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Restoration fire and wood-inhabiting fungi in a Swedish *Pinus sylvestris* forest

Jörgen Olsson[a,*], Bengt Gunnar Jonsson[b]

[a] *Department of Ecology and Environmental Science, Umeå University, SE-901 87 Umeå, Sweden*
[b] *Department of Natural Sciences, Engineering and Mathematics, Mid Sweden University, SE-851 70 Sundsvall, Sweden*

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ABSTRACT

A growing awareness of the negative consequences of efficient fire prevention in boreal Fennoscandia has resulted in an increasing use of fire as a restoration method. The primary purpose of restoration fire is to recreate features of natural forests that have been lost during long periods of fire suppression. We used the occurrence of fruiting bodies from wood-inhabiting fungi to assess the conservation value of and gain ecological information about restoration fire in a *Pinus sylvestris* dominated forest. The general pattern for the majority of the species was a drastic decline the first two years after the restoration fire. However, our results clearly demonstrate that most of the species that declined the first years after the fire rebounded after four years and were frequently found on charred wood. Species that increased after the fire and often occurred on charred logs were: *Antrodia sinuosa*, *Botryobasidium obtusisporum*, *Galzinia incrustans*, *Phlebia subserialis* and *Tomentella* spp. In addition, three threatened, red-listed and fire-favored species were also found on heavily charred logs: *Antrodia primaeva*, *Dichomitus squalens* and *Gloeophyllum carbonarium*. Our results indicate that fire disturbance creates a unique type of dead wood important for fungal species richness. The results also support the use of restoration fires in maintaining forest biodiversity.

1. Introduction

Fire is a fundamental process in the boreal forest ecosystem. The variation in fire frequency, severity, size and timing creates a mosaic forest landscape with stands in different successional stages after disturbance (Zackrisson, 1977; Niklasson and Granström, 2000; Ryan, 2002). The heterogeneity and variation created by fire is essential for maintaining forest biodiversity. For example, fires may create large input of dead wood, a key substrate for species richness (Harmon et al., 1986; Siitonen, 2001; Jonsson et al., 2005). The effective fire suppression during the last 150 years has reshaped the Fennoscandian boreal forest, and early post-fire successional stands have become rarer and smaller than they were historically (Linder et al., 1997; Uotila et al., 2002). Lack of fire has led to a shift in the forest structure, and many unmanaged stands previously dominated by *Pinus sylvestris* L. are increasingly dominated by the more shade tolerant and fire sensitive *Picea abies* (L.) Karst. (Engelmark, 1987). In addition, living and dead deciduous trees are becoming increasingly rare as succession proceeds (Linder et al., 1997; Niklasson and Drakenberg, 2001; Jönsson et al., 2009).

The natural fire return interval in Swedish dry *P. sylvestris* forests has varied depending on human impact, climate, altitude, and site type (Niklasson and Granström, 2000; Kouki et al., 2004), and the average fire return interval has historically ranged between 20 and 100 years (Zackrisson, 1977; Engelmark, 1984; Niklasson and Drakenberg, 2001).

Depending on the intensity and forest type, fires may create large inputs of dead wood (Spies et al., 1988; Linder et al., 1998; Siitonen, 2001). In addition, fire increases wood heterogeneity, ranging from wood unaffected by fire to heavily charred wood and often also provides new microclimate conditions. However, fire can also consume large amounts of dead wood (Knapp et al., 2005), particularly logs and snags in advanced decay stages (Eriksson et al., in preparation). The immediate fire effect on the existing fungal community seems to be a considerable decrease in both the species richness and diversity of fruiting wood fungi (Penttilä and Kotiranta, 1996; Junninen et al., 2008). At the same time, fire disturbance opens up opportunities for ruderal species as well as for the development of new fungal communities (Pugh and Boddy, 1988; Penttilä and Kotiranta, 1996). Because fire is a natural feature of the boreal forest and fire-affected dead wood is historically a common substrate, it seems that wood-inhabiting fungi should be adapted to, or some even dependent on, fire disturbance.

The growing awareness of the negative consequences of fire suppression has resulted in an increased use of fire as a restoration method in boreal Fennoscandia. Fire has long been used in forest management for soil preparation after clear-felling and to reduce forest fuels. However, the primary purpose of restoration fire is to recreate features of natural forests that have been lost during long periods of fire suppression. The value of restoration

* Corresponding author. Tel.: +46 90 786 66 34, fax: +46 90 786 67 05.
E-mail address: jorgen.olsson@emg.umu.se (J. Olsson).

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fires for insect biodiversity is emerging through several recent studies (Hyvärinen et al., 2006; Toivanen and Kotiaho, 2007). Based on controlled field experiments, Hyvärinen et al. (2006) showed that both species richness and number of individuals of red-listed and rare saproxylic species increased after restoration fire. Knowledge of the fire dependence of wood-inhabiting fungi is less developed. Studies by Penttilä and Kotiranta (1996) and Penttilä (2004) demonstrated strong positive effects of fire, but primarily as an effect of increased wood availability. Junninen et al. (2008) only found a minor increase in fruiting bodies of red-listed species fruiting in the first four years after fire. Thus, to what extent there exists a larger group of truly fire-favored wood fungi is still an open question. Since the use of restoration fire in the Fennoscandian forest is increasing, the ecological impact on key groups, such as saproxylic organisms needs to be evaluated.

The present study provides one of the first reports where the effects of a regular restoration fire on wood-inhabiting fungal communities have been explored. The experimental design allows comparison of pre- and post-treatment data with data from a nearby control area. Although unreplicated, the study is unique because it describes the fruiting patterns on individually mapped logs over a four-year period after fire. We hypothesize (i) that the restoration fire will change the pre-fire fungal community by negatively affecting some species and increasing the frequency of other species and (ii) that the fire will promote colonization of species rare or absent before the fire.

2. Methods

2.1. Study area

The study area is located 45 km north of Umeå, Västerbotten County, in the middle boreal zone (sensu Ahti et al., 1968) of Sweden. The study area consists of two coniferous forest stands, separated by about 200 m. At the center of each stand a 12 ha sampling site was selected. The disturbed site was burned in June 2001 while the other site was left as a control area. The altitude of the sites is 140–160 m asl. In this region the post-glacial seashore line is about 250 m above the current sea level, and hence the study area has strongly washed soils. The vegetation ranges from xeric dwarf-shrub type (lichen type; Arnborg, 1990) to dry dwarf-shrub type (*Vaccinium* type; Arnborg, 1990). These vegetation types are dominated by reindeer lichens (*Cladonia* spp.) together with *Vaccinium vitis-idea* L., *Calluna vulgaris* (L.) Hull, *V. myrtillus* L. and mosses like *Pleurozium schreberi* (Willd. ex Brid.) Mitt. and *Hylocomium splendens* (Hedw.) Schimp. Small portions of the study area are moister and the vegetation is of the mesic dwarf-shrub type (*Myrtillus* type; Arnborg, 1990). The canopy is dominated by *P. sylvestris*, with *P. abies* only occurring at mesic microsites and with scattered individuals of *Betula* spp. The study area is dominated by a low productive forest on shallow soils, and the standing volume of living trees ranged from lower than 100 $m^3\ ha^{-1}$ forests to 215 $m^3\ ha^{-1}$. Stand structure was influenced by historic selective harvest and fires. The fire history of the study area, based on fire-scarred trees and snags indicate at least six fires (1570, 1635, 1697, 1778, 1807 and 1828; David Rönnblom, Holmen Skog, personal communication). The oldest known *P. sylvestris* trees in the study sites are nearly 200 years old, generated after the 1807 and 1828 fires. The oldest known *P. sylvestris* tree in the area is more than 420 years old, but located outside the two study sites.

2.2. The restoration fire and sampling of experimental data

In September–October 2000, before the restoration fire, a total of 319 logs with ≥ 10 cm maximum diameter were analyzed and mapped, 150 in the fire site and 169 in the control site. In the previous winter, some logging occurred in the fire site, and only logs that were not in direct contact with the logging activity (<10 m from a felled tree) were included in the study. The rationale for this choice was to minimize the effects of artificial canopy gaps among the sampled logs. Each log was given an ID-number and the base and top diameter, length, stage of decay, percent ground contact, percent charred surface area, adjacent vegetation type, and position were recorded (Table 1). Log volume was estimated according to Smalian's formula (Husch et al., 1982). Fruiting bodies of wood-inhabiting fungi (mainly polypores and corticioids) were recorded. The presence–absence of fruiting bodies (e.g. Renvall, 1995; Berglund et al., 2005; Junninen et al., 2008) is the only feasible approach for large field studies. This method excludes non-fruiting species present only as mycelia. However, the use of DNA-analysis of each log is beyond the scope of this study.

Table 1
The variables recorded for each log before the restoration fire in 2000.

Base and top diameter (cm)
Length (m)
Decay stage
1. Freshly fallen trees with bark intact and needles remaining on the branches.
2. Wood hard, bark intact or broken up and fallen off but >50% remaining.
3. Wood hard, <50% bark remaining.
4. Wood is starting to get soft, no bark left or with small pieces of bark at the base.
5. Wood soft with small to large pieces of wood lost, mosses and lichens are often present
6. The log is collapsed or with cavities from the decaying heartwood, mosses and lichens are more or less covering the log
Ground contact (%), visually estimated
Ground fuel (cm): humus layer, litter, and low lichen and moss vegetation, measured by digging down to the mineral soil
Charred surface area (%), visually estimated
Vegetation type (Arnborg, 1990) around the log
ID-number, a metal plate were put into the soil at the base of the log
Position coordinates were measured at the base of the log using a GPS-device

Species that were difficult to identify in the field were collected for microscope identification (ca. 5000 specimens throughout the study). The number of logs each species was growing on was recorded (i.e. one or several fruiting bodies per log equals one record). Nomenclature follows the literature used for identification and all genera found in the study are present in: Eriksson and Ryvarden (1973, 1975, 1976); Eriksson et al. (1978, 1981, 1984); Hjortstam et al. (1987, 1988); Gilbertson and Ryvarden (1986); Ryvarden and Gilbertson (1993, 1994); Hansen and Knutsen (1997); Niemelä (1998). All specimens were identified to species except those within the genera *Tomentella* and *Tulasnella*. Definitions of coarse woody debris decay stages were adapted and modified from McCullough (1948; Table 1). If there were two or several decay stages in the same log, the dominant stage was recorded (i.e. the stage representing more than half of the log volume).

The fire site was burned June 27–29, 2001. The restoration fire was of low intensity with an average fire spread of about 1–2 m min^{-1} and the flame height was up to 2 m. About 30 ha were burned although the fire intensity varied throughout of the area. In September–October of 2001, 2003 and 2005, all logs in the fire- and control sites were re-examined with the same method as before the fire. Fruiting bodies occurring on newly charred wood were specifically noted.

The fungi fruiting on logs were divided into four different functional groups based upon their different nutritional strategies, white rot wood-decaying species, brown rot wood-decaying species, litter- and humus-decaying species, and mycorrhizal

Table 2
Recorded wood-inhabiting fungi (polypores and corticioids) from the control- and fire sites divided into functional groups based on different nutritional strategies: white rot = wood-decaying species causing white rot, brown rot = wood-decaying species causing brown rot, humus = litter and humus-decaying species, mycorrhiza = wood-inhabiting species with mycorrhiza.

White rot	Brown rot	Humus	Mycorrhiza
Ceraceomyces spp.	*Amyloathelia crassiuscula*	*Asterostroma laxum*	*Amphinema byssoides*
Ceriporiopsis mucida	*Amylocorticium cebennense*	*Athelia* spp.	*Piloderma* spp.
Conferticium ochraceum	*Anomoporia kamtschatica*	*Athelicium stridii*	*Sistotrema muscicola*
Dichomitus squalens	*Antrodia* spp.	*Athelopsis* spp.	*Tomentella* spp.
Diplomitoporus lindbladii	*Chaetoderma luna*	*Botryobasidium* spp.	*Tomentellopsis echinospora*
Galzinia incrustans	*Coniophora* spp.	*Botryohypochnus isabellinus*	*Tylospora* spp.
Globulicium hiemale	*Dacryobolus* spp.	*Hydrabasidium subviolaceus*	
Gloeocystidiellum subasperisporum	*Fomitopsis pinicola*	*Sistotrema autumnale*	
Hapalopilus salmonicolor	*Gloeophyllum* spp.	*Sistotrema brinkmannii*	
Hyphoderma spp.	*Jaapia ochroleuca*	*Sistotrema diademiferum*	
Hyphodontia spp.	*Leucogyrophana* spp.	*Sistotrema oblongisporum*	
Hypochnicium spp.	*Oligoporus* spp.	*Trechispora* spp.	
Ischnoderma benzoinum	*Pseudomerulius aureus*		
Junghuhnia luteoalba	*Serpula himantioides*		
Leptosporomyces galzinii			
Merulius tremellosus			
Odonticium romellii			
Peniophora pithya			
Phanerochaete spp.			
Phellinus viticola			
Phlebia spp.			
Phlebiella spp.			
Phlebiopsis gigantea			
Resinicium furfuraceum			
Sistotremastrum suecicum			
Skeletocutis spp.			
Stereum sanguinolentum			
Trichaptum spp.			
Tubulicrinis spp.			

species (Table 2). The classification is based on the literature used for identification and a number of previous publications (Kõljalg et al., 2007; Binder et al., 2005; Larsson et al., 2000).

2.3. Statistical analysis

We used nonmetric multidimensional scaling (NMS) to describe the species composition by year in the control- and fire sites before and after the restoration fire. The NMS ordination was preformed with PC-ORD software version 4.25 (McCune and Mefford, 1999). Species occurring on fewer than three logs were excluded from the ordination analysis to reduce the influence of rare species, and the species count data were log-transformed ($\log_{10}(x+1)$). Analysis parameters were set to Sørensen distance measure with 100 runs with real data and 500 randomized Monte Carlo runs. Dead wood characteristics in the control- and fire sites prior to the restoration fire were compared with Student's *t* and chi-square tests using SPSS software 16.0 (SPSS, 2007). Variations in average numbers of species per log over time were assessed with repeated measures ANOVA (SPSS, 2007) and heterosphericity was tested with Mauchly's test of sphericity. Between year variation was analyzed in a one-way ANOVA for the control- and fire sites separately, and differences between years were assessed with Tukey's HSD.

3. Results

3.1. Fungal community and study area variables

A total of 3342 records, representing 28 polypore species, 117 corticioid species and 9 species belonging to other fungal groups were recorded at the control- and fire sites (Appendix A). A few species dominated the study sites, while the majority (about 65%) only occurred on 1–3 logs in each site. Before the restoration fire, average number of species fruiting per log differed significantly between the sites ($t_{317} = 3.787$, $P < 0.001$) with 1.95 in the fire site and 2.66 in the control site (Fig. 1), with 15% of the logs in the fire site entirely lacking fruiting bodies compared with 8% in the control site (Table 3). Species richness distribution over the decay stages (Fig. 2) was similar at both sites, with the highest species richness in intermediate decay stages. Species composition was relatively similar between sites, with 84% of the species occurring in both sites. While the ordination indicated some separation between the sites, it was relatively small (Fig. 3).

Before the fire, log characteristics and adjacent vegetation types were largely comparable between the control- and the fire sites, although in several cases statistically different (Table 4). The xeric dwarf-shrub type was more frequent in the fire site while the mesic dwarf-shrub type was more common in the control site (Table 4). In addition, the fire site had more logs in decay stage 6 whereas the control site had more logs in decay stage 3 (Table 4). The restoration fire strongly affected the stand structure and the dead wood: twenty-three percent of the log volume was consumed (20.9 m^3 before and 16.1 m^3 after the fire). About 20% of logs in decay stages 4–6 lost more than 50% of their volume. However, 30% of the logs

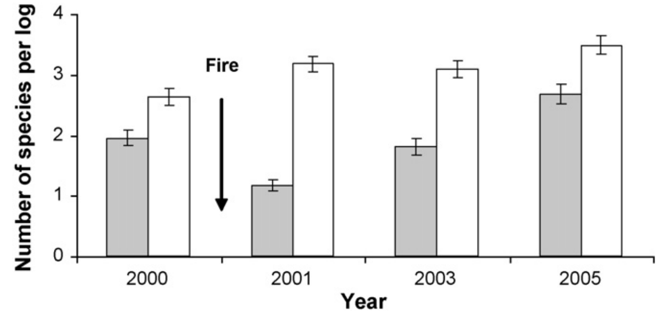

Fig. 1. Average number of wood-inhabiting fungi species (polypores and corticioids) per sampled log before and after fire ± S.E. Grey: fire site, $n = 150$ logs; white: control site, $n = 169$ logs.

Table 3
The number of records of wood-inhabiting species (polypores and corticioids) in the fire site ($n = 150$ logs) and control site ($n = 169$ logs). The proportion (%) of logs without species, remaining, lost and new species found before (year 2000) and after restoration fire in the fire- and control sites.

	Fire site				Control site			
Year of inventory	2000	2001	2003	2005	2000	2001	2003	2005
Number of species	69	53	52	67	83	93	82	92
Same species (%)	–	54	57	67	–	84	70	78
Missing species (%)	–	46	43	33	–	16	30	22
New species (%)	–	23	19	30	–	28	28	33
Logs without species (%)	15	33	19	15	8	6	2	4

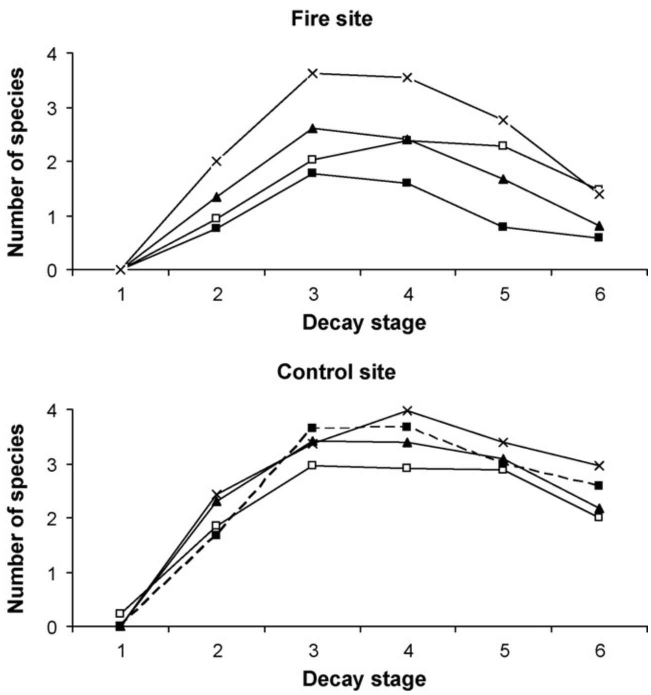

Fig. 2. Average number of fungal species per log sampled in each decay stage in the control site ($n = 169$) and fire site ($n = 150$), (□) year 2000, (■) year 2001, (▲) year 2003, (×) year 2005. Decay stages ranging from (1) "Freshly fallen trees with bark intact" to (6) "Log heavily decayed collapsed or with cavities and more or less covered with ground vegetation".

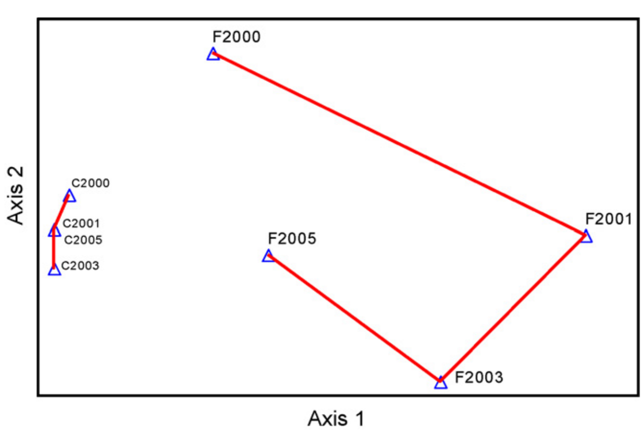

Fig. 3. Two-dimensional solution of the NMS ordination of the wood-inhabiting fungi species (polypores and corticioids) assemblages in the control site (C) and fire site (F), from the year 2000 to 2005. The stress value was low (<0.001) in the final two-dimensional solution, after 100 iterations indicating a stable solution. Only species that occurred on more than two logs per year are included in the analysis.

showed almost no consumption at all. On the other hand, most logs were heavily charred and 65% of the logs had more than 60% charred log surface. The fire also had a considerable effect on the log ground contact, which decreased from 60% before the restoration fire to 31% after the fire ($t_{298} = 8.417$, $P < 0.001$; Table 4). Before the restoration fire almost 50% had more than 80% ground contact but after the fire only 11% had more than 80% ground contact.

3.2. Effects of the restoration fire on species composition and species richness

There were major changes in the species composition in the fire site compared to the control site after the restoration fire, and between inventory years in the fire site (Fig. 3). Most of the polypores and corticioids decreased during the first season after the restoration fire. Of the species recorded at the fire site prior to the fire, only 54% were found the first autumn after the fire. This stands in strong contrast to the results from the control site where 84% of the originally recorded species were observed the autumn after the fire. Average numbers of species per log decreased significantly ($F_{3,599} = 20.449$, $P < 0.001$) at the fire site in the autumn after the fire (Fig. 1; Table 5), especially on logs in decay stages 4–6 (Fig. 2). By contrast, average numbers of species per log in the control site increased between 2000 and 2001 ($F_{3,675} = 6.404$, $P < 0.05$) (Fig. 1; Table 5). Species that showed strong post-fire declines in relation to the control site were; *Hyphoderma praetermissum*, *Hyphodontia hastata*, *Junghuhnia luteoalba*, *Trichaptum* spp. and *Tubulicrinis* spp. The relatively rare *Phlebia cretacea*, *Odonticium romellii* and *Skeletocutis lenis* disappeared after the fire and were still missing four years later (Appendix A). There were a few species that responded positively in the autumn immediate after the restoration fire, namely

Table 4
Characteristics of the logs studied before the restoration fire. Differences between the two sites tested with Student's *t*-test except for decay stages and vegetation type where chi-square test was applied.

	Fire site	Control site	*P*-value
Number of logs	150	169	–
Total log volume (m^3)	20.9	20.1	–
Mean log diameter (cm)	18.7	17.5	0.065
Mean decay stage	4.2	3.7	<0.001
Decay stage distribution (%)			
1	3.3	5.3	
2	5.3	7.7	
3	24.0	35.5	
4	23.3	21.9	
5	25.3	21.9	
6	18.7	7.7	
Mean log volume (m^3)	0.14	0.12	0.140
Mean ground contact (%)	59.7	42.1	<0.001
Mean charred wood (%)	–	<0.1	–
Logs without species (%)	16.0	7.7	<0.001
Vegetation type			
Xeric dwarf-shrub type (%)	79.3	73.3	–
Dry dwarf-shrub type (%)	9.3	8.3	–
Mesic dwarf-shrub type (%)	11.3	18.3	–
Average number of species per log	1.95	2.66	<0.001

Table 5
Tukey's HSD post hoc teats for average number of fungal species per log in the control- and fire sites tested with one-way ANOVA in the control- and fire sites, respectively.

Post hoc-test	*P*-value	
Year	Control site	Fire site
2000–2001	0.027	<0.001
2001–2003	1.000	0.001
2003–2005	0.403	<0.001
2000–2005	<0.001	0.014
2001–2005	0.438	<0.001

Botryobasidium obtusisporum, *Phanerochaete sordida*, *Phlebia subserialis* and *Trichoderma viride*. In addition, their fruiting bodies were frequently found on charred log surfaces. However, *T. viride* disappeared after the second year after the fire. Species that increased in abundance two years after the fire and were frequently on charred surfaces were *Athelia epiphylla*, *A. fibulata*, *Galzinia incrustans*, and *Sistotrema brinkmannii* (Appendix A).

The repeated measures ANOVA of the number of species per log revealed a significant interaction between years and site (within-subjects effects, $F_{3,315} = 22.001$, $P < 0.001$) and the control- and fire sites were significantly different (between-subjects effects, $F_{1,317} = 80.506$, $P < 0.001$). In addition, the average number of species increased significantly (one-way ANOVA, $F_{3,599} = 20.449$, $P < 0.001$) after the restoration fire (2001–2005) in the fire site (Table 5) and four years after the restoration fire, the number of species per log was higher than prior to the fire (Fig. 1). In comparison, the number of species per log was relatively stable between 2001 and 2005 at the control site (Table 5; Fig. 1). However, there was a small but significant increase at the control site in average number of species from 2000 to 2005 (Table 5; Fig. 1). The similarity between the species present in the fire site before and after the fire increased from 54% the autumn after the fire to 67% four years after the fire (Table 3). Fungal species occurring at intermediate decay stages showed the strongest positive post-fire responses four years after the fire (Fig. 2). Many of the species occurred on logs that were highly influenced by the restoration fire (degree of burn) and fruiting bodies were often found on charred log surfaces (Appendix A). Species that increased four years after the restoration fire and were growing on logs with more than 50% charred surface area were; *Anomoporia kamtschatica*, *Antrodia sinuosa*, *B. obtusisporum*, *P. subserialis*, and *Tomentella* spp. In addition, some rare threatened species were also recorded after the fire: *Antrodia primaeva*, *Dichomitus squalens* and *Gloeophyllum carbonarium*.

3.3. Fire effects on the functional groups

There were major changes in the white rot and humus-decaying species after the restoration fire. The relative abundance of white rot species decreased from 57% to 24% during the first two years after the fire. At the control site their relative abundance was more or less stable (Fig. 4). However, four years after fire they had increased, although not reaching the same relative abundance as before the restoration fire (Fig. 4). The humus-decaying species showed the reverse pattern, with a strong increase in relative abundance from 19% to 60% during the first two years after the fire. Four years after the fire they had decreased to a relative abundance close to that before the restoration fire (Fig. 4). In the control site they remained relatively stable at 30% relative abundance. For the brown rot and mycorrhizal species there was limited variation in their relative abundances after the restoration fire, although the brown rot species response partly mirrors that of the white rot species (Fig. 4).

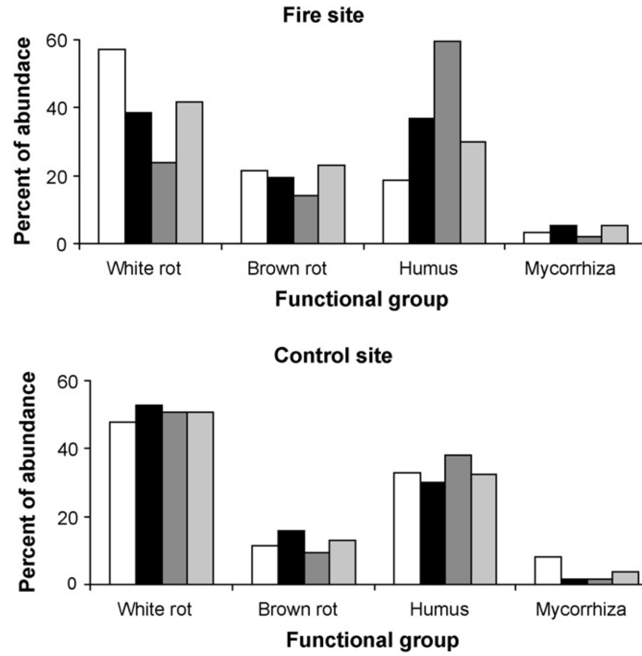

Fig. 4. The relative abundance of functional groups of wood-inhabiting fungi (Table 2) recorded from the control- and fire sites: white rot = wood-decaying fungi causing white rot, brown rot = wood-decaying fungi causing brown rot, humus = litter and humus-decaying fungi, mycorrhiza = wood-inhabiting fungi with mycorrhiza. White = before restoration fire (year 2000), black = same year as the fire (year 2001), dark grey = 2 years after fire (year 2003), light grey = 4 years after fire (year 2005).

4. Discussion

The species composition of wood-inhabiting fungi was strongly influenced by the restoration fire, and the variability in fungal community development following the restoration fire is striking (Fig. 3). The general pattern for the majority of the common wood-inhabiting fungi species was a drastic decrease the first two years after the restoration fire followed by an increase after four years. Further, they were frequently found on logs strongly influenced by the restoration fire and grew on charred log surface.

4.1. Early stage of fungal community development

Our result shows that the short-term effects of fire are a reduction in both species richness and species diversity, agreeing with other studies on the effect of fire on wood-inhabiting fungi (Penttilä and Kotiranta, 1996; Junninen et al., 2008). Besides the immediate destructive effect of fire on the resident fungal community, microclimate conditions are also altered after fire. The open stand conditions after the fire increase sun and wind exposure and decrease log moisture, a factor important for wood-inhabiting fungi (Boddy, 1983; Rayner and Boddy, 1988); this effect increases with decay stage (Sollins et al., 1987; Renvall, 1995). Logs in advanced decay stages are often covered with mosses and lichens, contributing to a more stable microclimate within the log. After the restoration fire, fungal communities were exposed to higher substrate temperature due to charred log surfaces and increased sun radiation. Logs became dryer due to the high amount of charred log surface, the reduced ground contact, and the loss of lichen and moss cover. These effects are particularly pronounced on more advanced decayed logs, and several of the species that decreased the first two years after the restoration fire were growing on logs in decay stage 4–6 (Fig. 2). Those apparently most vulnerable were species in the genera *Antrodia*, *Hyphodontia*, *Junghuhnia*, *Phlebia*, *Skeletocutis* and *Tubulicrinis*.

The early stages of fungal succession after disturbance are characterized by non-decaying fungi together with ruderal, less effective wood-decaying species, while in later stages, more competitive species become prevalent (Rayner and Boddy, 1988). Our results agree with these observations; during the first two years post-fire the developing fungal community is dominated by fungi with ruderal and stress-tolerant strategies, such as *B. obtusisporum*, *Athelia* spp., *T. viride* and *Costantinella* spp. *T. viride* is a blue-green anamorphic mould (ascomycetes) that is common on ephemeral substrate like food and soil that was very frequent the autumn after the restoration fire, often occurring on charred log surfaces (Appendix A). This clearly ruderal species had completely disappeared by two years after the fire.

After four years, most of the species that decreased during the first two years in the fire site had recovered and the average number of species per log exceeded the pre-fire richness (Fig. 1). Many of the fruiting bodies were found growing on charred log surfaces. However, species composition remained different from the pre-fire community (Fig. 3). The restoration fire changed the abundance of logs in the different decay stages and in some respect made the fire site and control site more similar as a large fraction of the decay stage 5 and 6 logs were consumed. This may explain why the trajectory in the ordination suggests that the species composition in the fire site is slowly approaching that of the control site (Fig. 3). Three threatened, red-listed species with preference for burned areas (Renvall, 1995; Penttilä, 2004; Stenlid et al., 2008) were found growing on heavily charred logs (*A. primaeva*, *D. squalens* and *G. carbonarium*). *A. primaeva* was observed on charred log surface the same year as the restoration fire and it is likely that it was already established in the log, waiting for suitable conditions. Similarly, Renvall (1995) found *A. primaeva* on 8 of 51 strongly charred *P. sylvestris* logs in old-growth forest in north-east Finland. Several wood-inhabiting fungal species found in this study have previously been found fruiting after fire and suggested to be favored by fire (Eriksson, 1958; Renvall, 1995; Lindgren, 2001; Penttilä and Kotiranta, 1996; Penttilä, 2004; Junninen et al., 2008), including; *A. sinuosa*, *A. xantha*, *A. primaeva*, *Athelia* spp., *B. obtusisporum*, *D. squalens*, *G. sepiarium*, *G. protractum*, *Oligoporus placenta*, *O. sericeomollis*, *Piloderma croceum*, *S. brinkmannii*, suggesting that the wood-inhabiting fungal community in dry *P. sylvestris* forest is evolutionarily adapted to fire disturbance.

Not all species re-appeared after the restoration fire in duration of the study, notably the red-listed species *Antrodia albobrunnea*, *O. romellii* and *S. lenis*. If these taxa depend on re-colonization from the surrounding landscape, the lack of dead wood and natural *P. sylvestris* forests with recent fire histories, their ability to migrate from areas of refugia may be strongly limited. The current degree of isolation for fire-dependent and fire-favored species is mostly likely very large in the study region.

4.2. Restoration fire effects on fungi with different nutritional strategies

Our results clearly show variation in relation to the nutritional strategies of associated fungi after the restoration fire and during the first years of fungal community development. The white rot species decreased the two first years after fire in the burn site and compared to the control site. Four years after the fire they had started to recover, although not reaching pre-fire levels (Fig. 4). The post-fire response of the brown rot species paralleled that of white rot species, and we predict that both brown rot and white rot species will continue to increase. Brown rotting species are known to increase after fire, including species such as *Antrodia* spp., *Coniophora arida*, *Gloeophyllum* spp., *Leucogyrophana romellii*, *O. placenta*, and *O. sericeomollis* (Eriksson, 1958; Renvall, 1995; Lindgren, 2001; Penttilä, 2004). However, many wood rot species growing on highly decayed logs depend on stable microclimate conditions and may be highly sensitive to the fire disturbance (Cooke and Rayner, 1984; Pugh and Boddy, 1988; Penttilä and Kotiranta, 1996). The humus-decaying species increased already the same year as the fire and two years post fire they accounted for 60% of the total abundance. However, four years after the fire they were close to the pre-fire levels and more or less equal to their abundance in the control (Fig. 4). The restoration fire provided competition-free substrate that is suitable for ruderal, stress-tolerant, and humus-decaying species. The larger species turnover in the fire site suggests that the occurrence of these species represent new colonization events. However, some species could have been present within the wood and not fruiting during the pre-fire inventory waiting for a disturbance like a forest fire to occur.

Several mycorrhizal and humus-decaying species utilize dead wood substrates for formation of fruiting bodies, but depend on soil conditions for their occurrence. Forest fires generally increase soil pH and release organically bound nutrients from the humus layer (MacLean et al., 1983). The charcoal produced by the fire also has the ability to absorb phytotoxic active phenolic compounds (Zackrisson et al., 1996) which can inhibit mycorrhizal function (Nilsson et al., 1993). In contrast to the strong effect of fire on the humus-decaying species, the mycorrhizal species were relatively unaffected (Fig. 4). Exceptions were *Tomentella* spp. and *Tomentellopsis echinospora* found only on heavily affected and charred logs with fruiting bodies common on charred surfaces (Appendix A). Mortality of ectomycorrhizal fungi correlates with fire severity and tree survival. In dry forests, mycorrhizal mycelia are located deeper in the mineral soil than in mesic forest, increasing their likelihood of survival (Stendell et al., 1999; Dahlberg et al., 2001). In our fire site, tree mortality was low and soil surface consumption patchy, contributing to the minimal effect of the restoration fire on the mycorrhizal community. However, the mycorrhizal fungal community maybe needs additional time to recover and show positive post-fire response similar to Renvall (1995), which found the mycorrhizal species *P. croceum* on 28 of 51 strongly charred *P. sylvestris* logs.

5. Conclusion

The present study provides empirical information on the development of the wood fungi community after a restoration fire. The results show highly dynamic early stages after the disturbance with a strong decrease in the number of fruiting species the first years after the fire. However, the fungal community rapidly recovered and a set of new species colonized logs affected by the restoration fire. This indicates that the fire provides a unique type of dead wood important for the species richness of associated fungi. The result thus lends support to the use of restoration fires in maintaining forest biodiversity, and that the negative effects on the wood fungi community are limited. However, every restoration fire is unique and site-specific effects depend on fire severity, edaphic conditions, and other environmental factors. Hence, additional studies are needed to support the development of a fire management that will better achieve specific objectives when designing restoration fires.

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Appendix A.

Species list of the recorded wood-inhabiting fungi and their abundance before (year 2000) and after the restoration fire (years 2001, 2003, 2005) in the fire site ($n = 150$ logs) and control site ($n = 169$ logs). Degree of burned surface is based on the area of charred log surface (%), divided into four classes: 1 = 0–25, 2 = 26–50, 3 = 51–75, 4 = 76–100. Fruiting bodies on burned log surface presented as frequency (%) of total records for the specific species. Red-listed species according to Gärdenfors (2005): EN = endangered, VU = vulnerable, NT = near-threatened. Corticioids and polypores were dominating throughout the study, however, some other fungal species were recorded: a = Ascomycota, ag = Agaricales and x = Hymenomycetidae, species traditionally not included within corticioids. (*) Only recorded ones or a few times in Sweden. (**) New for Sweden.

Species	No. of records fire site				No. of records control site				Degree of burn fire site			Fruiting bodies on burned surface		
	2000	2001	2003	2005	2000	2001	2003	2005	2001	2003	2005	2001	2003	2005
Hyphoderma praetermissum	26	11	9	33	28	48	39	45	2	2	3	–	22.2	66.7
Botryobasidium obtusisporum	18	33	76	67	62	70	68	59	4	3	3	66.7	81.6	89.6
Botryobasidium subcoronatum	16	11	9	15	20	27	31	37	3	2	3	45.5	33.3	73.3
Hyphodontia hastata	15	3	3	10	14	18	19	18	1	2	3	–	–	60.0
Trichaptum abietinum	12	2	5	4	11	12	7	4	2	3	2	–	20.0	25.0
Tubulicrinis subulatus	12	1	1	8	14	18	33	32	2	2	2	–	–	87.5
Botryobasidium botryosum	11	7	11	12	14	15	14	24	3	3	3	85.7	81.8	91.7
Hyphodontia breviseta	10	7	6	9	14	24	19	31	3	2	3	–	–	77.8
Tubulicrinis calothrix	10	4	2	9	1	–	1	3	3	4	3	–	–	55.6
Junghuhnia luteoalba NT	9	3	2	3	8	13	5	13	3	3	4	66.7	50.0	100.0
Dacryobolus karstenii	8	6	7	12	9	20	15	18	3	3	3	83.3	57.1	83.3
Antrodia sinuosa	7	1	6	36	2	5	4	9	1	3	3	–	100.0	97.2
Skeletocutis biguttulata	7	4	4	6	5	5	6	11	2	2	2	–	–	33.3
Coniophora arida	6	5	6	8	10	14	5	3	3	3	3	100.0	50.0	75.0
Fomitopsis pinicola	6	3	4	8	1	1	1	1	3	3	3	66.7	–	37.5
Trichaptum fusco-violaceum	6	–	1	2	11	8	4	4	–	2	2	–	–	
Anomoporia kamtschatica NT	5	1	3	8	3	3	1	5	4	3	4	–	–	75.0
Antrodia xantha	5	–	2	1	1	5	2	2	–	4	4	–	100.0	100.0
Ceraceomyces sublaevis	5	3	2	8	10	13	8	15	4	4	3	–	–	12.5
Phlebia cretacea	5	–	–	–	2	2	2	2	–	–	–	–	–	–
Phlebia lilascens	5	–	1	1	2	1	–	–	–	1	2	–	–	100.0
Phlebiella vaga	5	–	–	3	14	8	8	17	–	–	–	–	–	66.7
Hyphodontia subalutacea	4	3	2	7	4	8	6	6	2	2	2	–	–	42.9
Odonticium romellii NT	4	1	–	–	–	–	–	1	4	–	–	–	–	–
Skeletocutis lenis VU	4	1	–	–	–	–	–	2	4	–	–	–	–	–
Athelia fibulata	3	–	14	6	18	12	24	17	–	3	3	–	50.0	83.3
Chaetoderma luna	3	–	1	2	–	1	3	3	–	1	2	–	–	50.0
Dacryobolus sudans	3	–	–	–	5	10	4	3	–	–	–	–	–	–
Gloeophyllum sepiarium	3	1	3	4	3	4	1	1	3	3	3	–	–	50.0
Oligoporus sericeomollis	3	1	1	–	3	1	1	4	4	4	–	–	–	–
Tomentellopsis echinospora	3	5	4	7	15	5	2	8	4	4	4	40.0	50.0	57.1
Tubulicrinis gracillimus	3	–	–	1	1	3	5	3	–	–	1	–	–	–
Tubulicrinis borealis	3	4	5	16	6	11	27	21	2	3	3	25.0	20.0	62.5
Hyphoderma definitum	2	3	5	5	1	2	1	5	3	4	3	66.7	20.0	80.0
Hypochnicium punctulatum	2	2	1	5	8	12	8	9	3	4	3	50.0	100.0	80.0
Leptosporomyces galzinii	2	–	1	–	6	1	–	1	–	3	–	–	–	–
Leucogyrophana romellii	2	–	–	–	1	–	–	–	–	–	–	–	–	–
Oligoporus leucomallellus	2	–	–	–	1	3	1	2	–	–	–	–	–	–
Phanerochaete sanguinea	2	1	–	1	8	3	3	11	2	–	4	–	–	100.0
Piloderma sphaerosporum	2	1	–	3	11	1	3	8	2	–	2	–	–	–
Resinicium furfuraceum	2	1	2	3	3	5	5	5	1	2	2	50.0	–	33.3
Sistotremastrum suecicum	2	–	–	2	3	4	5	5	–	–	3	–	–	100.0
Stereum sanguinolentum	2	4	1	3	4	7	4	–	2	3	3	25.0	100.0	33.3
Tubulicrinis medius	2	–	2	3	6	7	16	8	–	2	3	–	–	33.3
Antrodia albobrunnea NT	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Athelia decipiens	1	3	3	4	1	–	2	1	3	3	3	33.3	66.7	100.0
Botryobasidium candicans	1	–	–	–	3	–	–	–	–	–	–	–	–	–
Ceraceomyces serpens	1	–	–	1	1	2	–	2	–	–	1	–	–	–
Globulicium hiemale	1	–	–	–	1	6	6	3	–	–	–	–	–	–
Hyphodontia abieticola	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Hyphodontia alutaria	1	–	1	1	–	–	–	1	–	3	3	–	–	100.0
Hyphodontia aspera	1	–	1	2	2	3	2	4	–	1	2	–	–	100.0
Hyphodontia crustosa	1	–	–	–	2	1	–	–	–	–	–	–	–	–
Hyphodontia pallidula	1	–	–	2	1	3	2	2	–	–	3	–	–	–
Jaapia ochroleuca	1	2	–	1	–	–	–	–	3	–	2	–	–	–
Oligoporus caesius	1	2	1	–	1	3	–	1	2	2	–	–	–	–
Oligoporus hibernicus NT	1	2	–	2	4	2	2	3	–	–	2	–	–	100.0
Oligoporus fragilis	1	1	–	1	2	3	2	5	3	–	3	–	–	100.0
*Oligoporus parvus**	1	1	1	–	–	–	–	–	–	2	2	–	–	–
Oligoporus tephroleucus	1	–	–	–	1	2	–	3	–	–	–	–	–	–
Phlebia tristis	1	–	–	–	–	–	1	1	–	–	–	–	–	–
Piloderma croceum	1	–	–	–	2	1	1	–	–	–	–	–	–	–
Sistotrema muscicola	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Skeletocutis kuehneri	1	–	–	–	–	–	–	–	–	–	–	–	–	–

Appendix A (*Continued*)

Species	No. of records fire site				No. of records control site				Degree of burn fire site			Fruiting bodies on burned surface		
	2000	2001	2003	2005	2000	2001	2003	2005	2001	2003	2005	2001	2003	2005
Tomentella spp.	1	2	1	10	4	–	1	1	4	3	4	–	100.0	70.0
Trechispora farinacea	1	–	–	2	2	4	1	7	–	–	2	–	–	50.0
Trechispora subsphaerospora	1	–	–	–	1	1	1	3	–	–	–	–	–	–
Tubulicrinis globisporus	1	–	–	–	1	1	2	2	–	–	–	–	–	–
Tylospora asterophora	1	–	–	–	1	–	–	1	–	–	–	–	–	–
Trichoderma viride (a)	–	25	–	–	–	–	–	–	3	–	–	80.0	–	–
Costantinella michenerii (a)	–	5	3	6	–	2	2	1	3	2	4	80.0	66.7	100.0
Athelia neuhoffii	–	4	3	1	–	2	1	4	4	3	4	75.0	66.7	100.0
Phanerochaete sordida	–	4	1	1	2	3	–	2	3	4	4	100.0	–	100.0
Phlebia subserialis	–	4	1	14	3	3	–	1	3	1	3	50.0	–	92.9
Sistotrema brinkmannii	–	4	7	1	–	4	3	1	3	3	4	50.0	85.7	100.0
Costantinella tillettei (a)	–	3	–	–	1	–	–	–	4	–	–	66.7	–	–
Athelia epiphylla	–	2	39	6	15	8	30	8	4	3	2	100.0	76.9	66.7
Coniophora olivacea	–	2	–	1	–	–	–	1	2	–	2	–	–	–
Amphinema byssoides	–	1	–	2	1	1	1	–	2	–	4	–	–	100.0
Amylocorticium cebennense	–	1	–	–	–	2	1	1	2	–	–	–	–	–
Antrodia primaeva EN	–	1	–	–	–	–	–	–	3	–	–	100.0	–	–
Botryohypochnus isabellinus	–	1	–	–	–	–	–	–	2	–	–	–	–	–
Ceraceomyces tessulatus	–	1	–	–	–	1	–	2	2	–	–	100.0	–	–
Ceriporiopsis mucida	–	1	–	–	1	–	–	–	4	–	–	–	–	–
Hydrabasidium subviolaceum	–	1	–	–	–	–	–	–	2	–	–	100.0	–	–
Hyphoderma setigerum	–	1	–	–	–	2	3	1	2	–	–	–	–	–
Leucogyrophana pseudomollusca	–	1	–	–	–	–	–	–	3	–	–	100.0	–	–
Panellus mitis (ag)	–	1	2	–	–	7	8	1	1	2	–	–	50.0	–
Sistotrema oblongisporum	–	1	–	–	–	–	–	–	4	–	–	100.0	–	–
Tulasnella spp. (x)	–	1	2	–	–	4	3	2	3	4	–	–	10.0	–
Galzinia incrustans	–	–	4	1	–	–	–	–	–	4	4	–	100.0	100.0
Athelia bombacina	–	–	2	6	–	2	10	20	–	4	3	–	–	16.7
Phlebiopsis gigantea	–	–	2	4	–	–	3	–	–	3	2	–	50.0	75.0
Amyloathelia crassiuscula	–	–	1	–	–	–	6	2	–	1	–	–	–	–
Athelicium stridii	–	–	1	–	–	1	6	1	–	1	–	–	–	–
Dichomitus squalens EN	–	–	1	–	–	–	–	–	–	3	–	–	100.0	–
Phlebia cornea	–	–	1	1	1	2	–	–	–	4	4	–	–	100.0
Phlebia diffissa	–	–	1	–	–	–	–	–	–	4	–	–	–	–
Pseudomerulius aureus	–	–	–	2	2	3	–	4	–	–	3	–	–	100.0
Antrodia sitchensis[*]	–	–	–	1	–	–	–	–	–	–	3	–	–	–
Diplomitoporus lindbladii	–	–	–	1	–	–	–	–	–	–	2	–	–	100.0
Gloeophyllum carbonarium VU	–	–	–	1	–	–	–	–	–	–	4	–	–	100.0
Hyphoderma sibiricum	–	–	–	1	1	1	1	1	–	–	4	–	–	100.0
Hypochnicium erikssonii	–	–	–	1	–	–	–	1	–	–	2	–	–	100.0
Phlebia firma	–	–	–	1	2	1	–	–	–	–	3	–	–	100.0
Phlebia radiata	–	–	–	1	–	1	–	2	–	–	3	–	–	100.0
Skeletocutis amorpha	–	–	–	1	2	4	3	2	–	–	3	–	–	–
Tubulicrinis sororius	–	–	–	1	–	–	1	–	–	–	2	–	–	100.0
Phlebia subcretacea	–	–	–	–	4	2	–	3	–	–	–	–	–	–
Ischnoderma benzoinum	–	–	–	–	3	2	3	1	–	–	–	–	–	–
Tylospora fibrillosa	–	–	–	–	3	1	1	3	–	–	–	–	–	–
Asterodon ferrugineus NT (x)	–	–	–	–	2	–	–	–	–	–	–	–	–	–
Phlebiella grisella	–	–	–	–	2	2	2	–	–	–	–	–	–	–
Asterostroma laxum	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Athelia singularis	–	–	–	–	1	4	2	1	–	–	–	–	–	–
Hapalopilus salmonicolor VU	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Hyphoderma cremeoalbum	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Peniophora pithya	–	–	–	–	1	1	–	1	–	–	–	–	–	–
Phellinus viticola	–	–	–	–	1	3	1	2	–	–	–	–	–	–
Phlebia segregata	–	–	–	–	1	2	–	–	–	–	–	–	–	–
Phlebiella borealis	–	–	–	–	1	2	–	2	–	–	–	–	–	–
Tubulicrinis angustus	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Tubulicrinis regificus	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Tubulicrinis strangulatus	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Antrodiella pallasii[*]	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Athelia subovata	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Athelopsis lacerata	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Cerinomyces crustulinus (x)	–	–	–	–	–	1	1	3	–	–	–	–	–	–
Hydnellum gracilipes EN (x)	–	–	–	–	–	1	–	1	–	–	–	–	–	–
Hyphoderma argillaceum	–	–	–	–	–	1	2	–	–	–	–	–	–	–
Hyphoderma occidentale	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Hypochnicium geogenium	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Hypochnicium subringescens	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Merulius tremellosus	–	–	–	–	–	1	1	1	–	–	–	–	–	–
Phanerochaete velutina	–	–	–	–	–	1	1	1	–	–	–	–	–	–
Sistotrema autumnale	–	–	–	–	–	1	1	–	–	–	–	–	–	–
Sistotrema diademiferum	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Trechispora byssinella	–	–	–	–	–	1	–	–	–	–	–	–	–	–

Appendix A (*Continued*)

Species	No. of records fire site				No. of records control site				Degree of burn fire site			Fruiting bodies on burned surface		
	2000	2001	2003	2005	2000	2001	2003	2005	2001	2003	2005	2001	2003	2005
Tubulicrinis accedens	–	–	–	–	–	1	1	–	–	–	–	–	–	–
Tubulicrinis hirtellus	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Tubulicrinis effugiens	–	–	–	–	–	–	3	1	–	–	–	–	–	–
Phlebia livida	–	–	–	–	–	–	2	–	–	–	–	–	–	–
Basidioradulum radula	–	–	–	–	–	–	1	2	–	–	–	–	–	–
Conferticium ochraceum	–	–	–	–	–	–	1	1	–	–	–	–	–	–
Crepidotus sphaerosporus (ag)	–	–	–	–	–	–	1	–	–	–	–	–	–	–
Hypochnicium bombycinum	–	–	–	–	–	–	1	–	–	–	–	–	–	–
Phlebiella christiansenii	–	–	–	–	–	–	1	–	–	–	–	–	–	–
Tubulicrinis propinquus	–	–	–	–	–	–	1	–	–	–	–	–	–	–
Botryobasidium intertextum	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Coniophora puteana	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Gloeocystidiellum subasperisporum NT	–	–	–	–	–	–	–	1	–	–	–	–	–	–
*Leucogyrophana montana***	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Phlebiella pseudotsugae	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Piloderma olivaceum	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Number of sampled logs	150	150	150	150	169	169	169	169	–	–	–	–	–	–
Number of species	69	58	55	68	85	98	87	97	–	–	–	–	–	–
Number of records	292	211	281	412	449	551	543	603	–	–	–	–	–	–

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