Severity of forest wildfire had a major influence on early successional ectomycorrhizal macrofungi assemblages, including edible mushrooms

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Abstract

Wildfires are likely to have a major influence on below-ground patterns and processes in forests but these effects and their consequences to forest succession are generally poorly known. Ectomycorrhizal macrofungi (ECM) is a key below-ground ecological group, mainly because of their functional relationships to trees. During severe fire disturbances, below-ground mycelia of ECM may be negatively affected. This study analyses long-term effects of a wildfire on ECM assemblages.

Using data from 12-years post-fire succession of ECM, we investigated the long-term fire effects on ECM, focusing on the effects of spatial variability in fire severity. The wildfire occurred in 1992 in eastern Finland, and covered 143 ha. We established sampling plots to four types of sites within the burned area, based on the observed fire severity, and also on unburned control sites. ECM assemblages were surveyed every autumn during the following 12 years period. A total of 133 ECM species and 14 469 ECM sporocarps were sampled.

Fire severity was closely associated with the post-fire ECM richness and assemblage patterns. The highest overall ECM species richness was in the low severity surface fire area, 87 species in total, followed by the intermediate ground fire area, 72 species; they both included post-disturbance ECM pioneer species but also species that are usually associated with old-growth forests. The high-severity crown fire area comprised only 15 ECM species and the high-severity treeless ground fire area 23 species. Assemblage composition (based on NMDS) was different in the two most severely burned areas, in comparison to less severely burned areas and controls.

We conclude that fire affects ECM assemblages and that the severity of a wildfire is connected to post-fire patterns of ECM richness and composition. The results suggest a functional link between wildfire and post-fire tree growth, mediated through the effects of fire on ECM. These connections may be important in maintaining small-scale, within-stand spatial heterogeneity in the natural post-disturbance forests.

Keywords: boreal forest, pine forest, post-fire, disturbance, spatial heterogeneity, succession

1. Introduction

Symbiotic associations of organisms, such as between ectomycorrhizal macrofungi (ECM) and their host trees, are important for the functioning and productivity of boreal ecosystems (Smith and Read 2008). In the boreal forests, both conifers and broadleaved trees are associated with ectomycorrhizal, and the majority of their root tips (>95%) are colonised by symbiotic ectomycorrhizal fungi (Melin 1927; Smith and Read 2008). These fungal associations have a multitude of positive influences on trees (Asai 1944; Smith and Read 2008).

Usually, the diversity of the ECM fungal communities decreases after a large-scale disturbance like wildfire due to the mortality of their host trees (Longo et al. 2011; Penttilä et al. 2013). However, the diversity of fungal communities can also increase, especially if the effect of fire is patchy (Zak and Wicklow 1980). Some studies also show that low-intensity fires do not seem to significantly affect ectomycorrhizal community richness (Jonsson et al. 1999). Overall, thus, the effects of fire on fungi assemblages and their mutualistic association with trees appear to vary remarkably after forest disturbances but this variation is not well understood (for a recent review, see Taudiere et al. 2017).

In general, fire affects many forest properties, including nutrient cycle, biological productivity and diversity of insects, plants and macrofungi. Fires create forest structures that are habitats or resources for many plant, insect and macrofungus species (Zackrisson 1977; Schimmel and

Granström 1996; Dahlberg et al. 1997; Dahlberg et al. 2001; Hyvärinen et al. 2005; Martin-Pinto et al. 2006; Ruokolainen and Salo 2006; Suominen et al. 2015; Heikkala et al. 2016). However, wildfires are not homogenous; within each fire there is typically a range of severity from high to low (e.g. Kafka et al. 2001). This spatial variation is particularly obvious in soil properties (e.g. Čugunovs et al. 2017). The effects of within-fire variation on specific plant, animal, and fungal communities are still poorly understood and most likely modified by local, within-fire patterns in fire severity. Additionally, most studies have been able to analyse only immediate fire effects, and long-term effects based on regular on-site monitoring are rare (for the general importance of long-term fungi monitoring, see e.g. Heegaard et al. 2017).

Some Fennoscandian studies indicate that the effects of fire on the ectomycorrhizal fungal community are low, but studies have mostly analysed only low-intensity or low-severity fires (Jonsson et al. 1999; Dahlberg 2002). For example, in the Mediterranean forests, high-intensity fires have been observed to strongly affect vegetation and fungal communities (Torres and Honrubia 1997; Mediavilla et al. 2014), and it is quite expected that high-severity fires may have a strong impact on fungal communities also in boreal regions, with possible consequences to post-fire tree growth and other ecosystem characteristics.

Ectomycorrhizal fungi play a fundamental role in the recovery of plant communities following fires, through soil stabilization and restoration of soil microflora (Claridge et al. 2009). ECM fungi absorb nutrients from the forest floor and, by transferring some of these nutrients to woody plant symbionts, they reduce nutrient loss from the ecosystem (Miller and Allen 1992). Post-fire succession, however, likely depends on multiple factors such as initial plant species composition, fire severity, seed bank availability and the ability of soil microbial communities to recover. The development of mycorrhizas and ectomycorrhizal sporocarps depends on the photosynthesis of the host trees (Lamhamedi et al. 1994). Ectomycorrhizal fungi particularly help plants in nutrient and water uptake by protecting them against pathogens (Finlay 2008; Hartmann et al. 2009). Thus, any significant changes that fire has on ECM assemblages may have consequences on post-fire tree growth and successional post-disturbance patterns in forest ecosystems (Clemmensen et al. 2013, 2015).

This study focuses on the long-term effects of a wildfire severity on ECM assemblages. The emphasis is on testing how fire severity modifies the assemblages during 12 years following the wildfire. More specifically, based on the previous findings, we set up two hypotheses for testing:
(1) successional patterns of the ectomycorrhizal macrofungus (ECM) species and their assemblages during early successional pine-dominated boreal forests is influenced by wildfire, and
(2) since there is often spatial variation in the within-fire severity, this variation is reflected also to the succession, diversity and structure of ECM community composition, including the edible ECM.

2. Materials and methods

2.1. Study area

The study was conducted in the Kitsi forest fire area - also known as Jäkäläkangas forest conservation area – located within the middle boreal vegetation zone in North Karelia, eastern Finland (63° 16’ N, 30° 45’ E) (Fig. 1). The area has elevation 185 - 190 m a.s.l. The effective temperature sum (no. of days and degrees above +5 °C, d.d.) of the area during the growing season is ca. 1000 d.d. and the average duration of the growing season (when daily temperature is at least +5 °C) in the study area ranges from 145 to 150 days. The mean annual precipitation was 601 mm and the mean annual temperature + 2.1 °C at the nearby Lieksa-Lampela weather station during the reference period 1971-2000 (Drebs et al. 2002).The mean monthly rainfall (mm) and temperatures

(°C) in 1993-2004 are shown in Appendixes 1 and 2 (data from Finnish Meteorological Institute 2007).

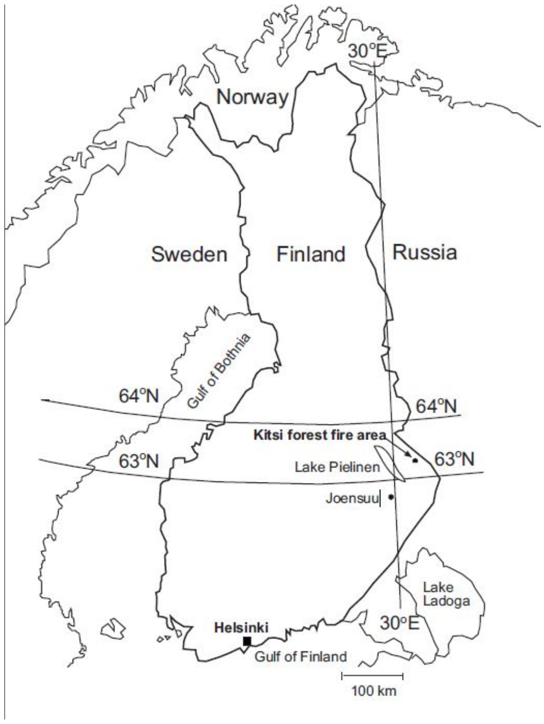


Fig. 1. The location of the study area.

The dominant tree species in the study area is Scots pine (*Pinus sylvestris*). Other tree species include Norway spruce (*Picea abies*) and birches (*Betula pendula*, *B. pubescens*). This dry pine heath (sub-xeric heath) forest in the mid-boreal vegetation zone belongs to the *Empetrum-Vaccinium* site type (EVT) in the Finnish site-type classification (Cajander 1921; Kalela 1961).

2.2. The fire

A forest wildfire started out in Kitsi on 7 June 1992, as an accidental result of prescribed silvicultural burning that took place in a clear-cut area about 500 m to north from the study area. The size of the burnt area expanded to an area covering 143 ha, and included heath forest areas and surrounding peatlands. The two main heath forest areas in Kitsi, Jäkäläkangas and Pöytäkangas, which total 55 ha, were old mature managed forests at the time of fire (Fig. 2). Based on tree core samples (five core samples were taken from 10 measurement plots across the area), the age of dominant pines was between 81-126 years in Jäkäläkangas and 99-147 years in Pöytäkangas in 1992. Last dendrochronologically dated fires on these sites occurred in years 1833, 1842 and 1892 (Lehtonen and Huttunen 1997).

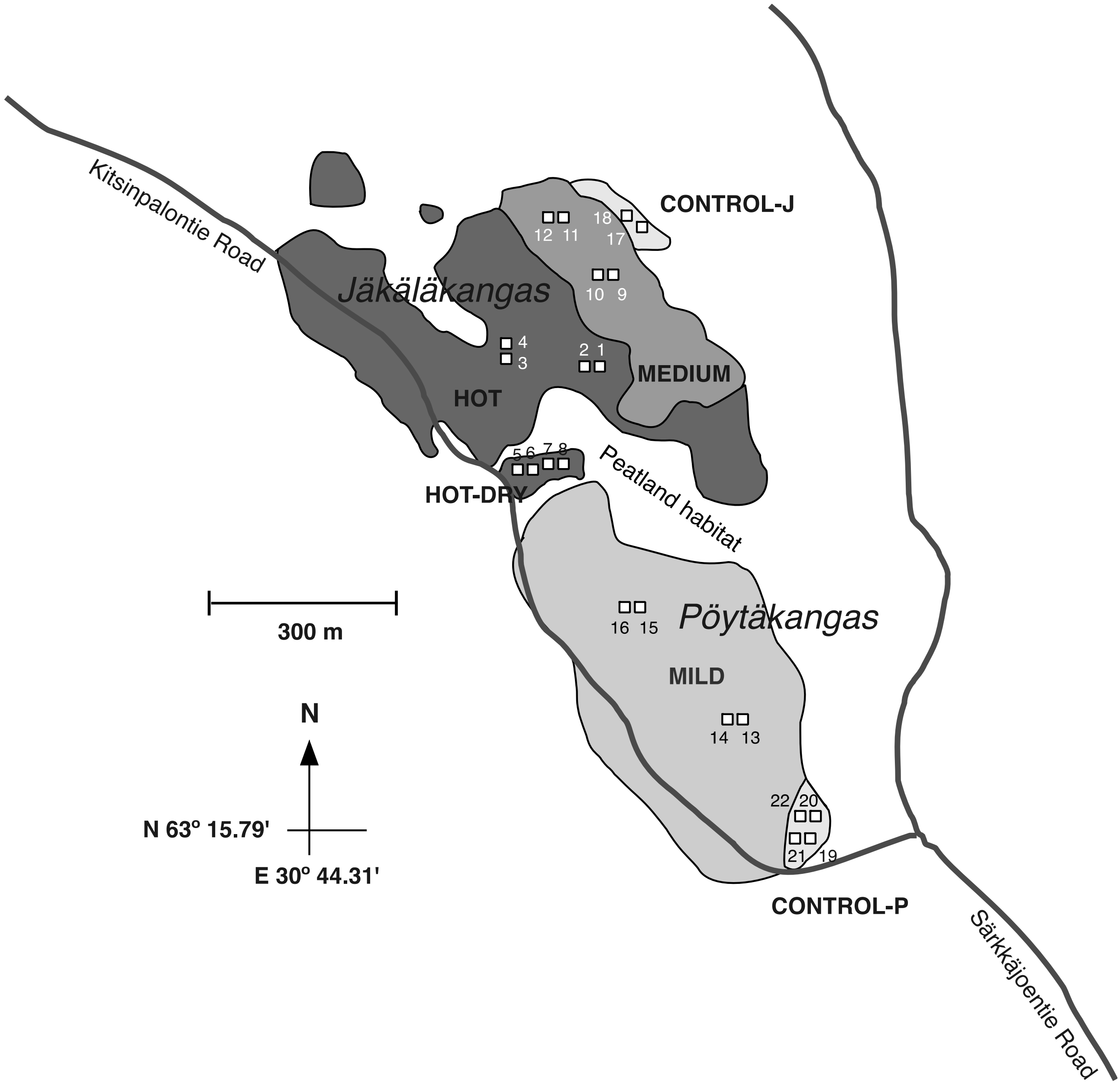


Fig. 2. Approximate locations of the macrofungal sample plots (squares no. 1-22; see also Table 1) in the Kitsi forest fire area. Note that the sampling plots (squares in the map) are not in scale, their actual size is 10 x 10 m^2 and the distance between two plots was at least 5 m. For more detailed explanation of fire severity classes HOT, HOT-DRY, MEDIUM and MILD, see chapter “Fire

severity and sampling design”. CONTROL-J is unburnt control site in Jäkäläkangas and CONTROL-P unburnt site in Pöytäkangas.

One year before the fire, in 1991, commercial thinning had been performed in Jäkäläkangas, leaving biomass harvest residues abundantly on the site. The dry logging residues probably increased the severity of the fire and led to intense crown fire in the thinned area. Practically all tall pines, spruces and birches were seriously damaged and were dead one year after the fire at latest. The burning was severe enough to strongly char also all the fallen trunks, stumps and branches. The humus and litter layer burnt from the top and was charred but in many places black humus formed a dense layer on top of the mineral soil. In the extinguishing work during and after the fire, forest tractors were used to carry water. Consequently, the wheels of the tractors compressed the burnt humus layer in part of the area. In Pöytäkangas area, fire did not reach crowns of tall trees and the fire remained as a lower severity ground or surface fire throughout the area.

2.3. Fire severity and sampling design

According to the initial visual post-fire inspection of the burned area, Jäkäläkangas area was a severe crown or intermediate ground fire area while Pöytäkangas represented less severe surface fire. Sample plots were designated to these areas so that they formed a representative sample of fire severities across the burnt area. A total of 22 permanent sample plots, each 10 m × 10 m in size, were established a year after the fire in 1993, including 16 plots on burned sites and 6 plots on unburned (control) sites (Fig. 2).

Two adjacent sample plots always formed a pair, and these pairs of plots were haphazardly placed within each severity area. Sample plots were situated in a south to north direction and between two plots there was a buffer zone of at least five metres in width.

Plots located on burned sites were further divided into four fire severity areas. Fire severity class (FS) was determined in the field by using a scale of 1 to 4, based on burnt or living trees, and how largely and intensively understorey vegetation, organic matter, humus, field and bottom vegetation layers had been burnt in the area (Fig. 2).

Area A, which included four sample plots (numbers 1-4) in Jäkäläkangas, represented a forest site where severe crown fire killed all the tall trees and shrubs, and trees that remained standing as well as the ground were covered by burnt litter. FS was 1 in these plots (Fig. 2), and these plots are hereafter referred as “HOT”, i.e. high severity. Area B (plots 5-8) is situated on a hillock, presenting ground fire in a previously clear-cut site (Fig. 2). Therefore, these sample plots were extremely dry during the initial study years. The forest fire had burnt most of the organic matter in the area. Tree stumps, branches and the upper layer of the humus were charred and FS was 2 (Fig. 2), and hereafter called “HOT-DRY”.

Area C (plots 9-12) was the ground fire area in Jäkäläkangas (Fig. 2), where ca. one third of the tree stock, mainly spruces and birches in the undergrowth, had died one year after the fire. Pines were mostly alive but the bark was charred on many trunks. The understorey vegetation, woody debris, litter, field and bottom layers were burnt by the ground fire. The humus layer was not burnt completely, but it became black and charred in places and FS was 3 (Fig. 2), and was denoted as “MEDIUM” severity.

Area D (plots 13-16) presented a surface fire in Pöytäkangas (Fig. 2), a pine dominated area that was thinned at the beginning of the 1970s. Trunks of the dominant tall pines blackened to the height of ca. three metres while undergrowth pines, spruces and birches died – a total of ca. 20 % of the tree stock. Fire burnt the surface litter and debris on the forest floor as well as the low vegetation, but the surface vegetation remained intact in many places. The lowest layer of the humus remained unburnt and there were some humus plots that remained completely unburnt in this area, and FS was 4 (Fig. 2), and denoted as “MILD” severity.

Unburnt control plots (plots 17-18 and 19-22) are located in the outskirts of the burned area (Fig. 2). Only a narrow strip of land in these comparable stands escaped fire, and consequently there was rather low number of control plots (Fig. 2). Although the control plots could not be established fully randomly (which is often the case in studies on wildfires), it is considered that the control areas adequately represent local conditions in the absence of fire (see also Ruokolainen and Salo 2009). Control plots next to Jäkäläkangas are denoted as CONTROL-J (or CJ in the Appendixes), and plots adjacent to Pöytäkangas are CONTROL-P (or CP in the Appendixes) sites.

2.4. Field and laboratory measurements

ECM fungi were inventoried from the permanent sample plots. All sporocarps of ECM found at different ages (young, medium and mature) were collected five or six times each year during the growing season from the beginning of August to the end of October in the period 1993-2004. In some years, the ECM inventory began in June and July. During the consecutive 12 years of ECM inventory, all the plots were visited several times each year. The total number of visits in every permanent sample plot varied from 60 to 72. During each sampling year, the sporocarps of ECM were gathered twice a month on average, with the total number of plot-surveys being 1476 (Table 1).

Table 1. Number of visits in the sample plots in years 1993–2004.

Total visits to all plots are 1476 while annual visits to each plot were between 5-6. Fire severity classes are explained in the text and the plots are shown in Fig. 2.

Fire severity class	Plot number	Sampling years	Total number of visits	Plots established
A, HOT	1	12	72	1993
A, HOT	2	12	72	1993
A, HOT	3	12	72	1993
A, HOT	4	12	72	1993
B, HOT-DRY	5	11	66	1994
B, HOT-DRY	6	11	66	1994
B, HOT-DRY	7	11	66	1994
B, HOT-DRY	8	11	66	1994
C, MEDIUM	9	12	66	1993
C, MEDIUM	10	12	66	1993
C, MEDIUM	11	11	66	1994
C, MEDIUM	12	11	66	1994
D, MILD	13	12	60	1993
D, MILD	14	12	60	1993
D, MILD	15	12	60	1993
D, MILD	16	12	60	1993
CJ, CONTROL-J	17	12	72	1993
CJ, CONTROL-J	18	12	72	1993
CP, CONTROL-P	19	12	72	1993
CP, CONTROL-P	20	12	72	1993
CP, CONTROL-P	21	11	66	1994
CP, CONTROL-P	22	11	66	1994

Macrofungi were identified in the field to the species level or to species groups and in some cases at the subgenus level in *Cortinarius*. The specification of subgenus *Telamonia* and their identification marks in fresh specimens were carried out and there were six unidentified ECM species in three sects of subgenus *Telamonia* and three ECM species in subgenus *Phlegmacium* (Appendix 3).

All the gathered macrofungus specimens were counted and their fresh weights were measured in sample plots. Occasionally, very small specimens that could not be identified readily were identified microscopically in the laboratory. For this, fresh specimens were sampled and dried in a drier at a temperature of 40 °C for 10-24 hours before identification. The dried specimens were archived to museum collections JOE, HKI and some specimens to TUR.

2.5. Classification and nomenclature of macrofungi

The taxonomy and nomenclature of basiodiomycete (agaricoid, boletoid and cyphelloid genera) follows Knudsen and Vesterholt (2008), including some checks according to Hansen and Knudsen (1992) and some *Cortinarius* species according to Brandrud et al. (1989-1998) and Niskanen et al. (2008).

We analysed separately also the edible mushrooms (hereafter “edible ECM”). The edible species were based on the classification in von Bonsdorff et al. 2013. List of edible mushrooms may vary, depending on how many species are identified as separate species in the groups of *Boletus* and *Leccinum*, the genus *Armillaria*, the species *Hydnum rufescens* coll., *Morchella* spp. and *Tuber* spp. In the list of nationally recommended edible mushrooms (Evira 2013), there are 33 recommended edible mushrooms that have commercial status (C), of which we observed in this study 15 species. Additionally, we observed 14 other edible species (E) and 5 species (M) that are marketed regionally in our study area in North Karelia, Finland (Appendix 3).

2.6. Data analysis

When reporting results from each fire severity class site and controls, we pooled the annual observations from the sample plots located in each stand because these are not true replicates of each fire “treatment” (severity class). This led us to apply quite descriptive numerical analytical tools when assessing the effects of fires severity. However, given that this is a case study of single fire that affect typically individual stands, we felt this a more justified approach than forming obvious pseudoreplications of the spatially and temporally repeated and related samples and measurements (Hurlbert 1984).

Non-metric multidimensional scaling (NMDS) was used to visualize macrofungal species composition and ECM community structure in burnt and unburnt study sites and years (Legendre and Legendre 1998). NMDS analyses were carried out using the package *vegan* in R software programme.

3. Results

3.1. Taxonomical and ecological composition and species richness of ECM

A total of 14 469 sporocarps of ECM were collected in 1993-2004. These included 133 species in 32 genera, 18 families, eight orders and three classes in Basidiomycota and Ascomycota (Appendix 3). The total biomass yield of all ECM sporocarps was 159 583 kg in fresh weight (fw) (Appendix 3).

Agaricales was the biggest order, containing seven families, ten genera and 81 species of ECM (Appendix 3). The most abundant genus was *Cortinarius* (44 species), with 33.1% of all ECM; the second most abundant was *Russula* (16, 12.0%), followed by *Tricholoma* (12, 9.0%), *Lactarius* (6, 4.5%) and *Inocybe* (6, 4.5 %). These five genera contained 63.2% of all ECM species (Appendix 3). In terms of frequencies, the most common ECM species was *Lactarius rufus* (freq. 97), followed by *Cortinarius semisanguineus* (freq. 94), *C. armeniacus* coll. (freq, 86), *Suillus variegatus* (freq. 84), *C. brunneus* coll. (freq. 79), *C. croceus* var. *croceus* (freq. 69) and *Laccaria laccata* coll. (freq. 63). These seven species contained 53.0% of all ECM sporocarps (Appendix 3).

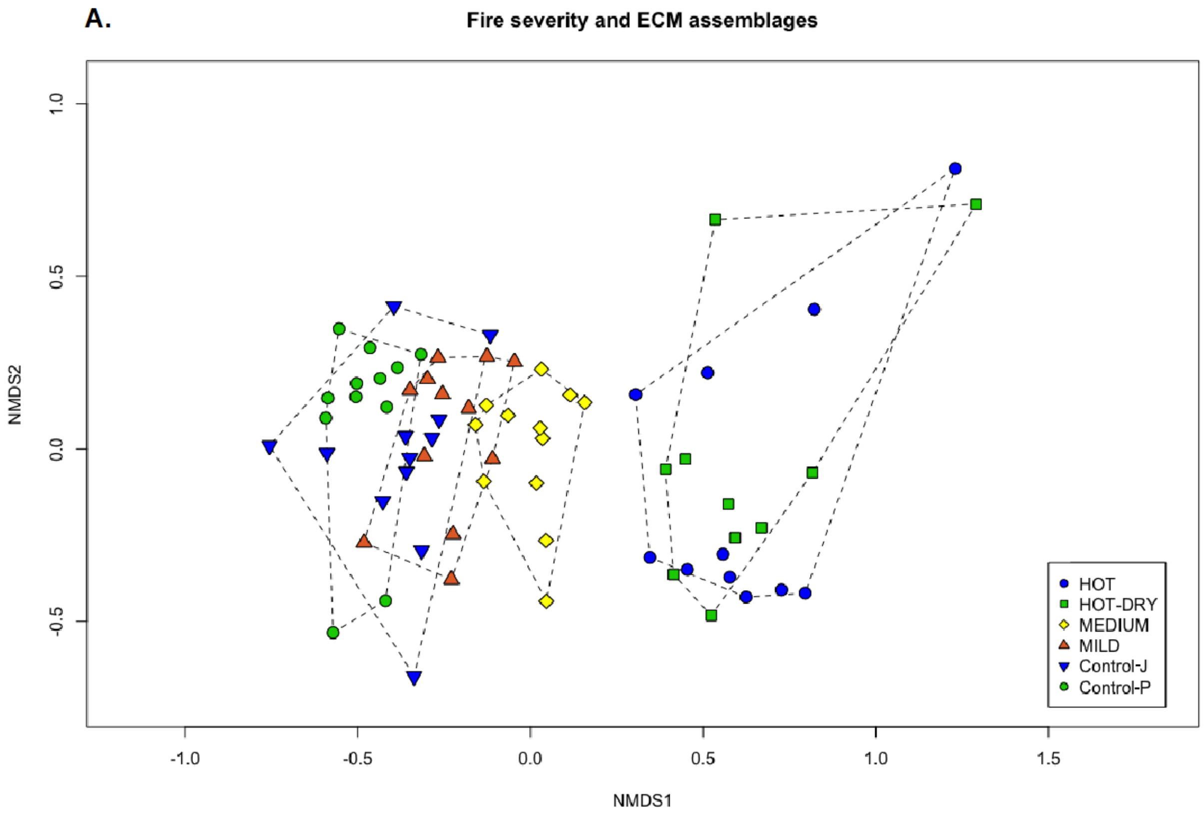
3.2. Fungal assemblages in relation to fire severity and time since fire

Fire severity was clearly connected to fungal assemblages while no clear temporal trends were evident. The effect of fire severity was evident both at the assemblage-level but also at species-level as detailed below.

The ECM diversity was highest in the surface fire area MILD where a total number of ECM species was 87, including many rare species, such as *Rhizopogon obtextus* and *Elaphomyces granulatus*, calciphilous agarics *Leucocortinarius bulbiger* (three sporocarps) and *Russula queletii* and a lime demanding red list species (NT) *Hygrophorus gliocyclus* (three sporocarps) (Appendix 3).

Seventy-two ECM species were found in the ground fire area MEDIUM, 59 species in CJ and 69 in CP (Appendix 3). In the totally burnt HOT sites, only 15 ECM species have been observed, and in the HOT-DRY burned areas 23 species (Appendix 3).

NMDS analyses revealed that the HOT and the HOT-DRY sites had quite distinct assemblages (Fig. 3a). Furthermore, there was no indication that these assemblages converged towards low-severity or control sites during the 12-years period (Fig. 3b). Consequently, the recovery of ECM species in HOT and HOT-DRY sites was slow after the fire (Appendix 4). During first four years only two ECM species were observed in HOT-DRY sites and the highest annual number of ECM species was ten in HOT sites and eleven in HOT-DRY sites in 2003 (Appendix 4). In these sites, also the annual variation in fungal richness was low, and much lower than in less-severely burned sites (Fig. 4)


A.
Fire severity and ECM assemblages
NMDS2
1.0
0.5
0.0
-0.5
NMDS1
-1.0
-0.5
0.0
0.5
1.0
1.5
● HOT
■ HOT-DRY
◆ MEDIUM
▲ MILD
▼ Control-J
● Control-P

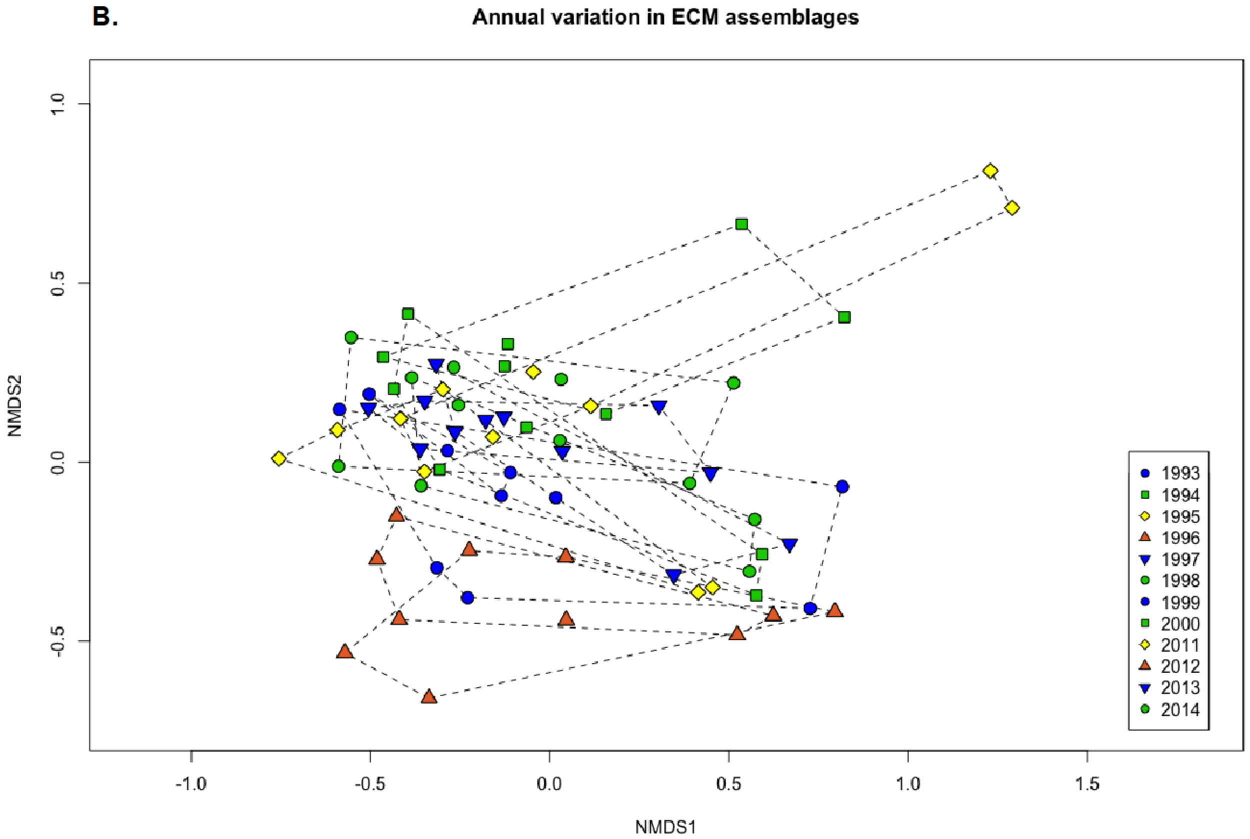

B.
Annual variation in ECM assemblages
NMDS2
1.0
0.5
0.0
-0.5
NMDS1
-1.0
-0.5
0.0
0.5
1.0
1.5
● 1993
■ 1994
◆ 1995
▲ 1996
▼ 1997
● 1998
● 1999
■ 2000
◆ 2011
▲ 2012
▼ 2013
● 2014

Fig. 3. ECM assemblage composition in different (A) fire severity classes and (B) study years, based on NMDS. Polygons delimit (a) fire severity classes and (b) study years. For explanations of the fire severity classes, see Material and Methods, and for their spatial occurrence, see Fig. 2. Final stress value of the two-dimensional NMDS solution is 0.153.

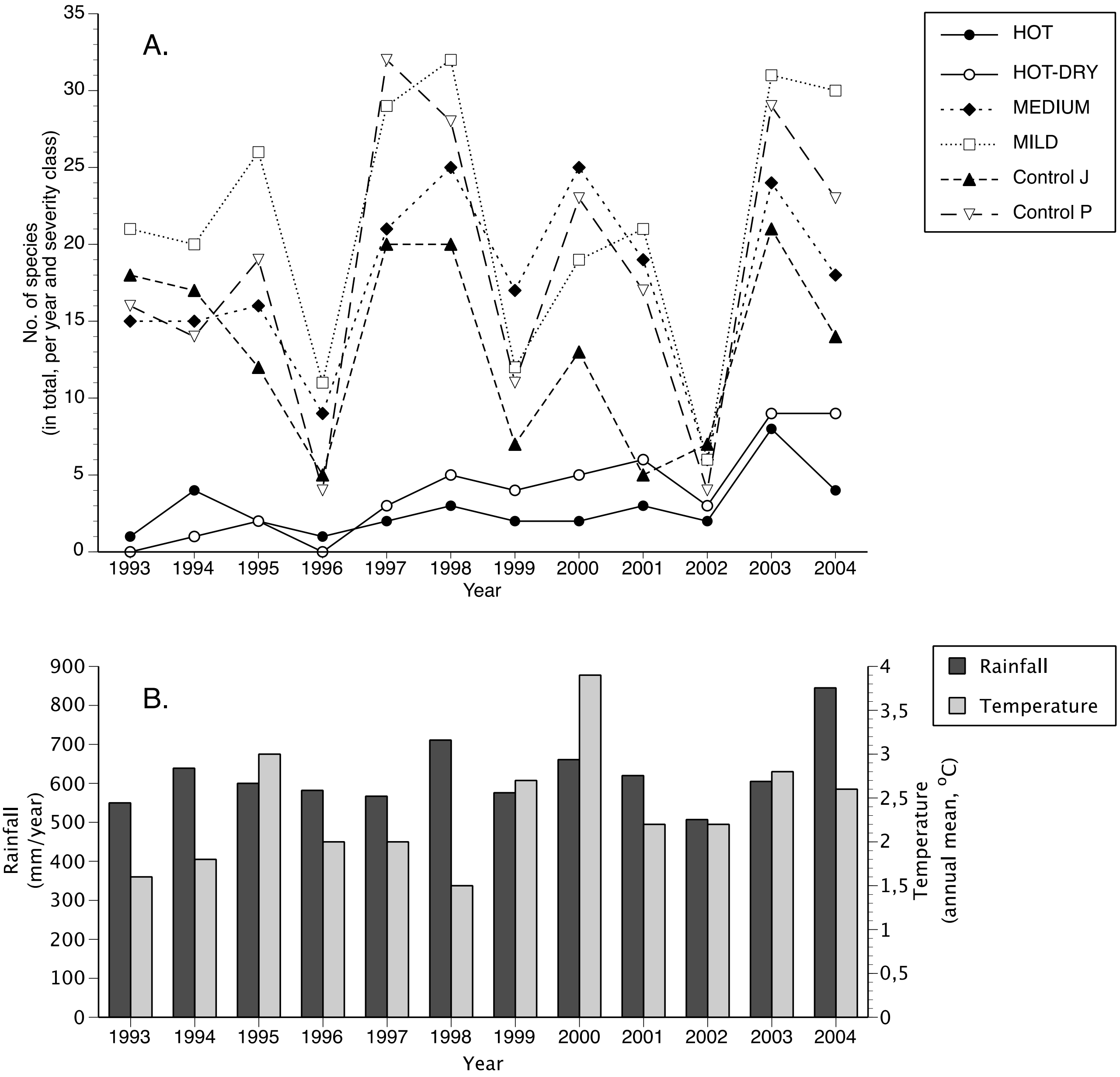


Fig. 4A. Total number of ECM species in severity classes HOT , HOT-DRY, MEDIUM and MILD and control plots Control-J (Jäkäläkangas) and Control-P (Pöytäkangas) in years 1993-2004. Y-axis values are sums of species observed in all sampling plots.

4B. Annual total rainfall (left axis, dark grey bars) and annual mean temperature (righ y-axis, light grey bars), measured in the Lieksa-Lampela weather station, during 1993-2004 (data: Finnish Meteorological Institute 2007).

At species and genus levels, there were a few notable patterns. *Naucoria* spp., *Laccaria laccata* coll., *Paxillus involutus*, *Inocybe grammata*, *I. lacera* var. *lacera* and *Thelephora terrestris* f. *terrestris* were fire-associated (i.e. were found exclusively on burned sites) and occurred mainly in HOT and HOT-DRY sites but also in MEDIUM and MILD sites. Sporocarps of these species were not found in CONTROL-J and CONTROL-P sites (Appendix 3). Of these species, *L. laccata* in particular was especially abundant on severely burned sites (Appendix 4). Fire-tolerant ECM species (species that commonly occurred also on burned sites) included *Russula decolorans*, *R. paludosa*, *Suillus variegatus*, *Boletus pinophilus*, all ECM species in genus *Tricholoma*, some species in *Cortinarius* and all species in Bankeraceae. These were found also in mature forest control sites, in addition to the MILD and MEDIUM sites (Appendix 3). *Lactarius rufus* had wide occurrence pattern living in every site but the highest total sporocarps and yield were in MILD and MEDIUM sites (Fig. 5, Appendix 3).

Less-severely burned sites showed strong annual variation (Fig. 4A). This variation was synchronous in different sites, suggesting that an external factor may cause the pattern. Indeed, according to the monthly rainfall data available from Lieksa-Lampela weather station (Appendix 1), in the summer months of July or August or together the lowest monthly rainfall levels were in 1996, 1999 and 2002 and the number of ECM species were low during these years (Fig. 4A). The correlation between the total annual number of ECM species by fire severity and monthly precipitation for months (June, July, August) and the aggregation groups of months (July and August, June, July and August) (Table 2) showed that precipitation in August, and July and August combined, had a strong positive correlation with the total number of the ECM species. In particular, it explained the richness of macrofungi in the MILD fire sites but also in control CP, MEDIUM and HOT-DRY sites (Fig.4). Annual climate variables (total annual rainfall and mean annual temperature; Fig. 4B)) did not reveal any correlations, except for the HOT-DRY sites where annual rainfall was related to the fungal species richness (r = 0.595, p=0.041).

Table 2. Correlation between total annual number of ECM species by fire severity and monthly precipitation obtained for summer months and the aggregation group months. Significance levels (2-tailed): *** < 0.01, ** < 0.05, * < 0.1.

Severity	**Correlation coefficient**				
	June	**July**	**August**	**July & August**	**June & July & August**
HOT	-0.354	-0.375	0.466	0.061	-0.121
HOT-DRY	0.283	0.024	0.527^{*}	0.376	0.462
MEDIUM	0.328	-0.157	0.566^{*}	0.279	0.401
MILD	-0.186	0.149	0.715^{***}	0.591^{**}	0.416
CONTROL-J	-0.205	-0.108	0.483	0.256	0.119
CONTROL-P	0.058	0.022	0.571^{*}	0.406	0.377

3.3. The occurrence of edible ectomycorrhizal macrofungi

Twenty-nine species of edible ECM (21.8% of all ECM species) were found over the period of 12 years and 22 of them belonged to Russulales and Boletales (Appendix 3). Eight edible ECM species in genus *Russula* and *Boletus* that are classified as excellent edible species and also one species in genus *Hygrophorus, Tricholoma, Cortinarius* and *Cantharellus* were observed (Appendix 3).

In the high-severity sites (HOT and HOT-DRY) the edible ECM occurred only occasionally (Fig. 5, Appendix 3). *Lactarius rufus, Suillus luteus* and *Leccinum versipelle* were the only edible species on the high-severity sites but all these species were more common in other fire severity classes (Appendix 3).

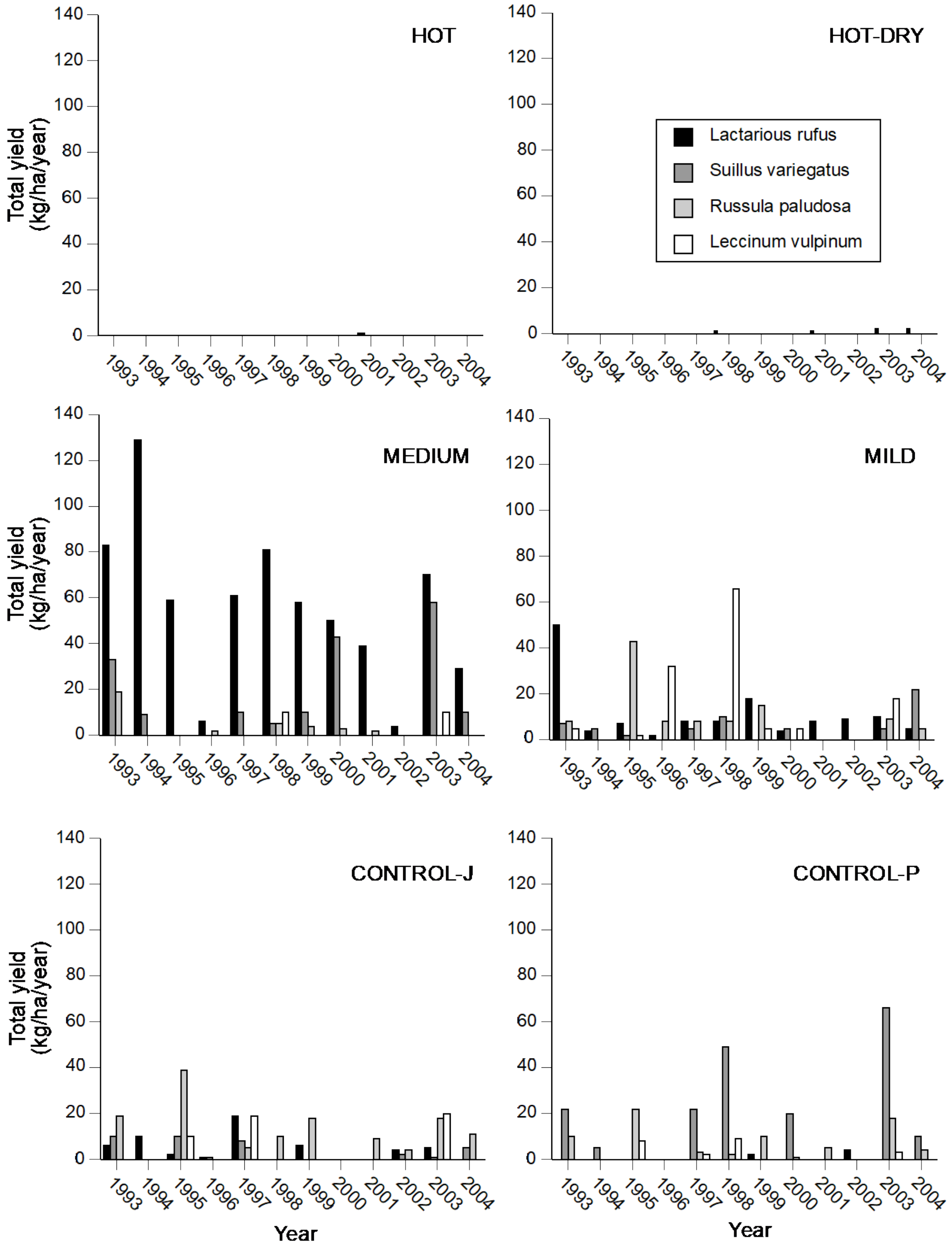


Fig. 5. The yield of the most productive edible ECM species in (fresh weigh, kg/ha) in fire severity classes HOT, HOT-DRY, MEDIUM, MILD and control plots CONTROL-J and CONTROL-P in years 1993-2004.

The most productive edible ECM species was *Lactarius rufus* in different years. The species prevailed in the ground fire area (MEDIUM) where the highest yield was 128.7 kg/ha (fresh weight) (10725 sporocarps per hectare) in 1994 (Fig. 5). *L. rufus* yields were high also in MILD sites, being 49.5 kg/ha in 1993 and 18.0 kg/ha in 1999 but low figures in totally burnt areas and control plots (Fig. 5). *Suillus variegatus* was abundant especially in control plots CP, the best yield being 66.0 kg/ha fresh weight in 2003 and 48.5 kg/ha in 1998, and was also common in the MEDIUM sites, the best yields being over 40.0 kg in 2000 and 2003 (Fig. 5).

Russula paludosa was most productive in the MILD surface fire area in 1995 and 1999, with yields being 43.0 kg/ha and 15.3 kg/ha (Fig. 5). Abundant yields occurred also in both control plots in 1993, 1995, 1999 and 2003 (Fig. 5). The *Leccinum vulpinum* yield was more abundant in MILD than in MEDIUM sites and no sporocarps were found in HOT or HOT-DRY sites (Fig. 5). The highest yields were in MILD, 66.0 kg/ha in 1998 and 32.2.kg/ha in 1996 (fresh weight, Fig. 5).

4. Discussion

This study is exceptional among the forest ECM studies due to its long post-fire temporal coverage, repeated within-season sampling, high degree of taxonomical representativeness, and inclusion of the spatial heterogeneity caused by a single fire event. Based on the results, fire severity was an important factor in the ECM succession. Temporal patterns were also evident although we could not find clear temporal trends in the recovery but rather annually fluctuating patterns that were more evident in less severely burnt sites.

4.1. ECM assemblages, fire severity and succession

Based on a recent review, majority of wildfire influences on ECM appear to be detrimental (Taudiere et al. 2017). Unfortunately, it is very rare that ECM studies can address the influence of variable fire severities using relatively long-term monitoring. Our study is first one representing fungal assemblage dynamics during a relatively long time-span in the Fennoscandian pine-dominated forests, a forest habitat that is usually assumed to be repeatedly affected by wildfires.

One of the main finding in the current study is that a single fire event – that typically include considerable spatial variation in fire severity – may have widely different effects on the ECM assemblages. Our results clearly support the hypothesis that fire severity plays a fundamental role here. In fact, it is quite possible that some of the controversial effects that fire may have on ECM (reported in Taudiere et al. 2017) may be due to variation in fire severity. Oftentimes, it is quite difficult to reliably measure fire severity, and many studies fail completely to report that. In general, this possibility has been recognized for quite long (e.g. Dahlberg 2002) but direct monitoring data supporting the idea are still scarce.

Interestingly, our results also point to a direction that mild or intermediate level fire-disturbance appears to increase ECM richness during the post-disturbance period, in comparison to both high-severity and undisturbed conditions. This is accordance of the classical idea that medium level of disturbance enhances species diversity (intermediate disturbance hypothesis, Grime 1973, Connell 1978). However, we do not know what the actual mechanism and processes behind this observation could be. Nevertheless, the intermediate disturbance – both the surface and ground fire – appear to lead to higher ECM diversity and quite distinct composition in our study areas, including edible ECM. This suggests than at least some ECM species can take advantage of mild soil disturbance by fire. Naturally, however, since we did not measure species richness at soil mycelia it is also possible that in these conditions ECM species just invest more on producing reproductive organs (sporocarps).

Temporal dynamics of ECM recovery after wildfire shows strikingly different patterns in previous studies (reviewed in Taudiere et al. 2017). It is quite likely that the variability is closely related to fire severity, and our results support this. Although we could not show that any of the burned sites returned to match the unburned control sites, both the species richness and its annual variability was close to control plots in the intermediate fires. Notably, our high severity sites did not even start to converge to control during the 12 years. Initially, this is probably due to lack of suitable host trees but it may also be due to altered soil conditions and lack of fungal colonisation. However, also the severely burned sites in our study areas were occupied by Scots pines towards the end of the monitoring period, and these pines could in principle maintain ECM assemblages comparable to intermediate or control sites.

Patterns of ECM fungi may have a multitude of effects on the forest succession and functional aspects of forests after the disturbance. For example, from the functional viewpoint, the association of trees and the ECM fungi appears to be related to the amount of carbon that is stored in forest soil (Clemmensen et. al. 2013, 2015). Our results suggest that the exact type and severity of disturbance may thus have also some consequences on functional features of forest ecosystems (see also Dahlberg et al. 2001). However, since we did not directly address or measure carbon, it may nevertheless be so that changes in fungal composition that we observed is not directly related to the carbon dynamics if there is functional redundancy in the system. This would mean that the remaining ECM species may compensate the activity of the lost species. This is definitely an issue that deserves further attention. If ECM and fire severity are linked to carbon cycling, then the predicted increase in fire frequencies due to climate change may have long-term effect on the ecosystem characteristics. However, as Clemmensen et al. (2013) have pointed out, the identity of fungal species rather than their total diversity may be overwhelmingly important to modify carbon cycling in soils.

4.2. Mushroom yields and forest fires

Edible mushrooms are an important non-timber product in boreal forests. However, the effect that different types of natural and anthropogenic disturbance have on the edible mushroom yield has remained elusive. Based on our results, also burned forests can produce high yields of edible mushrooms. Previous studies of the yield of *Lactarius rufus* – one of the main edible species – have revealed yields between 5-20 kg/ha in pine forests, with great deal of annual variation (Ohenoja and Koistinen 1984; Salo 1993). Compared to these values, the yield from medium-burned sites in this study were much higher during most study years. The same phenomenon was observed also in a few other species (*S. variegatus*, *R. paludosa, L. vulpinum*; Fig. 5). This suggest that this economically valuable species may actually benefit from fire disturbance if severity remains low.

In general, according to this study, the overall diversity and the yields of ECM in post-fire pine forests is high, provided that fire severity is low, pines remain alive, and that the field and ground vegetation and upper part of humus are only partly affected by fire. In contrast, crown and treeless fire areas (HOT and HOT-DRY sites) produce very low yields of edible ECM, at least during the 12 years after fire.

4.3. Implications for macrofungal surveys

Our study is based on long temporal coverage as well as on samplings that covered the main sporing production season each year. This effort sheds some light also on some methodological issues related to sampling and monitoring of ECM sporocarps. Many macrofungal surveys have limited temporal coverage, typically from two to four years only (Ohenoja and Koistinen 1984, Kalamees and Silver 1993, Väre et al. 1996, Bonet et al. 2004, Vasquez Gassibe et al. 2011, Hernandez-Rodrigues et al. 2013) while the importance of long-term monitoring is quite obvious and has recently gained new significant evidence (Heegaard et al. 2017).

It is quite evident that the number of ECM species has been underestimated in short-term studies. Based on our results, and quite as expected, the longer-term monitoring reveals many rare species that appear slowly in the data as monitoring years increase. Our results showed that as many as 90 very rarely and infrequently occurring ECM species (total frequencies being 1-9, 68 % of all ECM) were observed during the 12 years of the inventory (Appendix 3). Consequently, the distribution curve of ECM species according to the total frequencies (Appendix 3) followed a J-shaped distribution. This implies that sporocarps of ECM must be monitored a decade or more after the same permanent sample plots, if also rare ECM species is to be included in the study (see also Heegaard et al. 2017). Compared with the wood-decaying fungi (see Halme at al. 2009), ECM surveys based on sporocarps seem to require longer sampling effort to reveal full assemblages.

Fungi survey and monitoring is challenging also due to major effect that annual weather conditions have on this species group (e.g. Buntgen et al. 2011, Agreda et al. 2016, Taye et al. 2016). Our results showed this annual fluctuation clearly, but it was notable that the fluctuation seemed to depend also on fire severity. In medium-mild as well as in unburned sites, the survey results were more variable and more clearly related to prevailing weather. This implies that fungi in different fire severities cannot easily be compared using short-term data, if the observation probability of a fungus depends both on weather and the fire severity simultaneously. The (statistical) interactive effects between soil characteristics and weather patterns on fungi have been reported recently by Castano et al. 2017. Our study supports these ideas that soil characteristics interact with fungal sporocarp production. Our finding stresses that fire severity may be an important yet previously still poorly explored factor in triggering these climate effects.

5. Conclusions

Wildfires may become more common in the future due to warming and drying climate, and prescribed fires are also used nowadays more often for restoration purposes. Forest fires are most visible in their effect on above-ground parts of forests if they are severe enough to cause major mortality of prevailing, mature trees. However, it is evident that fires also affect several below-ground parts that, in turn, may influence longer-term recovery, biodiversity and productivity of forest ecosystems. We found that severe wildfire may cause decadal long shifts in ECM assemblages. Although these changes are likely to cause also functional consequences through changes in tree-ECM symbioses, we still need longer data to show how the ECMs return to burned sites and how this affects tree growth patterns. The mild and intermediate wildfires, on the contrary, appear to have only transient and small effect on ECM and they may even enhance ECM diversity. This is promising for prescribed burnings and restorative burnings as it suggests that low severity prescribed burnings can maintain favourable habitats for the diversity and production of ECM.

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Appendix 1. Mean monthly and total annual rainfall (mm) in 1993–2004 at Lieksa, Lampela weather station in 1993–2004 (Finnish Meteorological Institute 2007).

Month	Year											
	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
1	18.7	45.5	23.7	15.5	35.5	54.8	41.4	37.6	29.0	48.1	54.3	39.1
2	15.2	5.6	41.0	32.1	31.1	49.5	31.4	59.7	47.5	38.0	28.4	60.9
3	45.7	44.9	28.2	18.2	23.0	18.7	22.4	29.7	27.5	25.4	22.3	22.1
4	15.0	41.5	42.4	22.7	33.3	4.6	24.6	23.2	28.9	14.6	15.6	23.4
5	30.8	34.6	47.2	68.2	41.9	54.3	31.7	20.1	33.1	38.6	76.5	82.2
6	56.8	30.6	39.3	85.2	78.3	106.4	95.7	139.4	68.1	82.9	45.9	81.8
7	117.1	79.4	80.8	76.3	115.0	116.0	76.3	55.4	134.3	95.2	17.1	151.8
8	67.1	72.7	99.8	23.5	33.1	109.4	37.0	95.5	59.6	35.0	103.5	137.6
9	60.3	132.3	65.6	18.5	77.9	64.5	31.5	47.5	48.1	50.6	47.0	95.3
10	64.6	77.6	78.2	52.6	33.6	74.5	60.5	40.1	98.9	11.2	94.8	29.5
11	10.1	32.1	37.7	104.0	35.3	13.6	52.1	57.2	27.9	36.9	44.8	52.8
12	49.3	42.2	15.9	65.5	29.3	45.0	71.9	55.9	17.0	30.0	54.6	68.2
Total	550.7	639.0	599.8	582.3	567.3	711.3	576.5	661.3	619.9	506.5	604.8	844.7

Appendix 2. Mean monthly and annual temperature (°C) in 1993–2004 at Lieksa, Lampela weather station (Finnish Meteorological Institute 2007).

Month	Year											
	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
1	-7.5	-10.6	-5.7	-8.1	-11.6	-6.6	-13.3	-7.9	-5.8	-10.1	-17.6	-11.1
2	-6.8	-18.1	-4.4	-14.2	-8.4	-14.3	-11.3	-7.8	-12.0	-4.3	-7.9	-9.7
3	-3.6	-5.4	-1.5	-5.9	-4.1	-9.3	-4.7	-3.3	-8.7	-3.3	-2.7	-4.5
4	0.1	3.1	1.0	0.4	-1.5	-2.5	3.8	3.1	4.4	2.3	-0.4	1.1
5	9.9	5.9	7.6	6.3	6.1	7.2	5.0	8.5	6.9	9.7	9.9	7.9
6	10.3	13.0	15.8	13.0	14.6	13.4	17.9	13.7	14.6	14.8	11.0	12.8
7	15.3	17.3	14.0	14.2	17.4	16.2	16.9	17.0	18.3	18.0	19.9	16.5
8	12.9	13.6	13.6	15.6	15.1	12.5	12.2	13.4	13.6	14.9	14.4	14.2
9	4.3	8.8	9.0	7.0	8.9	9.6	9.9	8.0	10.0	7.9	9.7	10.4
10	0.2	2.8	5.4	4.2	0.7	4.1	5.2	6.6	3.4	-1.5	2.8	3.0
11	-7.9	-4.5	-6.0	1.6	-4.0	-5.1	-2.4	0.2	-5.2	-7.4	-0.4	-3.3
12	-7.6	-4.4	-12.7	-10.1	-8.7	-7.7	-6.4	-4.2	-12.8	-14.6	-4.9	-5.7
Mean	1.6	1.8	3.0	2.0	2.0	1.5	2.7	3.9	2.2	2.2	2.8	2.6

Appendix 3. Frequencies and biomass of the ectomycorrhizal macrofungus (ECM) species. Total frequency (Tot. freq.) has been counted from 255 sample plots, frequency in different fire severity classes (A–D; corresponding to classes HOT, HOT-DRY, MEDIUM, MILD) and control plots (CJ, CP), total number of ECM species in each fire severity (on line 3), total number of ECM sporocarps (Tot. sporos) and total yield in kilos in fresh weight (Tot. yield, kg fw) in all 22 plots (0.22 ha) in 12 years. Commercial status (C) and marketed (M) in North Karelia. E: Other edible ECM and edibility. Edibility codes of ECM: *** Excellent, ** Good, * Edible, ¤ Boiling before use, ¤¤ Cooking up well in a frying pan before use. *Boletopsis grisea* and *Hygrophorus gliocyclus* indicated as red list species (NT).

			Tot. freq	Freq. in the fire severity class						Tot. sporocarps	Tot. yield kg fw
				A	B	C	D	CJ	CP		
				15	23	72	87	59	69		
BASIDIOMYCOTA											
I. AGARICOMYCETES											
1. RUSSULALES											
Russulaceae											
C, M ¤**	*Lactarius*	*trivialis*	1			1				1	0.040
E¤*	*Lactarius*	*vietus*	3		1	1		1		72	0.343
E*	*Lactarius*	*glyciosmus*	1					1		1	0.006
E*	*Lactarius*	*mammosus*	54	4	3	25	18	4		448	4.253
	Lactarius	*helvus*	1			1				3	0.030
C. M ¤**	*Lactarius*	*rufus*	97	1	8	33	40	11	4	2 642	31.704
E***	*Russula*	*aeruginea*	4			1	2	1		5	0.164
C ***	*Russula*	*decolorans*	54			10	16	15	13	240	4.217
C ***	*Russula*	*paludosa*	58			6	17	16	19	279	10.664
C ***	*Russula*	*vesca*	1				1			1	0.020
C ***	*Russula*	*vinosa*	8			3	2	3		21	0.420
	Russula	*olivascens*	2		1	1				11	0.034
E***	*Russula*	*xerampelina coll.*	2					2		6	0.050
	Russula	*emetica*	1			1				1	0.005
	Russula	*rhodopus*	1						1	5	0.050
	Russula	*atrorubens*	8			8				43	0.193
	Russula	*betularum*	3		1	1	1			9	0.115
	Russula	*gracillima*	4		2	1		1		10	0.071
	Russula	*versicolor*	10		4	6				56	0.168
	Russula	*queletii*	2			2				8	0.051
	Russula	sp.1.	1			1				2	0.004
	Russula	sp.2.	3		1	2				7	0.022
2. BOLETALES											
Gomphidiaceae											
E**	*Chroogomphus*	*rutilus* var. *rutilus*	17			3	6	2	6	43	0.187
E**	*Gomphidius*	*glutinosus*	1						1	1	0.030
	Gomphidius	*roseus*	12			9	1	1	1	15	0.049
C **	*Suillus*	*luteus*	23	2		8	12	1		51	1.138
E*	*Suillus*	*bovinus*	13	4		4			5	87	1.514
C **	*Suillus*	*variegatus*	84			23	24	10	27	555	17.649
Paxillaceae											

	Paxillus	*involutus*	17		16		1			97	2.549
Boletaceae											
C, M ***	*Boletus*	*edulis*	1			1				1	0.080
C, M ***	*Boletus*	*pinophilus*	17			10	3	4		28	2.142
C ¤¤**	*Leccinum*	*vulpinum*	36			6	16	5	9	123	7.925
C ¤¤**	*Leccinum*	*versipelle*	17	2		5	3	7		43	3.753
E*	*Leccinum*	*scabrum*	15	4	3	4	3		1	31	0.820
	Tylophilus	*felleus*	1						1	1	0.040
E*	*Xerocomus*	*subtomentosus*	4	1		3				17	0.340
Rhizopogonaceae											
	Rhizopogon	*obtextus*	1				1			2	0.007
3. AGARICALES											
Hygrophoraceae											
E**	*Hygrophorus*	*olivaceoalbus*	1			1				1	0.002
E***	*Hygrophorus*	*hypothejus*	18			5	6	4	3	39	0.328
	Hygrophorus	*gliocyclus*	1				1			3	0.018
Amanitaceae											
	Amanita	*fulva*	1					1		1	0.020
	Amanita	*crocea*	1					1		1	0.017
	Amanita	*porphyria*	16				4		12	36	0.653
	Amanita	*rubescens* f. *rubescens*	5			1	1		3	7	0.162
	Amanita	sp.1.	1						1	1	0.012
Tricholomataceae											
	Tricholoma	*focale*	2				1		1	5	0.156
C ***	*Tricholoma*	*matsutake*	2				1		1	4	0.158
	Tricholoma	*inamoenum*	1			1				1	0.005
	Tricholoma	*virgatum*	2				2			4	0.142
	Tricholoma	*saponaceum* var. *saponaceum*	34			17	14	3		86	2.186
	Tricholoma	*imbricatum*	1			1				1	0.050
	Tricholoma	*fulvum*	1				1			2	0.050
	Tricholoma	*albobrunneum*	6			2	2		2	14	0.259
	Tricholoma	*pessundatum*	7			1	4		2	120	2.400
	Tricholoma	*aestuans*	1				1			1	0.005
	Tricholoma	*equestre*	12				6		6	28	0.439
E**	*Tricholoma*	*portentosum*	7			2	5			13	0.309
Entolomataceae											
	Entoloma	*cetratum*	26			2	6	5	13	73	0.138
Hydnangiaceae											
	Laccaria	*laccata* coll.	63	18	27	17	1			1 502	4.488
	Laccaria	*bicolor*	3			1	1	1		9	0.029
Cortinariaceae											
C ***	*Cortinarius*	*caperatus*	29			11	6	3	9	74	1.518
Subgen. Cortinarius sect. Dermocybe											
	Cortinarius	*sanguineus* var. *sanguineus*	1				1			1	0.006
	Cortinarius	*semisanguineus*	94			16	26	19	33	1 405	6.698
	Cortinarius	*cinnamomeus*	5			1	2	2		21	0.086

Cortinarius	*croceus* var. *croceus*	69		2	10	22	10	25	444	1.628
Cortinarius	*uliginosus* var. *uliginosus*	4				3	1		6	0.031
Cortinarius	*collinitus*	33			1	11	5	16	119	1.816
Cortinarius	*mucosus*	13				4	2	7	40	0.989
Subgen. Myxacium sect. Defibulati										
Cortinarius	*stillatitius*	5					2	3	8	0.149
Subgen. Myxacium sect. Vibratiles										
Cortinarius	*causticus*	6				1	1	4	115	0.742
Cortinarius	*vibratilis*	5						5	179	1.187
Subgen. Phlegmacium										
Cortinarius	*scaurus*	5			1	1	1	2	30	0.276
Cortinarius	*multiformis*	9				1	1	7	116	1.463
Cortinarius	*cf. multiformis*	1						1	1	0.016
Cortinarius	*balteatus*	12				3	3	6	56	1.113
Cortinarius	*turmalis*	1				1			1	0.024
Cortinarius	sp.5	4				2	1	1	30	0.300
Cortinarius	sp.6	6			1	2	2	1	38	0.344
Cortinarius	sp.7	3				1		2	20	0.116
Subgen. Telamonia sect. Armillati										
Cortinarius	*armillatus*	5			2	1		2	27	0.386
Subgen. Telamonia sect. Anomali										
Cortinarius	*anomalus*	20			1	5	6	8	187	0.933
Cortinarius	cf. *anomalus*	6					4	2	47	0.234
Subgen. Telamonia sects Pholidei and Fuscoperonati										
Cortinarius	*pholideus*	2				2			4	0.024
Subgen. Telamonia sects Brunnei, Cinnabarini, Colymbadini, Disjungendi and Uracei										
Cortinarius	*gentilis*	18				2	6	10	48	0.169
Cortinarius	*brunneus* coll.	79			3	27	15	34	1 411	11.055
Cortinarius	sp. 1	38			6	12	7	12	216	0.812
Cortinarius	sp.2	20	1	1	6	5	2	5	65	0.339
Subgen. Telamonia sects Telamonia and Camphorati										
Cortinarius	*camphoratus*	16			1	5	1	9	65	1.686
Cortinarius	*traganus* var. *traganus*	34				11	2	21	210	7.825
Subgen. Telamonia sect. Malachii										
Cortinarius	*malachius*	10			2	3	4	1	40	0.671
Subgen. Telamonia sects Balaustini, Lanigeri and Niveoglobosi										
Cortinarius	*laniger*	6			1	2		3	19	0.224
Subgen. Telamonia sects Bicolores and Duracini										
Cortinarius	*evernius*	3				1		2	29	0.290
Subgen. Telamonia sects Obtusi and Acetosi										
Cortinarius	*obtusus* s. lato	4				2	1	1	36	0.220
Cortinarius	sp.3	13		1	2	5	1	4	48	0.240
Cortinarius	sp.4	14		3	3	3	4	1	110	0.965

Subgen. Telamonia sects Firmiores, Urbici and Boulderenses

	Cortinarius	*biformis*	13			2	5	4	2	153	1.143
	Cortinarius	*armeniacus* coll.	86			8	32	13	33	1 120	6.591
	Cortinarius	sp.8	8			4	4			70	0.760
	Cortinarius	sp.9	3				2		1	48	0.282

Subgen. Telamonia sects Hinnulei and Safranopedes

	Cortinarius	*hinnuleus* s. lato	1						1	2	0.064

Subgen. Telamonia sects Incrustati, Helvelloides, Paleacei and Saniosi

	Cortinarius	*angelesianus*	7			2		1	4	48	0.090
	Cortinarius	*flexipes coll.*	3		1	1			1	28	0.056
	Cortinarius	cf. *flexipes*	1						1	2	0.008
	Cortinarius	*hemitrichus*	5				3		2	59	0.164

Hymenogasteraceae

	Hebeloma	*mesophaeum*	2				2			16	0.021
	Hebeloma	*crustuliniforme* s. lato	1						1	1	0.012
	Hebeloma	sp.1	8	1				1	6	31	0.118
	Hebeloma	sp.2	1					1		1	0.007
	Leucocortinarius	*bulbiger*	1				1			3	0.021
	Naucoria	*amarencens*	10	4	4	1	1			139	0.049
	Naucoria	*pseudoamarescens*	1		1					9	0.006
	Naucoria	sp. 1, nom. nud.	2		2					8	0.016
	Inocybe	*rimosa*	1						1	2	0.004
	Inocybe	*lacera* var. *lacera*	14	1	2	6	5			45	0.095
	Inocybe	*subcarpta*	8		3	3	1	1		46	0.121
	Inocybe	*lanuginosa*	7			4	2	1		16	0.026
	Inocybe	*grammata*	1	1						23	0.044
	Inocybe	sp.1	1				1			1	0.002

II. HYMENOMYCETES

4. CANTHARELLALES

Cantharellaceae

C, M ***	*Cantharellus*	*cibarius* var. *cibarius*	1			1				1	0.010

5. GOMPHALES

Ramariaceae

E*	*Ramaria*	*flava* sensu lat.	1				1			1	0.030

6. THELEPHORALES

Thelephoraceae

	Thelephora	*terrestris* f. *terrestris*	17	2	4	10	1			170	0.274
	Tomentella	sp.1	2		2					8	0.012

Bankeraceae

	Bankera	*fuligineoalba*	1						1	2	0.060
NT	*Boletopsis*	*grisea*	1						1	1	0.025
	Hydnellum	*caeruleum*	7			1	4	1	1	17	0.535
	Hydnellum	*aurantiacum*	1				1			3	0.015
	Hydnellum	*ferrugineum*	6			1	3	2		17	0.850
	Hydnellum	*peckii*	2				1	1		9	0.090
	Phellodon	*tomentosus*	10				7		3	154	0.417

	Phellodon	*niger*	1						1	4	0.049
	Sarcodon	*fennicus*	1						1	1	0.015
7. HYMENOCHAETALES											
Hymenochaetaceae											
	Coltricia	*perennis*	8	1		3	4			24	0.048
ASCOMYCOTA											
III. EUROTIOMYCETES											
8. EUROTIALES											
Elaphomycetaceae											
	Elaphomyces	*granulatus*	1				1			2	0.005
Total		133		15	23	72	87	59	69	14 469	159.583

Appendix 4. ECM species and number of sporocarps in fire severity classes A (HOT) and B (HOT-DRY) in years 1993-2004. Numbers are total numbers of sporocarps observed in all plots during each year. Total number of species was 31.

Species	1993		1994		1995		1996		1997		1998		1999		2000		2001		2002		2003		2004	
	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Laccaria laccata coll.			2		2		4		8	47	31	240	25	181	19	269	15	213	5	71	18	161	12	82
Thelephota terrestris f. terrestris			2									15					6					13		
Naucoria amarescens			45	37	21	9								15										
Inocybe grammata			23																					
Naucoria pseudoamarescens						9																		
Lactarius mammosus									4		5				10	3					3			66
Cortinarius sp. 2									1									3						
Cortinarius sp. 4										19														
Paxillus involutus										2		37		4		9		6				30		8
Hebeloma sp. 1											1													
Inocybe lacera var. *lacera*												3									2			2
Lactarius rufus												3					5	14				9		8
Naucoria sp. 1												8												
Xerocomus subtomentosus													1											
Russula olivascens														1										
Russula versicolor														4		7						30		
Inocybe subcarpta																5						6		
Russula betularum																		2						
Russula sp. 2																		2						
Suillus luteus																			1		15			
Cortinarius sp. 3																				5				
Russula atrorubens																					2	3	5	
Cortinarius semisanguineus																					3			
Suillus bovinus																					5		24	
Leccinum versipelle																					2		1	
Leccinum scabrum																					3	7	2	3
Coltricia perennis																					1			
Cortinarius croceus var. *croceus*																						3		1
Lactarius vietus																						72		9
Tomentella sp. 1																						8		
Russula gracillima																								4
Total no. of species	0	0	4	1	2	2	1	0	3	3	3	6	2	5	2	5	3	6	2	2	10	11	5	9