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Recent forest on abandoned agricultural land in the boreonemoral zone – Biodiversity of plants and fungi in relation to historical and present tree cover

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ABSTRACT

Recent forests may be an asset for green infrastructure and ecological restoration, but studies are needed of the variation in forest biodiversity among sites, and possible reasons for observed patterns. In boreonemoral Scandinavia, reforestation occurs on abandoned agricultural land, and we studied 27 such recent (40–80 years old) mixed forests with temperate deciduous trees and boreal trees including Norway spruce, and their communities of dead wood fungi and vascular plants. By analysing aerial photos from 1960 and 2017, we explored how species richness and composition within sites vary with historical and present tree cover, and separately spruce cover, at site scale (2 ha) and within the surroundings (12.5 ha). Tree cover, and the percentage spruce cover, had increased considerably from 1960 and 2017, while open areas had decreased accordingly, at both scales. We found no significant relationships between species richness of forest plants, or fungi on coarse woody debris, and tree cover at any scale. On the other hand, species richness of grassland plants, and fungi on fine woody debris, showed significant negative correlations with high tree cover, and thus the recent forests with the highest total species richness seem to occur in surroundings with lower tree cover, currently dominated by agriculture. The reason may be a correlation between richer soils and more agriculture; the area with the richest soil have been extensively cleared and cultivated, and therefore currently have lower tree cover and more fragmented forests. Furthermore, ordination analysis showed that several deciduous tree species were negatively correlated with tree cover, locally and in the surroundings, while the tree species preferring rich soil such as *Fraxinus* and *Ulmus* (and several associated fungal species), were positively correlated with spruce cover. A possible explanation is that spruce colonize well on abandoned grasslands and therefore tends to be associated with grassland plants and trees requiring the richer soils of these areas. We suggest that recent forests in boreonemoral areas could be used for instance for restoration of temperate deciduous woodland, especially in areas dominated by agriculture, but that recurrent management may be needed to avoid spruce domination.

1. Introduction

Spontaneous reforestation on abandoned pastures and fields has increased in the temperate zone during recent decades, due to rural depopulation and abandonment of extensive grazing (Nagaike et al., 2005; Chazdon, 2008; Lunt et al., 2010; Sitzia et al., 2010; Kolk et al., 2017; Buitenwerf et al., 2018). In Scandinavia, the area with high probability of future reforestation on marginal agricultural land is considerable (Bryn et al., 2013). The resulting recent forests may be an asset for planning of green infrastructure, ecological restoration and conservation, but studies are needed of the variation in forest biodiversity among sites, and possible mechanisms behind such patterns. The development of species communities in recent forests probably depend on several factors, such as habitat suitability (Flinn and Vellend, 2005), presence or absence of ecological legacies (Foster et al., 2003), habitat amount at various scales in the landscape, and the time required for colonization of various species (Nordén et al., 2014). Community development may also depend on taxa or guilds, with some taxa/guilds responding faster than others, with increase in species richness, and others decreasing in species richness as a result of secondary succession. Earlier studies have indicated greatly varying responses to forest recovery among taxa/guilds (Spake et al., 2015), and

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several taxa/guilds should ideally be evaluated to avoid taxonomic bias (Clark and May, 2002).

The recent forests in boreonemoral Scandinavia are often mixed forests with temperate deciduous trees and boreal trees, including Norway spruce *Picea abies* (Eriksson, 1991; Granhus et al., 2012; Bryn et al., 2013; Fridman and Wulff, 2018). Temperate deciduous forest (TDF) is one of the most severely degraded biomes worldwide and has been reduced to only a small fraction of its natural distribution area (Venter et al., 2016). In the southern, lowland parts of Scandinavia, clearing of land for pastures and fields has historically led to the decline of TDF (Lindbladh et al., 2007). TDF currently constitutes only 1.5% of the forested area in Norway (Granhus et al., 2012) and 2% in Sweden (Fridman and Wulff, 2018), but has the highest share of red-listed species per area of any biome in Scandinavia (Artdatabanken, 2015; Henriksen and Hilmo, 2015). Efforts should therefore be made not only to conserve the scattered remaining TDF patches, but also to increase the area of TDF through ecological restoration. While most emphasis on forest restoration in Scandinavia and northern Europe has been on boreal forests (Halme et al., 2013; Kuuluvainen et al., 2015), TDF deserves more attention due to its significance for the protection of biodiversity and as a measure to cope with the impacts of projected climate change (Nordén et al., 2019).

The objectives of forest restoration range from reforestation on degraded land, to promoting native species and biodiversity in existing forests (Stanturf and Madsen, 2005; Stanturf et al., 2014). In this context, natural regeneration of trees is much more economically and ecologically effective than planting and should be the basis of restoration when possible (Chazdon et al., 2020). However, the effectiveness of natural regeneration as a restoration measure will also depend on how close the composition of forest stands is to the desired restored state. In the case of TDF in southern Scandinavia, it is not known if reforestation on abandoned agricultural land offers a realistic opportunity for the restoration of TDF. The focus of this study is to assess the potential for restoring TDF stands from this kind of naturally regenerated recent forest.

We study how species richness and composition of vascular plants and fungi on dead wood, two organism groups with contrasting life-history strategies and ecology, vary with tree cover and land use history in recent forest sites on abandoned agricultural land in the southern parts of Norway and Sweden. We also study how the amount of spruce has developed and if spruce has any effects on diversity separate from tree cover. To refine our analyses, we analyse separately the following guilds: grassland plants and forest plants, and fungi predominantly found on coarse and fine woody debris, respectively. We pose the following specific research questions:

(1) How does the historical and present tree cover at site scale and in the surroundings (200 m radius, 12.5 ha), as well as the age of the recent forest sites, correlate with species richness and species composition of plants and fungi?
(2) How does the cover of spruce correlate with species richness and species composition of plants and fungi?
(3) How does the amount of dead wood correlate with species richness of fungi on fine and coarse woody debris, and is it related to historical and present tree cover at site scale and in the surroundings?

We hypothesize that overgrowing with trees and bushes will disfavour the majority of grassland plants, but that a few species may be able to persist for a long time under tree cover. Species richness of vascular plants is expected to be positively correlated with the degree of openness, while fungi are expected to increase with tree secondary succession. We expect spruce cover to be negatively associated with TDF species.

The history of tree cover greatly affect biodiversity in forests (Nordén et al., 2014), and we hypothesize that sites or surroundings with higher historical tree cover should be correlated with higher species richness of forest plants and fungi on dead wood.

We use our results to discuss the value of recent forests for biodiversity, their potential contribution to restoration, and the possible need for management interventions.

2. Materials and methods

2.1. Study area and site selection

We selected 27 recent (secondary succession) forest study sites, 14 in Norway and 13 in Sweden (Fig. 1, App. A). We used the following selection criteria: The sites should be mixed forests with relatively young (40–80 years) trees, have closed canopies, and should not have been used for harvest of timber or grazing for several decades. The sites were selected by contacting stakeholder organizations and landowners, by studying aerial photographs, and by field visits. The sites are situated in the lowland (5–138 m a.s.L.), and belong to the boreonemoral climatic region (Moen, 1998; Raab and Vedin, 1995), which is a transition zone between the boreal region landscape and the temperate (nemoral) region. The recent forests consisted of the temperate deciduous trees ash *Fraxinus excelsior*, elm *Ulmus glabra*, and oaks mainly pedunculate oak *Quercus robur* but also sessile oak *Q. petraea*, boreal deciduous trees such as birches *Betula pendula* and *B. pubescens,* aspen *Populus tremula* and goat willow *Salix caprea*, and the coniferous trees Norway spruce *Picea abies* and Scots pine *Pinus sylvestris* (Nordén et al., 2019).

Remnants of old fences, clearance cairns etc., as well as the position of the sites in the landscape close to farms, confirmed that these areas had generally been used for grazing, hay-making, and to a lesser extent for fields during earlier periods. Opportunistic interviews with landowners during fieldwork supported this view and indicated that agricultural use at the sites typically ended around just after World War 2, and that the sites were practically open at that time. We studied the degree of openness by analysing the oldest available aerial photos (from about 1960), see below. The sites lacked old deciduous trees that would indicate a history as wooded meadows. All forests had dry to mesic soil types and had relatively flat surface except two Norwegian sites that contained clay ravines.

Out of all sites, 12 had private, 5 had state, 8 municipal and 1 mixed private/state ownership. At each site we established two study plots (assigned for other purposes but both used here), each usually 100 × 100 m but sometimes rectangular (always one ha), usually situated close to each other.

2.2. Forest structure measurements

Basal area of trees was estimated in 4 (in a few cases 6) randomly chosen circular areas with radius 3.99 m (=50 m^2) in each plot (i.e. 8, or in a few cases 12 per site), and the mean value of the circles was used Nordén et al. (2019). We measured the diameter class with a ruler (2 cm interval; first class 5.0–6.9 cm) of all trees and bushes with > 5 cm DBH (diameter at breast height 1.3 m) and recorded the species. Smaller trees and bushes with diameter < 5 cm were counted, but not measured.

Coarse woody debris (CWD; dead wood > 10 cm diameter) was measured in two 25 m sections of two 10 × 100 m transects per plot (4 × 10 × 25 = 1000 m^2 per plot, or 2000 m^2 per site) in June 2016. The transects ran across the interior of each plot and were separated by at least 20 m. They were placed inside the forest, avoiding paths and other open areas. Only parts of dead wood objects inside the transects were included, and we measured length, top and bottom diameter of all dead wood objects, including standing dead trees and dead branches attached to living trees up to two m above ground. We noted tree species and decay stage 1–4 of the dead wood according to Hottola and Siitonen (2008). To measure fine woody debris (FWD; dead wood 5–10 cm diameter), we randomly placed one 2 × 2.5 m square in two 25 m sections, along the central axis of each transect. We measured top and

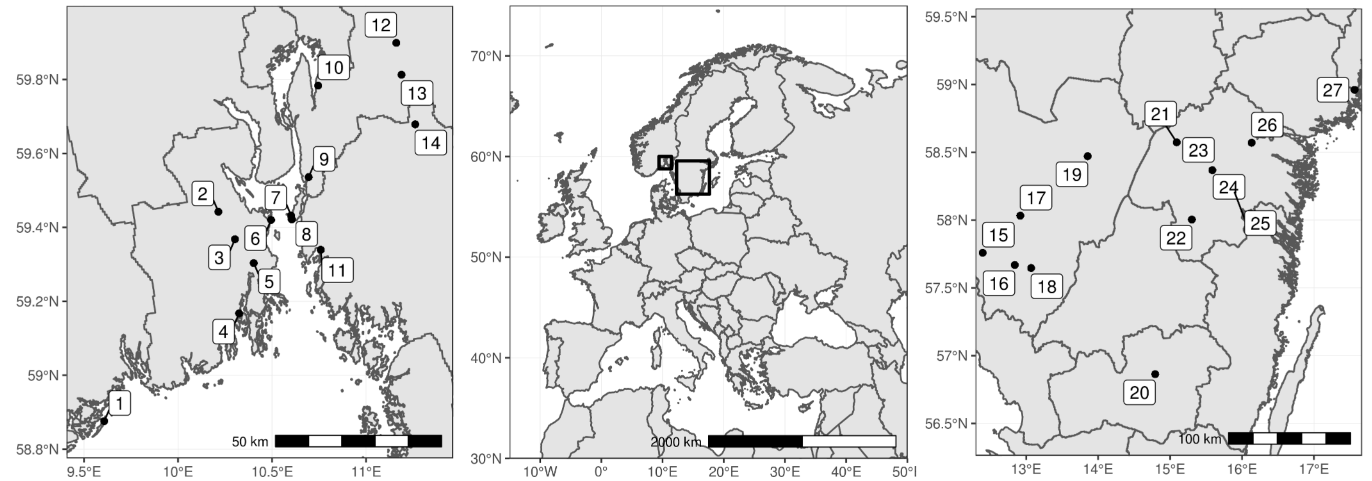

Fig. 1. Map of the sites. The left panel shows Norway and the right shows Sweden. 1. Jomfruland, 2. Kleiva, 3. Kåpe, 4. Sand, 5. Berg, 6. Karljohansvern, 7. Grønliparken, 8. Albyskogen, 9. Kolås, 10. Svartskog, 11. Tasken, 12. Bjanes, 13. Omberg, 14. Håkås, 15. Tvärsjönäs, 16. Bosnäs, 17. Remmene, 18. Aplared, 19. Stöpen, 20. Bokhultet, 21. Karshult, 22. Aspenäs, 23. Slaka, 24. Hovetorp, 25. Kvarntorp, 26. Klockaretorpet, 27. Tullgarn. See App. A for geographic, ownership and protection data on the sites.

bottom diameter of all dead wood objects inside the squares and noted tree species and decay stage (1–4) for each piece. The survey and calculation of CWD and FWD followed the methods in Nordén et al. (2004).

2.3. Species surveys

We surveyed vascular plants along two 1 × 25 m sections (50 m^2) of two 1 × 100 m transects per plot (in total 100 m^2 per plot and 200 m^2 per site) in June 2016, and recorded all species once per 25 m section (presence/absence). The transects were placed to cover the heterogeneity of the stands.

Fungi on dead wood were surveyed along two 3 × 25 m sections (75 m^2) of two 3 × 100 m transects per plot (in total 300 m^2 per plot, or 600 m^2 per site) after periods of rainfall in Sept-Oct 2016. All dead wood (CWD and FWD) within the transects (up to 2 m above ground, excluding branches of living trees not reaching the ground) were surveyed for ascomata and basidiomata. Among basidiomycetes we included all species with agaricoid (few), corticioid, polyporoid and stereoid fruitbodies, and for ascomycetes all pyrenomycetoid fungi and discomycetes with ascomata or stromata > 5 mm. Diameter, decay stage and tree species of the dead wood was noted for each record/collection.

2.4. Analysis of aerial photos

To study land-use history and tree cover, we analyzed digitized versions of the oldest available aerial photos covering the sites and the surroundings. These black and white photos were taken from airplanes between 1955 and 1965 (mean year 1959, SD 3.81 years), and are hereafter referred to as photos from '1960'. We next compared the historical land-use cover with the present vegetation cover using Google Maps satellite images (in color; mainly from 2016 and 2017, accessed Dec 10th 2017). In addition to the two one hectare plots, we analyzed the surroundings within a radius of 200 m (12.5 ha) around the intermediate coordinate between plots within the sites in the same way. We calculated the areas of each land use type as polygons in QGIS 2.18.0 (QGIS Development Team, 2016) with GRASS 7.0.5 (Grass Development Team, 2012). For examples of historical and recent aerial photographs with digitized polygons, see App. B. We divided the vegetation cover into field, forest, pasture, pasture with scattered trees, spruce plantations, built areas, and water bodies. For analyses, we pooled the data into the following three categories: 1) 'Forest', representing areas with >95% closed canopies (including 1–2.5% of spruce plantations in the surroundings); 2) 'Open', representing non-forested vegetated areas such as meadows or pastures, and fields. Pasture with scattered trees were included in the open category since the trees were mainly young and indicated an earlier open pasture; 3) 'Other', constituting water, buildings, and roads. In addition, we estimated the total cover of spruce trees in mixed forest for both the historical and recent aerial photos. Spruce was distinguished by its dark green color and star-shaped branching pattern. For the black and white aerial photos from 1960, spruce was more difficult to detect, and three photos had to be discarded. Spruce trees were generally scattered and mixed with deciduous trees, and of varying sizes indicating that they had spread to the area spontaneously and were not planted.

2.5. Species functional groups

Non-woody plant species were classified as either forest species, grassland species or ruderal species following Götmark et al. (2005a), complemented by expert opinion for species not included in that publication. To increase the relevance for conservation and restoration, we highlighted the number of plant species indicating old forest (Hermy et al., 1999) or areas of special value for biodiversity (Woodland Key Habitat (WKH) Indicator species; Skogsstyrelsen, 2014) in ordination analyses. To help explain patterns, we used Ellenberg indicator values for light influx, nutrient availability and pH (Ellenberg et al., 1992), complemented by values from Hill et al. (1999) for species lacking in the first list or there classified as 'indifferent'. A list of species and their classifications is provided in App. C.

Similar classifications are not available for most fungal species on dead wood, but species on coarse dead wood such as big logs can only occur in old forests. Based on Nordén et al. (2004) and personal experience, we therefore classified the fungal species based on whether they predominantly occur on coarse woody debris (CWD, dead wood with a diameter > 10 cm) or fine woody debris (FWD, dead wood with a diameter < 10 cm), or are generalists (App. D). We also classified each species as specialized on dead wood from deciduous or coniferous trees, or generalists (App. D).

2.6. Statistical analyses

We used mixed effects models to examine the relationships between tree cover and DBH, and the response variables species richness of non-woody vascular plants (forest and grassland/open species separately), species richness of fungi (FWD fungi and CWD fungi separately) and the volume of dead wood (FWD and CWD separately). Tree cover (%) in the plots and in the surroundings, as well as mean DBH, were used as fixed variables. Spruce cover (%) in the plots and in the surroundings were initially included as fixed variables, but removed due to convergence problems. However, these initial analyses indicated that there were few significant relationships between the response variables and spruce cover. Separate analyses were conducted for the historical and present tree cover. Note that historical and present tree cover in the surroundings were correlated ($r = 0.84$), which makes it difficult to completely separate the effects of these two factors. DBH was only included in the models with present tree cover. To account for the nested design, initial models included random intercepts for transect nested in plot, site and country. The appropriate random effects structure was found using likelihood ratio tests in a backward selection procedure where country was kept as the minimum random structure. Similar likelihood ratio tests were used to find the appropriate fixed effects structure. All species richness models were run with a Poisson error distribution and checked for over-dispersion. The dead wood model was run with a Gaussian error distribution and square root transformed response variables. We used similar mixed effects models to examine the relationship between the volume of dead wood and species richness of FWD fungi and CWD fungi, respectively. FWD and CWD volume (m^3) were used as fixed variables in separate models. Two extreme outliers, one for FWD and one for CWD volume, were excluded from all analyses due to their strong influence on the parameter estimates.

Next, we used global non-metric multidimensional scaling (GNMDS) to examine how species composition of canopy layer trees, dead wood, and non-woody field layer vegetation varied with tree cover (%) and spruce cover (%) in the plots and in the surroundings, both historically (1960) and at present (2017), and with mean diameter of trees (DBH). The two-dimensional GNMDS was run with Bray-Curtis dissimilarity measure, 100 initial configurations, maximum 200 iterations and stress tolerance 10^{-6}. The correlation coefficient between the ordination axes and environmental variables was tested using the non-parametric Kendall's τ. A similar GNMDS was used to examine the relationship between fungi species composition and the same environmental variables, but due to low numbers of species found in each transect, the fungi data were aggregated to the site scale. All statistical analyses were conducted in R version 3.1.2 (R Core Team, 2014) using the packages lm4 (Bates et al., 2014) and vegan (Oksanen et al., 2015).

3. Results

3.1. Changes in land-use from 1960 to 2017

Tree cover (mean ± 1SD) in the study sites increased from 71.2 ± 29.7% in 1960 to 99.2 ± 3.9% in 2017 (Table 1). At most of the sites, reforestation with young trees occurred in 1960, and only two sites lacked trees entirely in 1960. There were no spruce plantations at site scale in 1960, and spruce plantations covered only 0.4+/-1.6% in 2017. However, the share of spruce in the category Forest increased from 19.8 ± 21.7 to 30.2 ± 19.3 during the same time period.

From 1960 to 2017, tree cover in the surroundings increased from 47.0 ± 29.7% to 63.3 ± 22.6% (Table 1). The area of spruce plantations in the surroundings increased from 1.1+/−3.7 to 2.7 +/−6.4, while the share of spruce in the category Forest increased from 25.8 ± 25.3 to 42.3 ± 24.3%. Old-growth patches and protected areas were lacking in the surroundings. Further details on land use categories are available in App. E.

Table 1
Land use categories (%) at the sites and within the 200 m surroundings as judged from historical and recent aerial photos. Numbers are mean ± SD.

Scale	Year	Forest (% spruce*)	Open	Other
Site	1960	71.2 ± 29.7 (19.8 ± 21.7)	28.8 ± 48.2	0.00 ± 0.00
Site	2017	99.2 ± 3.9 (30.2 ± 19.3)	0.70 ± 2.60	0.1 ± 0.4
Surroundings	1960	47.0 ± 29.7 (25.8 ± 25.3)	44.2 ± 49.3	8.8 ± 12.6
Surroundings	2017	63.3 ± 22.6 (42.3 ± 24.3)	27.4 ± 30.7	9.3 ± 13.1

* This share relates to the percentage spruce of the total area of forest cover, not of the total area).

3.2. Tree cover and tree species composition

The basal area in the dense forests sites consisted of on average 38 ± 23% SD temperate deciduous trees, 26 ± 28% SD conifers, and 36 ± 25% SD of other (boreal) deciduous trees. The trees with the largest diameter were Scots pine, oaks, and birches. Tree species were generally well mixed in the plots, with 9.7 ± 2.1 SD tree species per site. The canopy was often even aged but with a few older pines and oaks at some sites. Main regeneration was from young ash seedlings. For further details on forest composition and forest structure see Nordén et al. (2019).

Regarding species composition of trees, ordination axis 1 was uncorrelated with tree cover ($p > 0.05$), but significantly correlated with both historical ($\tau = -0.20$, $p = 0.006$) and present ($\tau = -0.19$, $p = 0.002$) spruce cover in the plots, as well as historical spruce cover in the surroundings ($\tau = -0.16$, $p = 0.028$) (Fig. 2). Ordination axis 2 was significantly correlated with tree cover in the surroundings both historically ($\tau = 0.17$, $p = 0.007$) and at present ($\tau = 0.18$, $p = 0.004$), and with present spruce cover in the surroundings ($\tau = 0.22$, $p = 0.001$). Spruce cover in the plots was positively associated with present tree cover, whereas most deciduous trees, such as oaks, aspen, rowan *Sorbus aucuparia*, beech *Fagus sylvatica* and European crab apple *Malus sylvestris*, were negatively associated with tree cover in general (Fig. 2). The red-listed (Henriksen and Hilmo, 2015; ArtDatabanken, 2015) tree species elm (CR in Sweden, VU in Norway) and ash (EN in Sweden, VU in Norway) were more common in sites with a high present tree cover, thus co-occuring with high spruce cover (Fig. 2). Ordination axis 1 seemed to be associated with soil nutrients and pH, with more nutrient poor and more acid conditions to the right, as shown by the position of rich soil trees such as elm and ash to the left, and more acidic soil trees such as *Q. robur* and *P. tremula* to the right (Fig. 2).

3.3. Tree cover and dead wood

The studied forests had on average 9.8 m^3 CWD per ha, which is slightly lower than the national average in productive forest outside of nature reserves in Norway (10.6 m^3/ha; Storaunet and Rolstad, 2015), but higher than the corresponding average value for Sweden (8.1 m^3/ha; Nilsson et al., 2017). The mean volume of dead wood including FWD was 14.4 m^3/ha. There was no relationship between tree cover at any spatial scale, or of average DBH, and the volume of FWD (Table 2). However, the volume of CWD was significantly higher in plots with a high tree cover and a higher average DBH (Table 2).

Regarding species composition of dead wood, the patterns of species occurrences largely followed that of the tree layer, for instance dead wood of *U. glabra* and *F. excelsior* positively associated with high spruce cover (App. I). Ordination axis 1 was significantly correlated with present tree cover in the landscape ($\tau = 0.20$, $p = 0.038$), whereas ordination axis 2 was significantly correlated with present spruce cover in the surroundings ($\tau = -0.29$, $p = 0.003$).

3.4. Field layer plants

In total, we recorded 197 vascular plant species, including 153 non-woody species (App. C). Of the latter, 76 were grassland/open habitat plants (27 grassland species, 49 open area species), 60 were forest species, and 17 were ruderals. Of the forest species, 45 were TDF species, while 15 were typical for coniferous forest. One herb species, *Campanula cervicaria*, found in Sweden, was on the Swedish red-list (NT, ArtDatabanken, 2015), 34 species were ancient forest plants according to Hermy et al. (1999) and 16 were WKH Indicator species (Skogsstyrelsen, 2014)

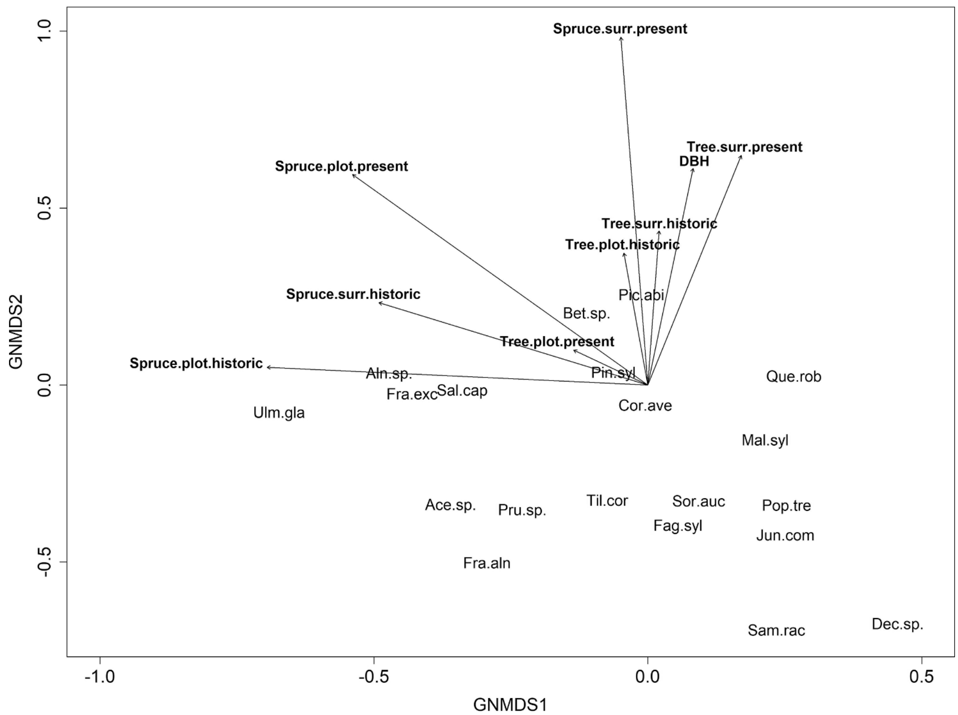

Fig. 2. GNMDS ordination plot of tree and shrub layer species composition. Arrows indicate the correlation between the ordination and tree cover (%) and spruce cover (%) in the plots and in the surroundings historically (1960) and at present (2017), as well as DBH. The length of the arrows are proportional to the correlation strength. The position of some species names were slightly adjusted to avoid overlap. For species abbreviations, see App. F.

Table 2
Parameter estimates (Coef) and standard errors (SE) for fixed effects of mixed-effects models for the relationship between volume of dead wood, including both fine woody debris (FWD) and coarse woody debris (CWD), and tree cover (%) in the plots and in the surroundings historically (1960) and at present (2017), as well as DBH. p-values are indicated by asterisks (*p < 0.05, **p < 0.01, ***p < 0.001). Non-significant variables (–) were excluded during model selection.

	FWD				CWD			
	Historical		Present		Historical		Present	
	Coef	SE	Coef	SE	Coef	SE	Coef	SE
Intercept	0.47	0.058	0.47	0.058	0.85	0.166	0.51	0.26
Tree plot	–	–	–	–	0.004	0.002*	–	–
Tree surroundings	–	–	–	–	–	–	–	–
DBH			–	–			0.04	0.02*

(App. C). We found on average 23.8 ± 12.0 SD species of non-woody plants per site.

There was no significant relationship between species richness of forest plants and tree cover at any spatial scale (App. G). Species richness of grassland plants was significantly higher in sites with a low tree cover in the surroundings both historically and at present (Table 3, Fig. 3). Mean DBH had no correlation with species richness of neither forest species nor grassland species (Table 3).

Species composition of the field layer vegetation (including both forest and grassland species) was correlated with both the plot tree cover and tree cover in the surroundings, as well as with spruce cover (Fig. 4). Both ordination axes were significantly correlated with tree cover in the surroundings both historically (axis 1: $\tau = 0.13$, $p = 0.005$, axis 2: $\tau = -0.19$, $p < 0.001$) and at present (axis 1: $\tau = 0.13$, $p = 0.007$, axis 2: $\tau = -0.20$, $p < 0.001$), as well as present spruce cover in the surroundings (axis 1: $\tau = -0.13$, $p = 0.015$, axis 2: $\tau = 0.11$, $p < 0.019$), but not mean DBH (axis 1: $\tau = 0.04$, $p = 0.38$, axis 2: $\tau = 0.004$, $p = 0.92$). Further, ordination axis 1 was significantly correlated with historic plot tree

Table 3
Parameter estimates (Coef) and standard errors (SE) for fixed effects of mixed-effects models for the relationship between plant species richness and tree cover (%) in the plots and in the surroundings historically (1960) and at present (2017), as well as DBH. p-values are indicated by asterisks (*p < 0.05, **p < 0.01, ***p < 0.001). Non-significant variables (–) were excluded during model selection.

	Grassland species				Forest species			
	Historical		Present		Historical		Present	
	Coef	SE	Coef	SE	Coef	SE	Coef	SE
Intercept	1.79	0.272	2.13	0.488	1.61	0.180	1.61	0.180
Tree plot	–	–	–	–	–	–	–	–
Tree surroundings	−0.01	0.005 **	−0.02	0.007 *	–	–	–	–
DBH			–	–			–	–

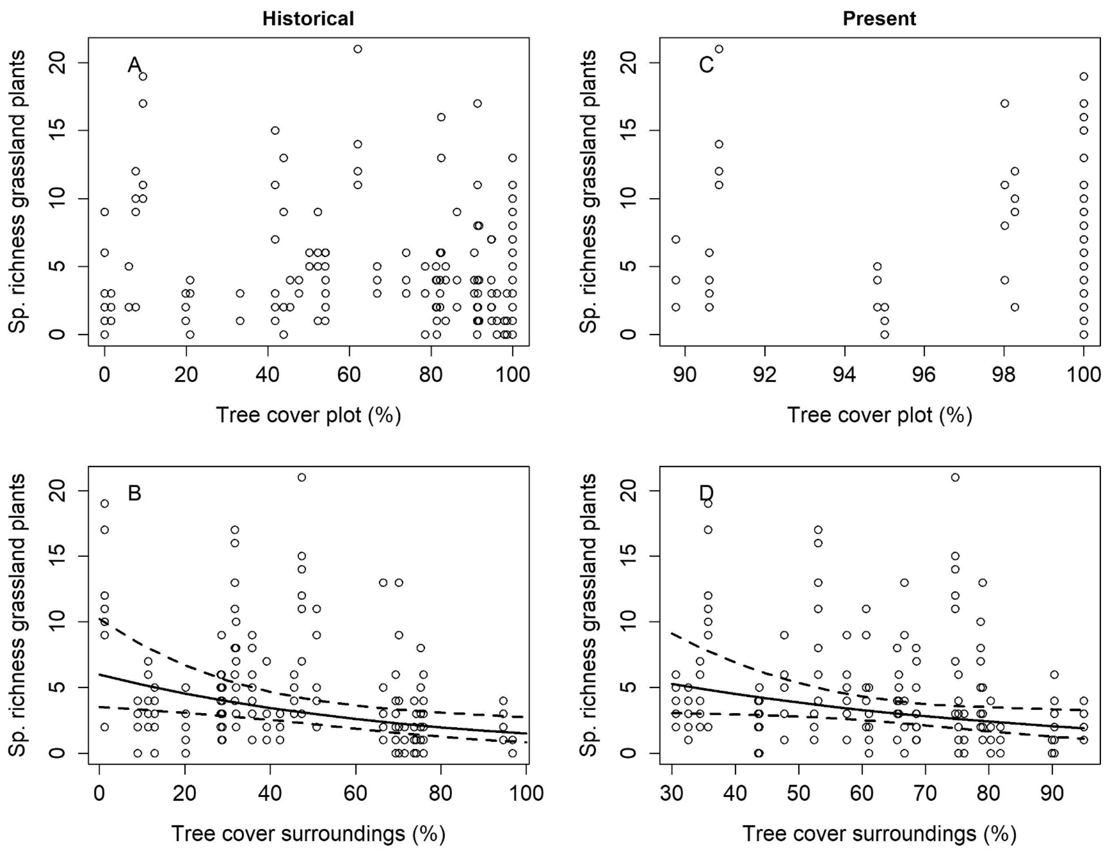

Fig. 3. Species richness of grassland plants in the recent forest sites in relation to tree cover (%) in the plots (A, C) and in the surroundings (B, D) historically (1960; A, B) and at present (2017; C,D). Solid lines represent the fitted values from the model in Table 3. Dashed lines denote 95% confidence intervals (1.96 × SE). Only significant relationships are shown. Note that some of the data points in the figure overlap.

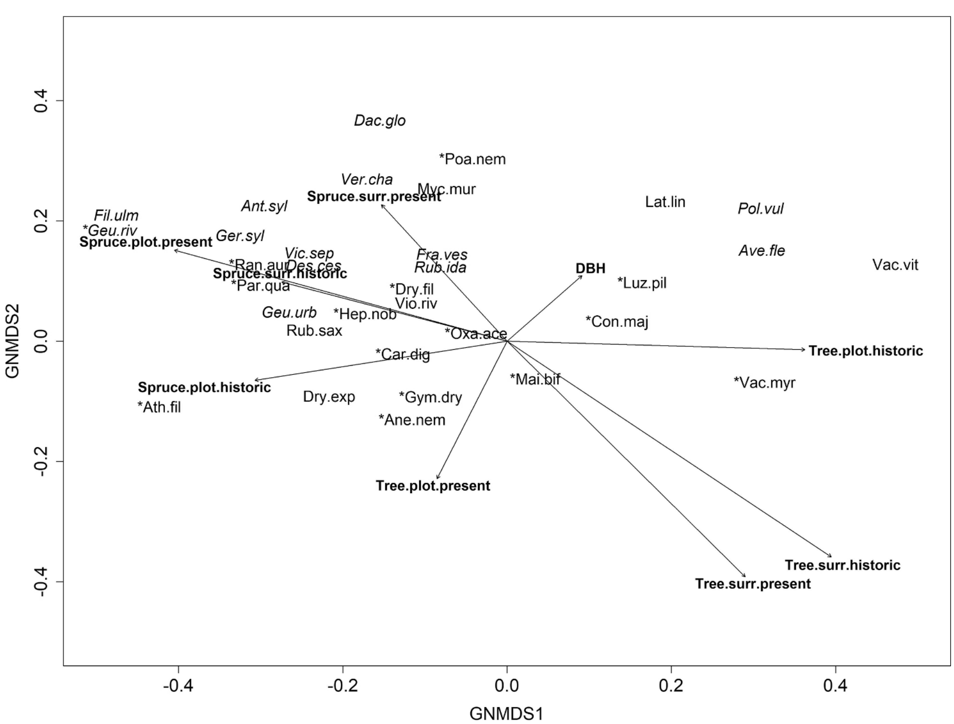

Fig. 4. GNMDS ordination of field layer vascular plant species composition in the recent forest study sites. Grassland species are shown in italics and forest species in regular font. Arrows indicate the correlation between the ordination and tree cover (%) and spruce cover (%) in the plots and in the surroundings historically (1960) and at present (2017), as well as DBH, with the length of the arrows proportional to the correlation strength. For species abbreviations, see App. C. Only the most common species are shown, and the position of some species names were slightly adjusted to avoid overlap. * denote Indicator species, see App. C.

cover (axis 1: $\tau = 0.16$, $p = 0.001$) and plot spruce cover both historically (axis 1: $\tau = -0.16$, $p = 0.003$) and at present (axis 1: $\tau = -0.23$, $p < 0.001$), whereas ordination axis 2 was significantly correlated with plot tree cover at present (axis 2: $\tau = -0.16$, $p < 0.005$). Similar to tree species composition, ordination axis 1 seemed to be associated with soil richness, as shown by the position of rich soil herbs such as *Hepatica nobilis, Viola riviniana, Carex digitata, Rubus saxatilis* and *Paris quadrifolia* to the left, and acidic soil herbs such as *Vaccinium myrtillus, V. vitis-idaea, Avenella flexuosa*, *Convallaria majalis* and *Luzula pilosa* on the right (Fig. 4). The mean Ellenberg indicator values for nutrient and pH along the same ordination axes indicates the same pattern (App. J). Further, rich soils were negatively associated with tree cover in the surroundings and historical plot tree cover (Fig. 4, App. J). Most grassland species (e.g. *Deschampsia cespitosa, Veronica chamaedrys, Vicia sepium*) were negatively associated with tree cover in general, although seemed to be positively associated with spruce cover, while forest species such as *Vaccinium vitis-idaea* and *V. myrtillus* were positively associated with especially historical plot tree cover. Indicator species (App. C) were scattered throughout the ordination plot (Fig. 4).

3.5. Fungi on dead wood

We recorded a total of 193 fungal species (69 ascomycetes and 124 basidiomycetes); 53 species classified as FWD fungi and 88 classified as CWD fungi. We found 161 species on FWD and 98 species on CWD. Five red-listed species were found in Norway (two VU and three NT; Henriksen and Hilmo, 2015), and three in Sweden (NT; ArtDatabanken, 2015).

Species richness of fungi on FWD decreased significantly with both the historical and present tree cover in the surroundings, whereas there was no correlation with plot tree cover (Table 4, Fig. 5). There was no correlation between tree cover and the richness of fungi on CWD at any spatial scale (Table 4, App. H), and mean DBH showed no correlation with species richness of neither FWD nor CWD fungi (Table 4).

Species richness of FWD fungi increased with the plot volume of FWD, but not with the plot volume of CWD, while species richness of CWD fungi increased with the volume of both FWD and CWD (Table 5, Fig. 6).

Species composition of fungi on dead wood was not significantly correlated with tree or spruce cover at any spatial scale or DBH ($p > 0.05$ for all correlations with both GNMDS axes, Fig. 7). Individual species of FWD fungi, especially ascomycetes such as *Diatrype disciformis, Euepixylon udum, Eutypella sorbi* and *Rosellinia helvetica,* seemed to be negatively associated with tree cover in the surroundings, both historically and at present, although seemed to be positively associated with present spruce cover. DBH of the living trees was positively associated with several fungal species occurring on CWD, mainly basidiomycetes such as *Cerioporus mollis, Chondrostereum purpureum, Fomitopsis pinicola, Ganoderma applanatum, Stereum gausapatum, Trametes hirsuta* and *Trechispora hymenocystis*.

4. Discussion

4.1. Biodiversity in the recent forests

Taxa or guilds in which species have restricted colonization ability, or are restricted by lack of microhabitats such as old trees, tree hollows and dead wood (Nordén et al., 2014), may be species poor in recent forests. For example, Spake et al. (2015) found that ectomycorrhizal fungi on average needed 90 years, and epiphytic lichens 180 years to reach 90% of old-growth values in species richness. In contrast, non-saproxylic beetle richness, decreased as site age of broadleaved forests increased, which might be an effect of less light influx and cooler condition in older forests.

Considering the heavy historic degradation of the boreonemoral forest landscape (Lindbladh et al., 2007; 2014), we expected the recent forests to have a rather impoverished flora mainly composed of generalist species. Verheyen et al. (2003) and others have shown that differences between ancient and recent forests in species composition and life-form spectra may persist for many decades. Nevertheless, we found on average 23.8 species of non-woody plants per plot, which is higher than Götmark et al. (2005b) who recorded on average 20.4 species per plot with a similar design but in older forests in Sweden. The communities in our recent forests consisted of 39.2% forest species, 17.3% ancient forest indicators, 8.1% WKH indicator species, possibly indicating that some of the sites historically maintained microhabitats with trees or bushes where these species have managed to survive during the most open period (Sitzia, 2007). However, we found no pattern of ancient forest/ WKH Indicator species in relation to tree cover. 60.8% of all plant species were open area species (17.6% strict grassland species), indicating that these species are able to survive as legacies of earlier land-use for a long time. The result indicate a mix of species from various habitats forming relatively species rich communities.

Intuitively, sites and surroundings with higher historical tree cover should lead to higher species richness of forest plants, but we found no evidence for this hypothesis. The reason may have to do with the slow colonization of forest plants, especially ancient forest indicators (Brunet and von Oheimb, 1998; Hermy et al., 1999). On average 80 years may be needed for colonization of individual herb species from adjacent remnant patches (Brunet, 2007). Since such patches were lacking in the surroundings, colonization at our sites probably mainly rely on rare long-distance dispersal events.

Fungal surveys may give varying results due to local weather conditions. However, fungi on dead wood often have more long-lived ascomata and basidiomata than ground-living species and about 25% are even perennial (stereoid, hard polyporoid, stromatoid, et c). We therefore assume that the surveys gave a representative and comparable estimation of the diversity of these fungi across sites. Regarding species richness, Nordén et al. (2004) studied fungal diversity in woodland key habitats in S Sweden, using similar methods as in the present study. Excluding smaller species not surveyed in the present study, they found 217 species on FWD and 170 species on CWD, to compare with our 161 fungal species on FWD and 98 on CWD. Biodiversity of wood fungi is probably roughly proportional to the amount of dead wood, which was

Table 4
Parameter estimates (Coef) and standard errors (SE) for fixed effects of mixed-effects models for the relationship between fungi species richness and tree cover (%) in the plots and in the surroundings historically (1960) and at present (2017). p-values are indicated by asterisks (*p < 0.05, **p < 0.01, ***p < 0.001). Non-significant variables (–) were excluded during model selection.

	FWD fungi				CWD fungi			
	Historical		Present		Historical		Present	
	Coef	SE	Coef	SE	Coef	SE	Coef	SE
Intercept	0.96	0.290	1.22	0.479	0.48	0.090	0.48	0.090
Tree plot	–	–	–	–	–	–	–	–
Tree surroundings	−0.02	0.005 ***	−0.02	0.007 *	–	–	–	–
DBH			–	–			–	–

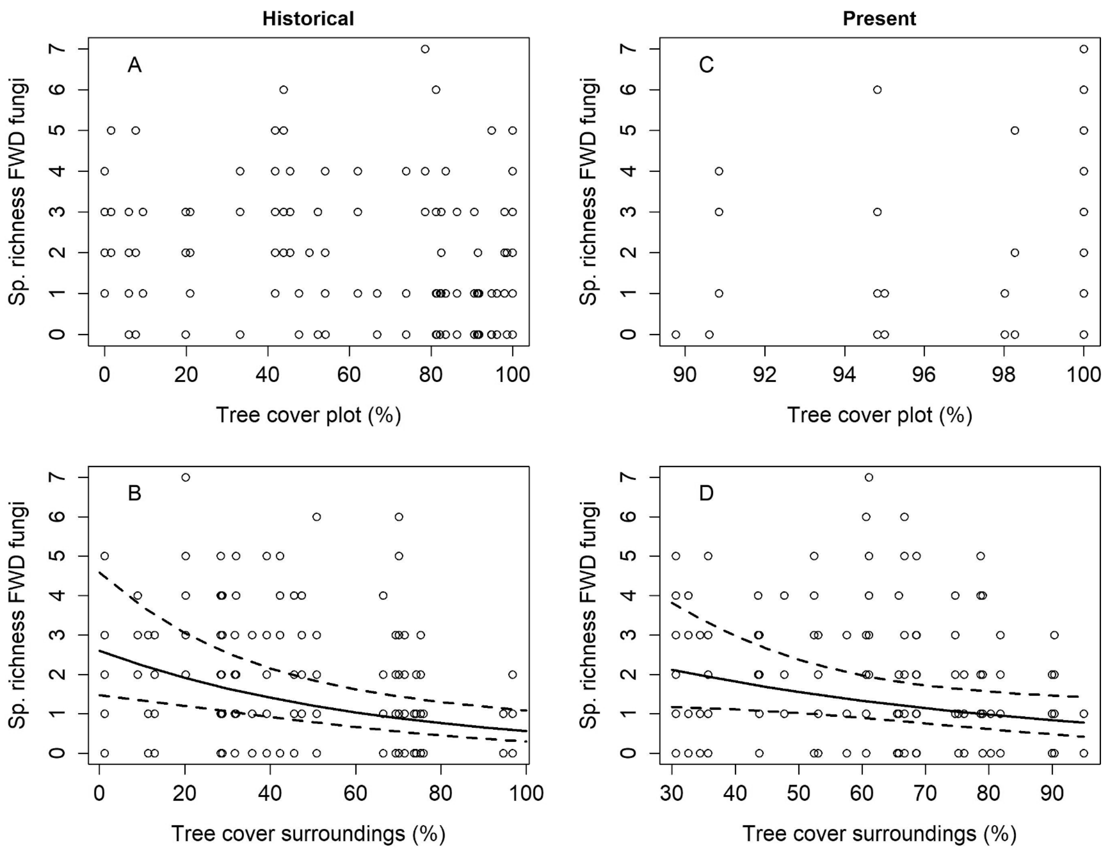

Fig. 5. Species richness of FWD fungi in the recent forest sites in relation to tree cover (%) in the plots (A, C) and in the surroundings (B, D) historically (1960; A, B) and at present (2017; C, D). Solid lines represent the fitted values from the model in Table 4. Dashed lines denote 95% confidence intervals, C.I. (1.96 × SE). Only significant relationships are shown. Note that some of the data points in the figure overlap.

Table 5
Parameter estimates (Coef) and standard errors (SE) for fixed effects of mixed-effects models for the relationship between species richness of FWD and CWD fungi and the volume (m^3) of fine woody debris (FWD) and coarse woody debris (CWD). p-values are indicated by asterisks (*p < 0.05, **p < 0.01, ***p < 0.001). Non-significant variables (–) were excluded during model selection.

	FWD fungi		CWD fungi	
	Coef	SE	Coef	SE
Intercept	0.003	0.158	0.22	0.103
FWD volume	0.81	0.173 ***	0.78	0.165 ***
Intercept	0.25	0.208	0.29	0.097
CWD volume	–	–	0.07	0.014 ***

higher in Nordén et al. (2004), especially FWD (12.0 m^3 CWD and 11.2 m^3 FWD per ha, compared to our 9.8 m^3 CWD and 4.6 m^3 FWD per ha), and this may explain the difference between the two studies. Forest structure at the present sites has developed to the level that they now hold as much CWD as the average in production forests (Tomter et al., 2010; Fridman and Wulff, 2018). The amount of dead wood will probably increase rather rapidly due to fast growth and self-thinning, and many fungi can probably track the increase in dead wood, at least generalist species (Komonen and Müller, 2018).

Colonization of wood-decaying fungi will probably continue for a long time, and there are indications that some species colonize mainly after a certain threshold of CWD volume has been reached (Nordén et al., 2018). Wood-decaying fungi generally produce a high amount of spores with the possibility to travel long distances (Komonen and Müller, 2018), and the surroundings may not be decisive for site species richness. However, despite their high dispersal capacities, legacies have previously been observed for wood-decaying fungi. Paltto et al. (2006) found that the amount of old-growth forest within 1 km radius 120 years ago better explained the occurrence of fungal Red List species than the current amount of old-growth forest. While Paltto et al. (2006) studied red-listed species in older forests, we mainly found generalist species, which may be less dependent on spatiotemporal connectivity than red-listed species and (WKH) Indicator species (Nordén et al., 2018).

The negative association between the most temperate deciduous trees and tree cover indicate that stands with a higher proportion of temperate deciduous trees may be younger and/or grow more slowly than sites with a high proportion of spruce. That average DBH was not correlated with species richness or species composition of plants or fungi, may be because DBH is a function of several factors in addition to site age, including site index, competition and local climate. However, certain CWD fungi species, mainly basidiomycetes, seemed to occur mainly in stands with higher average DBH as was expected.

4.2. *Biodiversity in relation to tree cover and land use history*

Our studies of aerial photos highlight the increase in tree cover that has occurred in S Scandinavia during the last century (Eriksson, 1991; Granhus et al., 2012; Bryn et al., 2013). Tree cover had increased considerably while open areas had decreased accordingly. However, species richness of forest plants did not increase as expected with forest cover. Instead, the recent forests with the highest total species richness occurred in surroundings with lower tree cover, dominated by agriculture. The reason may be the correlation between richer soils, agriculture and certain tree species; areas with rich soils have been extensively cleared and cultivated, and therefore currently have lower tree cover and more fragmented forests. Areas with higher forest cover obviously had fewer grassland plants, but also fewer rich soil trees such as for instance *Fraxinus* and *Ulmus,* and fewer of their associated fungal

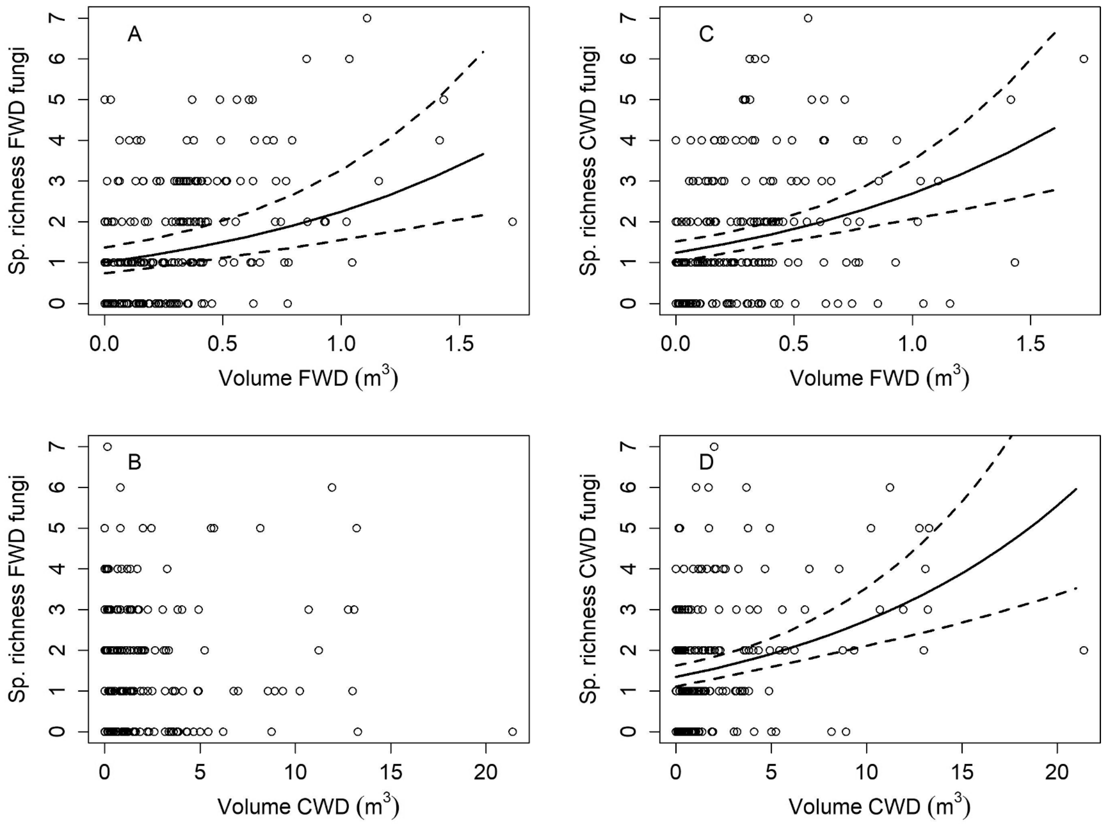

Fig. 6. Species richness of FWD fungi (A, B) and CWD fungi (C, D) in the recent forest plots in relation to FWD volume (m^3/ha (A, C) and CWD volume (m^3/ ha) (B, D). Solid lines represent the fitted values from the model in Table 5. Dashed lines denote 95% confidence intervals (1.96 × SE). Only significant relationships are shown. Note that some of the data points in the figure overlap.

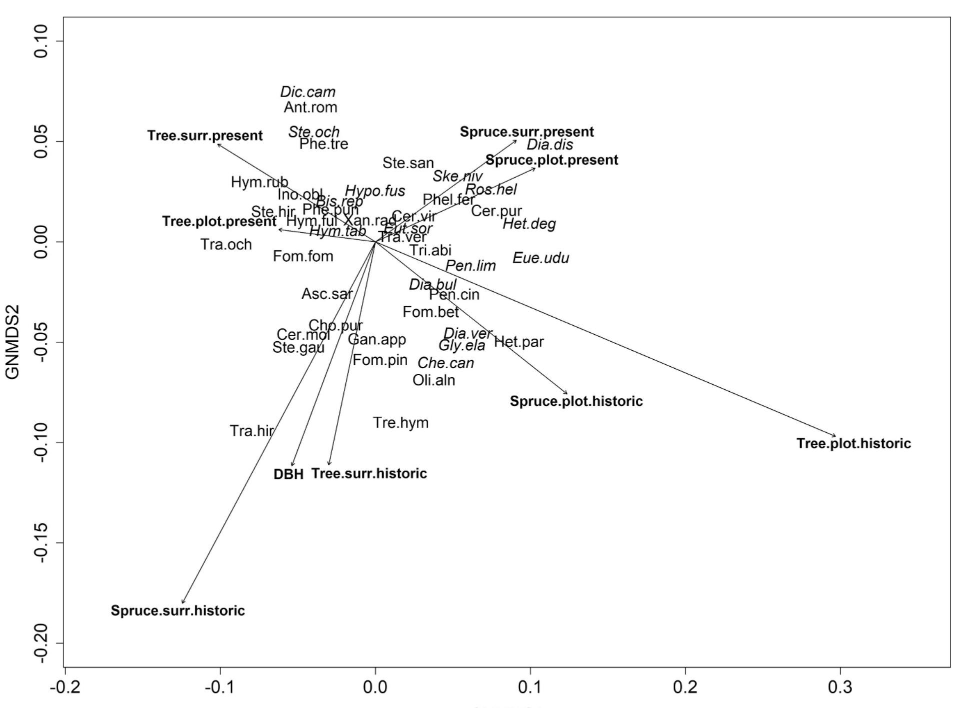

Fig. 7. GNMDS ordination of dead-wood fungi species composition in the recent forest study sites. FWD fungi are shown in italics and CWD fungi in regular font. Generalist fungi are not shown. Arrows indicate the correlation between the ordination and tree cover (%) and spruce cover (%) in the plots and in the surroundings historically (1960) and at present (2017), as well as DBH, with the length of the arrows proportional to the correlation strength. For species abbreviations, see App. D. Only the most common species are shown, and the position of some species names were slightly adjusted to avoid overlap.

species. The lack of correlation between species richness of forest plants and CWD fungi with forest cover may be an effect of the relatively short time for colonization (Hermy and Verheyen, 2007; Jogiste et al., 2018), and microhabitat (CWD) formation, respectively.

Spruce cover may also affect biodiversity in the recent forests. The increase in spruce cover over time indicates that there is a high seed pressure from adjacent areas and that spruce is competitive in the overgrowth phase. Without intervention, the forest may become dominated by spruce as it colonizes and competes with TDF species (Swedish environmental protection agency, 2013; Lindbladh et al., 2014). The often dense and dark conditions and the acidic litter layer in forests dominated by spruce may disfavour many TDF plants (Verstraeten et al., 2013), and other biodiversity. Due to the development of modern forestry, the current forest landscape in southern Scandinavia is dominated by Norway spruce, while TDF occur only as small fragments that may become invaded by spruce. However, the risk of sprucification has been questioned, at least for mature deciduous forests where the proportion of spruce seems to be relatively stable over time in closed stands (Hedwall and Mikusiński, 2016). The fragments of TDF are very important considering their potential to maintain species and an ecosystem adapted to the future climate, which is expected to greatly disfavor spruce during this century (Löf et al., 2012). Also for this reason, restoration of TDF is urgently needed.

The lower species richness of grassland plants with higher tree cover in the surroundings was expected. Moreover, species composition of vascular plants was significantly correlated with both tree cover and spruce cover. The significant correlation between species composition of vascular plants and spruce cover indicate that spruce often co-occur with grassland plants such as *Deschampsia cespitosa, Veronica chamaedrys* and *Vicia sepium* (Fig. 4). Species composition of trees was uncorrelated with plot tree cover, but significantly correlated with spruce cover and apparently related to soil type, with trees on rich soil in the left of the figure and trees on poorer soil to the right (Fig. 2), and there was thus more *Ulmus glabra* and *Fraxinus excelsior* where there was more spruce. A possible explanation for these patterns is that spruce is faster to expand on open (agricultural) areas than inside forests, and that it therefore tends to be associated with grassland plants and trees requiring the richer soils of these areas.

Also for wood fungi and their microhabitats a positive effect of (especially historical) tree cover would be expected, but the volume of FWD was not correlated with tree cover, and for FWD fungi, species richness was lower in sites with a higher tree cover in the surroundings. The reason for the latter may be the tendency of temperate deciduous trees such as *Fraxinus excelsior* and *Ulmus glabra* to be negatively correlated with high tree cover. These trees support many species of FWD fungi (Nordén et al., 2004), and in our recent forests the fungal community was rich in species on branches and other FWD mainly from deciduous trees (App. D). Deciduous trees produce more FWD per basal area than spruce, and FWD from deciduous trees harbor different and more species rich communities than spruce FWD (Nordén et al., 2004). Several fungal species typical of *F. excelsior* and *U. glabra* branches, such as *Ceriporia purpurea, Heterochaetella deglubens* and *Skeletocutis nivea*, were associated with spruce cover in the plot 2017, since higher spruce cover co-occurred with these trees.

4.3. Can this kind of forest be used for TDF restoration?

It is possible that recent forests could be used to increase area and connectivity of TDF in line with the Nagoya commitments to restore 15% of degraded ecosystems. The mix of forest species and grassland species of vascular plants opens the question of how to define the goal of restoration in this forest type. While grassland plants should not be main priority for forest restoration, it is possible that some of them may persist under semi-open canopies. We suggest that the target for restoration could be to improve conditions for forest plants, with species richness slowly increasing as a result of colonization, while maintaining some of the open area species by creating a semi-open canopy woodland. The flora in restored forests will vary with soil richness, which seems to explain most of the variation in vascular plant species composition. Similarly, the funga will vary with tree species composition, which also vary with soil richness. When possible, sites with legacies from earlier TDF, or adjacent to ancient TDF, should be prioritized for restoration to enable future colonization of forest species.

Regardless of the risk for sprucification, extraction of spruce may be a useful and economically feasible (Nordén et al., 2019) management option to enable restoration of temperate deciduous woodland. Such ‘restoration cutting’ may create a semi-open canopy that may for instance allow the regeneration of oak (Götmark, 2007), and may be beneficial for biodiversity and ecosystem services associated with semi-open canopy, such as insects and pollination (Proctor et al., 2012; Sebek et al., 2015). Recurrent extraction of spruce may be needed since this tree species may be quick to regenerate in the created gaps (Leonardsson, 2015).

5. Conclusions

The recent forests, as expected, seem to be of moderate importance for biodiversity of forest plants and wood-decaying fungi at present, but they may be an asset for restoration of for instance TDF. Our study indicates that the most biodiversity rich recent forests in this respect occur in surroundings currently dominated by agriculture and with lower tree cover. The increase in spruce over time and the apparent competition with other tree species, plants and fungi on richer soils may have negative effects on biodiversity. It is possible that reforestation on abandoned agricultural land may offer a realistic opportunity for the restoration of TDF, but active restoration and management may be required.

CRediT authorship contribution statement

Björn Nordén: Conceptualization, Data curation, Funding acquisition, Investigation, Writing - original draft. **Siri Lie Olsen:** Formal analysis, Methodology, Project administration, Writing - review & editing. **Solveig Haug:** Formal analysis, Visualization. **Graciela Rusch:** Funding acquisition, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Geographic, ownership and protection data for the sites.

Number	Site	County	Municipality	Owner type	Protection form[xx]
	Norway				
1.	Jomfruland	Telemark	Kragerø	Private, state	NP
2.	Kleiva	Vestfold	Re	Private	–
3.	Kåpe	Vestfold	Re	Private	–
4.	Sand	Vestfold	Sandefjord	Private	–
5.	Berg	Vestfold	Tønsberg	State	–
6.	Karljohansvern	Vestfold	Horten	State	PWPA
7.	Grønliparken	Østfold	Moss	Private	LPA, NR
8.	Alby	Østfold	Moss	State	LPA
9.	Kolås	Akershus	Vestby	Private	NR
10.	Svartskog	Akershus	Oppegård	Private	LPA
11.	Tasken	Østfold	Råde	Private	Partly NR
12.	Bjanes	Akershus	Fet	Municipality	–
13.	Omberg	Akershus	Enebakk	Private	–
14.	Håkås	Østfold	Trøgstad	Private	–
	Sweden				
15.	Tvärsjönäs	Västergötland	Lerum	Private	Partly WKH
16.	Bosnäs	Västergötland	Borås	Municipality	–
17.	Remmene	Västergötland	Herrljunga	State	SNUS
18.	Aplared	Västergötland	Borås	Municipality	–
19.	Stöpen	Västergötland	Skövde	Municipality	Partly WKH
20.	Bokhultet	Kronoberg	Vaxjo	Municipality	NR, Natura 2000
21.	Karshult	Östergötland	Motala	Municipality	–
22.	Aspenäs	Västergötland	Lerum	Private	WKH, planned NR
23.	Slaka	Östergötland	Linköping	Municipality	–
24.	Hovetorp	Östergötland	Linköping	Private	-?
25.	Kvarntorp	Östergötland	Åtvidaberg	Private	Partly WKH
26.	Klockaretorpet	Östergötland	Norrköping	Municipality	–
27.	Tullgarn	Stockholm	Södertälje	State	–

[x]UTM 32. [xx]LPA = Landscape protection area, NR = Nature reserve, NP = National park, PWPA = Plant and wildlife protection area, WKH = Woodland key habitat, SNUS = Protection-worthy state owned forest.

Appendix B. Examples of historical and recent aerial photographs with digitized polygons. a. The site Svartskog in 1960, showing fields and pasture in about half of the plot area. b. The same site in 2017 showing nearly total tree cover.

a.

b.

Appendix C. Data and classification of the non-woody plant species. Species were classified as either forest species, grassland species or ruderal species following Götmark et al. (2005), Hermy et al. (1999) for ancient forest species and the Swedish woodland key habitat survey guide for indicator species (Skogsstyrelsen, 2014). Ellenberg indicator values for light influx, nutrient availability and pH were gathered from Ellenberg et al. (1992), complemented by values from Hill et al. (1999) for species lacking in the first list (11 species).

Species	Author	Abbreviation	Sites	Land type	Indicator species*	Ellenberg light	Ellenberg nutrient	Ellenberg pH
Achillea millefolium	L.	Ach.mil	1	Grassland		7	4	6
Actaea spicata	L.	Act.spi	4	Forest	A, S	3	6	8
Adoxa moschatellina	L.	Ado.mos	1	Forest	A, S	4	5	6
Aegopodium podagraria	L.	Aeg.pod	2	Open		6	7	6
Agrostis capillaris	L.	Agr.cap	8	Grassland		6	4	4
Ajuga pyramidalis	L.	Aju.pyr	1	Open		7	2	5
Alchemilla sp.		Alc.sp.	2	Open		NA	NA	NA
Anemone nemorosa	L.	Ane.nem	24	Forest	A	5	4	5
Angelica sylvestris	L.	Ang.syl	3	Open		7	5	6
Anthoxanthum odoratum	L.	Ant.odo	8	Grassland		7	3	4
Anthriscus sylvestris	(L.) Hoffm.	Ant.syl	9	Grassland		6	7	7
Athyrium filix-femina	(L.) Roth	Ath.fil	11	Forest	A	5	6	5
Avenella flexuosa	(L.) Drejer	Ave.fle	21	Open		6	3	2
Avenula pubescens	(Huds.) Dumort	Ave.pub	1	Open		7	3	7
Calamagrostis arundinacea	(L.) Roth	Cal.aru	9	Forest		3	6	7
C. canescens	(F.H. Wigg.) Roth	Cal.can	1	Open		7	5	7
C. phragmitoides	Hartm.	Cal.phr	2	Forest		8	2	3
Callitriche cophocarpa	Sendtn.	Cal.cop	1	Open		7	4	5
Calluna vulgaris	(L.) Hull	Cal.vul	1	Forest		6	4	5
Caltha palustris	L.	Cal.pal	2	Open		7	3	6
Campanula cervicaria	L.	Cam.cer	1	Open		7	2	3
C. rotundifolia	L.	Cam.rot	2	Open		4	6	6
Cardamine amara	L.	Car.ama	3	Forest		7	2	5
C. bulbifera	(L.) Crantz	Car.bul	1	Forest	S	4	5	6
Carex digitata	L.	Car.dig	16	Forest	A	6	5	4
C. echinata	Murray	Car.ech	2	Open		8	5	8
C. leporina	L.	Car.lep	1	Grassland		7	2	2
C. pallescens	L.	Car.pal	6	Grassland	A	7	4	6
C. pilulifera	L.	Car.pil	4	Forest		6	4	8
C. remota	L.	Car.rem	1	Forest	S	6	6	7
C. sylvatica	Huds.	Car.syl	1	Forest		5	4	8
Cerastium fontanum	Baumg.	Cer.fon	3	Grassland		7	4	5
Chamaenerion angustifolium	(L.) Holub	Cha.ang	1	Ruderal		6	5	6
Chelidonium majus	L.	Che.maj	1	Ruderal		6	7	8

(continued on next page)

(*continued*)

Species	Author	Abbreviation	Sites	Land type	Indicator species*	Ellenberg light	Ellenberg nutrient	Ellenberg pH
Chrysosplenium alternifolium	L.	Chr.alt	4	Forest	A, S	5	6	6
Cirsium palustre	(L.) Scop.	Cir.pal	1	Ruderal		7	4	5
Convallaria majalis	L.	Con.maj	19	Forest	A	5	5	6
Crepis paludosa	(L.) Moench	Cre.pal	1	Forest	S	6	4	6
Cystopteris fragilis	(L.) Bernh	Cys.fra	2	Open		6	4	8
Dactylis glomerata	L.	Dac.glo	14	Grassland		5	5	5
Dactylorhiza maculata ssp. *fuchsii*	(Druce) Hyl.	Dac.mac	1	Forest	A, S	7	6	7
Deschampsia cespitosa	(L.) P.Beauv	Des.ces	17	Grassland		7	3	7
Dryopteris expansa	(C.Presl) Fraser-Jenk. and Jermy	Dry.exp	13	Forest		6	4	5
D. filix-mas	(L.) Schott	Dry.fil	21	Forest	A	7	2	3
Elymus caninus	(L.) L.	Ely.can	1	Forest	A, S	7	4	5
Elytrigia repens	(L.) Nevski	Ely.rep	2	Ruderal		5	5	5
Epilobium montanum	L.	Epi.mon	5	Ruderal	A	7	8	7
Equisetum arvense	L.	Equ.arv	3	Ruderal		7	7	7
E. pratense	Ehrh	Equ.pra	7	Forest		6	6	6
E. sylvaticum	L.	Equ.syl	6	Forest	A	7	6	6
Festuca ovina	L.	Fes.ovi	5	Open		8	5	6
F. rubra	L.	Fes.rub	3	Grassland		7	2	4
Ficaria verna	Huds.	Fic.ver	6	Forest		6	6	6
Filipendula ulmaria	(L.) Maxim	Fil.ulm	11	Open		7	5	6
Fragaria vesca	L.	Fra.ves	22	Open		6	4	6
Galeopsis sp.		Gal.sp.	4	Ruderal		6	8	7
Galium album	Mill.	Gal.alb	1	Open		7	3	7
G. aparine	L.	Gal.apa	4	Forest		6	6	5
G. boreale	L.	Gal.bor	2	Grassland		7	4	5
G. elongatum	C. Presl	Gal.elo	1	Open		6	5	6
G. palustre	L.	Gal.pal	1	Open		4	7	7
Geranium robertianum	L.	Ger.rob	6	Grassland		7	6	6
G. sylvaticum	L.	Ger.syl	7	Open		7	4	7
Geum rivale	L.	Geu.riv	9	Open	A	5	6	6
G. urbanum	L.	Geu.urb	21	Open		6	4	6
Glechoma hederacea	L.	Gle.hed	8	Open		6	7	7
Glyceria fluitans	(L.) R.Br.	Gly.flu	1	Open		7	6	6
Gymnocarpium dryopteris	(L.) Newman	Gym.dry	12	Forest	A	4	4	4
Hepatica nobilis	Schreb.	Hep.nob	11	Forest	A, S	6	2	4
Hieracium sect. *Hieracium*		Hie.Hie	11	Forest		4	5	7
H. umbellatum	L.	Hie.umb	1	Open		4	4	5
Hylotelephium maximum	(L.) Holub	Hyl.max	4	Open		7	5	7
Hypericum maculatum	Cratz	Hyp.mac	6	Grassland		6	5	5
Impatiens noli-tangere	L.	Imp.nol	3	Forest	S	4	8	7
I. parviflora	DC.	Imp.par	1	Ruderal		4	6	7
Juncus effusus	L.	Jun.eff	4	Grassland		7	4	4
Knautia arvensis	(L.) Coult.	Kna.arv	2	Grassland		7	4	8
Lapsana communis	L.	Lap.com	1	Open		5	3	5
Lathyrus linifolius	(Reichard) Bässler	Lat.lin	19	Forest		8	3	4
Lilium martagon	L.	Lil.mar	1	Ruderal	A	7	5	7
Luzula multiflora	(Ehrh) Lej.	Luz.mul	2	Grassland		6	7	7
L. pilosa	(L.) Willd	Luz.pil	24	Forest	A	6	3	4
Lycopodium annotinum	L.	Lyc.ann	1	Forest		3	6	7
Lysimachia europaea	(L.) U.Manns and Anderb.	Lys.eur	8	Forest		7	3	3
L. thyrsiflora	L.	Lys.thy	1	Open		6	3	3
L. vulgaris	L.	Lys.vul	1	Open		5	3	3
Maianthemum bifolium	(L.) F.W.Schmidt	Mai.bif	12	Forest	A	4	2	2
Matteuccia struthiopteris	(L.) Tod.	Mat.str	1	Forest	S	3	3	3
Melampyrum pratense	L.	Mel.pra	6	Forest	A	5	7	7
M. sylvaticum	L.	Mel.syl	7	Forest		5	3	2
Melica nutans	L.	Mel.nut	9	Forest	A	4	3	7
Mentha arvensis	L.	Men.arv	1	Open		6	6	7
Milium effusum	L.	Mil.eff	7	Forest	A	4	5	6
Moehringia trinervia	(L.) Clairv.	Moe.tri	7	Forest		4	6	7
Molinia caerulea	(L.) Moench	Mol.cae	1	Open		7	2	3
Mycelis muralis	(L.) Dumort.	Myc.mur	11	Forest		4	5	7
Myosotis arvensis	(L.) Hill	Myo.arv	1	Ruderal		7	6	6
Orthilia secunda	(L.) House	Ort.sec	1	Forest		5	3	5
Oxalis acetosella	L.	Oxa.ace	23	Forest	A	4	4	4
Paris quadrifolia	L.	Par.qua	14	Forest	A, S	5	3	7
Phegopteris connectilis	(Michx.) Watt	Phe.con	7	Forest		7	6	7
Phleum pratense	L.	Phl.pra	3	Grassland		7	5	6
Pilosella officinarum	L.	Pil.off	1	Open		3	6	7
Plantago major	L.	Pla.maj	1	Ruderal		4	4	4
Platanthera bifolia	(L.) Rich.	Pla.bif	1	Grassland		8	6	7
Poa nemoralis	L.	Poa.nem	22	Forest	A	8	2	7
P. palustris	L.	Poa.pal	1	Open		7	7	6

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(continued)

Species	Author	Abbreviation	Sites	Land type	Indicator species*	Ellenberg light	Ellenberg nutrient	Ellenberg pH
P. pratensis	L.	Poa.pra	3	Grassland		6	2	6
Polygonatum multiflorum	(L.) All.	Pol.mul	2	Forest	A, S	4	5	6
P. odoratum	(Mill.) Druce	Pol.odo	2	Open		4	6	7
Polypodium vulgare	L.	Pol.vul	13	Open		5	3	4
Potentilla erecta	(L.) Raeusch.	Pot.ere	8	Open		7	2	3
Primula veris	L.	Pri.ver	2	Grassland		7	3	7
Prunella vulgaris	L.	Pru.vul	1	Grassland		7	4	6
Pteridium aquilinum	(L.) Kuhn	Pte.aqu	10	Open	A	6	3	3
Pyrola sp.		Pyr.sp.	1	Forest		NA	NA	NA
Ranunculus acris	L.	Ran.acr	10	Grassland		7	3	4
R. auricomus	L.	Ran.aur	13	Forest	A	6	5	6
R. repens	L.	Ran.rep	7	Ruderal		6	7	6
Rubus idaeus	L.	Rub.ida	24	Open		7	4	7
R. saxatilis	L.	Rub.sax	19	Forest		7	4	6
Rumex acetosa	L.	Rum.ace	2	Open		6	5	5
R. acetosella	L.	Rum.acet	2	Open		7	4	5
Sanicula europaea	L.	San.eur	1	Forest	A, S	4	2	2
Schedonorus giganteus	(L.) Holub	Sch.gig	1	Forest		7	7	6
Scrophularia nodosa	L.	Scr.nod	2	Forest	A	4	7	6
Scutellaria galericulata	L.	Scu.gal	1	Open		5	3	4
Silene dioica	(L.) Clairv	Sil.dio	3	Open		4	5	7
Solidago canadensis	L.	Sol.can	1	Ruderal		5	7	7
S. virgaurea	L.	Sol.vir	5	Open		5	6	7
Stachys sylvatica	L.	Sta.syl	4	Forest	A	7	5	6
Stellaria graminea	L.	Ste.gra	2	Grassland		5	7	6
S. longifolia	Muhl. Ex Wild.	Ste.lon	1	Open		8	6	6
S. media	(L.) Vill.	Ste.med	1	Ruderal		6	8	7
S. nemorum	L.	Ste.nem	3	Forest	A, S	7	4	5
Taraxacum sp.		Tar.sp.	10	Ruderal		7	6	7
Trifolium medium	L.	Tri.med	2	Forest		7	4	6
Tussilago farfara	L.	Tus.far	1	Open		7	6	6
Urtica dioica	L.	Urt.dio	10	Ruderal		6	8	7
Vaccinium myrtillus	L.	Vac.myr	22	Forest	A	6	5	6
V. vitis-idaea	L.	Vac.vit	12	Forest		6	4	4
Valeriana sambucifolia	Mikan f.	Val.sam	5	Forest		7	2	3
Veronica beccabunga	L.	Ver.bec	1	Open		6	4	5
V. chamaedrys	L.	Ver.cha	12	Grassland		7	5	6
V. officinalis	L.	Ver.off	7	Open		8	4	6
V. serpyllifolia	L.	Ver.ser	2	Ruderal		6	2	2
Vicia cracca	L.	Vic.cra	2	Grassland		6	2	2
V. sepium	L.	Vic.sep	10	Grassland		7	5	6
Viola mirabilis	L.	Vio.mir	2	Forest	S	7	6	6
V. palustris	L.	Vio.pal	2	Open	A	7	5	7
V. riviniana	Rchb.	Vio.riv	22	Forest		6	6	6
V. tricolor	L.	Vio.tri	2	Open		4	NA	8
Viscaria vulgaris	Bernh.	Vis.vul	1	Grassland		8	2	4

*A = Ancient forest species (Hermy et al., 1999), S = Indicator species (Skogsstyrelsen, 2014).

Appendix D. Occurrence and classification of the fungal species. Based on Nordén et al. (2004) and personal experience, fungal species were classified based as predominantly occurring on CWD (CWD fungi) or FWD (FWD fungi), or as generalists, and if specialized on dead wood from deciduous or coniferous trees.

Species	Author	Abbreviation	No of sites	CWD[1]	FWD[2]	Broadl[3]	Conif.[4]
Amyloporia sinuosa	(Fr.) Rajchenb., Gorjón and Pildain	Amy.sin	1	1			1
Amylostereum chailletii	(Pers.) Boidin	Amy.cha	1		1		1
A. laevigatum	(Fr.) Boidin	Amy.lae	1		1		1
Amylostereum sp.		Amy.sp.			1		1
Antella niemelaei	(Vampola and Vlasák) Miettinen	Ant.nie	1		1	1	
Antrodia serialis	(Fr.) Donk	Ant.ser	2	1			1
A. xantha	(Fr.) Ryvarden	Ant.xan	3	1			1
Antrodiella faginea	Vampola and Pouzar	Ant.fag	2	1	1	1	
A. romellii	(Donk) Niemelä	Ant.rom	4	1		1	
A. semisupina	(Berk. and M.A. Curtis) Ryvarden	Ant.sem	1	1		1	
A. serpula	(P. Karst.) Spirin and Niemelä	Antr.ser	1	1		1	
Antrodiella sp.		Ant.sp.	1			1	
Ascocoryne sarcoides	(Jacq.) J.W. Groves and D.E. Wilson	Asc.sar	8	1		1	
Auricularia auricula-judae	(Bull.) J. Schröt.	Aur.aur	4		1	1	
Bertia moriformis	(Tode) De Not.	Ber.mor	10	1	1	1	1
Biscogniauxia cinereolilacina	(J.H. Mill.) Pouzar	Bis.cin	1	1		1	
B. marginata	(Fr.) Pouzar	Bis.mar	1	1		1	

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(*continued*)

Species	Author	Abbreviation	No of sites	CWD[1]	FWD[2]	Broadl[3]	Conif.[4]
B. repanda	(Fr.) Kuntze	Bis.rep	14		1	1	
Bisporella citrina	(Batsch) Korf and S.E. Carp.	Bis.cit	11	1	1	1	
Bjerkandera adusta	(Willd.) P. Karst.	Bje.adu	1	1		1	
Byssomerulius corium	(Pers.) Parmasto	Bys.cor	5	1	1	1	
Calocera furcata	(Fr.) Quél.	Cal.fur	3	1	1	1	
C. viscosa	(Pers.) Fr.	Cal.vis	7	1	1	1	
Camarops tubulina	(Alb. and Schwein.) Shear	Cam.tub	1	1			1
Capronia nigerrima	(R.R. Bloxam) M.E. Barr	Cap.nig	1		1	1	
C. sp.		Cap.sp.	1	1		1	1
Ceratostomella rostrata	(Fr.) Sacc.	Cer.ros	1	1		1	
Cerioporus leptocephalus	(Jacq.) Zmitr. and Kovalenko	Cer.lep	1	1		1	
C. mollis	(Sommerf.) Zmitr. and Kovalenko	Cer.mol	4	1		1	
C. varius	(Pers.) Zmitr. and Kovalenko	Cer.var	1	1		1	
Ceriporia purpurea	(Fr.) Donk	Cer.pur	4	1		1	
C. reticulata	(Hoffm.) Domanski	Cer.ret	4	1		1	
C. sp.		Cer.sp.	4			1	
C. viridans	(Berk. and Broome) Donk	Cer.vir	5	1		1	
Ceriporiopsis sp.		Ceri.sp.	1			1	1
Cheimonophyllum candidissimum	(Berk. and M.A. Curtis) Singer	Che.can	5		1	1	
Chlorencoelia versiformis	(Pers.) J.R. Dixon	Chl.ver	1		1	1	
Chlorociboria aeruginascens	(Nyl.) Kanouse ex C.S. Ramamurthi	Chl.aer	19	1	1	1	
Chondrostereum purpureum	(Pers.) Pouzar	Cho.pur	4	1		1	
Corticium roseum	Pers.	Cor.ros	1	1		1	
Crepidotus cesatii	(Rabenh.) Sacc.	Cre.ces	1		1		1
C. mollis	(Schaeff.) Staude	Cre.mol	1		1	1	
C. sp.		Cre.sp.	2			1	1
Cryptosphaeria sp.		Cry.sp.	1	1	1	1	
Daedalea quercina	(L.) Pers.	Dae.que	2	1		1	
Daedaleopsis confragosa	(Bolton) J. Schröt.	Dae.con	3	1	1	1	
Diatrype bullata	(Hoffm.) Fr.	Dia.bul	4		1	1	
D. decorticata	Rappaz	Dia.dec	1		1	1	
D. disciformis	(Hoffm.) Fr.	Dia.dis	1		1	1	
D. quercina	(Pers.) Berk. and Broome	Dia.que	1		1	1	
D. sp.		Dia.sp.	3			1	
D. stigma	(Hoffm.) Fr.	Dia.sti	3		1	1	
Diatrypella favacea	(Fr.) Ces. and De Not.	Dia.fav	1		1	1	
D. verruciformis	(Ehrh.) Nitschke	Dia.ver	9		1	1	
Dichomitus campestris	(Quél.) Domanski and Orlicz	Dic.cam	4		1	1	
Euepixylon udum	(Pers.) Füisting	Eue.udu	4		1	1	
Eutypa flavovirens	(Pers.) Tul. and C. Tul.	Eut.fla	5	1	1	1	
E. sp.		Eut.sp.	8			1	
E. sparsa	Romell	Eut.spa	1		1	1	
Eutypella cerviculata	(Fr.) Sacc.	Eut.cer	1		1	1	
E. sorbi	(Alb. and Schwein.) Sacc.	Eut.sor	10		1	1	
E. sp.		Euty.sp.	1			1	
E. stellulata	(Fr.) Sacc.	Eut.ste	2		1	1	
Exidia glandulosa	(Bull.) Fr.	Exi.gla	2		1	1	
Fomes fomentarius	(L.) Fr.	Fom.fom	14	1		1	
Fomitopsis betulina	(Bull.) B.K. Cui, M.L. Han and Y.C. Dai	Fom.bet	7	1		1	
F. pinicola	(Sw.) P. Karst.	Fom.pin	13	1			1
Ganoderma applanatum	(Pers.) Pat.	Gan.app	11	1		1	
Gelatoporia dichroa	(Fr.) Ginns	Gel.dic	1	1		1	
Gloeophyllum odoratum	(Wulfen) Imazeki	Glo.odo	3	1			1
Gloeoporus taxicola	(Pers.) Gilb. and Ryvarden	Glo.tax	1		1		1
Glyphium elatum	(Grev.) H. Zogg	Gly.ela	4		1	1	
Hapalopilus rutilans	(Pers.) Murrill	Hap.rut	1		1	1	
Heterobasidion parviporum	Niemelä and Korhonen	Het.par	5	1			1
Heteroradulum deglubens	(Berk. and Broome) Spirin and Malysheva	Het.deg	4		1	1	
Hydnocristella himantia	(Schwein.) R.H. Petersen	Hyd.him	1	1		1	
Hydnomerulius pinastri	(Fr.) Jarosch and Besl	Hyd.pin	1	1			1
Hymenochaete cinnamomea	(Pers.) Bres.	Hym.cin	2	1		1	
H. fuliginosa	(Pers.) Lév.	Hym.ful	5	1		1	1
H. rubiginosa	(Dicks.) Lév.	Hym.rub	13	1		1	
Hymenochaetopsis tabacina	(Sowerby) S.H. He and Jiao Yang	Hym.tab	8		1	1	
Hyphodontia quercina	(Pers.) J. Erikss.	Hyp.que	1	1	1	1	
Hypocreopsis riccioidea	(Bolton) P. Karst.	Hyp.ric	1		1	1	
Hypoxylon fragiforme	(Pers.) J. Kickx f.	Hyp.fra	3	1	1	1	
H. fuscoides	J. Fournier, P. Leroy, M. Stadler and Roy Anderson	Hyp.fus	1		1	1	
H. fuscum	(Pers.) Fr.	Hypo.fus	14		1	1	
H. julianii	L.E. Petrini	Hyp.jul	1	1	1	1	
H. petriniae	M. Stadler and J. Fourn.	Hyp.pet	2	1	1	1	
H. rubiginosum	(Pers.) Fr.	Hyp.rub	15	1	1	1	
H. sp.		Hyp.sp.	7			1	
H. subticinense	Y.M. Ju and J.D. Rogers	Hyp.sub	1	1		1	
H. vogesiacum	(Curr.) Sacc.	Hyp.vog	1	1		1	
Immotthia atrograna	(Cooke and Ellis) M.E. Barr	Imm.atr	1	1	1	1	

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Species	Author	Abbreviation	No of sites	CWD[1]	FWD[2]	Broadl[3]	Conif.[4]
Inonotus obliquus	(Ach. ex Pers.) Pilát	Ino.obl	4	1		1	
Ischnoderma benzoinum	(Wahlenb.) P. Karst.	Isc.ben	1	1			1
Jackrogersella multiformis	(Fr.) L. Wendt, Kuhnert and M. Stadler	Jac.mul	18	1	1	1	
Junghuhnia nitida	(Pers.) Ryvarden	Jun.nit	8	1	1	1	
Kretzschmaria deusta	(Hoffm.) P.M.D. Martin	Kre.deu	3	1		1	
Lasiosphaeria sp.		Las.sp.	1			1	1
Lasiosphaeris hirsuta	(Fr.) A.N. Mill. and Huhndorf	Las.hir	1	1	1	1	
Lenzites betulina	(L.) Fr.	Len.bet	2	1		1	
Lopadostoma turgidum	(Pers.) Traverso	Lop.tur	1		1	1	
Lophium mytilinum	(Pers.) Fr.	Lop.myt	2		1		1
Melanopsamma pomiformis	(Pers.) Sacc.	Mel.pom	1	1		1	
Moristroma quercinum	Nordén	Mor.que	1		1	1	
Mycoacia aurea	(Fr.) J. Erikss. and Ryvarden	Myc.aur	2	1	1	1	
M. fuscoatra	(Fr.) Donk	Myc.fus	2	1	1	1	
Nemania confluens	(Tode) Læssøe and Spooner	Nem.con	1		1	1	
N. serpens	(Pers.) Gray	Nem.ser	11	1	1	1	
N. sp.		Nem.sp.	16			1	
Neobarya parasitica	(Fuckel) Lowen	Neo.par	2	1	1	1	1
Oligoporus alni	(Niemelä and Vampola) Piatek	Oli.aln	5	1		1	
O. romellii	(M. Pieri and B. Rivoire) Niemelä	Oli.rom	1	1			1
Ostropa barbara	(Fr.) Nannf.	Ost.bar	2		1	1	
O. cubicularis	(Fr.) Fuckel	Ost.cub			1	1	
Oxyporus corticola	(Fr.) Ryvarden	Oxy.cor	1	1		1	
O. populinus	(Schumach.) Donk	Oxy.pop	2	1		1	
Panellus serotinus	(Pers.) Kühner	Pan.ser	1	1		1	1
P. stipticus	(Bull.) P. Karst.	Pan.sti	1	1		1	
Peniophora cinerea	(Pers.) Cooke	Pen.cin	8	1		1	
P. junipericola	J. Erikss.	Pen.jun	1		1		1
P. limitata	(Chaillet ex Fr.) Cooke	Pen.lim	15		1	1	
P. quercina	(Pers.) Cooke	Pen.que	2		1	1	
Phellinopsis conchata	(Pers.) Y.C. Dai	Phe.con	3	1		1	
Phellinus chrysoloma	(Fr.) Donk	Phe.chr	1	1			1
P. ferreus	(Pers.) Bourdot and Galzin	Phe.fer	1	1		1	
P. ferruginosus	(Schrad.) Pat.	Phel.fer	11	1		1	
P. laevigatus	(Fr.) Bourdot and Galzin	Phe.lae	1	1		1	
P. punctatus	(P. Karst.) Pilát	Phe.pun	8	1		1	
P. sp		Phe.sp.	1			1	
P. tremulae	(Bondartsev) Bondartsev and P.N. Borisov	Phe.tre	3	1		1	
P. viticola	(Schwein.) Donk	Phe.vit	1	1			1
Phlebia radiata	Fr.	Phl.rad	7	1	1	1	
P. rufa	(Pers.) M.P. Christ.	Phl.ruf	2	1	1	1	
P. tremellosa	(Schrad.) Nakasone and Burds.	Phl.tre	3	1		1	
Plicaturopsis crispa	(Pers.) D.A. Reid	Pli.cri	2		1	1	
Polycephalomyces sp		Pol.sp.	1	1		1	1
Polypore sp.		Poly.sp.	6			1	1
Postia alni	Niemelä and Vampola	Pos.aln	2	1	1	1	
P. caesia	(Schrad.) P. Karst.	Pos.cae	5	1	1		1
P. populi	Spirin and Miettinen	Pos. pop	1	1	1	1	
P. rufescens	Spirin and Miettinen	Pos.ruf	1	1			1
P. tephroleuca	(Fr.) Jülich	Pos.tep	1	1			1
P. undosa	(Peck) Jülich	Pos.und	3	1			1
Protocrea farinosa	(Berk. and Broome) Petch	Pro.far	3	1	1	1	
Quaternaria dissepta	(Fr.) Tul. and C. Tul.	Qua.dis	1		1	1	
Resupinatus applicatus	(Batsch) Gray	Res.app	1	1		1	
Rigidoporus sp.		Rig.sp.	1			1	1
Rosellinia helvetica	L.E. Petrini, Petrini and S.M. Francis	Ros.hel	3		1	1	
R. sp.		Ros.sp.	1			1	1
Rutstroemia firma	(Pers.) P. Karst.	Rut.fir	1		1	1	
Ruzenia spermoides	(Hoffm.) O. Hilber	Ruz.spe	1	1		1	
Scutellinia sp.		Scu.sp.	2	1		1	1
Scytinostroma portentosum	(Berk. and M.A. Curtis) Donk	Scy.por	2	1		1	
Sidera vulgaris	(Fr.) Miettinen	Sid.vul	2	1		1	
Sillia ferruginea	(Pers.) P. Karst.	Sil.fer	2		1	1	
Skeletocutis amorpha	(Fr.) Kotl. and Pouzar	Ske.amo	2	1			1
S. biguttulata	(Romell) Niemelä	Ske.big	3	1		1	1
S. carneogrisea	A. David	Ske.car	1	1			1
S. exilis	Miettinen and Niemelä	Ske.exi	1	1			1
S. nivea s. lat	(Jungh.) Jean Keller	Ske.niv	23		1	1	
Steccherinum fimbriatum	(Pers.) J. Erikss.	Ste.fim	15	1	1	1	
S. lacerum	(P. Karst.) Kotir. and Saaren.	Ste.lac	2		1	1	
S. ochraceum	(Pers. ex J.F. Gmel.) Gray	Ste.och	10		1	1	
Stereum gausapatum	(Fr.) Fr.	Ste.gau	6	1		1	
S. hirsutum	(Willd.) Pers.	Ste.hir	12	1		1	
S. rugosum	Pers.	Ste.rug	22	1	1	1	
S. sanguinolentum	(Alb. and Schwein.) Fr.	Ste.san	4	1			1
S. subtomentosum	Pouzar	Ste.sub	1	1	1	1	

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Species	Author	Abbreviation	No of sites	CWD[1]	FWD[2]	Broadl[3]	Conif.[4]
Tomentella crinalis	(Fr.) M.J. Larsen	Tom.cri	1	1		1	1
Trametes hirsuta	(Wulfen) Pilát	Tra.hir	3	1		1	
T. ochracea	(Pers.) Gilb. and Ryvarden	Tra.och	6	1		1	
T. pubescens	(Schumach.) Pilát	Tra.pub	2	1		1	
T. sp.		Tra.sp.	1			1	
T. versicolor	(L.) Lloyd	Tra.ver	4	1		1	
Trechispora candidissima	(Schwein.) Bondartsev and Singer	Tre.can	1	1			1
T. hymenocystis	(Berk. and Broome) K.H. Larss.	Tre.hym	3	1			1
T. mollusca	(Pers.) Liberta	Tre.mol	3	1			1
Trichaptum abietinum	(Pers. ex J.F. Gmel.) Ryvarden	Tri.abi	9	1			1
T. fuscoviolaceum	(Ehrenb.) Ryvarden	Tri.fus	1	1			1
Trichoderma piluliferum	J. Webster and Rifai	Tri.pil	1	1		1	
T. protopulvinatum	(Yoshim. Doi) Jaklitsch and Voglmayr	Tri.pro	1	1			1
T. pulvinatum	(Fuckel) Jaklitsch and Voglmayr	Tri.pul	1	1		1	
T. sp.		Tri.sp.	1			1	1
T. strictipile	Bissett	Tri.str	1		1	1	
Tyromyces lacteus	(Fr.) Murrill	Tyr.lac	1	1		1	
Vuilleminia comedens	(Nees) Maire	Vui.com	2		1	1	
V. coryli	Boidin, Lanq. and Gilles	Vui.cor	3		1	1	
Xanthoporia radiata	(Sowerby) Tura, Zmitr., Wasser, Raats and Nevo	Xan.rad	7	1		1	
Xylaria hypoxylon	(L.) Grev.	Xyl.hyp	13	1	1	1	
Xylodon paradoxus	(Schrad.) Chevall.	Xyl.par	7	1	1	1	
X. radula	(Fr.) Tura, Zmitr., Wasser and Spirin	Xyl.rad	8		1	1	
X. raduloides	Riebesehl and E. Langer	Xylo.rad	3		1	1	

[1]Classified as predominantly occuring on CWD (>10 cm). [2]Classified as predominantly occuring on FWD (1–10 cm). [3]Classified as predominantly occuring on wood of broadleaf trees. [4]Classified as predominantly occuring on wood of coniferous trees.

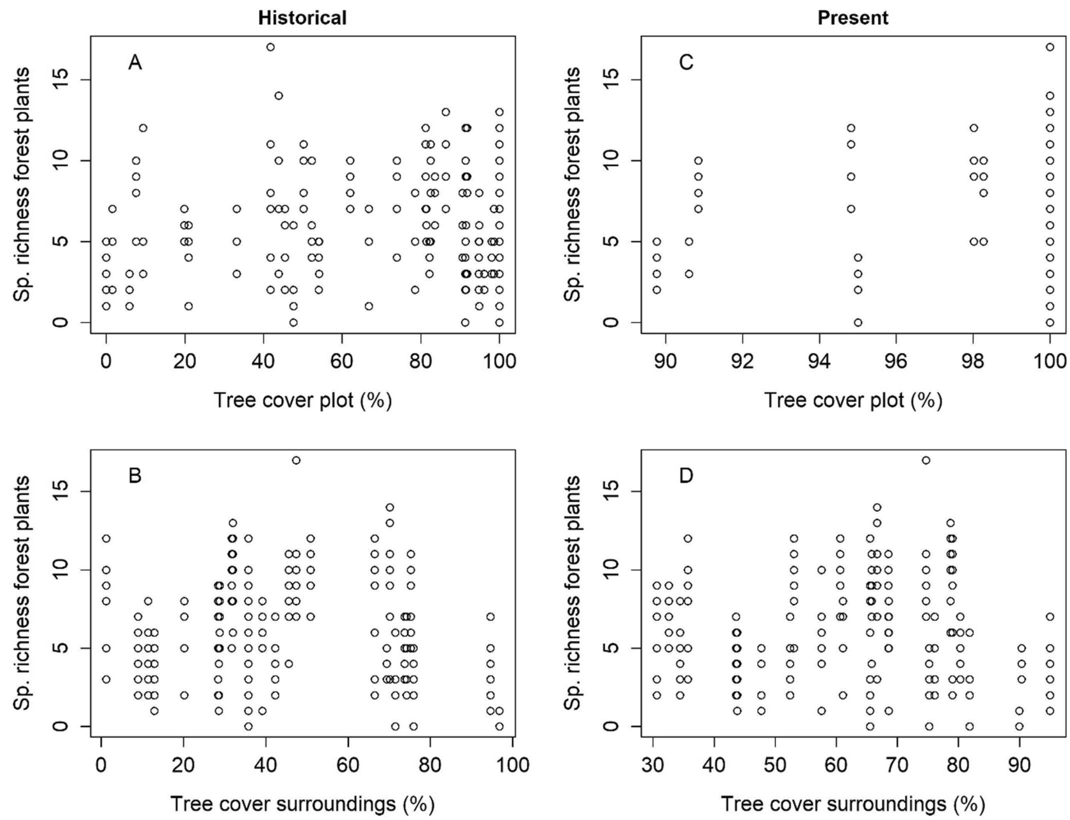
Appendix E. Data on land-use categories in % (mean+/-SD) in 1960 and 2017 at the sites and in the surroundings.

Scale	Year	Field	Forest	Pasture	Pasture w trees	Built	Spruce plantation	Water
Site	1960	3.30 ± 9.9	71.2 ± 29.7	18.1 ± 25.9	7.4 ± 12.4	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.1
Site	2017	0.0 ± 0.0	98.8 ± 2.3	0.3 ± 1.3	0.3 ± 1.3	0.1 ± 0.2	0.4 ± 1.6	0.0 ± 0.2
Surroundings	1960	20.5 ± 20.3	45.9 ± 25.9	19.2 ± 20.8	4.5 ± 8.2	3.5 ± 3.8	1.1 ± 3.7	5.2 ± 8.8
Surroundings	2017	17.6 ± 18.7	60.6 ± 16.1	6.8 ± 7.0	3.0 ± 4.9	4.6 ± 4.8	2.7 ± 6.4	4.7 ± 8.3

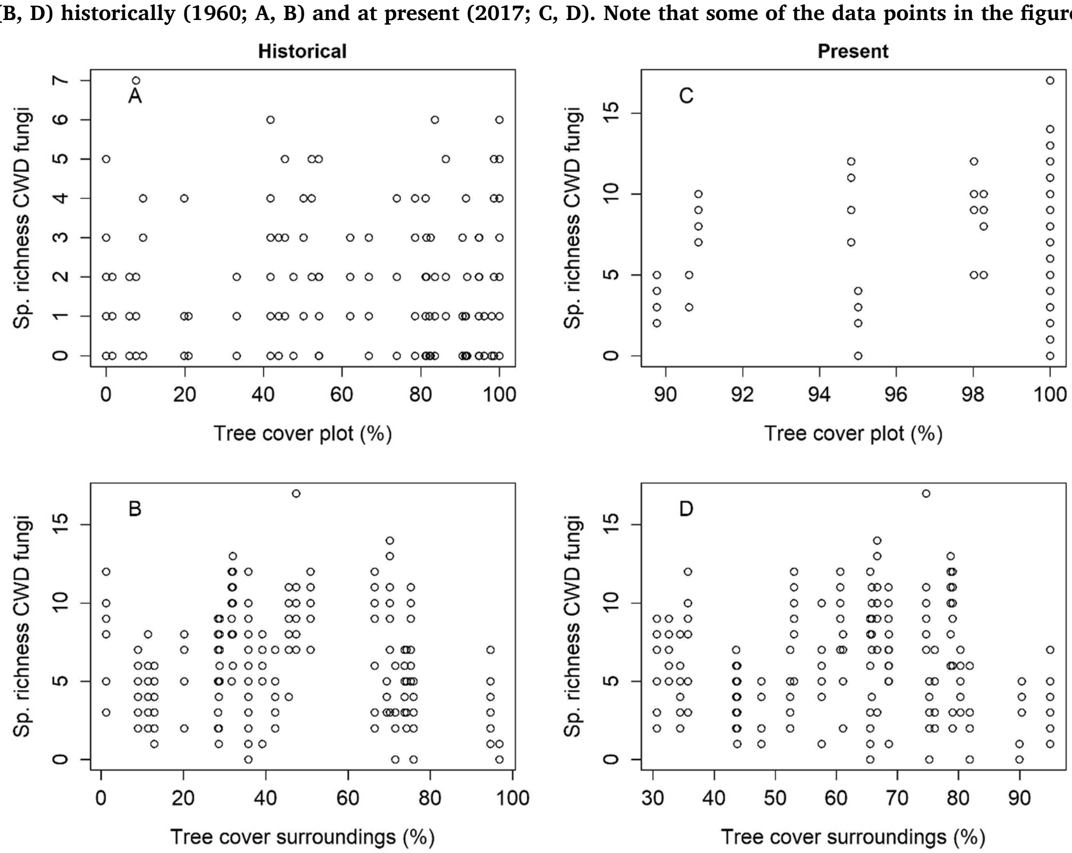
Appendix F. Names, authors and number of sites with occurrences of tree and shrubs species.

Species	Author	Abbreviation	No of sites
Acer sp.		Ace.sp.	17
Alnus sp.		Aln.so.	13
Betula sp.		Bet.sp.	27
Corylus avellana	L.	Cor.ave	21
Unknown deciduous tree		Dec.sp.	1
Fagus sylvatica	L.	Fag.syl	7
Frangula alnus	Mill.	Fra.aln	2
Fraxinus excelsior	L.	Fra.exc	19
Juniperus communis	L.	Jun.com	5
Malus sylvestris	(L.) Mill.	Mal.syl	2
Picea abies	(L.) H.Karst.	Pic.abi	23
Pinus sylvestris	L.	Pin.syl	17
Populus tremula	L.	Pop.tre	20
Prunus sp.		Pru.sp.	11
Quercus robur	L.	Que.rob	25
Salix caprea	L.	Sal.cap	13
Sambucus racemosa	L.	Sam.rac	1
Sorbus aucuparia	L.	Sor.auc	23
Tilia cordata	Mill.	Til.cor	8
Ulmus glabra	Huds.	Ulm.gla	8

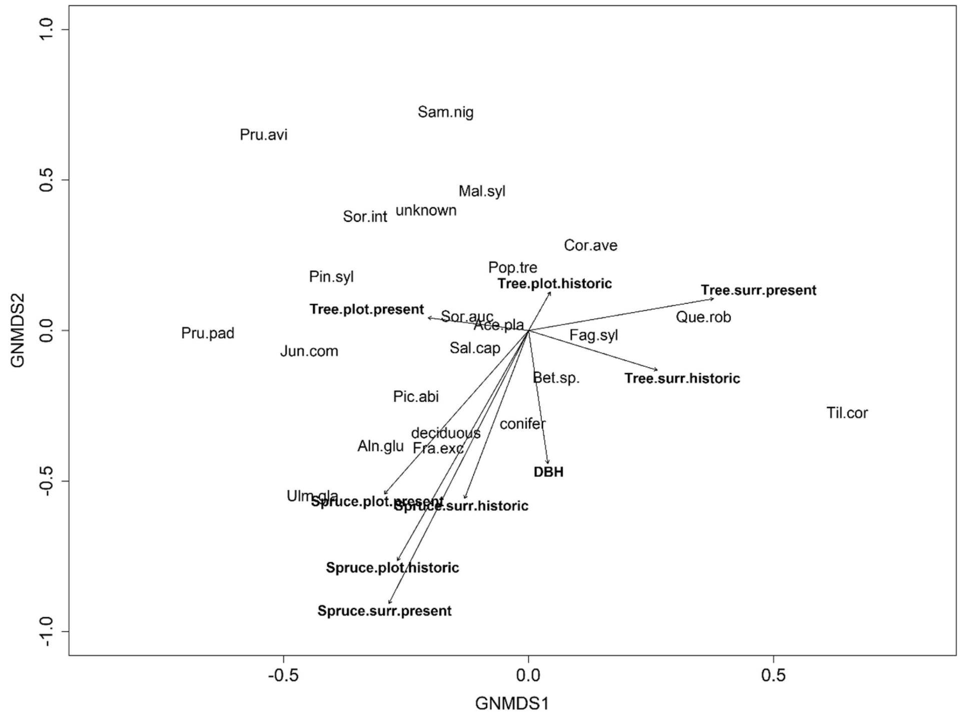
Appendix G. Species richness of forest plants in the recent forest sites in relation to tree cover (%) in the plots (A, C) and in the surroundings (B, D) historically (1960; A, B) and at present (2017; C, D). Note that some of the data points in the figure overlap.



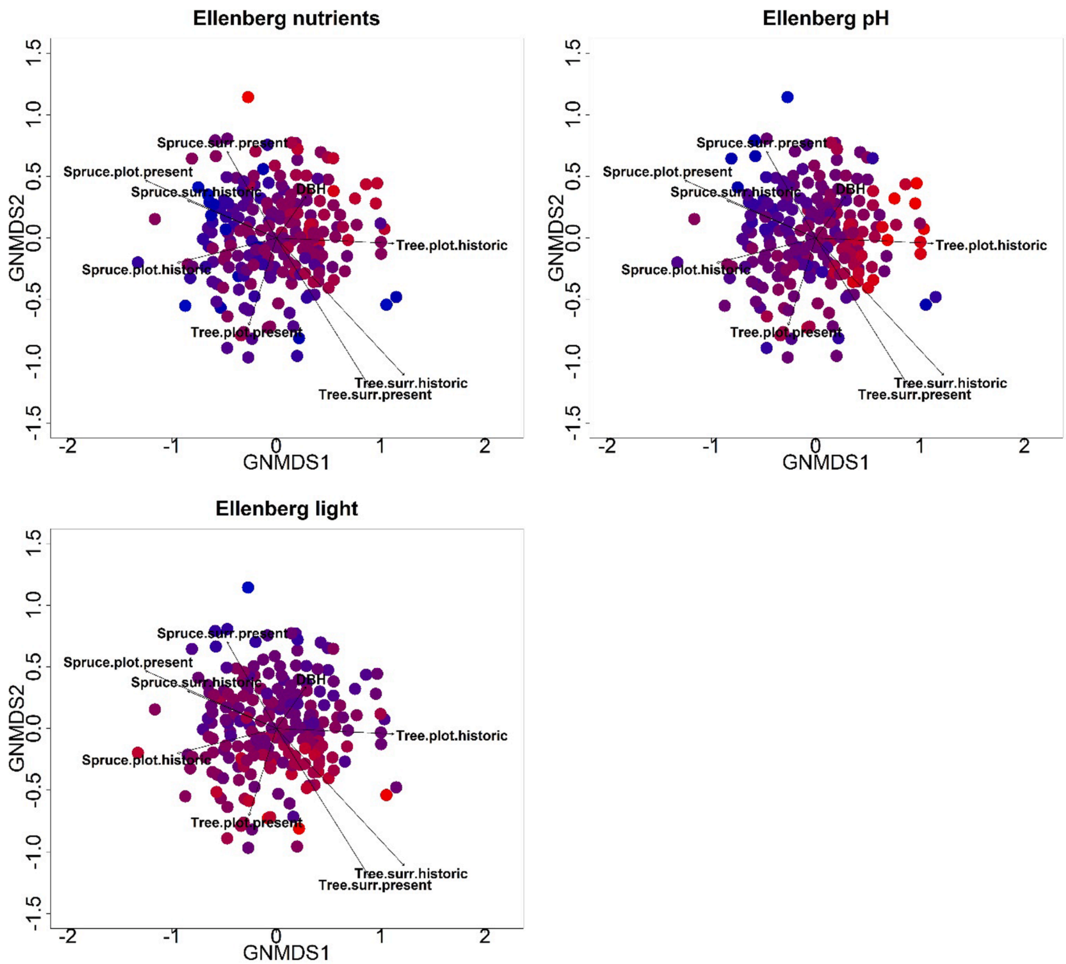
Appendix H. Species richness of fungi on CWD in the recent forest sites in relation to tree cover (%) in the plots (A, C) and in the surroundings (B, D) historically (1960; A, B) and at present (2017; C, D). Note that some of the data points in the figure overlap.



Appendix I. GNMDS ordination plot of dead wood tree species composition. Arrows indicate the correlation between the ordination and tree cover (%) and spruce cover (%) in the plots and in the surroundings historically (1960) and at present (2017), as well as DBH. The length of the arrows are proportional to the correlation strength. For species abbreviations, see App. F.



Appendix J. GNMDS ordination of field layer vascular plant species composition in the recent forest study sites showing mean Ellenberg indicator values for nutrients, pH and light, respectively. Each dot represents one transect section, and the dot color indicates the mean indicator value from low (red) to high (blue). Arrows indicate the correlation between the ordination and tree cover (%) in the plots and in the surroundings historically (1960) and at present (2017), as well as DBH, with the length of the arrows proportional to the correlation strength.



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