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Forest fire drives long-term community changes of wood-decaying fungi in a boreal forest archipelago

Mikael Gudrunsson



Mittuniversitetet

MID SWEDEN UNIVERSITY

Campus Härnösand Universitetsbacken 1, SE-871 88. **Campus Sundsvall** Holmgatan 10, SE-851 70 Sundsvall.

Campus Östersund Kunskapens väg 8, SE-831 25 Östersund.

Phone: +46 (0)771 97 50 00, Fax: +46 (0)771 97 50 01.

MID SWEDEN UNIVERSITY

Department of Natural Sciences

Examiner: Bengt-Gunnar Jonsson, Bengt-Gunnar.Jonsson@miun.se

Supervisor: Mattias Edman, Mattias.Edman@miun.se

Author: Mikael Gudrunsson, migu1202@student.miun.se

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Mikael Gudrunsson

Supervisor:
Mattias Edman, Mid Sweden University

Department of Natural Sciences
Mid Sweden University, SE-851 70 Sundsvall, Sweden

ABSTRACT

Conservation of wood-decaying fungi requires improved knowledge about the long-term effects of forest management; regarding habitat loss, fragmentation and fire suppression. To better understand such effects, I examined the influence of area, isolation, fire history and forest stand characteristics on communities of wood-decaying fungi. Species richness and composition were studied along a gradient of 22 forested islands varying in size (0.16 to 17.58 ha) and fire history (spanning 5000 years) in a boreal forest archipelago in northern Sweden. A total of 490 records of 41 polypore species were found in 33 circular plots, each 0.1 ha in size. Species richness and the number of red-listed species were analyzed using generalized linear models (GLMs), while species composition was examined using non-metric multidimensional scaling (NMDS) ordination. The species composition was clearly different between recent-fire (< 300 years since last fire) and old-fire (\geq 300 years since last fire) islands, mirroring the shift in tree species composition as pine-associated fungal species were replaced by spruce-associated fungal species. The volume of logs was the only variable influencing the species richness, although the diversity of logs showed a clear trend of also influencing species richness positively. The results demonstrate the importance of having both recent-fire and old-fire forests as landscape-level habitats and species pools, where fire naturally would constitute a key role for maintaining forest biodiversity in the boreal forest landscape. The results also stress the importance of dead wood for species richness at the individual forest stands.

Keywords: wood-decaying fungi, polypores, species richness, species composition, fire history, disturbance, spatiotemporal dynamics, forest succession, species-area relationship, dead wood, boreal forest

SAMMANFATTNING

I boreala skogar spelar vedsvampar en nyckelroll för skapande och nedbrytning av död ved; en viktig faktor för biologisk mångfald som ca 20-25 % av alla skogslevande arter är direkt beroende av. I Sverige har industriella skogsbruksmetoder medfört att variationen och mängden död ved kraftigt minskat i svenska skogar. Många vedsvampar har därav påverkats negativt och för närvarande är ca 30 % rödlistade. För bevarande av Sveriges vedsvampar krävs ökad kunskap om skogsbrukets långsiktiga effekter; dels angående förlust och fragmentering av livsmiljöer, dels angående förlust av naturlig störningsdynamik (orsakad av brandbekämpning). För att bättre förstå hur sådana effekter påverkar vedsvampar undersökte jag hur skogars storlek, isolering och brandhistoria påverkar vedsvampssamhällen. Artsammansättning och artrikedom studerades utmed en gradient bestående av 22 öar med varierande storlek (från 0.16 till 17.58 ha) och brandhistorik (från 70 till 5150 år sedan senaste brand) i två angränsande sjöar (Hornavan och Uddjaure) i Arjeplogs kommun, Norrbottens län. Sammanlagt påträffades 490 fynd av 41 arter inom 33 provytor (vardera 0.1 ha). Det fanns en tydlig skillnad i artsammansättning mellan öar som nyligen brunnit (< 300 år sedan sista brand) och öar som varit utan brand under längre tid (≥ 300 år sedan sista brand), där arter förknippade med tall ersattes av arter förknippade med gran. Volymen liggande död ved var den enda faktor som påverkade artrikedomen (med ökande antal arter med ökande volym), även om variationen av liggande död ved visade en tydlig trend mot att positivt påverka artrikedomen. Sammantaget visar studien på vikten av att bibehålla skogar med olika stadier av brandsuccession på landskapsnivå för att tillgodose en nödvändig variation av livsmiljöer för vedsvampar. I ett bevarandebiologiskt perspektiv utgör skogsbränder därmed en viktig faktor för bevarande av biologiska mångfald i boreala skogslandskap. Studien understryker också vikten av död ved för de enskilda skogarnas artrikedom av vedsvamp.

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1. INTRODUCTION

Wood-decaying fungi constitute an important organism group in the boreal forest ecosystem, essential for a wide range of forest living organisms and ecosystem processes (Jonsson et al. 2005; Lonsdale et al. 2008; Stenlid et al. 2008). Parasitic wood-decaying fungi act as disturbance agents by weakening and killing trees and thus creating dead wood; important for nutrient cycling, carbon storage and a key factor for biodiversity (Siitonen 2001; Jonsson et al. 2005; Edman et al. 2007). Wood-decaying fungi also play a major role in the decomposition and succession of dead wood, making nutrients available and creating structural heterogeneity that increase the diversity of habitats and resources (Jonsson et al. 2005; Siitonen 2001). In addition, mycelia and fruiting bodies of wood-decaying fungi serve as an important food source and breeding ground for insects (Jonsell et al. 1999; Jonsell et al. 2001; Johansson et al. 2006).

Most species of wood-decaying fungi are highly specialized in their habitat requirements (e.g. tree species, size and decay stage of substrate, microclimatic conditions and biotic interactions) and thus sensitive to changes in the environment (Penttilä et al. 2006; Junninen & Komonen 2011). The occurrence (spatial and temporal variation) and properties (quantity and quality) of dead wood are well recognized for being important for the species richness and composition of wood-decaying fungi at the individual forest stand level (Bader et al. 1995; Rolstad et al. 2004; Berglund & Jonsson 2005; Penttilä et al. 2006; Hottola et al. 2009), whereas forest stand size and structure of the surrounding landscape have been found to affect species occurrences and long-term persistence (Penttilä et al. 2006; Jönsson et al. 2008). At the substrate level, microclimatic factors such as moisture and temperature are highly important (Olsson et al. 2011). For example, the species composition at exposed clear-cut edges of a forest stand has been shown to differ from more moist interior areas, where the low water content of logs can affect moist-sensitive species negatively, while favoring species adapted to a dry and sunny microclimate (Siitonen et al. 2005). Further, the occurrence of wood-decaying fungi is affected by species interactions, resulting in various successional pathways with different combinations of successor and predecessor species (Renvall 1995; Niemelä et al. 1995).

In Fennoscandian boreal forests, 20-25 % of all known forest-inhabiting species are considered to be dependent on dead wood habitats, with macro fungi as the most species-rich organism group accounting for ca. 35 % of these species (Siitonen 2001). The ecological importance and sensitivity of wood-decaying fungi makes species belonging to this group suitable as indicators of forest continuity and conservation value (Karström 1992; Nitare 2010). As a result of intensive industrial forest management, i.e. the destruction and fragmentation of natural forests combined with effective fire suppression and creation of even-aged coniferous monocultures, a large proportion (ca. 30 %) of wood-decaying fungi are considered threatened in Sweden (Gärdenfors 2010). Since 1950, approximately 60 % of Sweden's productive forest land has been clear cut and with current development all forests without formal protection are predicted to follow the same transformation within 20 years (Larsson 2011), fundamentally altering the boreal forests in Sweden. Habitat loss stands

for the most obvious threat to the diversity of wood-decaying fungi as both quantity and quality of dead wood is deficient in managed forests (Siitonen et al. 2000), causing declining populations and rare species more prone to extinction (Penttilä et al. 2006). At the broader temporal and spatial scales, fragmentation of natural forests is a major concern for the long-term survival of the threatened species as successful colonization between available habitats is reduced (Jönsson et al. 2008). This also includes decreased genetic diversity and reduced spore vitality (Högberg et al. 1998, Edman et al. 2004a). In addition, fire suppression has eliminated natural disturbance dynamics, causing a decline in species favored by fires or dependent on biological legacies created by fire such as increased amount of dead wood (Junninen et al. 2008).

For conservation of wood-decaying fungi there is a need to assess the effects of environmental variables related to forestry practices (e.g. habitat loss, fragmentation and fire suppression). Earlier studies indicate that forest stand size, isolation, successional stage and properties of dead wood are important factors influencing species richness and composition of wood-decaying fungi (Junninen & Komonen 2011). The importance of area and isolation has been widely discussed, since these factors have been shown to interact with species extinction and colonization rates (MacArthur & Wilson 1967; Hanski 1999). The theory of island biogeography predicts increasing species richness with increasing area because larger areas will gain more species through immigration (larger area to colonize) and hold larger populations that are less prone to stochastic extinction (MacArthur & Wilson 1967), while increasing isolation will result in less immigration (larger distance to overcome). However, species-area relationships have also been explained as an effect of passive sampling (i.e. the number of immigrating individuals, often positively correlated with species richness, will increase with island area purely by chance; Connor & McCoy 1979) and habitat diversity (i.e. larger islands tend to have a greater variety of habitats, thus permitting existence of a variety habitat specialists and species requiring multiple habitats; Williams 1964). In addition, empirical studies show that a set of small patches generally has higher cumulative species richness than a single large area (e.g. Quinn & Harrison 1988), implying that the relative importance of habitat loss versus habitat fragmentation has to be considered (Fahrig 2003). Metapopulation theory emphasize the importance of habitat configuration (i.e. number of habitat patches or relative isolation among them) for species to regionally persist as metapopulations (Levins 1969; Hanski 1999). The dispersal of individuals from local populations between habitat patches is predicted to enable recolonizations of empty patches, as well as persistence of local populations with negative growth rate (source-sink dynamics; Pulliam 1988) or by means of decreased extinction risk (the rescue effect; Hanski 1999) through sufficient immigration from other populations.

For the community structure of wood-decaying fungi, the influence of successional stage has received increasing attention as it can reflect how species compositions change over time, both at community and substrate levels (Renvall 1995; Junninen et al. 2006; Ylisirniö et al. 2012; Rajala et al. 2012). Succession, the process of temporal change in species composition at a site, has since long been one of the major themes in ecology (Tansley 1935; Diamond 1975; Connell & Slatyer 1977) and in its conceptual framework three driving mechanisms

have become widely accepted, where the early arriving species can either (1) promote (facilitation), (2) have no effect (tolerance) or (3) reduce (inhibition) the establishment of later arriving species (Connell & Slatyer 1977). Furthermore, succession can be divided into two main types: primary succession (occurs in a new habitat with no species prior to succession, requires colonization of species) and secondary succession (occurs in damaged or disturbed habitats, with dispersal or expansion of species already present, as well as colonization of species). How species composition changes over time can result from a variety of factors, where disturbance constitutes a key factor for the successional dynamics in boreal forests (Kuuluvainen 2002). The effect of a disturbance depends on characteristics such as frequency, extent, and severity (Kuuluvainen 2002), where four main types of disturbance-succession dynamics have been recognized (Kuuluvainen & Aakala 2011): (1) even-aged stand dynamics following stand-replacing disturbances, (2) cohort dynamics driven by partial disturbances, (3) patch dynamics driven by tree mortality at intermediate scales ($> 200 \text{ m}^2$) and (4) gap dynamics driven by tree mortality at fine scales ($< 200 \text{ m}^2$). In Fennoscandia, partial and small scale disturbance is the most commonly documented types of disturbance, whereas stand-replacing disturbances may play a smaller role (Kuuluvainen & Aakala 2011).

Fire is a major disturbance in boreal ecosystems and well recognized as a fundamental process for maintaining community and landscape biodiversity (Zackrisson 1977; Ryan 2002; Bergeron et al. 2002). Fire creates environmental heterogeneity and provides new substrates and opportunities for new species to colonize as well as for new fungal communities to develop (Dahlberg 2002). Previous studies have found that the fungal community on dead wood is different a few years after fire compared with the pre-fire fungal community (Penttilä et al. 1996; Olsson & Jonsson 2010; Berglund et al. 2011). The early fungal community following fire is characterized by species with effective dispersal and fast colonization ability being less effective in decaying wood, and thus replaced by more competitive species in later stages. In addition, heat resistance seems common among many species confined to pine (Carlsson et al. 2012) and may help species to survive in a log during a forest fire and thus allow for expansion of less competitive species. However, the long-term effects of forest fire and fire suppression on wood-decaying fungi are yet to be explored. Given that the tree species composition and structure of boreal forests change with time since fire and that different boreal tree species host partly different fungal species (Renvall 1995), fungal communities are likely to change with time since fire as well. In addition, fire creates unique dead wood substrates such as charred wood, which probably influence the species composition of fungi.

In this study, a system with 22 forested islands in two adjacent lakes in the boreal forest zone of northern Sweden was used to examine how communities of wood-decaying fungi vary along spatial and temporal gradients in a natural boreal forest landscape. Across the studied islands, spatial gradients for area and isolation and a temporal gradient for fire history were present. The specific objectives of the study were to investigate how (1) species richness and number of red-listed species and (2) species composition of wood-decaying fungi are influenced by forest stand size, degree of isolation and fire disturbance history.

2. MATERIALS AND METHODS

2.1 STUDY AREA

The study area is located in the municipality of Arjeplog in northern Sweden (Fig. 1). The area belongs to the northern boreal vegetation zone (Ahti et al. 1968) and is characterized by a boreal forest landscape with a number of large lakes (being parts of the large lake system of the Skellefte River). The mean annual precipitation in the area is 750 mm, and the mean temperature is -14 °C in January and +13 °C in July.

I used a set of 22 forested islands in two adjacent lakes, Hornavan and Uddjaure (65°55' - 66°09' N, 17°43' - 17°55' E), of which 20 had been used in previous studies (e.g. Wardle et al. 1997, 2003, 2012). All islands were formed from glacial deposits when land ice retreated about 9000 years ago (Wardle et al. 1997). They vary in size from 0.16 to 17.58 ha, and the size of the islands determines the history of lightning ignited fires (i.e. large islands burn more frequently than small islands). The fire history of the islands ranges from 70 to 5150 years since last fire, being the only major extrinsic factor that differs between the islands (Wardle et al. 1997). The variation in fire history results in the islands being at different successional stages. Large islands are at an early successional stage with Scots pine (*Pinus sylvestris*) as dominant tree species, while small islands are at a much later stage dominated by Norway spruce (*Picea abies*) (Wardle et al. 1997). Further, differences in the successional stage is characterized by small islands having lower plant productivity, slower decomposition of litter, increasing below-ground carbon sequestration and less available soil nutrients than large islands (Wardle et al. 1997, 2003, 2012). At all islands hairy birch (*Betula pubescens*) is a common species. All islands show relatively low influences of human activities, even though a small amount of cut stumps from selective logging is present on each island.

2.2 SITE SELECTION AND DATA COLLECTION

On each island a circular study plot of 0.1 ha was randomly placed (exceptional patches with high amount of rocks and boulders were excluded) at a set distance of 5 meters from the shoreline to avoid differences in inland environments depending on island size, and thus controlling for the influence of edges (using ArcGIS 10, ESRI 2011). Similarly, additional plots were placed on large islands (> 1.5 ha) for better representations of these islands. In total 33 study plots were used; 15 islands with 1 study plot each, 4 islands with 2 study plots each, 2 islands with 3 study plots each and 1 island with 4 study plots.

Within each study plot all living trees and dead wood pieces with a minimum diameter of 5 cm and 1 m in length were searched through for fruiting bodies of wood-decaying fungi. Thus, the presence of species not fructifying at the time of the inventory was omitted from the study. However, the use of fruiting bodies is likely to provide sufficient information about the reproductive capacity and population dynamics of the species, as wood-decaying fungi primarily disperse by spores (Rayner & Boddy 1988). All substrate originating from a single tree were considered as one substrate unit and all fruiting bodies of a particular species at each substrate unit were counted as one single occurrence. Dead perennial fruiting bodies

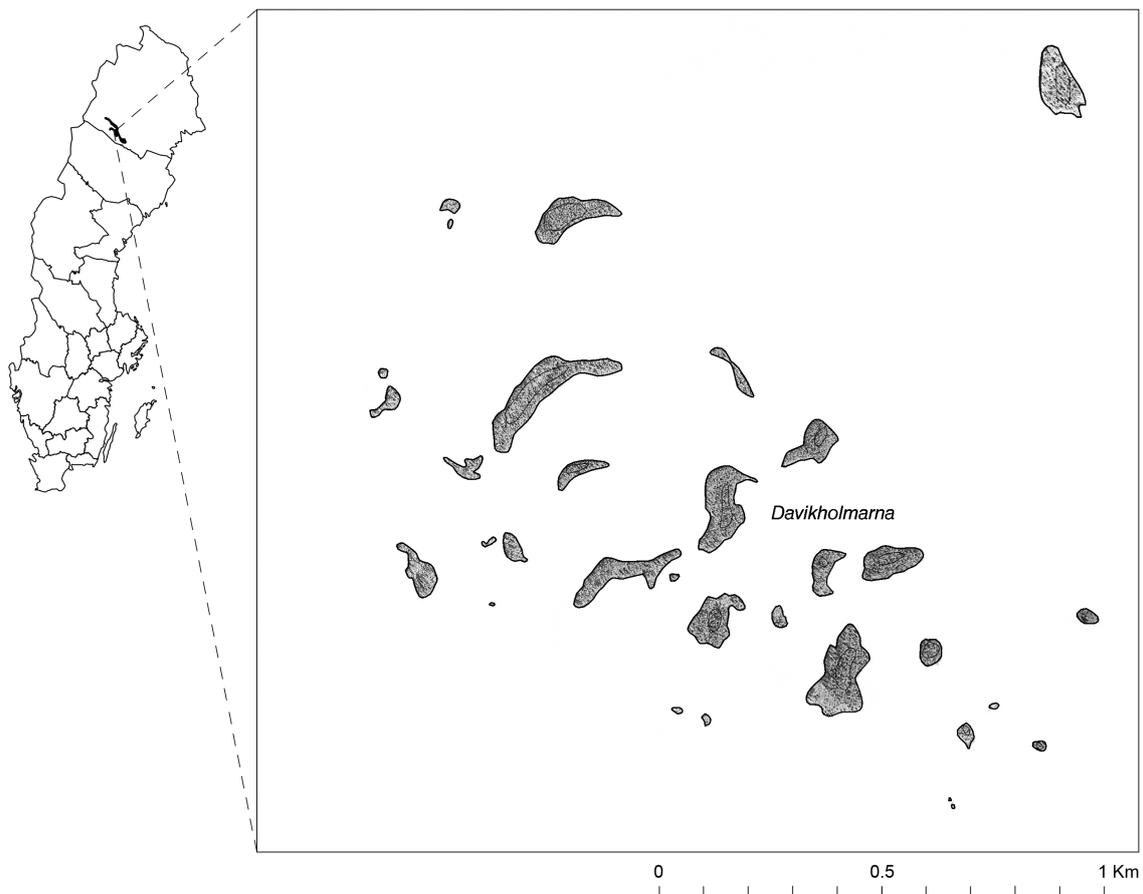


Fig. 1. Map of Sweden with county borders (left), showing a section of the archipelago in Lake Hornavan, including some of the studied islands (right).

were not recorded. The species inventory was made during August and September when species with annual fruiting bodies fruitify. In total, 1910 substrate units composed of 543 logs, 86 standing dead trees and 1282 living trees were examined. Species that could not be identified in field were collected for later microscopical identification. Red-listed species were classified according to the latest Red Data Book of Sweden (Gärdenfors 2010), including both threatened (classes VU and EN) and near-threatened (NT) species. Nomenclature of wood-decaying fungi follows Niemälä (2005).

Additional data were collected for environmental variables known to effect wood-decaying fungi, such as substrate properties and forest stand characteristics (Bader et al. 1995; Renvall 1995; Junninen & Komonen 2011). Size, substrate type and decay stage were recorded for each substrate unit. For standing substrates size was measured as DBH (diameter at breast height) and used for calculations of basal area, while length and min/max diameter was measured for logs and used for volume calculations following the conic-paraboloid formula recommended by Fraver et al. (2007). Substrate types were classified as (1) living trees; (2) entire dead standing trees; (3) broken snags (at least 1/3 of the upper part of the stem broken off, height ≥ 1.3 m); (4) natural stumps (height < 1.3 m); (5) uprooted logs; (6)

broken logs; (7) cut trees/trunks/tops; (8) fallen branches. Decay stages follow a modified classification of Renvall (1995): (1) wood hard, a knife penetrates by pushing only a few mm into the wood; (2) wood relatively hard, knife penetrates 1–2 cm; (3) wood relatively soft, knife penetrates 3–5 cm; (4) wood soft, knife penetrates through the wood easily; (5) wood very soft, almost completely decomposed and can be molded by hand. Diversity of dead wood was calculated for statistical analyses as a number of combinations formed by the following variables: tree species, substrate types (entire dead trees, broken snags, logs) decay stages (1–2, 3, 4–5) and 10 cm DBH/maximum diameter classes (5–9 cm, 10–19 cm, 20–29 cm etc.) present on each stand (modification of Hottola & Siitonen 2008; Siitonen et al. 2000). Cut trees, trunks and tops were included in logs, while stumps and branches were ignored. In addition, diversity of logs was calculated separately in a similar way, excluding other substrate types than logs. Forest stand characteristics included vegetation type, basal area of living trees (DBH \geq 5 cm) and number of cut stumps at each plot. Diversity of living trees was calculated similarly as substrates, including only tree species and DBH classes as variables.

For island variables, a vector based map of the study area was used to measure the area and calculate an index of isolation for each island (using ArcGIS 10; ESRI 2011). The index of isolation represents the proportion of water in the surrounding area of each island, calculated as $(a - b)/a$, where a is the total area around the entire island between the shoreline and a set distance from the shoreline and b is the total landmass in the surrounding area (modification of Jonsson et al. 2009). For each island, two values of the index were calculated for two different distances from the shoreline: 300 m and 1200 m. These distances are approximations of short and long distance dispersal, since spore deposits from wood-decaying fungi is known to rapidly decrease with distance (Norros et al. 2012). For fire history, data from Wardle et al. (2012) with records of time since the last major fire for each island was used (based on carbon-14 dating of charcoal), except for three islands where time since last fire was determined with additional sampling and dating of the last fire scar from one pine tree per island. All fire records were ranked among the islands to avoid uncertainties in the precision of the fire dating.

2.3 STATISTICAL ANALYSIS

Environmental variables measured as areas and volumes were log-transformed, and number of stumps was square root transformed in all statistical analysis. For islands with more than one study plot, average values were calculated and used for analysis of species richness and number of red-listed species. For analysis of species composition all 33 study plots were used; represented as either recent-fire (< 300 years since last fire) or old-fire (\geq 300 years since last fire) forest stands. Two-sample Wilcoxon rank sum tests were used for comparing forest stand characteristics between recent-fire and old-fire islands.

Variations in species composition between study plots were examined using non-metric multidimensional scaling (NMDS) ordination. NMDS is an unconstrained ordination method that avoids assumptions about linear relationships among variables, and is considered a robust

method for representing species compositions of communities (Clarke 1993; McCune et al. 2002). The ordination was based on Bray-Curtis dissimilarities calculated from abundance data (for 41 polypore species at 33 study plots) with Wisconsin double standardization (shifting the focus of the analysis from absolute abundances to relative abundances). These two standardizations often improve the quality of ordinations and have been generally recommended for ecological data (Legendre & Gallagher 2001). To determine the number of dimensions for the NMDS, stress values were assessed. The stress value reflects how much the distances in the reduced ordination space depart from the dissimilarities in the original data, i.e. how well the ordination represents the relationships among the samples. The lower stress value, the better match; values up to 20 are ecologically interpretable and useful (Clarke 1993). Final three-dimensional stress value of 18.793 was acceptable. The result was rotated so that the first axis accounted for most of the variance in the data, with each subsequent axis containing progressively less information. This makes it possible to visualize the main structures in the data by plotting the first two axes against each other.

The relationship between environmental variables and species composition were examined by vector fitting, using multiple regression of environmental variable with ordination axes in order to find a direction (vector) across the ordination, along which the environmental variable have a linear correlation. Significance of correlations was tested using 1000 random permutations, with one test of significance per environmental variable. Species were mapped into the ordination space using weighted-averaging and expanded so that species and site scores have equal variances. This makes species closely located to the study plots they occur in. Differences in species composition between recent-fire and old-fire forest stands were tested for significance with a pairwise comparison test (PERMANOVA) using the scores of the study plots.

Generalized linear models (GLMs) were used to analyze the effects of environmental variables on species richness and the number of red-listed species. As the response variable was count data, a Poisson error distribution with a logarithmic link function was used (O'Hara & Kotze 2010). The effect of each environmental variable on species richness and the number of red-listed species was initially tested with single predictor models. To further analyze the combined effects of environmental variables, several of the variables were included simultaneously in multiple predictor models. Due to strong correlation between some of the environmental variables (Appendix 2), variance inflation factors (VIF) were used to find a set of variables without collinearity. In VIF, the relationship of each environmental variable and all other environmental variables were tested separately with linear regression (Montgomery & Peck 1982). A high VIF value (over 5) is an indication of collinearity and suggests elimination of that variable from further analysis (Montgomery & Peck 1982). As a result, island area, basal area of living pine, number of logs and diversity of logs were excluded from the multiple predictor models. A manual backward selection procedure with stepwise deletion of non-significant terms (Chi-square test based on residual deviance) was used to determine the best multiple predictor model. Only main factors were included in the models since none of the biologically reasonable two-way interactions between the environmental variables proved to be significant. All models were submitted to residual

analyses for validation of model fit.

All statistical analyses were performed using R version 3.0.0 (R Development Core Team 2013), applying the vegan package (Oksanen et al. 2013) for species composition analysis. All statistical tests were considered significant at $\alpha \leq 0.05$.

3. RESULTS

3.1 FOREST STAND CHARACTERISTICS

A summary of the environmental variables are listed in Table 1. The basal area of living and dead spruce and pine were the only forest stand characteristics that significantly differed between recent-fire and old-fire islands, clearly showing different tree species composition for the different successional stages (Fig. 2).

3.2 SPECIES COMPOSITION

The non-metric multidimensional scaling (NMDS) ordination of species composition showed distinct community differences between the recent-fire and old-fire islands (Fig. 3).

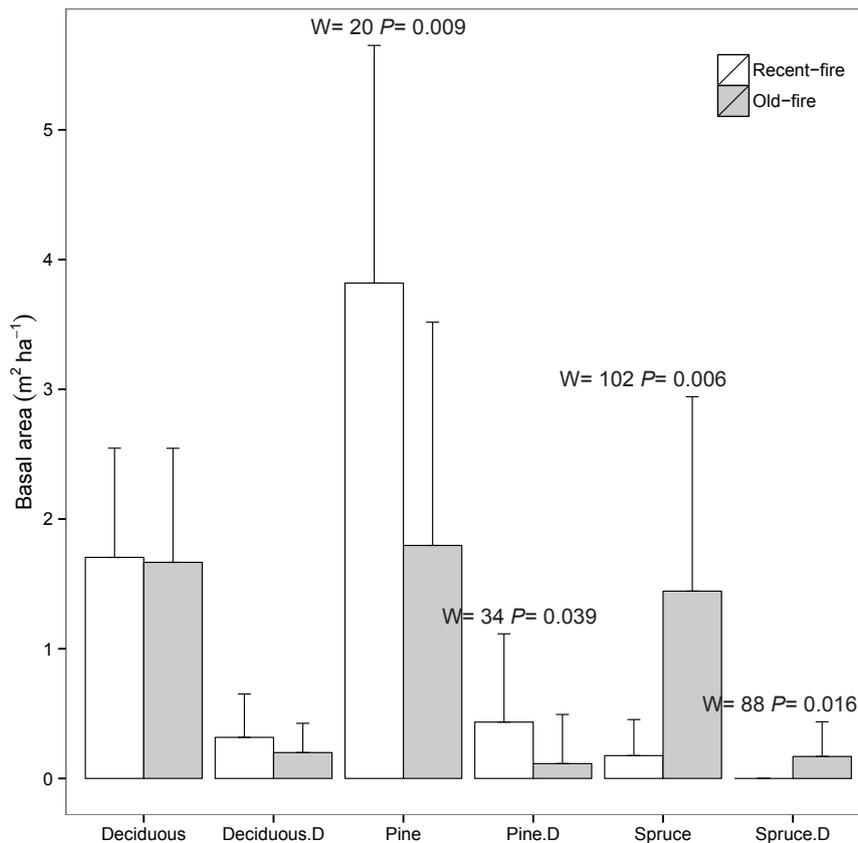


Fig. 2. Basal area (mean per island \pm SD) of different tree species between recent-fire ($n=11$) and old-fire islands ($n=11$). Basal area of pine and spruce, living and dead respectively, were significantly different between the groups. W- and P-values based on two-sample Wilcoxon rank sum tests.

Table 1. Summary of all environmental and dependent variables for the 22 studied islands. Isolation represents the proportion of water in the surrounding area of each island. Diversity is measured as the number of combinations of different types of living trees, standing dead wood and logs respectively.

Environmental variables		Mean	SD	Min	Max
Area (ha)		2.85	4.83	0.15	19.58
Isolation	300 m	0.94	0.05	0.83	1.00
	1200 m	0.94	0.04	0.86	0.99
Time since last fire (years)		1475.68	1516.71	70	5150
Basal area (m ² ha ⁻¹)	Living spruces	3.02	4.17	0	16.21
	Dead spruces	0.27	0.65	0	2.68
	Living deciduous	5.36	2.68	2.22	10.77
	Dead deciduous	0.64	0.61	0	2.44
	Living pine	8.49	6.70	0	19.31
	Dead pine	0.98	1.85	0	5.14
	Total	18.54	5.94	6.68	29.96
No. of cut stumps (ha ⁻¹)		26.36	34.16	0	110
No. of logs (ha ⁻¹)		153.64	44.57	80	250
Volume of logs (m ³ ha ⁻¹)		17.40	9.31	3.48	44.09
Diversity	Living trees	5.69	1.09	4	8
	Dead wood	11.5	2.13	8	17
	Logs	9.07	1.77	5	12
<i>Dependent variables</i>					
Species richness		8.77	2.50	4	14
No. of red-listed species		1.86	1.13	0	4

The pairwise comparison test (PERMANOVA) also confirmed that the two groups were significantly different (Pseudo-F = 3.5996, $P < 0.0001$).

The weighted averages for species showed that species associated with spruce (e.g. *Phellinus chrysoloma*, *Phellinus ferrugineofuscus*, *Skeletocutis chrysella*) and pine (e.g. *Antrodia albobrunnea*, *Cinereomyces lenis*, *Junghuhnia luteoalba*) were separated between the recent-fire and old-fire islands, while the species associated with deciduous trees (e.g. *Cerrena unicolor*, *Inonotus obliquus*, *Piptoporus betulinus*) had their optimum somewhere in between the groups (Fig. 4).

The fitted vectors for environmental variables on the NMDS ordination revealed some clear trends (Fig. 5, Table 2). Time since last fire had the highest linear correlation ($R^2 = 0.5442$, $P = < 0.001$) among all environmental variables studied, with increasing values towards the old-fire islands, together with basal area of living and dead spruce as well as diversity of dead wood. In the opposite direction, towards the recent-fire islands, went the fitted vectors of basal area of living pine, island area and volume of logs.

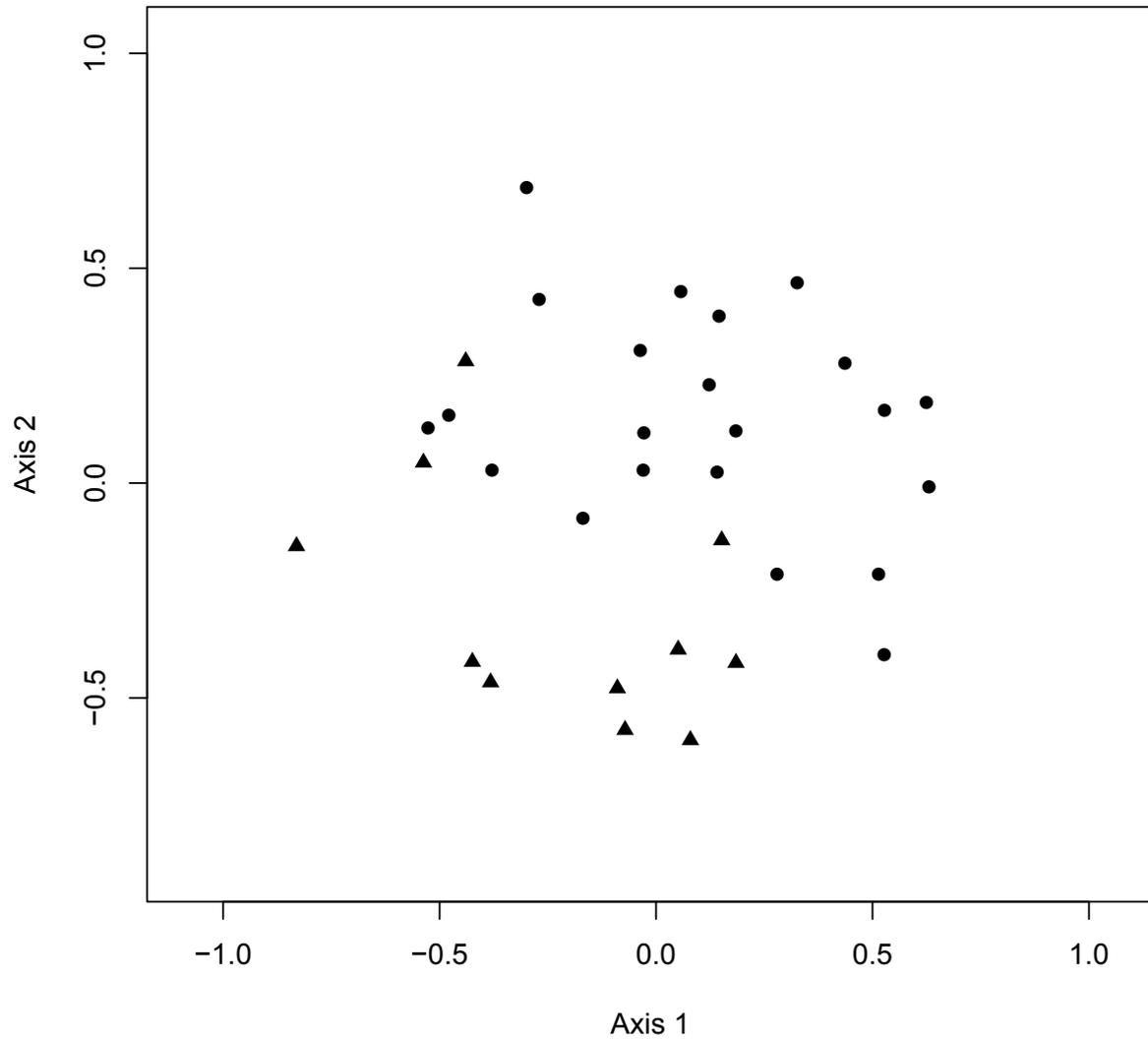


Fig. 3. Non-metric multidimensional scaling ordination (NMDS; stress value = 18.793) of fungal species composition. Points represent the sample scores for study plot ($n=33$), categorized as either recent-fire (circles) or old-fire (triangles) islands. The two best axes, accounting for most of the variance of scores, were selected from a three dimensional solution. The NMDS output is scaled in half-change units where unit distance corresponds to halving of community similarity (50% turnover in species composition).

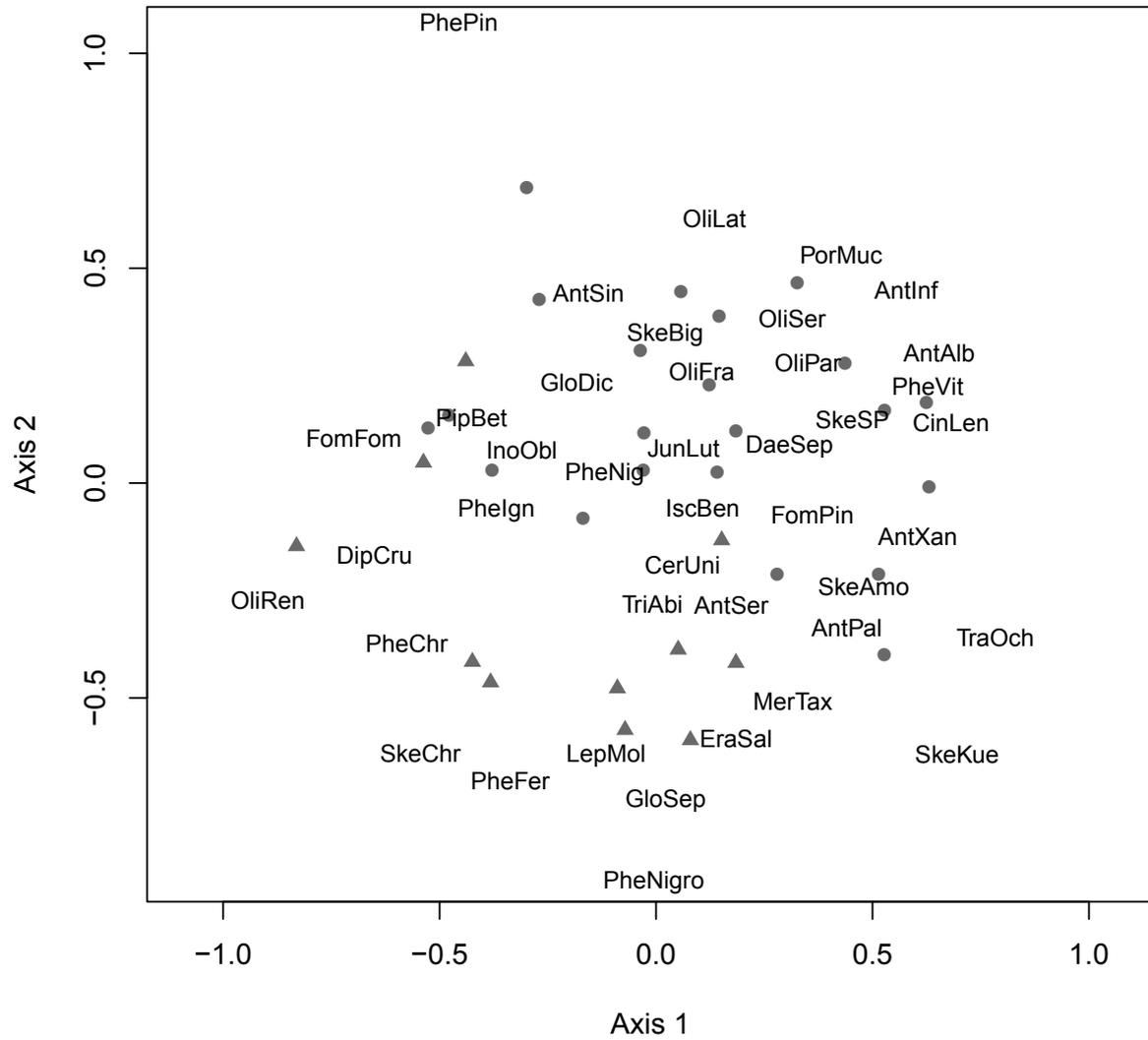


Fig. 4. NMDS ordination (same as in Fig. 3) showing the species scores derived as weighted averages of sample scores. The abbreviations of the species consists of the first three letters of both genus and species name (nomenclature according to Niemelä 2005; Appendix 1).

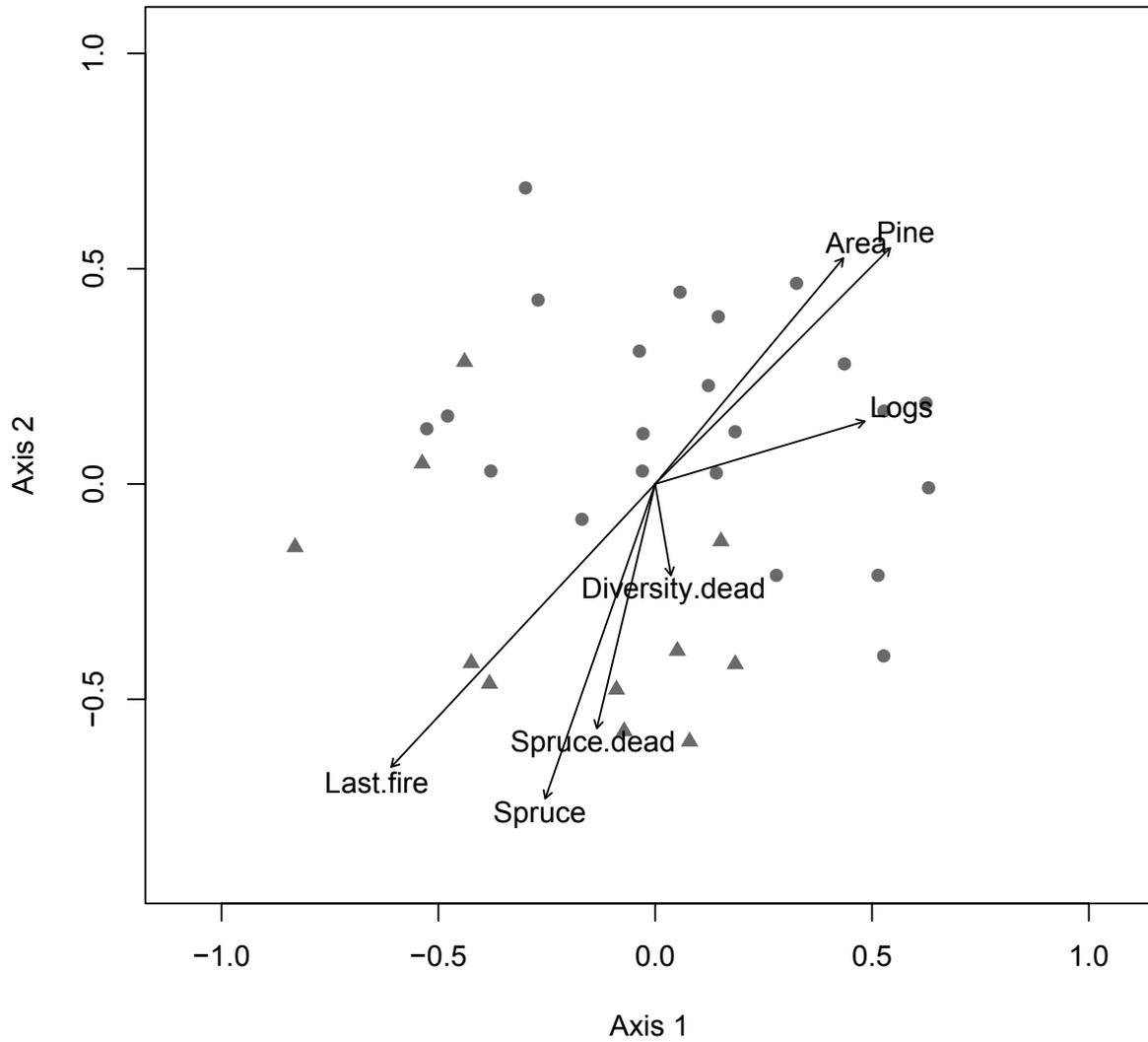


Fig. 5. NMDS ordination (same as in Fig. 3) showing environmental variables significantly correlated with ordination scores (Table 2). The fitted vectors show the direction in the ordination space that has maximal correlation with each environmental variable.

Table 2. Correlation coefficients between environmental variables and NMDS ordination scores. R² shows the proportion of variance explained, P-values based on a post-hoc permutation test ($n = 1000$).

Environmental variables	NMDS1	NMDS2	NMDS3	R ²	P
Area	0.59	0.73	-0.35	0.31	0.017 *
Isolation, 300 m	-0.04	-0.76	0.65	0.09	0.426
Isolation, 1200 m	0.90	-0.37	0.25	0.04	0.761
Time since last fire	-0.63	-0.73	0.27	0.54	<0.001 ***
Basal area, living spruce	-0.28	-0.89	0.36	0.44	0.002 **
Basal area, dead spruce	-0.19	-0.92	0.34	0.25	0.026 *
Basal area, living deciduous	-0.95	-0.32	-0.03	0.18	0.136
Basal area, dead deciduous	-0.04	-0.07	-1.00	0.11	0.346
Basal area, living pine	0.58	0.64	-0.49	0.49	0.002 **
Basal area, dead pine	0.98	0.20	-0.01	0.14	0.210
Basal area, total	0.80	0.06	-0.60	0.17	0.136
No. of cut stumps	0.56	0.75	0.35	0.15	0.161
No. of logs	0.85	0.31	-0.42	0.12	0.247
Volume of logs	0.68	0.26	-0.68	0.29	0.016 *
Diversity, living trees	-0.37	-0.86	0.36	0.02	0.860
Diversity, dead wood	0.04	-0.26	-0.96	0.26	0.036 *
Diversity, logs	0.78	0.39	-0.49	0.18	0.118

* < 0.05 ** < 0.01 *** < 0.001

3.3 SPECIES RICHNESS AND NUMBER OF RED-LISTED SPECIES

In total, 490 records of 41 polypore species were found at the study plots, of which 16 were red-listed species (Appendix 1). Many species were rare; 23 species (56 %) occurred in five or less (15 %) of the study plots. Only 6 species (14.6%) occurred in more than half of the study plots, and 5 of these species were associated with birch (*Betula pubescens*). Mean number of species and red-listed species per study plot was 9 and 2 respectively (Table 1).

Results of the generalized linear models (GLMs) exploring for environmental variables influencing species richness and the number of red-listed species are listed in Table 3. The GLMs of the individual effects of the environmental variables showed that the volume of logs was the only significant variable influencing species richness ($P = 0.035$), although the diversity of logs were on the edge of being significant ($P = 0.058$).

The volume of logs was the only remaining environmental variable in the best model with multiple predictors, explaining 27.7 % of the variation in species richness with a significant positive relationship (Fig. 6).

No significant environmental variables were found for the number of red-listed species (Table 3).

Table 3. Results of generalized linear models (GLMs) for all 22 islands studied, showing the individual effect of environmental variables on species richness and number of red-listed species, followed by the best multiple predictor model. For islands with more than one study plot, an average value was used. Environmental variables excluded from the multiple predictor models due to collinearity are shown in bold. Chi-square and P-values ($df=1$) of likelihood ratio tests are presented.

Environmental variables	Species richness		Red-listed species	
	χ^2	<i>P</i>	χ^2	<i>P</i>
<i>Single predictor</i>				
Area	1.04	0.309	0.03	0.869
Isolation, 300 m	1.22	0.269	1.38	0.241
Isolation, 1200 m	0.46	0.499	2.49	0.114
Time since last fire	2.23	0.136	0.03	0.854
Basal area, living spruce	0.00	0.966	1.21	0.272
Basal area, dead spruce	0.00	0.952	0.07	0.794
Basal area, living deciduous	0.48	0.491	0.20	0.651
Basal area, dead deciduous	0.08	0.774	0.12	0.724
Basal area, living pine	0.71	0.401	0.01	0.935
Basal area, dead pine	2.72	0.099	1.83	0.176
Basal area, total	3.12	0.077	2.19	0.139
No. of cut stumps	0.01	0.930	0.10	0.748
No. of logs	1.35	0.245	0.11	0.745
Volume of logs	4.44	0.035 *	0.40	0.529
Diversity, living trees	0.01	0.925	0.54	0.463
Diversity, dead wood	0.27	0.601	0.18	0.673
Diversity, logs	3.59	0.058	< 0.01	0.972
<i>Best multiple predictor model</i>				
Volume of logs	4.44	0.035 *		

* < 0.05

4. DISCUSSION

Species composition was clearly different between recent-fire and old-fire islands, mirroring the shift in tree species composition as pine-associated fungal species were replaced by spruce-associated fungal species. Time since last fire was the most influential environmental variable for species composition, followed by dominant tree species (basal area of living pine and spruce), island area and properties of dead wood (volume of logs, diversity of dead wood, basal area of dead spruce). The influence of fire on species composition could consist of both direct and indirect effects. Directly, fire can create large amounts of dead wood and certain substrate qualities like charred and resin-impregnated wood, supporting species with fast colonization or stress-tolerant strategies as well as species specifically fruiting on charred logs (Niemelä et al. 2002; Olsson & Jonsson 2010; Carlsson et al. 2012). Indirectly, fire

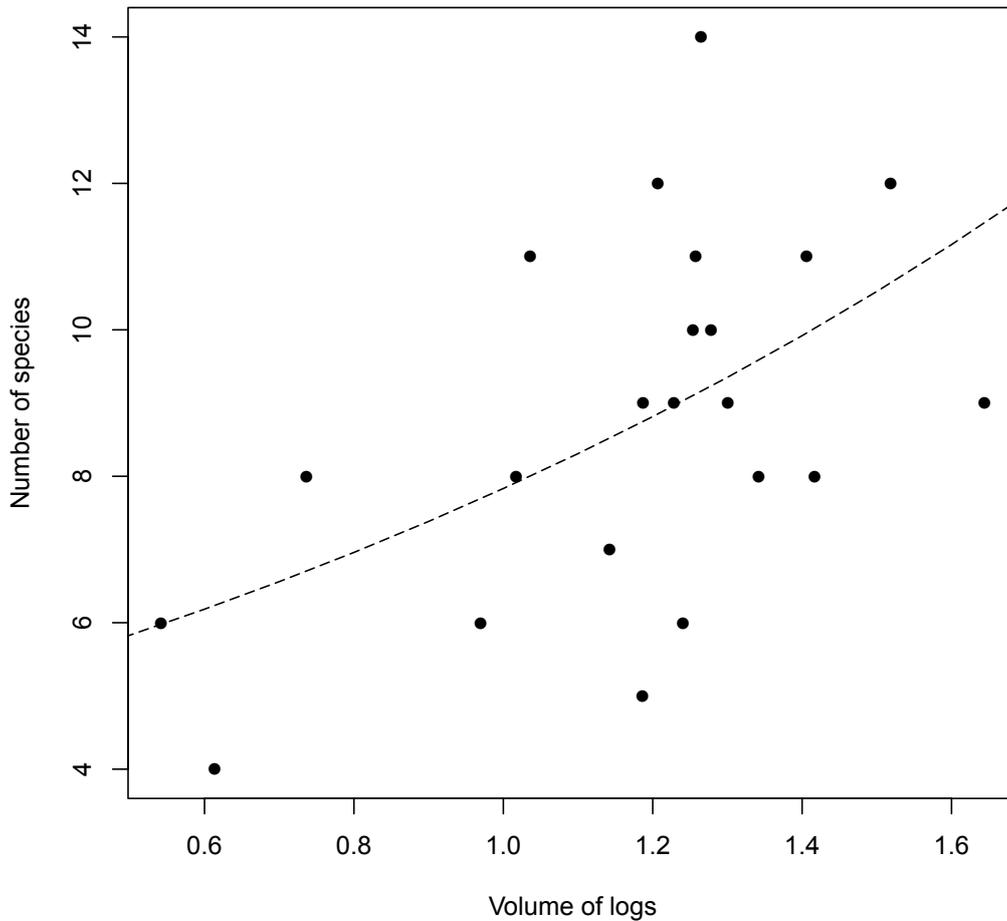


Fig. 6. Relationship between species richness and volume of logs (log-transformed) with fitted Poisson GLM curve (dotted line). Points represents islands ($n=22$), for islands with more than one study plot average values were used.

generally creates a more open forest structure with changed environmental conditions for the fungal community. It is well known that moisture and temperature are the two most important factors regulating the activity of wood-decaying fungi, and that different species have different optima for these factors (Schmidt 2006). Therefore it is likely that the increased solar radiation and wind flow in fire characterized forests make substrates drier and warmer, which in turn should influence the species composition of fungi. In addition, fire favors pine and thus indirectly the pine-associated fungal species.

Time since last fire was strongly correlated with island area ($r = -0.71$, $P = < 0.001$), and the individual effects of these variables are questionable. The influence of island area on species composition could consist of both direct area effects, such as passive sampling (Connor & McCoy 1979) and area-dependent extinction (MacArthur & Wilson 1967), and indirect area effects, such as increased habitat diversity and decreased influence of edges with increasing area (Williams 1964; Murcia 1995). However, the strongest influence of island area on species composition is most likely indirect by affecting the frequency of fire, as fungal communities on the islands primarily depends on tree species composition determined

by fire history. In addition, the influence of edges was controlled for in this study and the correlation between species composition and diversity of dead wood does not appear to be an indirect area effect as area and diversity of dead wood show no correlation.

Despite the high proportion of water in the surrounding area of each island there was no effect of isolation on species composition. This is probably a matter of scale, as the longest included distance of 1200 m may not exceed the dispersal ability of many species. For example, studies of wood-decaying fungi sensitive to forestry, *Phellinus nigrolimitatus* (Kausserud & Schumacher 2002) and *Phlebia centrifuga* (Franzen et al. 2007), have shown that a substantial gene flow could take place even in fragmented populations. Also, wood-decaying fungi are known for their massive spore production with dispersal abilities up to several kilometers even for rare, red-listed species (Edman & Gustafsson 2003, Edman et al. 2004b). On the other hand, spore deposition has been shown to rapidly decrease with distance and the amount of spores is likely to be an important factor for the actual establishment of wood-decaying fungi (Norros et al 2012; Edman et al 2004c). However, in a long term perspective the reduced establishment of long distance dispersal may be overshadowed by the chance of a successful colonization after numerous attempts.

The volume of logs was the only environmental variable that had a significant effect on species richness in this study, while the diversity of logs showed a clear trend. This finding highlights the importance of substrate properties for wood-decaying fungi, consistent with earlier observation of high correlation between species richness and quantity and quality of dead wood (Junninen et al. 2006; Hottola et al. 2009; Josefsson et al. 2011). The relationship between volume of logs and species richness could be seen as a more local equivalent of the species-area relationship of islands, i.e. volume is important per se, as well as a species-habitat relationship, i.e. volume is important for generating substrate heterogeneity. In addition, the diversity of logs is likely to be an equally important factor for species richness, as the life cycle and the ecological requirements of wood-decaying fungi are highly variable between species (Bader et al. 1995; Sippola et al. 2001; Penttilä et al. 2004). For example, small-diameter logs have been shown to be important for species with short life cycle and low competitive ability (Kruys & Jonsson 1999; Nordén et al. 2004), while many red-listed species depend on intermediate or well-decayed large-diameter logs (Tikkanen et al. 2006; Josefsson et al. 2011). Furthermore, the infrequent occurrence of many species in this study supports the notion that most species of wood-decaying fungi are specialized to specific environmental conditions and have developed specific adaptations to utilize different dead wood qualities (Rayner & Boddy 1988). Similar frequency distribution patterns have been reported in several studies of wood-decaying fungi in boreal old-growth forests (Berglund et al. 2005), including studies with species registration by DNA sequencing of mycelia within dead wood (Allmér et al. 2006; Kubartova et al. 2012). In fact, the pattern with many rare species and only a few common ones is close to an ecological rule and has been recorded for many different organism groups and ecosystems (e.g. Hanski 1999; Lawton 1999; Magurran & Henderson 2003).

For the number of red-listed species, no effect of the environmental variables was found. In earlier studies, environmental variables such as island area (Berglund & Jonsson

2001), isolation (Paltto et al. 2006), successional stage (Ylisirniö et al. 2012) and dead wood properties (Ylisirniö et al. 2012; Hottola et al. 2009) have been shown to affect the number of red-listed species. The dead wood variables used in this study may have been too general for detecting effects on the number of red-listed species, as these species are known to be sensitive in their habitat demands (using mainly large-diameter logs in certain decay stages). Alternatively, the size of the study plots may have been too small to detect differences in the number of red-listed species among the islands. However, although the environmental variables showed no effect on the number of red-listed species, the NMDS ordination indicated that they influence the composition of red-listed species. There was a clear division of red-listed species between the recent-fire and old-fire islands. For example, red-listed species known to depend on natural pine forests with a history of reoccurring fires, e.g. *Antrodia albobrunnea*, *Cinereomyces lenis* and *Oligoporus lateritius*, were only found at the recent-fire islands, while species known to prefer old-growth spruce forests, e.g. *Leptoporus mollis*, *Phellinus ferrugineofuscus* and *Skeletocutis chrysella*, were only found at the old-fire islands. This result highlights the fact that long-term survival of the red-listed species depends on the persistence of different types of forests in the landscape.

For conservation, the question of fire is central and needs to be assessed with a long-term perspective. The absence of fire in boreal forest landscapes due to effective fire suppression threatens to transform natural pine forests into spruce forests (Engelmark 1987). Under the successional transition the effects on red-listed species can be expected to be delayed as the decomposition of large logs of pine is a slow process, up to several hundred years for charred or resin-impregnated wood (Niemelä et al. 2002). On the positive side, this means that the time frame for implementing conservation measurements becomes extended, but it could also have a negative effect if conservation planning fails to recognize the extinction debt in time. The need for restoration fire has been well-recognized for being an important active measurement for conservation of natural pine forest ecosystems (Granström 2001; Shorohova et al. 2011), but the scale of implementation is still small in comparison to the natural extent of fire in a boreal forest landscape (Zackrisson 1977; Niklasson & Granström 2000). In fact, at present the percentage of area burnt annually (including all types of fires) rarely exceeds 0.001% of the total forest area (Drobyshev et al. 2012), while at least 1 % of the forest land burned prior to effectively fire suppression (before the end of the 19th century) (Niklasson & Granström 2000). Also, the quality of fires (e.g. fire intensity and severity) is an important factor of the natural fire regime, where much of the prescribed burnings so far have had a high tree mortality and low impact on the organic soil layer in contrast to typical fires of the natural boreal landscape with considerable tree survival and deep burn in organic soils (Granström 2001). Further, the question of where to apply restoration fire has been shown to be important in order to prevent sensitive types of dead wood (e.g. dead pine wood in late decay stages that is important for many red-listed species) from being destroyed by fire (Eriksson et al. 2013). Consequently, increasing the amount and scale of fires while considering the quality and choice of the burned areas is probably crucial for the conservation of wood-decaying fungi dependent on natural pine forest ecosystems.

5. CONCLUSION

This study shows that forest fire drives long-term community changes of wood-decaying fungi in a boreal forests archipelago. Species composition in natural recent-fire forests are characterized by being associated to pine, while old-fire forests are composed by species associated with spruce. Whereas the difference in tree species composition between different successional stages are well-documented for boreal forests (Bergeron et al. 2002), this study provides an improved understanding in how wood-decaying fungi can respond to long-term succession following a fire. For conservation, this implies that the red-listed species within each forest type has to be treated differently in respect to their habitat demands, where fire naturally would constitute a key role for maintaining forest biodiversity in the boreal forest landscape. In addition, this study highlights the importance of dead wood (volume and diversity) for species richness of wood-decaying fungi. This result stress the importance of maintaining high levels of dead wood in the individual forest stands, and suggests that more active measures are needed to increase the amount of dead wood in managed forests.

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Appendix 1. Percentage of species occurrence at the 22 islands studied. Nomenclature follows Niemelä (2005). Red List categories according to Gärdenfors (2010): EN endangered, VU vulnerable, NT near-threatened.

Species	%	Species	%
<i>Inonotus obliquus</i>	95.5	<i>Phellinus viticola</i>	22.7
<i>Piptoporus betulinus</i>	68.2	<i>Skeletocutis subincarnata/papyracea</i>	22.7
<i>Cerrena unicolor</i>	63.6	<i>Antrodiella pallasii</i> (VU)	13.6
<i>Trichaptum abietinum</i>	63.6	<i>Porpomyces mucidus</i>	13.6
<i>Phellinus igniarius</i>	59.1	<i>Gloeoporus dichrous</i>	13.6
<i>Phellinus nigricans</i>	59.1	<i>Skeletocutis amorpha</i>	13.6
<i>Antrodia sinuosa</i>	50.0	<i>Antrodia serialis</i>	9.1
<i>Phellinus chrysoloma</i> (NT)	45.5	<i>Daedaleopsis septentrionalis</i>	9.1
<i>Fomes fomentarius</i>	40.9	<i>Diplomitoporus crustulinus</i> (VU)	9.1
<i>Junghuhnia luteoalba</i> (NT)	36.4	<i>Leptoporus mollis</i> (NT)	9.1
<i>Oligoporus parvus</i> (NT)	36.4	<i>Oligoporus rennyi</i>	9.1
<i>Skeletocutis biguttulata</i>	36.4	<i>Phellinus ferrugineofuscus</i> (NT)	9.1
<i>Antrodia xantha</i>	31.8	<i>Skeletocutis chrysella</i> (VU)	9.1
<i>Oligoporus fragilis</i>	31.8	<i>Antrodia infirma</i> (EN)	4.5
<i>Oligoporus sericeomollis</i>	31.8	<i>Erastia salmonicolor</i> (VU)	4.5
<i>Cinereomyces lenis</i> (VU)	27.3	<i>Oligoporus lateritius</i> (VU)	4.5
<i>Gloeophyllum sepiarium</i>	27.3	<i>Phellinus nigrolimitatus</i> (NT)	4.5
<i>Ischnoderma benzoinum</i>	27.3	<i>Phellinus pini</i> (NT)	4.5
<i>Antrodia albobrunnea</i> (VU)	22.7	<i>Skeletocutis kuehneri</i> (NT)	4.5
<i>Fomitopsis pinicola</i>	22.7	<i>Trametes ochracea</i>	4.5
<i>Meruliopsis taxicola</i>	22.7		
		Total 41 species (16 red-listed)	

Appendix 2. Correlation coefficients of environmental variables. For full variable names see Table 1.

Variable	Area	Iso.300	Iso.1200	Last.fire	Spruce	Spruce.d	Decid.	Decid.d	Pine	Pine.d	Ba.total	Stumps	No.logs	V.logs	Div.l	Div.d
Area																
Iso.300	-0.06															
Iso.1200	-0.15	0.06														
Last.fire	-0.67***	0.24	0.03													
Spruce	-0.39	0.48*	0.34	0.57**												
Spruce.d	-0.32	0.23	0.05	0.39	0.69***											
Decid.	-0.19	0.17	-0.26	0.06	0.07	0.18										
Decid.d	0.35	-0.15	-0.2	-0.07	-0.21	-0.29	-0.31									
Pine	0.51*	-0.51*	-0.04	-0.56**	-0.74***	-0.62**	-0.39	0.58**								
Pine.d	0.64**	-0.01	0.06	-0.44*	-0.27	-0.22	-0.50*	0.3	0.53*							
Ba.total	0.33	-0.18	0.1	-0.2	-0.05	0.11	0.02	0.38	0.45*	0.50*						
Stumps	0.03	-0.3	0.15	-0.11	-0.2	-0.12	-0.05	0.21	0.37	0.24	0.47*					
No.logs	0.47*	-0.42	0.02	-0.34	-0.22	-0.22	-0.14	0.52*	0.57**	0.55**	0.67***	0.28				
V.logs	0.52*	0.22	-0.08	-0.49*	0.05	-0.1	-0.1	0.19	0.13	0.18	0.18	-0.2	0.23			
Div.l	-0.4	-0.17	0.19	0.33	0.42	0.43*	0.27	0.18	-0.11	-0.18	0.37	0.21	0.22	-0.19		
Div.d	0.31	0.12	-0.05	-0.18	0.1	-0.03	-0.19	0.70***	0.19	0.13	0.2	0.02	0.34	0.47*	-0.03	
Div.logs	0.44*	-0.16	0.01	-0.45*	-0.12	-0.16	-0.28	0.70***	0.53*	0.47*	0.58**	0.14	0.68***	0.49*	0.15	0.69***