Master of Science Thesis

Predicting species richness of wood-inhabiting fungi, epiphytic bryophytes and lichens based on stand structure and indicator species

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ABSTRACT

Global biodiversity loss has become a significant concern in last few decades. Temperate broadleaved forests are one of the most anthropogenically disturbed biomes and especially old natural forests have become rare. It is widely acknowledged that in addition to global and landscape scale factors, disturbance history, forest management and ecological continuity affect structural diversity in a forest and hence, species richness. Many species groups are however, poorly studied and it is not completely understood which are the main factors affecting species richness in a forest stand and what finally causes the extinction of a population. I studied temperate broadleaved forests in Denmark and aim of my study was to investigate what are the different elements in forest stand structure affecting the species richness of wood-inhabiting fungi, epiphytic lichens and bryophytes. I also tested whether ancient forest plant species or local indicator species could be used as an indicator group for estimating the species richness of these three species groups. Or whether some of the elements in a forest stand structure could be used as a structural indicator for species richness in the area. The data was collected from a nature reserve called Lille Vildmose, in North Jutland, Denmark, during 2013-2014. I used Analysis of Covariance to analyse which of the factors in stand structure correlated with the species richness of epiphytic lichens, epiphytic bryophytes and wood-inhabiting fungi and Pearson correlation to test the correlation between the occurrence of my study species and potential indicators. Stand age, average water level and basal area of broadleaved trees were the most significant factors correlating with the species richness of epiphytic lichens. Species richness of living trees, basal area of broadleaved trees and stand age correlated significantly with the species richness of epiphytic bryophytes. And dead wood volume, number of dead wood tree species, stand age and average dead wood diameter correlated significantly with the species richness of woodinhabiting fungi. The results were consistent with several previous studies and showed that old forest stands and high volume of dead wood are essential factors in maintaining species richness in temperate broadleaved forests. The correlations between the occurrence of ancient forest plant species and my study species were not significant enough that ancient forest plant species could be used as indicator group for the study species. Also the correlations between the occurrence of local indicator species and my study species were too weak that local indicator species could be used as indicator group for the study species either.

Abbreviations

BA	Basal area
DBH	Diameter at breast height
SD	Standard deviation

JYVÄSKYLÄN YLIOPISTO, Matemaattis-luonnontieteellinen tiedekunta

Bio- ja ympäristötieteiden laitos Ekologia ja evoluutiobiologia

Väätäinen M.;	Lahottajasienten ja epifyyttisammalten ja –jäkälien lajirunsauden ennustaminen metsän rakennepiirteiden ja indikaattorilajien perusteella
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Hakusanat: lahopuu, lauhkeat lehtimetsät, isäntäpuu, metsien suojelu, metsälaikun ikä, mikroilmasto, pohjaveden korkeus, putkilokasvit indikaattoreina

TIIVISTELMÄ

Maailmanlaajuinen monimuotoisuuden vähentyminen on ollut suuri huolenaihe jo useiden vuosikymmenten ajan. Lauhkeat lehtimetsät ovat yksi eniten ihmisen vaikutuksesta kärsineistä biomeista ja eteenkin vanhat, luonnontilaiset metsät ovat vähentyneet huolestuttavasti. Ilmaston ja maisemallisten tekijöiden lisäksi metsän historia, häiriödynamiikka, metsätalous ja ekologinen jatkuvuus vaikuttavat metsän rakenteelliseen monimuotoisuuteen ja näin ollen myös lajirunsauteen. Monet lajiryhmät ovat kuitenkin huonosti tunnettuja ja vaikeasti havaittavissa, eikä lopullisia syitä lajin häviämiseen alueelta pystytä varmasti sanomaan. Tutkimukseni tarkoitus oli selvittää, mitkä elementit metsän rakenteessa vaikuttavat metsän lajirunsauteen ja olisiko joitakin metsän rakennepiirteitä mahdollista käyttää indikaattoreina ennustamaan alueen lajirunsautta. Lisäksi selvitin, olisiko ikimetsille tyypillisiä putkilokasvilajeja tai paikallisia indikaattorilajeja mahdollista käyttää indikaattori lajiryhmänä ennustamaan muiden lajien runsautta. Tutkimukseni kohteena olivat Tanskan lauhkeat lehtimetsät ja niiden lahottajasienet, epifyyttijäkälät ja sammalet. Aineisto on kerätty Lille Vildmosen luonnonsuojelualueelta, Pohjois-Jyllannista, vuosina 2013–2014. Tulosten analysoinnissa käytin kovarianssianalyysiä, selvittääkseni metsän rakenteessa vaikuttavat epifyyttijäkälien, mitkä tekijät -sammalten ia lahottajasienten lajirunsauteen ja Pearsonin korrelaatiota tutkiakseni potentiaalisten indikaattoreiden toimivuutta. Tärkeimmät epifyyttijäkälien lajirunsauteen vaikuttavat tekijät olivat pohjaveden pinta-ala ja metsälaikun ikä ja tärkeimmät epifyyttisammalten lajirunsauteen vaikuttavat tekijät olivat elävien puiden lajirunsaus, lehtipuiden pinta-ala ja metsälaikun ikä. Lahottajasienten lajirunsauteen vaikutti selkeästi eniten lahopuun määrä. Tulokset tukivat useita aikaisempia tutkimustuloksia, joissa on osoitettu, että vanhat metsät ja lahopuun määrä ovat avainasemassa metsien lajirunsauden turvaamisessa. Sekä korrelaatio ikimetsille tyypillisten putkilokasvien ja tutkittujen lajiryhmien välillä että paikallisten indikaattorilajien ja tutkittujen lajiryhmien välillä oli niin heikko, ettei niitä tämän tutkimuksen perusteella voida käyttää indikaattoriryhminä näiden lajiryhmien lajistolliselle runsaudelle tällä alueella. Yksittäisistä rakennepiirteistä lahopuun määrä korreloi kaikkein voimakkaimmin tutkimuslajien yhteenlasketun lajirunsauden kanssa.

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1. INTRODUCTION

Already twenty two years ago in Rio de Janeiro, The United Nations Convention on Biological Diversity was held (CBD 1993), and today 193 nations are parties of the convention and 168 have signed it (United Nations 2009). Despite this global battle and later actions, including the strategic plan in 2002 to halt the loss of biodiversity by 2010 (CBD 2002), the goals have not been reached (Butchart *et al.* 2010). International agendas and agreements are certainly needed to reach these goals but without understanding the ecological patterns determining diversity in ecosystems, efficient conservation of biological diversity would be inconceivable (Ehrlich 1996, Norton 1996). Biodiversity as a whole is a complex ensemble and factors affecting species richness and diversity varies in different scales.

1.1. Factors affecting species richness at global and landscape scale

Geographical variation in species diversity has long been one of the great interests in biological research and it is a well described fact that species richness is highest in the Tropics and reduces towards Poles (Wallace 1878). However, factors underlying this latitudinal gradient are still discussed (MacArthur 1965, Stevens 1989, Hawkins *et al.* 2003). Species richness varies also among the latitudes and on the contrary, in some species groups species richness increases toward Poles (MacArthur 1965, Valdovinos *et al.* 2003). According to species-energy theory and more individuals -hypothesis, local energy availability is the most important determinant behind local species richness (Wright 1983, Srivastava & Lawton, 1998, Hawkins *et al.* 2003). Topography, vegetation and distance to the ocean or other large water system cause local variation in climatic conditions as well and naturally, climate affects the soil and resource availability (Whittaker 1972).

Landscape scale factors on species richness have been widely acknowledged as well (Dunning et al. 1992, Bennett 1999, Hanski 1999, Henle et al. 2004, Jonsson et al. 2005). Heterogeneity in the landscape has been showed to increase the species richness in many species groups (Atauri & Lucio 2000). Nevertheless, fragmentation of the landscape and habitats is showed to be among the major factors creating global habitat and biodiversity loss (Tilman et al. 2001, Haila 2002, Helm et al. 2005, Cushman 2006, Krauss et al. 2010, see also Fahrig 2003). Fragmentation influences the spatial population dynamics, for example by creating dispersal barriers, thus especially hindering species with poor dispersal capacity or narrow ecological niche (Hanski 2005). It is also closely linked to area reduction which has major effect on species loss (MacArthur & Wilson 1967). Study of Nordén et al. 2013 showed that fragmented landscape decreases the number of red-listed species in the retaining habitat patches while some generalist species become more common. Also one of the reasons why habitat fragmentation is so harmful for a population is that it increases the edge effects in the ecosystem, hence changing the quality of the habitat (Lindenmayer & Fischer 2006). Still, it is not completely understood what eventually causes the extinction of a population (Hanski 2005).

1.2. Factors affecting species richness at stand scale

In general, the geographical history, bedrock, local climatic conditions and also more recent actions, like forest management have shaped and defined the stand quality which further affects the local species richness (Heilmann-Clausen *et al.* 2014). During the last centuries, human impact has critically decreased the number, size and quality of natural forests around the Globe and temperate broadleaved forests are among the most disturbed biomes in the world. Large areas in Central Europe would naturally, without human impact, be covered by forests, largely dominated by European beech (*Fagus sylvatica*). Due to rarity of unmanaged

and especially old temperate forests, the number of studies on natural dynamics and regeneration cycles of the temperate forests is scarce. Majority of the European forests in natural or near-natural state are located in northern parts of Europe, hence studies on boreal forest dynamics are more common (Kuuluvainen & Aakala 2011). According to studies on boreal forests and on few remnants of natural or near-natural temperate forests, quite similar forest dynamics and patterns occur in both boreal- and temperate forests.

Disturbances create succession cycles and typical forest dynamics for particular forest. In natural forests, disturbances like storms and wildfires cover the widest areas and for example wildfires can ravage thousands of hectares of forest (Conard & Ivanova 1997). In the other end, a death of a single mature tree covers relatively small area, still creating dead wood and diversity in light regimes and canopy cover, hence diversity in stand structure. Natural forest dynamics are commonly divided in three different types, according to the characteristics of the predominant disturbance-succession cycles in the forest: 1) disturbances creating stand-replacing dynamics 2) cohort dynamics, related to partial disturbances and 3) small scale disturbances, including the death of a single tree, or small tree groups, creating gap dynamics (Angelstam & Kuuluvainen 2004).

In natural forest, disturbances creating stand-replacing forest dynamics, hence affecting the whole forest stand, are typically forest fires, violent windstorms or wide-ranging insect outbreaks or fungal diseases (Kuuluvainen & Aakala 2011). In stand-replacing disturbances the tree mortality is comprehensive and forest succession starts over. In the beginning shade intolerant species and species with good dispersal ability colonize the area and gradually the forest goes through changes in species composition until it reaches the stable climax stage or next disturbance occurs (Shugart 1984). Partial disturbances, covering intermediate scales and creating cohort dynamics in a forest are caused for example by weaker windstorms, insect outbreaks or fungal diseases. Small scale disturbances, including single damaged trees, wind falls or other single tree or small tree group mortality create gab dynamics in a forest. Partial and small scale disturbances, creating cohort and gab dynamics, create a mosaic structure in a forest and terms mosaic-cycle or shifting mosaic, are also commonly used describing patchy tree age distribution and relatively small scale disturbance-succession regimes in a forest (Emborg 1998, Emborg *et al.* 2000).

Naturally, these different forest dynamics are not totally distinct and for example between two stand-replacing disturbances, different smaller scale disturbances can dominate. Also, predominant disturbance cycles can differ a lot, even between two relatively close forest stands. However, some forest dynamics are usually more common in particular forests than the others. In natural temperate forests, mosaic-cycle, including gap dynamics and medium scaled partial disturbances, is typically the predominating disturbance succession-cycle (von Oheimb *et al.* 2005, Emborg *et al.* 2000). Natural regeneration cycles in temperate forests develop very slowly (Emborg 1998, Emborg *et al.* 2000). For example European beech (*Fagus sylvatica*) can live up to 250-350 years, hence, after stand-replacing disturbances it can take hundreds of years when the forest reaches the mosaic structure with diverse tree age distribution and structure (von Oheimb *et al.* 2005). Today the most common disturbance in temperate broadleaved forest is forest management, especially logging. As a result of forest management, for example wildfires have been reduced and many other disturbances, including logging and introduced species have become common (Conard & Ivanova 1997).

The forest history including natural forest dynamics, succession and forest management, are crucial in determining species richness (Franklin 1988). Disturbances and ecological continuity create structural diversity, increasing the number and diversity of available niches, hence increasing the forest species richness (Franklin 1988, Fischer *et al.* 2013). Structural diversity in stand structure means for instance diversity in tree species, tree

size and age distribution, amount and type of dead wood, shrub layer and canopy closure. For example tree species composition affects species diversity in many forest dwelling species groups (Ódor et al. 2013). In temperate broadleaved mixed forest stands, presence of oak and pine has been shown to increase the species diversity in epiphytic bryophytes and lichens (Ódor et al. 2013, Király et al. 2013). Tree age distribution can also increase the species richness in a forest and many studies have shown that species richness is higher in old forest stands (Laiolo 2002, Jonsson et al. 2005, Moning & Müller 2009, Lõhmus & Lõhmus 2011). Old trees have both a wider surface and more diverse microhabitats for specialized forest species. Many microhabitats, like hollow trees, rot holes and tree cavities require a long period of time to be formed and they are essential habitats for many forestdwelling species (Fritz & Heilmann-Clausen 2010). Studies have illustrated that these structures are more abundant in natural forests than in managed forests (Remm & Lõhmus 2011). Furthermore, old unmanaged forests typically contain larger volume of dead wood which is considered as one of the major factors underlying higher species richness in old forests (Jonsson et al. 2005, Aakala et al. 2009). Also the term ecological continuity is often used when explaining the species richness in old forests (Fritz et al. 2008). Ecological continuity means that in a long time period, diverse microclimates and microhabitats can evolve and also many species with poor dispersal capacity have enough time for colonization.

Plenty of studies demonstrate dead wood's significance in determining species diversity in many forest dwelling species groups (Harmon *et al.* 1986, Siitonen 2001, Similä *et al.* 2003, Penttilä *et al.* 2004, Ódor *et al.* 2006, Raabe *et al.* 2010). Being an important component in nutrient cycling in forest, dead wood is a crucial factor in forest ecosystem functions (Harmon *et al.* 1986). It is also a habitat and nutrient for remarkable amount of species, including many fungal, invertebrate and bryophyte groups (Jonsell *et al.* 1998, Humphrey *et al.* 2002, Jonsson *et al.* 2005, Stokland *et al.* 2012). Not only the amount of dead wood, affect species richness in a forest but also the variation in dead wood quality (Stokland *et al.* 2012). When estimating the biodiversity values of a forest stand, the decay stage of dead wood and the amount of coarse wood debris (CWD), including logs and snags, can be used (Nordén *et al.* 2004). Furthermore, fine woody debris (FWD) and dead wood attached in living trees and roots can indicate the biodiversity values of a forest stand (Kruys & Jonsson 1999, Nordén *et al.* 2004, Bässler *et al.* 2010).

Light is also one of the important factors affecting species diversity in a forest, naturally due to its direct effect on autotrophs but also due to its effect on microclimates, hence niche quality (Jennings *et al.* 1999). Thus, canopy structure, affecting the light regimes in a forest, has clear impact on biodiversity in a forest (Ishii 2004). Especially lichen communities and fungi living on fine woody debris have been showed to be sensitive for light availability and its effects on microclimates (Bässler *et al.* 2010, Ódor *et al.* 2013). In old temperate broadleaved forests, canopy layer effectively reduces the amount of light in understory, thus openings in canopy have an effect on microclimates in a forest. When mature tree dies, formed gap is rapidly filled with saplings. Due to closed canopies, shrub layer in old temperate broadleaved forests is rather scarce.

1.3. Human impacts on species richness in forests

Certainly, humans have impacted biodiversity and many of the human actions can have impacts on long distances. Among many other human actions, the history of agriculture and forest management is very long (Wallenius *et al.* 2010). Since the implementation of agriculture in Europe, landscape fragmentation, habitat loss and impoverishment of ecosystems have increased (Harris 1996, Hoekstra *et al.* 2005, Wallenius 2010). Most of the forests in natural state today have been a pastureland in the past or part of the forest

management and hence, it is difficult to find a temperate forest stand without management history (Wallenius *et al.* 2010). Human impacts on woodlands have been significant (Dupouey *et al.* 2002, Wallenius 2010) and especially old forest stands in ecologically natural successional state have become rare (Franklin 1988).

The primary aim in modern forest management is to maximize the harvest. Measures for reaching this goal unfortunately reduce the structural diversity and especially dead wood volume, in the forest. Forest management impoverish the forest ecosystems by maintaining monocultures and reducing the structural diversity causing decline in availability of different niches for specialized forest species (Dettki & Esseen 1998, Halme et al. 2013). Studies indicate that for example slash removal and stump harvesting affect soil waters (Staaf & Olsson 1994). Many studies have shown that species richness is higher in unmanaged than in managed forests (Paillet et al. 2010). Managed forests are mainly monocultures with same aged trees. Especially the amount of veteran trees and dead wood is smaller in managed than in unmanaged forests. Hence, many forest-dwelling species are endangered or have already become extinct (Hanski 2005). In management forests, the succession cycle is short and old forest stands or even single veteran trees are rare. Especially increased slash removal and stump harvesting remarkably decreases the amount of dead wood in the forest causing decline especially in dead wood dependent species (Bouget et al. 2012). Clear-cuttings can cover large areas having major effects on functions of a forest ecosystem (Likens et al. 1978). Removal of a canopy cover exposes the understory to higher amounts of sunlight, hence affecting the microclimates and diversity of many species groups, including lichens, wood decaying fungi and bryophytes (Hedenås & Ericson 2003, Bässler et al. 2010, Ódor et al. 2013).

1.4. Study species

Wood-inhabiting fungi and epiphytes, including lichens and bryophytes are essential species groups in temperate broadleaved forest ecosystem (Esseen *et al.* 1997, Longton 1997, Boddy 2001, Ellis 2011). Epiphytic lichens and -bryophytes affect mineral cycling and water balance (Pike 1978, Turetsky 2003, Pypker *et al.* 2006a, 2006b) and wood-inhabiting fungi have an important role in nutrient cycling by decaying processes in terrestrial habitats (Boddy 2001, Stokland *et al.* 2012). These species groups have also a significant role in forest food-webs and influence the ecological succession of other forest-dwelling species (Henderson & Hackett 1986, Hayward & Rosentreter 1994, Petterson *et al.* 1995, Gunnarson *et al.* 2004, Flaherty *et al.* 2010, Stokland *et al.* 2012). As a result of forest management and decreasing number of old growth forests, many wood-inhabiting fungi, epiphytic lichen and bryophyte species have become endangered (Dettki & Esseen 1998, Jonsson *et al.* 2005, Paillet *et al.* 2010). Compared to many other species groups, epiphytic lichens and bryophytes and wood-inhabiting fungi are poorly studied (Fazey *et al.* 2005). This is mainly due to the great extent of the species richness of these groups and difficulty in their detectability, monitoring and species identification (Fazey *et al.* 2005, Lõhmus 2009).

1.5. Biodiversity surrogates

Measuring the diversity of many species groups, including wood-inhabiting fungi and epiphytes, is rather challenging. Even in a small scale, the total number of species present is impossible to survey and studies easily end up with lower number of detected species than the area really contains. With larger study areas, more time and repeated surveys, inaccuracy could be reduced but comprehensive surveys are very laborious and expensive. Hence, different kinds of surrogates or indicator groups, predicting the biological diversity in the area, without need to survey the complete diversity, are commonly used. In literature, several meanings for indicator can be found but according to Lindenmayer *et al.* 2000, indicators of

biological diversity in forests can be divided in two groups; biological or taxon-based indicators and structure-based indicators. Taxon-based indicators are practically indicator species or groups (McGeoch 1998) and structure-based indicators include for example stand complexity, heterogeneity and connectivity (Lindenmayer *et al.* 2000, Humphrey *et al.* 2005).

Because of the difficulty in detecting causal pathways, many studies can usually be generalized only in a very small scale or in a particular area. Hence, in addition to, or instead of structural characteristics, different species groups are commonly used as indicators for biodiversity. Several studies have shown that vascular plants could be used as indicators for different taxa (Wolters *et al.* 2006, Hofmeister *et al.* 2014, see also McMullan-Fisher *et al.* 2010). As an important autotrophic components in terrestrial ecosystems, vascular plants clearly have a significant role in nutrient and water cycling in a forest which further affects the substrate availability for other species and hence, the species composition in a forest ecosystem. Effectiveness of particular species groups, as indicators, varies a lot and naturally, it is impossible to find a complete congruence in species richness between two different species groups. Hence, the suitability of an indicator has to be studied carefully (Stephens *et al.* 2015). Many studies have still shown, that surrogates, especially indicator groups consisted of species among different taxa could be profitable for indicating the biodiversity in a particular area (Jonsson & Jonsell 1999, Rodrigues and Brooks 2007, Larsen *et al.* 2009).

1.6. Aim of the study

My study focused on temperate broadleaved forests, located in North Jutland, Denmark. The aim was to investigate what are the most important elements in forest stand structure affecting species richness of wood-inhabiting fungi, epiphytic lichens and epiphytic bryophytes. I also investigated whether two potential biodiversity surrogate groups, the so called "ancient forest plant species" or Danish "local indicator species", could be used as a surrogate species groups for indicating the species richness of my three study species groups. In addition, I investigated whether some of the structural elements in a forest stand could be used as a structural indicator for the species richness of all the three species groups combined.

My detailed study questions were the following: 1) How different elements of forest stand structure affect the species richness of i) epiphytic lichens ii) epiphytic bryophytes and iii) wood-inhabiting fungi? 2) Are there some structures which maximize the number of all of these species groups combined? 3) Could some of these structures work as an indicator predicting species richness of these species groups on forest stand scale? 4) Could ancient forest plant species or local indicator species act as an indicator group for these three species groups?

2. MATERIALS AND METHODS

2.1 Study area

The study area – two nearby forests (c. 10 km apart); Tofte Skov and Høstemarks Skov - are located in the nature reserve called Lille Vildmose in the municipalities of Aalborg and Mariagerfjord, North Jutland, Denmark (Anonymous 2012). Lille Vildmose is Denmark's largest protected land area covering 76 km² and comprising of coniferous, broadleaved and mixed forests, lakes, moors and the biggest raised bog in lowland Northwest Europe. The area has been actively used for peat mining and farming for decades and from

the original 55 km² of the raised bog, only 22 km² is preserved today (Anonymous 2012). The area is one of the Natura 2000 areas and part of the European Union's LIFE+ Nature and Biodiversity funding programme which started in September 2011 and will continue until 31st of December 2016 (Anonymous 2011, Anonymous 2012).

The objective of this extensive project is to secure the preserved areas of raised bog and also create a basis for the restoration of degraded raised bog (Anonymous 2012). Several actions will be carried out during the project, including restoration of Lake Birkesø as a shallow lake with a surface area of 130 ha, raising the water levels on 770 ha, establishing a stock of red deer living in the central areas of Lille Vildmose, cutting down 200 ha of tree growth in Portlandmosen and Paraplymosen and reducing the numbers of racoon dog, American mink, and red fox. The study forests, Tofte Skov and Høstemarks Skov are mainly characterized by mixed broadleaved forest, beech forest and mixed coniferous forest (Anonymous 2012). Due to high grazing pressure of red deer, area is relatively open creating unique microhabitats especially for epiphytes. The restoration project and following rise in water levels in the area will certainly have an effect on the forests as well. Especially in the areas where the raise in water levels will be highest, some tree mortality can occur due to increasing wetness of the ground.

2.2. Data

The total forest area was divided in 22 forest compartments, each including five circular study plots. The study plots were randomly chosen by using GIS. Three of them were lacking trees hence, the final amount of study plots used in the analyses was 107, except for fungal species which had data only from 106 study plots due to one missing datasheet. Only criteria for study plots were 30 m minimum distance between plots and 15 m minimum buffer area to the forest edge. The radius of every study plot was 15 m.

In every study plot, following measurements were made: 1) All the dead wood items with diameter ≥ 10 cm and length ≥ 1 m were measured, identified to species and classified in decay stage by using five point scale (Òdor & van Hees 2004). 2) DBH (diameter breast height) of all the live trees with diameter ≥ 10 cm were measured and identified to species. 3) Canopy closure was measured by viewing from a single spot in the middle of the study plot by using a Concave Spherical Densiometer (Werner 2009). 4) Water levels were measured from 4 different points, each 5 meters from the centre of the study plot. If water level was above ground, distance from ground to water surface was measured and the value was positive. Otherwise, small hole was dug and distance from the ground level to the raised water surface in the hole was measured and the value was negative. If no water rose when 40 cm depth was reached, the value was recorded as ">-40cm". 5) The area covered with water in the study plot, precisely water coverage was estimated with approximately 50 cm² accuracy. 5) Floral species were listed from 5 m circle plots in the centre of the study plot. 6) Epiphytic lichen species (including micro-lichens) were recorded if present per every standing live and dead tree with DBH \geq 10cm from 0 up to 2 m height in each study plot. Stumps higher than breast height (1.5 m) were also included, whereas logs and twigs, below 2 m, were excluded from the survey. 7) Epiphytic bryophytes were recorded as lichens. 8) For wood-inhabiting fungi, individual species list per dead wood item in the study plot were recorded. 9) Stand age estimations were based on the age of the oldest trees in a study plot.

Concerning all the species surveys, the identification of the occurrence of the species was carried out in the field conditions if possible. Specimens were taken for later microscopic identification if needed. Species statuses and nomenclature for fungal species followed indexfungorum.org. Epiphytes were monitored in 2013 in three periods; 19 plots in April, 54 in August and 32 in October. Vegetation was monitored for all plots in summer

2013 and fungi in all plots during two visits, first in late August and second in October. Water levels were measured in all plots in two visits in February 2014.

2.3. Data analyses

2.3.1. Species richness models

Altogether, 19 variables were used in the Analysis of Covariance (Table 1) to analyse which of the factors in stand structure correlated with the species richness of these three species groups. Stand age was used as a fixed factor and it was classified in three classes (1 = before 1800, 2 = late 1800, 3 = 1900). To avoid errors resulting from zeroes in some variables, logarithmic transformation was used for species richness of wood-inhabiting fungi and square root transformation was used for dead wood volume.

	Epiphytic	Epiphytic	Wood-
	lichens	bryophytes	inhabiting fungi
Average DBH of live trees	х		
Average dead wood diameter			х
Average decaystage plot			х
Average water level	х		
BA of broadleaved trees	х	х	
BA of coniferous trees	х		
Dead wood volume			х
No. dead wood tree species			х
Species richness of living trees		х	
No. lying dead wood			х
No. trees with hollows			х
No. trees with rotten parts	х		
SD of DBH of live trees	х		
Stand age	х	х	х
Water coverage			х
Average DBH of live trees * Average water level	х		
BA of broadleaved trees * Average water level	х		
BA of coniferous trees * Average water level	х		
No. dead wood tree species * Dead wood volume			x

Table 1. Variables used in three final models of The Analysis of Covariance.

The final models included combination of variables chosen by backward elimination to find the highest Adjusted R Squared value. To see whether the forest site variable (Tofte Skov or Høstemarks Skov) had effect on species richness, it was first included to the model as a random factor. As it did not have any significant effects, it was excluded from the models. I also reported partial eta squared (eta2), which shows the variance explained by a given variable after excluding variance explained by other predictors. All analyses were conducted using PASW Statistics, version 18.

2.3.2. Indicators of the species richness

Pearson correlations were conducted to see how ancient forest plant species' occurrence correlated with the occurrence of epiphytic lichens, epiphytic bryophytes and wood-inhabiting fungi and whether ancient forest plant species could be used as an indicator group for these tree species groups. Pearson correlation was also conducted between the occurrence of all the three study species groups combined and the occurrence of "local indicator species", including total 17 Danish fungal, bryophyte and lichen species. List of the ancient forest plant species was taken from the study of Hermy *et al.* 1999. According to the list, my data included total 38 ancient forest plant species (Appendix 1). For comparison, Pearson correlations were also conducted to see whether some of the structural elements could be used as indicator for these three study species groups.

3. RESULTS

Altogether 120 lichen, 66 bryophyte and 194 fungal species were recorded (Appendix 1). Rank-abundance curves were heavily skewed towards the dominance of the most abundant species (Figure 1). In lichens and bryophytes there were a few generalist species which were present in almost all the study plots, while in fungi, the most abundant species were present in less than 50 % of the study plots (Figure 1).

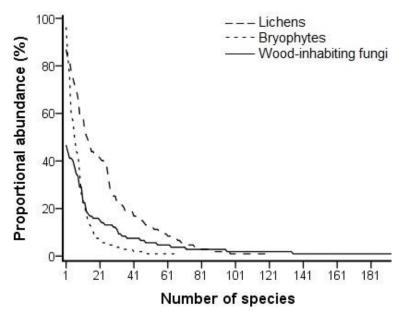


Figure 1. Species rank abundance curves showing the proportional abundance of each species in all study plots (epiphytic lichens and bryophytes n = 107, wood-inhabiting fungi n = 106).

3.1. Species richness of epiphytic lichens

The final model of the Analysis of Covariance for epiphytic lichen species included main effects of 6 variables and 3 interactions with Adjusted R Squared 0.475 (Table 2). Main effect of stand age was clearly the most significant factor having a positive correlation with the species richness of epiphytic lichens (Table 2). The only factors having a negative effect on species richness of epiphytic lichens in the final model were basal area of coniferous trees and average DBH of live trees (Table 2).

	MS	df	В	F	Р	eta ²
Average water level	398.7	1	0.53	14.20	<0.001	0.144
BA of coniferous trees	242.1	1	-12.90	9.11	0.003	0.093
Stand age	228.1	2		8.58	<0.001	0.162
SD of DBH of live trees	80.8	1	0.18	3.04	0.085	0.033
Average DBH of live trees	58.0	1	-0.11	2.18	0.143	0.024
No. trees with rotten parts	43.1	1	0.16	1.62	0.206	0.018
BA of broadleaved trees	15.6	1	0.88	0.59	0.446	0.007
BA of coniferous trees * Average water level	258.9	1	-0.45	9.74	0.002	0.099
BA of broadleaved trees * Average water level	135.5	1	-0.13	5.10	0.026	0.054
Average DBH of live trees * Average water level	127.4	1	-0.01	4.79	0.031	0.051
Error	26.6	89				

Table 2. Variables affecting species richness of lichens. The Analysis of Covariance, Adjusted $R^2 = 0,475$, n = 107.

3.2. Species richness of epiphytic bryophytes

The final model of the Analysis of Covariance for bryophytes included main effects of 3 variables with Adjusted $R^2 = 0,230$, n = 107 (Table 3). Species richness of living trees had the most significant positive correlation with species richness of epiphytic bryophytes.

Table 3. Variables affecting the species richness of bryophyte species. The Analysis of Covariance, Adjusted $R^2 = 0,230$, n = 107.

	MS	df	В	F	Р	eta ²
Species richness of living trees	123.5	1	0.92	12.80	0.001	0.122
BA of broadleaved trees	44.9	1	0.93	4.65	0.034	0.048
Stand age	42.8	2		4.43	0.015	0.088
Error	9.7	92				

3.3. Species richness of wood-inhabiting fungi

The final model of the Analysis of Covariance for wood-inhabiting fungi included main effects of 8 variables and 1 interaction with Adjusted $R^2 = 0,714$, n = 106 (Table 4). Most of the variables correlating significantly with the species richness of wood-inhabiting fungi were related to dead wood. The total dead wood volume was clearly the most significant factor affecting species richness of wood-inhabiting fungi (Table 4). Also the number of dead wood tree species and stand age had significant results. Variables having a negative effect on species richness of wood-inhabiting fungi were the interaction between the number of dead wood tree species and dead wood volume and the main effect of average dead wood diameter (Table 4).

	MS	df	В	F	Р	eta ²
Dead wood volume	1.68	1	0.55	43.49	<0.001	0.341
No. dead wood tree species	0.83	1	0.19	21.56	<0.001	0.204
Stand age	0.24	2		6.14	0.003	0.128
Average dead wood diameter	0.17	1	-0.01	4.36	0.040	0.049
Average decaystage plot	0.12	1	0.06	3.09	0.083	0.035
No. trees with hollows	0.07	1	0.02	1.81	0.183	0.021
No. lying dead wood	0.07	1	0.01	1.76	0.188	0.021
Water coverage	0.06	1	<0.01	1.58	0.212	0.018
No. dead wood tree species * Dead wood volume	0.55	1	-0.11	14.25	<0.001	0.145
Error	0.04	84				

Table 4. Variables affecting the species richness of wood-inhabiting fungi. The Analysis of Covariance, Adjusted $R^2 = 0.714$, n = 106.

3.4. Indicators of the species richness

There was no significant correlation between the occurrence of ancient forest plant species and species richness of epiphytic lichens (Table 5). The positive correlation between species richness of epiphytic bryophytes and occurrence of ancient forest plant species was significant but relatively weak (Table 5). For fungal species, positive correlation with ancient forest plant species' occurrence was also significant but even weaker than for bryophytes (Table 5). Positive correlation between the occurrence of "local indicator species" and the species richness of all three study species groups combined was clearly more significant (Pearson correlation = 0.59, n = 107, p < 0.001), still not strong enough that it could be used as an indicator group for these three study species groups.

Both species richness of epiphytic lichens and species richness of epiphytic bryophytes had a significant positive correlation with 4 variables (Table 6, Table 7). Species richness of wood-inhabiting fungi had a significant positive correlation with dead wood volume and number of dead wood species (Table 8). The correlation between species richness of epiphytic lichens and species richness of epiphytic bryophytes was significant but relatively weak (Pearson Correlation = 0.39, n = 107, p < 0.001) when species richness of wood-inhabiting fungi had even weaker correlation with both epiphytic lichen (Pearson Correlation = 0.25, n = 106, p = 0.009) and epiphytic bryophyte species richness (Pearson Correlation = 0.25, n = 106, p = 0.011).

Variable having the strongest positive correlation with all the three study species groups combined was dead wood volume (Pearson Correlation = 0.62, n = 106, p < 0.001). Dead wood volume didn't have significant correlation either with species richness of epiphytic lichens (Pearson correlation = 0.14, n = 106, p = 0.153) nor species richness of epiphytic bryophytes (Pearson correlation = 0.14, n = 106, p = 0.152). Furthermore, stand age had a significant negative correlation with all the three species groups combined (Pearson Correlation = -0.42, n = 107, p < 0.001).

	n	r	р
Epiphytic lichens	107	0.136	0.162
Epiphytic bryophytes	107	0.308	0.001
Wood-inhabiting fungi	106	0.219	0.024

Table 5. Pearson Correlations between occurrence of ancient forest plant species and species richness of epiphytic lichens, epiphytic bryophytes and wood-inhabiting fungi.

Table 6. Variables having a significant Pearson Correlations with epiphytic lichen species richness

	n	r	р
BA of coniferous trees	107	-0.43	<0.001
BA of broadleaved trees	107	0.34	<0.001
Species richness of living trees	107	0.34	<0.001
SD of DBH of live trees	107	0.23	0.015

Table 7. Pearson Correlations with epiphytic bryophyte species richness.

	n	r	р
BA of coniferous trees	107	-0.43	<0.001
BA of broadleaved trees	107	0.40	<0.001
SD of DBH of live trees	107	0.33	<0.001
Average DBH of live trees	107	0.285	0.003

Table 8. Pearson Correlations with species richness of wood-inhabiting fungi.

	n	r	р
Dead wood volume	106	0.76	<0.001
No. dead wood tree species	106	0.41	<0.001

4. DISCUSSION

4.1. Factors affecting the species richness of the study species

According to the results, most of the significant factors affecting the species richness in all the study species groups were related to nutrient or substrate availability. For fungal species richness, both quality and volume of available dead wood were clearly the most significant factors having a positive correlation with the species richness. In both epiphytic species groups, the significance of the variables related to living host-trees was emphasized. Similar results emphasizing the significance of nutrient and substrate availability have been attained in several previous studies (Harmon *et al.* 1986, McGee & Kimmerer 2002, Jonsson *et al.* 2005, Cleavitt *et al.* 2009, Fritz & Heilmann-Clausen 2010) but this study revealed also some interesting new aspects. In this study, the average water level had a significant positive correlation with the species richness.

Stand age was the most significant factor having a positive correlation with the species richness in all the study species groups. Old stands include higher amounts of veteran trees,

which are key elements for epiphytic lichen and bryophyte diversity due to differences in bark chemistry, nutrient availability and variety in special niches, including rot holes and dead branches (Fritz & Heilmann-Clausen 2010). There are many previous studies where tree or stand age and amount of old trees have been shown to be among the most significant factors affecting epiphytic lichen and bryophyte diversity and species richness (Gustafsson *et al.* 1992, Kuusinen & Siitonen 1998, Uliczka & Angelstam 1999, Fritz *et al.* 2008, Fritz *et al.* 2009, Brunialti *et al.* 2010). For fungal species richness, the most important thing related to stand age is that old forests usually include higher volume of dead wood (Jonsson *et al.* 2005, Aakala *et al.* 2009).

Also in this study, dead wood volume was the most significant factor affecting the species richness of wood-inhabiting fungi, which supports the present understanding of the link between dead wood and fungal species richness. Studies have shown that species richness of wood-inhabiting fungi is strongly affected by both, volume and diversity of dead wood (Harmon *et al.* 1986, Jonsson *et al.* 2005, Stokland *et al.* 2012, Heilmann-Clausen *et al.* 2014). Wood-inhabiting fungi are enormously large species group with lots of old forest dependent specialists and as heterotrophic organisms which use the woody parts as their main substrate, it is logical that also in this study the number of dead wood species correlated significantly with fungal diversity. Also the average decay stage, number of trees with hollows and volume of lying dead wood correlated significantly with the species richness of wood-inhabiting fungi. This also underlines the importance of maintaining the variability in dead wood quality in a forest.

Most of the other significant factors having positive correlations with the species richness of both epiphyte groups were somehow related to substrate availability as well. Species richness of living trees was the most significant factor correlating with the species richness of epiphytic bryophytes. Also basal area of broadleaved trees correlated significantly with epiphytic bryophyte species richness. Results were consistent with many previous studies (McGee & Kimmerer 2002, Cleavitt et al. 2009, Király et al. 2013, Ódor et al. 2013). However, basal area of coniferous trees had a significant, yet quite weak, negative effect on species richness of lichens. Majority of the coniferous trees in the study area were introduced Picea abies trees, or Picea sitchensis trees, also introduced in Denmark, which might explain this result. Coniferous trees decrease effectively the light availability in a forest, which further affects the lichen community (Ódor et al. 2013). Studies have also indicated that coniferous trees are usually inhabited by lower number of epiphyte species than deciduous trees (Kuusinen 1996, see also Coote et al. 2007). Additionally, many deciduous trees have more specialized epiphytes than conifers (Uliczka & Angelstam 1999 Jüriado et al. 2003). It is also notable that the model for epiphytic bryophytes explained only a bit more than 20 % of the species richness in this group. Bryophytes are autotrophic organisms, which use the living or dead wood mainly as their platform for growing and studies have indicated that compared to substrate quality, local climatic factors have a major impact on epiphytic bryophytes (Heilmann-Clausen et al. 2014). However, it is interesting that neither of the variables linked to air humidity, precisely average water level and water coverage in this study, were not significant enough to be included in the model for epiphytic bryophytes.

What was new and also quite interesting result was that average water level had a significant positive correlation with the species richness of epiphytic lichens. Some previous studies on air humidity and epiphytic lichens have been done, but they have mainly focused on the community level and species composition rather than species richness (Heylen *et al.* 2005). Several studies have shown that epiphytic bryophytes are affected by air humidity while epiphytic lichens are mainly affected by light availability in a forest (Király *et al.* 2013,

Ódor *et al.* 2013, Heilmann-Clausen *et al.* 2014). However, according to this study, air humidity may have some effects on epiphytic lichens as well.

Also several interactions were significant enough to be included in the species richness models. Interactions are typically very difficult to explain and interpret but according to the other results, at least some speculation could be made. In all the three interactions having a significant correlation with the species richness of epiphytic lichens, average water level was the other interacting variable. And in the whole model, the main effect of average water level was, with the stand age, the most significant factor correlating with the species richness of epiphytic lichens. In addition, the interaction between number of dead wood tree species and dead wood volume could be somehow related to dead woods' significance on species richness of wood-inhabiting fungi generally. It is also notable that some of the explanatory factors may be correlating together which can further affect the results. However, this is not assumed to affect the significance of the results remarkably.

4.2. Correlations and indicators of the species richness

The correlation between the occurrence of ancient forest plant species and epiphytic lichens, bryophytes and wood-inhabiting fungi was relatively weak. Hence, according to this study, ancient forest plant species should not be used as an indicator group for these three species groups. The strongest positive correlation was between the occurrence of ancient forest plants and epiphytic bryophytes, still only 0.308. It is a fact that factors affecting the species richness are complicated. Also suitability of a particular species or species groups as indicators varies a lot in different scales and hence, calibration of a particular indicator group is very important (Stephens *et al.* 2015). Despite the previous studies in which the occurrence of ancient forest plant species correlated strongly with the occurrence of other species groups, including macro fungi (Hofmeister *et al.* 2014), this subject should be studied more carefully. However, there was a stronger correlation between the occurrence of local indicator species and our study species. Still, the correlation was not strong enough that even these local indicator species could act as an indicator group for the three study species groups in this area.

The potential structural indicators were also investigated and the total volume of dead wood had the strongest positive correlation with occurrence of all the three species groups combined. Anyway, some caution should be made if dead wood volume is used as a structural indicator, because this result might have been mainly due to very strong correlation between dead wood volume and species richness of wood-inhabiting fungi. The correlations between dead wood volume and both, epiphytic lichens and bryophytes, were very weak.

4.3. Future aspects

In a natural state, the forests in Lille Vildmose would be even more humid, due to flatness of the area, not much above sea level, and nearby bogs. Nowadays high grazing pressure keeps the area relatively open which, in addition to light regimes, also affects the air humidity. Because of the long history of human impacts and dehydration in the area, availability of suitable host-trees for epiphytes, and nutrients like dead wood for fungal species, might have been, at least occasionally, scarce. Many epiphytes species are specialized in substrates, like veteran trees which develop very slowly. Also many fungal species are specialized in a particular dead wood type which has been decaying for several decades. Fungal species form important links in nutrient cycling in a forest, and hence have a major role in forest food-webs (Jonsson *et al.* 2005, Stokland *et al.* 2012). Many of the species are also dependent on other fungal species and for example colonize logs only after particular fungal species. Studies have also indicated that forest management is very harmful especially for those species with strong associative links to others species (Abrego 2014).

According to these results, it is crucial to maintain the sufficient volume, variability and continuity of dead wood in forests. So, forest and habitat continuity is important for both epiphytes and wood-inhabiting fungi and gaps in local substrate and nutrient availability can harm especially species with poor dispersal ability.

At the last, the link between species richness of epiphytic bryophytes and air humidity has been recognized in earlier studies (Király *et al.* 2013, Ódor *et al.* 2013, Heilmann-Clausen *et al.* 2014) but this study showed that increasing air humidity, which is naturally affected by water level in a forest stand, could be beneficial for epiphytic lichens as well. The sensitivity to microclimates and air humidity makes the species also more vulnerable to environmental changes. However, the effect of ground water level and air humidity on species richness of epiphytic lichens should be studied more carefully in the future.

4.3. Conclusions

The main results of this study supported basically the same ideas as in many previous studies. Factors related to substrate and nutrient availability, like stand age, dead wood volume and diversity in tree species were among the most significant factors having a positive correlation with the species richness of the studied species groups. Average water level and stand age had the most significant positive correlation with species richness of epiphytic lichens. Alternatively, basal area of coniferous trees had a significant negative correlation with species richness of lichens. Species richness of living trees, basal area of broadleaved trees and stand age had the strongest positive correlation with the species richness of epiphytic bryophytes. However, for bryophytes, the model explained only a bit more than 20 % of the species richness. For wood-inhabiting fungi, dead wood volume was clearly the most significant factor having a positive correlation with the species richness. Also different elements in dead wood quality correlated significantly and the whole model explained even more than 70 % of the species richness of wood-inhabiting fungi.

In this study, the correlation between occurrence of ancient forest plant species and species richness of epiphytic lichens, epiphytic bryophytes and wood-inhabiting fungi was not strong enough that ancient forest plant species could be used as a surrogate group for the these species groups in temperate broadleaved forests. With more study on the subject, there is a little possibility that local forest indicator species could be potential surrogate for these species groups. However, according to this study alone, they should not be used as an indicator group for these three species groups either.

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APPENDIXES

Lichens	local indicator species
Amandinea punctata	
Anisomeridium biforme	
Anisomeridium polypori	
Arthonia didyma	
Arthonia radiata	
Arthonia ruana	
Arthonia spadicea	
Arthonia vinosa	
Arthopyrenia sp.	
Bacidia circumspecta	
Bacidia incompta	
Bacidia rosella	
Bacidia rubella	
Bacidina arnoldiana	
Bacidina phacodes	
Bactrospora corticola	
Biatora globulosa	
Buellia griseovirens	
Calicium salicinum	
Calicium viride	
Caloplaca lucifuga	
Caloplaca luteoalba	
Candelariella efflorescens	
Candelariella xanthostigma	
Chaenotheca brachypoda	
Chaenotheca chlorella	
Chaenotheca chrysocephala	
Chaenotheca ferruginea	
Chaenotheca furfuracea	
Chaenotheca hispidula	
Chaenotheca stemonea	
Chaenotheca trichialis	
Chaenothecopsis cf pusilla	
Chaenothecopsis cf vainoiana	
Chrysothrix candelaris	
Cladonia sp.	
Cliostomum griffithi	
Dactylospora parasitica	
Dimerella pineti	
Evernia prunastri	

Graphis scripta	
Haematomma ochroleucum	
Hypogymnia physodes	
Hypocenomyce scalaris	
Hypotrachyna revoluta	
Lecanactis abietina	x
Lecania cyrtella	A
Lecania cyrtellina	
Lecanora allophana	
Lecanora argentata	
Lecanora carpinea	
Lecanora chlarotera	
Lecanora expallens	
Lecanora glabrata	
Lecanora intumescens	
Lecanora pulicaris	
Lecanora symmicta	
Lecidella elaeochroma	
Lepraria incana	
Lepraria lobificans	
Lepraria membranacea	
Lepraria rigidula	
Leptorhaphis epidermis	
Lobaria pulmonaria	Х
Megalaria pulverea	
Melanelixia glabratula	
Melanelixia subaurifera	
Micarea peliocarpa	
Micarea prasina	
Mycoblastus fucatus	
Normandina acroglypta	
Normandina pulchella	
Ochrolechia androgyna	
Ochrolechia microstictoides	
Ochrolechia subviridis	
Opegrapha atra	
Opegrapha niveoatra	
Opegrapha ochrocheila	
Opegrapha rufescens	
Opegrapha sorediifera	
Opegrapha varia	
Opegrapha vermicellifera	Х
Opegrapha viridis	
Opegrapha vulgata	
Pachyphiale carneola	
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Parmelia ernstiae	
Parmelia saxatilis	
Parmelia sulcata	
Parmeliopsis ambigua	
Peltigera cf praetextata	
Pertusaria albescens	
Pertusaria amara	
Pertusaria coccodes	
Pertusaria flavida	
Pertusaria hemisphaerica	
Pertusaria hymenea	
Pertusaria leioplaca	
Pertusaria multipuncta	
Pertusaria pertusa	
Phlyctis argena	
Physcia pulverulenta	
Physcia tenella	
Physconia perisidiosa	
Placyntiella sp.	
Platismatia glauca	
Pseudosagedia aenea	
Pyrenula nitida	Х
Pyrrhospora quernea	
Ramalina farinacea	
Rhaphidicyrtis trichosporella	
Ropalospora viridis	
Schismatomma decolorans	
Sclerophora peronella	
Scoliciosporum chlorococcum	
Stenocybe pullatula	
Thelotrema lepadinum	Х
Trapeliopsis flexuosa	
Trapeliopsis pseudogranulosa	
Xanthoria parietina	
Xanthoria polycarpa	

Bryophytes	local indicator species
Antitrichia curtipendula	
Brachythecium rutabulum	
Brachythecium cf salebrosum	
Bryum capillare	
Bryum moravicum	

Calypogeia sp.	
Cephalozia bicuspidata	
Ceratodon purpureus	
Chiloscyphus sp.	
Dicranella heteromalla	
Dicranoweissia cirrata	
Dicranum majus	
Dicranum montanum	
Dicranum scoparium	
Eurhynchium striatum	
Frullania dilatata	
Frullania fragilifolia	
Frullania tamarisci	
Homalia trichomanoides	
Homalothecium sericeum	X
Hypnum andoi	
Hypnum cupressiforme	
Hypnum jutlandicum	
Isothecium alopecuroides	Х
Isothecium myosuroides	Х
Kindbergia praelonga	
Lejeunea cavifolia	
Lepidozia reptans	
Leucobryum glaucum	
Loeskeobryum brevirostre	
Lophocolea heterophylla	
Lophocolea bidentata	
Metzgeria furcata	
Mnium hornum	
Neckera complanata	Х
Orthotrichum affine	
Orthotrichum diaphanum	
Orthotrichum lyellii	
Orthotrichum pulchellum	
Orthotrichum speciosum	
Orthotrichum stramineum	
Orthotrichum striatum	
Plagiomnium affine	
Plagiomnium cuspidatum	
Plagiomnium undulatum	
Plagiothecium curvifolium	
Plagiothecium denticulatum	
Plagiothecium laetum	
Plagiothecium latebricola	
Plagiothecium nemorale	
C 1	

Plagiothecium undulatum	
Pleurozium schreberi	
Polytrichastrum formosum	
Porella platyphylla	х
Ptilidium pulcherrimum	
Radula complanata	
Rhizomnium punctatum	
Rhytidiadelphus loreus	х
Rhytidiadelphus squarrosus	
Rhytidiadelphus triquetrus	
Scleropodium purum	
Sphagnum fimbriatum	
Tetraphis pellucida	
Thuidium tamariscinum	
Ulota crispa	
Zygodon rupestris	х

Wood-inhabiting fungi	local indicator species
Amylostereum chailletii	
Amylostereum laevigatum	
Antrodiella faginea	
Antrodiella serpula	
Armillaria lutea	
Armillaria ostoyae	
Ascocoryne cylichnium (Tul.) Korf	
Ascocoryne sarcoides (Jacq.: Fr.) Groves & Wilson	
Ascocoryne sp (brun)	
Ascotremella faginea	
Biscogniauxia marginata	
Bjerkandera adusta (Willd.: Fr.) P.Karst.	
Bolbitius reticulatus (Pers.: Fr.) Rick.	
Bulgaria inquinans (Pers.: Fr.) Fr.	
Calocera cornea (Batsch) Fr.	
Camarops polysperma	
Ceriporia excelsa (Lund.) Parm.	
Ceriporia reticulata (Hoffm.: Fr.) Dom.	
Ceriporia viridans (Berk. & Broome) Donk	
Ceriporiopsis resinascens	
Cerrena unicolor	
Chlorociboria aeruginascens	
Chondrostereum purpureum	
Cineromyces vulgaris	
Clitopilus hobsonii (Berk.) P.D.Orton	

Conocybe subpubescens P.D.Orton	
Coprinus micaceus (Bull.: Fr.) Fr.	
Crepidotus mollis (Schaeff.: Fr.) Staude	
Cylindrobasidium evolvens (sprækkehinde)	
Cystoderma carcharias	
Dacrymyces stillatus	
Daedaleopsis confragosa (Bolt.: Fr.) Schroet.	Х
Daldinia decipiens	
Datronia mollis (Sommerf.: Fr.) Donk	
Delicatula integrella	
Entoloma conferendum	
Entoloma cryptocystidiata (cfr)	
Entoloma jahnii	
Entoloma juncinum	
Entoloma neglectum	
Entoloma triste (cfr)	
Eutypa spinosa (Pers.: Fr.) Tul. & C.Tul.	х
Exidia nucleata	
Exidia pithya	
Exidia plana	
Exidia thuretiana	
Flammula alni	
Fomes fomentarius (L.: Fr.) Fr.	Х
Fomitopsis pinicola (Swartz: Fr.) P.Karst.	х
Fuscoporia ferrea	
Galerina marginata (Batsch) Kuhner	
Galerina sp.	
Galerina triscopa	
Ganoderma lipsiensis (Batsch) Atk.	
Ganoderma lucidum	
Gymnopilus penetrans (Fr.) Murrill	
Hemimycena cephalotricha	
Hemimycena delectabilis	
Henningsomyces candidus (Pers.: Fr.) O.K.	
Henningsomyces puber	
Heterobasidion annosum	
Hohenbuehelia fluxilis	
Hohenbuehelia mastrucata	
Hydropus floccipes	
Hygrophoropsis aurantiaca	
Hymenochaete rubiginosa	Х
Hyphodontia radula (Pers.: Fr.) E.Langer & Vesterh.	
Hypholoma capnoides	

Hypholoma fasciculare (Huds.: Fr.) P.Kumm.	
Hypholoma lateritium	
Hypocrea rufa (Pers.) Fr. (s.lato)	
Hypoxylon cohaerens (Pers.: Fr.) Fr.	
Hypoxylon fragiforme (Pers.: Fr.)	
Kickx Hypoxylon macrocarpum Pouz.	
Hypoxylon multiforme (Fr.: Fr.) Fr.	
Hypoxylon petriniae	
Hypoxylon rubiginosum (Pers.: Fr.)	
Fr.	
Inonotus obliquus (Pers.: Fr.) Pilat	
Ischnoderma benzoinum	
Kretzschmaria deusta (Hoffm.) P.M.D. Martin	
Kuehneromyces mutabilis	
Lycoperdon perlatum Pers.: Pers.	
Lycoperdon pyriforme Schaeff.: Pers.	
Marasmiellus ramealis	
Marasmius rotula	
Megacollybia platyphylla (Pers.: Fr.)	
Kotl. & Pouz.	
Mensularia nodulosa (Fr.) T. Wagner & M. Fisch.	
Mensularia radiata	
Meripilus giganteus	
Mutinus caninus	
Mycena abramsii (Murrill) Murrill	
Mycena cinerella (P.Karst.) P.Karst.	
Mycena crocata (Schrad.: Fr.)	
P.Kumm.	
Mycena epipterygia	
Mycena erubescens	
Mycena filopes	
Mycena galericulata (Scop.: Fr.) Quél.	
Mycena galopus	
Mycena haematopus (Pers.: Fr.) P.Kumm.	
Mycena hiemalis	
Mycena inclinata	
Mycena maculata	
Mycena meliigena	
Mycena metata	
Mycena olida	
Mycena polygramma	
Mycena pseudocorticola	
Mycena pura (Pers.: Fr.) P.Kumm.	
Mycena renati Quél.	
Mycena sanguinolenta	
Mycena speirea	
ingeena speriea	

Mycena stipata	
Mycena vitilis	
Mycetinis alliaceus (Jacq.) Earle	
Nemania chestersii	
Nemania serpens (Pers.: Fr.) Gray	
Neobulgaria pura	
Neonectria coccinea (Pers.) Rossman & Samuels	
Oligoporis stipticus	
Oligoporus immitis	
Oudemansiella mucida (Schrad.: Fr.) Höhn.	
Panaeolus acuminatus	
Panellus stipticus (Bull.: Fr.) P.Karst.	
Peziza varia	
Phlebia livida (Pers.: Fr.) Bres.	
Phlebia radiata	
Phlebia rufa (Pers.: Fr.) M.P.Christ.	
Phlebia tremellosa (Schrad.: Fr.) Burds. & Nakas.	
Phlebia uda	
Phleogena faginea (Fr.: Fr.) Link	
Pholiontina brunnea	
Pholiota adiposa	
Pholiota flammans	
Physisporinus sanguinolentus (Alb. & Schwein.) Pilát	
Piptoporus betulinus	
Pleurotus ostreatus	
Pleurotus pulmonarius (Fr.) Quél.	
Pluteus cervinus (Batsch) Singer	
Pluteus insidiosus	
Pluteus luctuosus Boud.	
Pluteus phlebophorus (Dittm.: Fr.) P.Kumm.	
Pluteus plautus (Weinm.) Gillet	
Pluteus podospileus Sacc. & Cub.	
Pluteus romellii	
Pluteus salicinus (Pers.: Fr.) P.Kumm.	
Pluteus semibulbosus (Lasch) Gillet	
Pluteus umbrosus (Fr.) P.Kumm.	
Polyporus brumalis	
Polyporus ciliatus	
Polyporus leptocephalus	
Postia caesia	
Postia lactea	
Postia subcaesia	
Postia tephroleuca	
Psathyrella cernua	

Psathyrella fagetophila Psathyrella nolitangere	
Psathyrella nolitangere	
Psathyrella piluliformis (Bull.: Fr.) P.D.Orton	
Psathyrella spadiceogrisea	
Pseudoclitocybe cyathiformis	
Quaternaria quaternata	
Ramaria stricta	
Resinicium bicolor	
Resupinatus applicatus	
Resupinatus porineformis	
Resupinatus trichotis	
Rhodocollybia butyracea	
Sarcomyxa serotina	
Schizophyllum commune	
Scopoloides rimosa	
Scutellinia scutellata	
Simocybe centunculus (Fr.: Fr.) P.Karst.	
Simocybe sumptuosa	
Skeletocutis carneogrisea	
Skeletocutis nivea (Jungh.) Keller	
Steccherinum ochraceum (Pers.: Fr) Gray	
Steccherinum sp.	
Stereum gausapatum	
Stereum hirsutum	
Stereum rugosum (Pers.: Fr.) Fr.	
Stereum sanguinolentum	
Stereum subtomentosum Pouz.	
Trametes gibbosa (Pers.: Fr.) Fr.	
Trametes hirsuta (Wulfen: Fr.) Pilat	
Trametes versicolor (L.: Fr.) Quel.	
Trechispora hymenocystis	
Tremella mesenterica	
Trichaptum abietinum (Pers.: Fr.) Ryvarden	
Tubaria conspersa	
Tubaria furfuracea	
Volvariella taylori	
Xerula radicata (Relhan: Fr.) Dörfelt	
Xylaria hypoxylon (L.: Fr.) Grev.	
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Vascular plants	ancient forest plant species
Acer platanoides	
Acer pseudoplatanus	

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Achillea millefolium	
Achillea ptarmica	
Aegopodium podagraria	
Agrostis canina	
Agrostis capillaris	
Agrostis gigantea	
Agrostis stolonifera	
Alnus glutinosa	
Andromeda polifolia	
Anemone nemorosa	Х
Anthoxanthum odoratum	
Arenaria serpyllifo ssp. serpyllifo	
Athyrium filix-femina	Х
Atrichum undulatum	
Bellis perennis	
Betula pendula	
Betula pubescens	
Betula species	
Bladmos	
Botrychium lunaria	
Brachythecium rutabulum	
Briza media	
Calamagrostis arundinacea	
Calamagrostis canescens	
Calamagrostis epigejos	
Calliergonella cuspidata	
Callitriche species	
Calluna vulgaris	
Campanula rotundifolia	
_	
Campylopus introflexus Cardamine amara	
Cardamine flexuosa	
Cardamine pratensis	
Carex acutiformis	
Carex arenaria	
Carex canescens	
Carex demissa	
Carex echinata	
Carex elata ssp. elata	
Carex elongata	
Carex flava	
Carex nigra var. nigra	
Carex nigra var. recta	
Carex ovalis	
Carex pallescens	Х
Carex panicea	
Carex pilulifera	
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Carex remota	х
Carex rostrata	
Carex sylvatica	X
Carex vesicaria	
Cerastium fontanum ssp. vulgare	
Chrysosplenium alternifolium	X
Chrysosplenium oppositifolium	X
Circaea alpina	
Circaea lutetiana	X
Cirsium arvense	
Cirsium palustre	
Cirsium vulgare	
Cladonia sp., s.s	
Convallaria majalis	X
Cornus suecica	
Corylus avellana	X
Crataegus laevigata	X
Crataegus monogyna	
Crataegus species	
Crepis paludosa	
Cynosurus cristatus	
Dactylis glomerata ssp. glomerata	
Dactylis glomerata ssp. lobata	
Dactylorhiza maculata ssp. maculata	
Danthonia decumbens	
Deschampsia cespitosa	
Deschampsia flexuosa	
Dicranella heteromalla	
Dicranum scoparium	
Doed Organic Material	
Dryopteris carthusiana	X
Dryopteris dilatata	^
Eleocharis palustris ssp. vulgaris	
Elymus repens	
Epilobium adenocaulon	
Epilobium angustifolium	
Epilobium hirsutum	
Epilobium obscurum	
_	
Epilobium palustre	
Epilobium roseum	
Epilobium species	
Epilobium tetragonum	
Equisetum arvense	
Equisetum fluviatile	
Equisetum palustre	
Equisetum pratense Equisetum sylvaticum	v
Equisetum sylvaticum	X

Erica tetralix	
Eriophorum angustifolium	
Eriophorum vaginatum	
Euphrasia species	
Euphrasia stricta var. stricta	
Fagus sylvatica	
Festuca gigantea	Х
Festuca ovina	
Festuca pratensis	
Festuca rubra	
Filipendula ulmaria	
Fomes fomentarius	
Frangula alnus	
Fraxinus excelsior	
Galeopsis bifida	
Galeopsis tetrahit	
Galium aparine	
Galium palustre	
Galium saxatile	
Galium uliginosum	
Galium verum	
Geranium robertianum	
Geum rivale	X
Geum urbanum	
Glyceria fluitans	
Glyceria fluitans Hedera helix	
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Hedera helix	
Hedera helix Hieracium pilosella	
Hedera helix Hieracium pilosella Hieracium umbellatum	
Hedera helix Hieracium pilosella Hieracium umbellatum Holcus lanatus	
Hedera helix Hieracium pilosella Hieracium umbellatum Holcus lanatus Holcus mollis	
Hedera helix Hieracium pilosella Hieracium umbellatum Holcus lanatus Holcus mollis Homalothecium sericeum	
Hedera helix Hieracium pilosella Hieracium umbellatum Holcus lanatus Holcus mollis Homalothecium sericeum Hottonia palustris	
Hedera helix Hieracium pilosella Hieracium umbellatum Holcus lanatus Holcus mollis Homalothecium sericeum Hottonia palustris Hydrocotyle vulgaris	
Hedera helixHieracium pilosellaHieracium umbellatumHolcus lanatusHolcus mollisHomalothecium sericeumHottonia palustrisHydrocotyle vulgarisHypnum cupressiforme	X
Hedera helix Hieracium pilosella Hieracium umbellatum Holcus lanatus Holcus mollis Homalothecium sericeum Hottonia palustris Hydrocotyle vulgaris Hypnum cupressiforme Hypochoeris radicata	X
Hedera helix Hieracium pilosella Hieracium umbellatum Holcus lanatus Holcus mollis Homalothecium sericeum Hottonia palustris Hydrocotyle vulgaris Hypnum cupressiforme Hypochoeris radicata Ilex aquifolium	X
Hedera helix Hieracium pilosella Hieracium umbellatum Holcus lanatus Holcus mollis Homalothecium sericeum Hottonia palustris Hydrocotyle vulgaris Hypnum cupressiforme Hypochoeris radicata Ilex aquifolium Impatiens noli-tangere	X
Hedera helix Hieracium pilosella Hieracium umbellatum Holcus lanatus Holcus mollis Homalothecium sericeum Hottonia palustris Hydrocotyle vulgaris Hypnum cupressiforme Hypochoeris radicata Ilex aquifolium Impatiens noli-tangere Iris pseudacorus	X
Hedera helix Hieracium pilosella Hieracium umbellatum Holcus lanatus Holcus mollis Homalothecium sericeum Hottonia palustris Hydrocotyle vulgaris Hypnum cupressiforme Hypochoeris radicata Ilex aquifolium Impatiens noli-tangere Iris pseudacorus Isothecium alopecuroides	X
Hedera helix Hieracium pilosella Hieracium umbellatum Holcus lanatus Holcus mollis Homalothecium sericeum Hottonia palustris Hydrocotyle vulgaris Hypnum cupressiforme Hypochoeris radicata Ilex aquifolium Impatiens noli-tangere Iris pseudacorus Isothecium alopecuroides Isothecium myosuroides	X
Hedera helix Hieracium pilosella Hieracium umbellatum Holcus lanatus Holcus mollis Homalothecium sericeum Hottonia palustris Hydrocotyle vulgaris Hydrocotyle vulgaris Hypnum cupressiforme Hypochoeris radicata Ilex aquifolium Impatiens noli-tangere Iris pseudacorus Isothecium alopecuroides Isothecium myosuroides Juncus articulatus	X
Hedera helixHieracium pilosellaHieracium umbellatumHolcus lanatusHolcus mollisHonalothecium sericeumHottonia palustrisHydrocotyle vulgarisHypnum cupressiformeHypochoeris radicataIlex aquifoliumImpatiens noli-tangereIris pseudacorusIsothecium alopecuroidesIsothecium myosuroidesJuncus articulatusJuncus bufonius	X
Hedera helix Hieracium pilosella Hieracium umbellatum Holcus lanatus Holcus mollis Homalothecium sericeum Hottonia palustris Hydrocotyle vulgaris Hydrocotyle vulgaris Hypnum cupressiforme Hypochoeris radicata Ilex aquifolium Impatiens noli-tangere Iris pseudacorus Isothecium alopecuroides Isothecium myosuroides Juncus articulatus Juncus bufonius Juncus bulbosus	X
Hedera helixHieracium pilosellaHieracium umbellatumHolcus lanatusHolcus mollisHonalothecium sericeumHottonia palustrisHydrocotyle vulgarisHypnum cupressiformeHypochoeris radicataIlex aquifoliumImpatiens noli-tangereIris pseudacorusIsothecium alopecuroidesIsothecium myosuroidesJuncus articulatusJuncus bufoniusJuncus conglomeratus	X
Hedera helix Hieracium pilosella Hieracium umbellatum Holcus lanatus Holcus mollis Homalothecium sericeum Hottonia palustris Hydrocotyle vulgaris Hypnum cupressiforme Hypochoeris radicata Ilex aquifolium Impatiens noli-tangere Iris pseudacorus Isothecium alopecuroides Isothecium alopecuroides Juncus articulatus Juncus bufonius Juncus bulbosus Juncus conglomeratus	X

Lapsana communis	
Larix kaempferi	
Lathyrus linifolius	
Lathyrus pratensis	
Lecanactis abietina	
Lemna minor	
Leontodon autumnalis	
Leucodon sciuroides	
levermos	
Linaria vulgaris	
Lobaria pulmonaria	
Lolium perenne	
Lonicera periclymenum	x
Lotus corniculatus	A
Luzula campestris	
Luzula multiflora	
Luzula pilosa	X
Luzula sylvatica	X
Lychnis flos-cuculi	
Lycopodium clavatum	
Lycopus europaeus	
Lysimachia vulgaris	
Lythrum salicaria	
Maianthemum bifolium	х
Malus sylvestris	х
Matricaria perforata	
Melampyrum pratense	
Melica uniflora	Х
Mentha arvensis	
Mentha species	
Mentha x verticillata	
Milium effusum	Х
Mnium hornum	
Moehringia trinervia	
Molinia caerulea	
Montia fontana	
Mycelis muralis	1
Myosotis laxa ssp. caespitosa	1
Myosotis scorpioides	
Myrica gale	
Nardus stricta	
Neckera complanata	
Odontites verna	
Oxalis acetosella	X
Oxyrrhynchium praelongum	
Paris quadrifolia	X
Persicaria amphibia	
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Persicaria hydropiper	
Persicaria lapathifol ssp. pallida.	
Persicaria minor	
Peucedanum palustre	
Phalaris arundinacea	
Phleum pratense ssp. pratense	
Phragmites australis	
Picea abies	
Picea glauca	
Picea sitchensis	
Pinus mugo	
Pinus sylvestris	
Piptoporus betulinus	
Plagiomnium undulatum	
Plantago lanceolata	
Plantago major	
Pleurozium schreberi	
Poa annua	
Poa pratensis	
Poa trivialis	
Polygala species	
Polygonatum verticillatum	
Polygonum aviculare ssp. aviculare	
Polytrichum formosum	
Polytrichum juniperinum	
Populus tremula	
Porella platyphylla	
Potentilla anserina	
Potentilla erecta	
Primula elatior	X
Prunella vulgaris	X
Prunus avium	
Prunus cerasifera	
Prunus padus	
Prunus spinosa	
Pteridium aquilinum	X
Quercus petraea	A
Quercus robur	
Quercus rubra	
Ranunculus acris	
Ranunculus auricomus agg.	X
Ranunculus ficaria	л
Ranunculus flammula	
Ranunculus repens	
Ranunculus species Rhytidiadelphus loreus	
Rhytidiadelphus squarrosus	
reny autacipitus squartosus	

Roegneria canina	
Rosa canina ssp. canina	
Rosa species	
Rubus idaeus	
Rubus sect. rubus	
Rumex acetosa	
Rumex acetosella	
Rumex sanguineus	
Rumex thyrsiflorus	
Sagina procumbens	
Sagina procumbens	
Salix aurita	
Salix caprea	
Salix cinerea	
Salix repens ssp. repens var. Repens	
Sambucus nigra	
Scleropodium purum	
Scrophularia nodosa	X
Scutellaria galericulata	
Senecio jacobaea	
Senecio species	
Senecio sylvaticus	
Senecio vulgaris	
Silene dioica	
Sonchus oleraceus	
Sorbus aucuparia	
Sorbus intermedia	
Sphagnum capillifolium	
Sphagnum cuspidatum	
Sphagnum fallax	
Sphagnum fimbriatum	
Sphagnum magellanicum	
Sphagnum palustre	
Sphagnum rubellum	
Sphagnum species	
Sphagnum squarrosum	
Stachys palustris	
Stachys sylvatica	Х
Stellaria alsine	

Stellaria graminea	
Stellaria holostea	Х
Stellaria media	
Stellaria nemorum	Х
Stellaria palustris	
Succisa pratensis	
Taraxacum species	
Thelotrema lepadinum	
Thelypteris palustris	
Tilia cordata	X
Trichophor cespitosum ssp.	
germanicum	
Trientalis europaea	
Trifolium campestre	
Trifolium dubium	
Trifolium pratense	
Trifolium repens	
Urtica dioica	
Vaccinium myrtillus	Х
Vaccinium oxycoccos	
Vaccinium uliginosum	
Vaccinium vitis-idaea	
Valeriana sambucifol ssp. procurrens	
Veronica beccabunga	
Veronica chamaedrys	
Veronica officinalis	
Veronica serpyllifolia	
Viburnum opulus	X
Vicia cracca	
Vicia sylvatica	
Viola canina	
Viola palustris	
Viola reichenbachiana	X
Viola riviniana	1
Viola species	1
Zygodon species	1
	1