Master's thesis

Effects of forest-fuel harvesting on the diversity of dead wood and epixylic macrolichens in clear-cuts

Mari Jäntti

The University of Jyväskylä
The Department of Biological and Environmental Science
Ecology and Evolutionary Biology
16.4.2016

THE UNIVERSITY OF JYVÄSKYLÄ, Faculty of Mathematics and Science

The Department of Biological and Environmental Science
Ecology and Evolutionary Biology

Jäntti, M.: Effects of forest-fuel harvesting on the diversity of dead wood and epixylic macrolichens in clear-cuts

Master's seminar: 33 p.
Supervisors: Doc. Panu Halme, MSc Jenna Purhonen
Inspectors:
April 2016

Keywords: bioenergy, disturbances, habitat heterogeneity, logging residues, macrolichens, *Picea abies*, saproxylic species, species-area relationship (SAR)

ABSTRACT

Forest-fuel harvesting (FFH) is a growing industry in countries of intensive forest management. FFH is the collection of logging residues for energy production interconnected with thinning and clear-cutting, and it reduces especially the amount of fine woody debris (FWD) and stumps on clear-cuts. With dead wood already being a scarce resource in managed forests, the practice may cause further species loss among dead wood dependent, saproxylic species. This is why it is important to study the effects of FFH on biodiversity. Some of the most important theories for species richness are the theories of species-area relationship (SAR) and the theory of habitat heterogeneity. According to the SAR, when the available area decreases, the number of species it can support decreases as well. The theory can be applied to species that use dead wood primarily as a substrate, such as epixylic lichens. According to the theory of habitat heterogeneity, when the heterogeneity of the habitat decreases, the same often happens considering the species richness. In this study, the effects of FFH on the diversity of dead wood and epixylic lichens (that grow on dead wood) were studied on 12 spruce (*Picea abies*) dominated sites. The sites were located in Central Finland and Northern Savonia and had been clear-cut about 8 years earlier. FFH had been conducted on 7 sites, and 5 sites without FFH were controls. Different dead wood characteristics were measured and all epixylic macrolichen species surveyed on 3 sampling plots on each site. Even though the overall volume and surface area of dead wood did not significantly differ between treatments, FFH seemed to reduce the amount of stumps and logs. However, FFH additionally increased the aboveground amount of dead wood by lifting uprooted stumps and roots on the surface. There were less lichen species growing on the branches of FFH than of control sites, and the species richness on stumps tended to be lower on FFH than on control sites. However, no effect on the overall species diversity was found. It may be that the availability of other substrates can compensate the loss of branches and stumps for the common macrolichens that were found in the study. A positive SAR was found between coarse woody debris (CWD) and lichen richness, whereas lichen richness did not correlate with the diversity of dead wood. Therefore, the hypothesis of dead wood diversity affecting lichen species richness was not supported. CWD consisted of logs and uprooted stumps in the present study, which indicates that uprooted stumps might be a valuable substrate for lichens along with logs. Although, in the light of the present study, the effects of FFH on the diversity of lichens do not seem severe, FFH does decrease the amount of dead wood, and thus the effects on other saproxylic species need to be studied as well.

JYVÄSKYLÄN YLIOPISTO, Matemaattis-luonnontieteellinen tiedekunta

Bio- ja ympäristötieteiden laitos
Ekologia ja evoluutiobiologia

Jäntti, M.:	Energiapuun korjuun vaikutukset lahopuun ja lahopuulla elävän makrojäkälälajiston monimuotoisuuteen hakkuualoilla
Pro Gradu –tutkielma:	33 s.
Työn ohjaajat:	Dos. Panu Halme, FM Jenna Purhonen
Tarkastajat:	
Huhtikuu 2016	

Hakusanat: bioenergia, habitaatin heterogeenisyys, hakkuutähteet, häiriöt, lahopuusta riippuvaiset lajit, lajimäärä-pinta-ala-suhde (SAR), makrojäkälät, *Picea abies*

TIIVISTELMÄ

Energiapuuta käytetään yhä enemmän uusiutuvan energian lähteenä. Energiapuun korjuussa hakkuutähteitä eli kantoja, oksia ja latvuksia kerätään päätehakkuun ja harvennuksen yhteydessä hakkuualoilta. Tämä vähentää erityisesti pienikokoisen lahopuun ja kantojen määrää. Lahopuu on tärkeä resurssi boreaalisissa metsissä, mutta sen määrä talousmetsissä on alhainen luonnonmetsiin verrattuna. Määrän väheneminen edelleen energiapuun korjuun seurauksena voi johtaa lahopuusta riippuvaisen monimuotoisuuden vähenemiseen, minkä vuoksi on tärkeää tutkia energiapuun korjuun monimuotoisuusvaikutuksia. Teoriat pinta-alan ja habitaatin heterogeenisyyden vaikutuksesta lajimäärään ovat yksiä tärkeimmistä lajimäärää määrittävistä teorioista. Jäkälät käyttävät lahopuuta kasvualustanaan, jolloin lahopuun pinta-alan sekä sen heterogeenisyyden vähenemisen voidaan ennustaa vaikuttavan jäkälien lajimäärään. Tässä tutkimuksessa tutkittiin energiapuun korjuun vaikutuksia lahopuun sekä lahopuulla elävien eli epiksyylisten makrojäkälien monimuotoisuuteen. Tutkimuksessa käytettiin 12:sta noin 8 vuotta sitten hakattua hakkuuaukkoa Keski-Suomessa. Korjuu aloilta energiapuu, eli suurin osa kannoista ja muista hakkuutähteistä kuten oksista, oli kerätty päätehakkuun yhteydessä, ja kontrollialoilta ei. Tietoa kerättiin jokaisella hakkuualalla 3 koealalta mitatuista lahopuun määrästä, ominaisuuksista ja lahopuulla elävästä makrojäkälälajistosta. Vaikka lahopuun kokonaispinta-ala tai tilavuus ei eronnut käsittelyjen välillä, energiapuun korjuu näytti vähentävän ainakin kantojen ja runkojen määrää hakkuualoilla. Energiapuun korjuu vaikuttaa kuitenkin lahopuun määrään ristiriitaisesti, sillä se myös nostaa kannonkappaleita ja juuria maan pinnan yläpuolelle. Korjuualojen oksilla kasvoi vähemmän jäkälälajeja kuin kontrollialojen oksilla, ja myös korjuualojen kannoilla näytti kasvavan vähemmän jäkälälajeja kuin kontrollialojen kannoilla. Korjuun vaikutusta kokonaislajimäärään tai -monimuotoisuuteen ei kuitenkaan havaittu, mikä saattoi johtua siitä, että muiden kasvualustojen saatavuus riitti korvaamaan oksien ja kantojen menetyksen. Jäkälälajimäärän ja suurikokoisen lahopuun pinta-alan välillä havaittiin positiivinen suhde, kun taas lahopuun monimuotoisuus ja jäkälälajimäärä eivät korreloineet keskenään. Hypoteesi lahopuun monimuotoisuuden vaikutuksesta jäkälälajimäärään ei siis saanut tukea. Tämän tutkimuksen suurikokoinen lahopuu koostui rungoista ja nostetuista kannoista. Rungot ovat tunnetusti tärkeä kasvualusta jäkälille, mutta nostettujen kantojen roolia jäkälien ja muidenkin lahopuusta riippuvaisten lajien kasvualustana olisi mielenkiintoista tutkia lisää. Vaikka tämän tutkimuksen tulosten perusteella energiapuun korjuun vaikutukset jäkäliin eivät vaikuta kovin vakavilta, myös muiden lajiryhmien vasteet energiapuun korjuuseen täytyy ottaa huomioon.

Contents

APPENDIXES

1. INTRODUCTION

Increasing the use of renewable energy resources has a big role in the EU's strategy against climate change (European Commission 2014). Countries with intensive forestry such as Finland and Sweden have responded to this target by using increasing proportions of wood for energy production (Ericsson *et al.* 2004, Helmisaari *et al.* 2014). Forest-fuel harvesting (FFH) is one way to utilize wood for this purpose. In this thesis, FFH is referred to as the collection of logging residues, stumps, branches, and tops, as well as stemwood for energy production in connection with thinning and clear-cutting forests (Äijälä *et al.* 2010). Using large amounts of forest-fuel for energy production is a rather new phenomenon and its scale is increasing rapidly (Verkerk *et al.* 2011). Drivers behind this rapid development lie in political will, subsidies, and investment in research and technology of the forest energy sector (Björheden 2006, Hakkila 2006). Finland has committed to increase the usage of renewable energy up to 38 % by 2020 (Valtioneuvosto 2008) and reaching this goal depends heavily on the use of forest chips, which are produced from logging residues collected from clear-cuts and thinnings, for energy (Hakkila 2006, Helmisaari *et al.* 2014). In 2012, stumps were collected from about 10 % and other logging residues from about 30 % of all clear-cuts, and there is potential for increase (Asikainen *et al.* 2013). Therefore, the impact of FFH on the biodiversity in managed forests will also increase in the near future (Bouget *et al.* 2012).

In Finland, it is estimated that there are 4 000–5 000 species which are dependent on dead wood, which is 20–25 % of all the forest-dwelling species (Siitonen 2001). Clear-cutting is an anthropogenic disturbance that removes most of the wood and future dead wood away from the forest affecting also the deadwood-dependent species diversity (e.g. Fridman & Walheim 2000, Siitonen *et al.* 2000, Gibb *et al.* 2005). The amount and quality of dead wood is already one of the most noteworthy differences between managed and natural forests (Kruys *et al.* 1999, Gibb *et al.* 2005). FFH can be seen as an additional disturbance adjacent to the clear-cutting or thinning, or as intensifying the effects of the existing disturbance. FFH causes further dead wood losses (Rudolphi & Gustafsson 2005, Eräjää *et al.* 2010), soil disturbance (Walmsley & Godbold 2009, Kataja-aho *et al.* 2011, 2012), and a potentially further decrease in biodiversity (Bouget *et al.* 2012). The decrease in biodiversity can be predicted based on one of the most explored and proved theory explaining species richness patterns – species-area relationship (SAR) (Arrhenius 1921, Gleason 1922, Rosenzweig 1995), which states that with decreasing area, such as the area of dead wood resource, species richness will decrease as well.

As the scope of FFH constantly increases, it is important to study the effects of this management on biodiversity. Being a new phenomenon on a large scale, the studies concerning the effects of FFH are still scarce and concentrate only on a few species groups (Bouget *et al.* 2012). In order to implement FFH in a sustainable manner from a biodiversity point of view, more information is needed. This thesis discusses the effects of FFH on the amount and quality of dead wood together with the effects on the epixylic lichen diversity.

1.1. Biodiversity and patterns of species richness

1.1.1. Biodiversity

Biodiversity can be viewed on three levels: species, community, and landscape (Gaston 1996, Purvis & Hector 2000, Hooper *et al.* 2005). Genetic diversity is observed at the species level, whereas species diversity is measured at the community level. The landscape level considers larger areas that contain different communities i.e. different assemblages of populations of different species that exist together in space and time. At this level habitat connectivity and the abundance of different habitats become important (Cain *et al.* 2011).

The focus of this thesis is at the community level and thus at species diversity. The term “species diversity” signifies the combination of species evenness (relative abundances of species) and species richness (number of species) (Cain *et al.* 2011). In a community where species richness is high but most individuals belong to few species, species diversity is lower than in a community where with equal richness the abundances of different species are more even (Purvis & Hector 2000).

1.1.2. Patterns of species richness: area, energy and habitat heterogeneity

The theories of species-energy relationship (SER) and species-area relationship (SAR) are some of the most studied and demonstrated theories of species richness (Connor & McCoy 1979, Rosenzweig 1995, Evans *et al.* 2005). It was already observed in 1808 by Alexander von Humboldt that species richness increases from the poles towards the Equator (von Humboldt 1808 cited by Hawkins *et al.* 2003). This pattern has been explained by the greater amount of solar energy at the Equator relative to the poles, and has led to the theory of species-energy relationship (SER) (Wright 1983, Rosenweig 1995). Species-area relationship (SAR) is another phenomenon that has been observed for a long time – the number of species tends to grow with increasing area (Arrhenius 1921, Gleason 1922). However, the theories are interconnected, because a larger area also receives more solar energy than a smaller area. Thus, area is often seen as a proxy of energy (Wright 1983, Hawkins *et al.* 2003, Honkanen *et al.* 2010).

The availability of energy can be measured not only by the amount of solar energy but also by the amount of productive energy – energy that can be converted into biomass by photosynthetic organisms (Evans *et al.* 2005). There are some contradictory results on whether productive energy or solar energy better predicts species richness (Hawkins *et al.* 2003, Honkanen *et al.* 2010). Different species groups respond to the amount of productive energy in different ways, and the relationship of diversity and productivity can be positive, negative, hump shaped, or something in between, depending also on the scale that is being observed (Rosenzweig 1995). Some organisms, such as lichens, get their energy from photosynthesis and are therefore not dependent on productive energy in the form of biomass. In cases like this, the species richness should be restricted by area as SAR predicts.

There are three main hypotheses to explain SAR (see Connor & McCoy 1979, Shen *et al.* 2009). The first and simplest explanation is the random placement hypothesis that suggests that ecological processes do not explain SAR, but that in a larger area there are more likely more individuals and thus more species than in a smaller area (Arrhenius 1921, Connor & McCoy 1979). The range over which the species richness grows within this phenomenon depends on the organisms and ecosystems under observation (Whittaker & Fernández-Palacios 2007). The second hypothesis is based on the theory of island biogeography (MacArthur & Wilson 1967) where the species richness is determined by the dynamics of immigration and extinction rates in relation to the size and degree of isolation of the island (Whittaker & Fernández-Palacios 2007). According to the theory, there are more species on a larger island than on a smaller one because the size of the island enables larger population sizes and thus lowers the extinction risk of species. However, many other explanations for the phenomenon have been demonstrated as well (Schoener 2010). Thirdly, the hypothesis of habitat diversity states, that with increasing area there are more likely to be more new habitats and thus more species (Williams 1964, MacArthur & Wilson 1967, Lack 1969).

Another, but closely related theory for species richness is the theory of habitat heterogeneity (MacArthur & MacArthur 1961, Lack 1969, Nilsson *et al.* 1988). The theory originated as the hypothesis of habitat diversity explaining SAR but was later on mixed with habitat heterogeneity (Nilsson *et al.* 1988). According to the diversity hypothesis, species richness grows with area because more habitats are added, whereas habitat heterogeneity would include also the within habitat variation in addition to between habitat variation. However, the terms of diversity and heterogeneity have been used mixed in the literature (Nilsson *et al.* 1988).

There has been a lot of discussion about the driving forces of SAR. Study results range from either area *per se* or habitat diversity/ heterogeneity being seen as the only driving force of SAR to both having an equally important role in it (e.g. Nilsson *et al.* 1988, Mac Nally & Watson 1997, Tews *et al.* 2004, Jüriado *et al.* 2006, Kallimanis *et al.* 2008). However, disentangling the effects of area and heterogeneity has been found to be difficult since they tend to correlate with each other (MacArthur & Wilson 1967, Rosenzweig 1995, Kallimanis *et al.* 2008).

1.2. The structure and disturbance dynamics of managed forests

Habitat transformation, mainly by humans, is the single largest threat to biodiversity (Vitousek *et al.* 1997). Forests all over the world are under heavy management, which is one reason for a major decline in biodiversity (Foley *et al.* 2005). The largest differences between managed and natural forests are in the structure of the forest (e.g. age and tree species distribution) and the amount of dead wood (e.g. Siitonen 2001, Jonsson *et al.* 2005) which is reflected also in species richness (e.g. Juutilainen *et al.* 2014). Species richness is correlated with dead wood volume especially in boreal forests (Siitonen 2001, Lassauce *et al.* 2011), but the volume and quality of dead wood indicate the diversity of dead wood dependent species more so than the overall diversity (Juutinen *et al.* 2006). The landscape structure differs between managed and natural forests as well: managed forests are more fragmented, in smaller patches, and simpler shapes. Many old-growth species do not appear on managed forest patches because the patches do not reach old enough age or are too far apart for colonization (Nordén *et al.* 2013). The proportion of forest reserves in the landscape is too low to preserve all forest biodiversity (Hanski 2000). For example, in southern Finland the proportion of old-growth forests is only 0.5 %. Therefore, in order to preserve the remaining biodiversity of boreal forests, new forestry practises are needed that can mimic natural disturbance dynamics better than the management of today (Niemelä 1999, Bengtsson *et al.* 2000).

The most important natural disturbances that can initiate secondary succession in boreal forests are fire, storm fellings, snow, browsing, or insect outbreaks (Niemelä 1999, Gromtsev 2002). All of the most important disturbances can create gaps of different sizes in boreal forests (Kuuluvainen 1994). Large-scale disturbances such as fires are rare which emphasizes the role of gap phase dynamics in forest regeneration. However, fire has been seen as the most prominent disturbance in natural forests although its importance in boreal ecosystems may have been overemphasized (Engelmark 1999, Bergeron & Fenton 2012). Disturbances differ in their size, intensity, and frequency (Turner *et al.* 1998), and diversity is often highest on intermediate disturbances (Rosenzweig 1995). Fire is a disturbance of spatially variable intensity, size, and frequency, according to the predominant climate, dominant tree species, etc. (Gromtsev 2002). Fire has often been compared to clear-cutting because they both can start secondary succession in a forest and can be similar in their intensity and size (Niemelä 1999). However, the dynamics of artificial tree removal differ from natural disturbances in several ways: the frequency is lower, clear-cut is a more uniform disturbance than fire, it leaves less organic material behind, and does not create charred wood of which many species are dependent on. Although fire instantly kills many organisms, the long-term effects on biodiversity are positive (Vanha-Majamaa *et al.* 2007).

1.3. Dead wood as a resource: availability and quality

1.3.1. Abiotic and biotic factors affecting the characteristics of dead wood

When a tree dies, it becomes dead wood, and its productive energy is released for the use of dead wood dependent organisms (Stokland *et al.* 2012). A tree may die either from abiotic or biotic factors: for example, suddenly in a storm, fire, or drought, or slowly by old age, competition, or fungal disease. The cause of death can also be an anthropogenic disturbance such as felling.

The surrounding environment also affects the biotic factors, such as the growth rate of a tree, which can affect the tree's chemical composition and thus the saproxylic organisms (defined as "any species that depend, during some part of their life cycle, upon wounded or decaying material from living, weakened, or dead trees") (Stokland *et al.* 2012). The chemical properties of a tree change again when the tree dies and decomposition starts. Fungi are the most important decomposers in terrestrial ecosystems (Boddy *et al.* 2008, Stokland *et al.* 2012), but wood is decomposed also by, for example, a large number of invertebrates (Ulyshen 2016) and bacteria (Greaves 1971). Different decomposition processes produce dead wood with different physical and chemical properties, and different decomposers create different kind of microhabitats, such as loose bark or trunk cavities (Stokland *et al.* 2012). The rate of decay depends for example on the tree species, size, and the decomposer organism (Harmon *et al.* 1986). Dead wood is inhabited by decomposers but also by other members of the saproxylic food web, such as lichens that grow on the surface of dead wood, or birds and mammals (Stokland *et al.* 2012).

Both abiotic and biotic factors affect the characteristics of the forming dead wood and the saproxylic species diversity (Stokland *et al.* 2012). Abiotic factors of dead wood, such as temperature and moisture, are determined by the surrounding environment, and can define the habitat suitability for a species or species group. For example, many invertebrates favour dry and sun-exposed habitats (Jonsell *et al.* 1998, Lindhe *et al.* 2005). A clear-cut is an open habitat that can offer substitutive sun-exposed habitats for organisms. On these open habitats, it matters how the piece of dead wood is situated, whether it is standing or lying, and whether it is exposed to sun or buried in the soil (Stokland *et al.* 2012). Lichens can favour this kind of habitats as well. When comparing lichens and their competitors bryophytes on dead wood, bryophytes prefer moist logs in advanced stages of decay whereas lichens are more abundant on standing dead trees and decorticated stems (Caruso & Rudolphi 2009, Stokland *et al.* 2012). Environmental factors, such as moisture and temperature, can also affect the rate of decay (Harmon *et al.* 1986). Fluctuating temperature can enhance both the rate of decay and species richness of wood-decaying fungi (Toljander *et al.* 2006).

The tree species defines much of the species diversity it hosts (Stokland *et al.* 2012). Coniferous trees differ from deciduous trees in their chemical and physical structure, and many wood-inhabiting organisms are strictly confined to either coniferous or deciduous trees (Jonsell *et al.* 1998, Stokland *et al.* 2012). Different tree species differ also in the thickness of bark, which affects the colonization of species and provides insulation against environmental changes especially in the early stages of decay when the bark is still firmly attached to the trunk (Stokland *et al.* 2012).

1.3.2. Volume and size of dead wood

In natural boreal forests, the volume of dead wood typically varies between 60 and 120 $m^3 ha^{-1}$ (Siitonen 2001). Modern forestry has reduced the volume of dead wood (especially of large diameter) in managed forests drastically, with estimates for dead wood quantity varying between 2 and 30 % of the amount in natural forests (Fridman & Walheim 2000, Siitonen 2001, Gibb *et al.* 2005). Often the dead wood volume in managed forests is estimated to be between 4–10 m^3 ha^{-1} (Jonsson *et al.* 2005) but the estimates have traditionally covered only large diameter deadwood. There are a few key aspects to the amount of dead wood: the number of dead wood pieces, the size of dead wood, and the quality of dead wood (which is determined by the above-mentioned dead wood characteristics such as decay stage or moisture content).

Tree size is an important characteristic of dead wood because many saproxylic species are able to inhabit trunks of only a certain diameter range. This has been best documented on fungi (Nordén *et al.* 2004, Juutilainen *et al.* 2014) and beetles (Foit 2010, Brin *et al.* 2011). The size of dead wood is usually described by diameter. It is important to bear in mind that tree diameter increases with age, and the characteristics also change with time, and therefore, it can be difficult to disentangle the reasons behind the species richness patterns (Stokland *et al.* 2012).

Dead wood of large diameter i.e. coarse woody debris (CWD) (usually ≥ 10 cm) is often more species rich and often has more red-listed species than small diameter dead wood i.e. fine woody debris (FWD) (usually < 10 cm) (Kruys *et al.* 1999, Nilsson *et al.* 2001, Schmit 2005). There are several reasons for this. Conditions such as moisture, temperature, diameter, or decay stage are more variable in large logs – they can offer more microhabitats than smaller logs (Samuelsson *et al.* 1994, Halme *et al.* 2013). Large logs can for example reach later stages of decay than FWD without being overgrown by vegetation (Kruys *et al.* 1999). In addition, large logs are simply larger in volume and so forth more spacious and able to provide resources for more species. Thirdly, large logs persist longer in the environment resulting in a longer colonization period (Samuelsson *et al.* 1994, Stokland *et al.* 2012) because FWD decays faster than CWD (Boddy *et al.* 2008).

However, Kruys & Jonsson (1999) compared equal surface areas of spruce (*Picea abies*) FWD and CWD and found that the species richness of cryptogams between them did not differ. When comparing equal volumes of dead wood, FWD actually had more species than CWD. This suggests that the amount of total surface area of dead wood can have a surprisingly great effect on the species richness. Thus, in managed forests where the amount of dead wood and especially CWD is low in general, the importance of small diameter dead wood increases (Kruys & Jonsson 1999). FWD has been observed to be important especially for many species of fungi (Nordén *et al.* 2004, Juutilainen *et al.* 2011), and the species composition between FWD and CWD can be largely different (Allmér *et al.* 2006). Ignoring FWD in species inventories can lead to biased population size estimates and incomplete species lists of saproxylic species (Juutilainen *et al.* 2011). However, it has to be noted, that only few red-listed fungi are found from FWD on clear-cuts (Allmér *et al.* 2006, Toivanen *et al.* 2012).

In addition to the size, the form and location of dead wood matter to the saproxylic species (Stokland *et al.* 2012). Dead wood varying in size, form, and abiotic factors can offer different kinds of microhabitats for saproxylic species. Logs are usually the most species rich substrate especially for fungi in natural forests (Hottola 2009, Toivanen *et al.* 2012). However, on clear-cuts, stumps can harbour fauna at least as species-rich as logs (Jonsell & Hanson 2011). Stumps are a new artificial dead wood resource that can act as key alternative microhabitat for many saproxylic species in managed forests where naturally formed deadwood is in low quantities (Walsmley & Godbold 2009, Bouget *et al.* 2012). Species that are able to use stumps are often opportunistic pioneer species that can quickly utilize a suitable resource (Svensson *et al.* 2013). Stumps can host more fungi and lichen species than other logging residues (Allmér *et al.* 2006, Caruso *et al.* 2008).

1.4. Epixylic lichen diversity

Dead wood is also important for species that use its surface as a substrate – the so-called epixylic species (Stokland *et al.* 2012). Epixylic species get their energy primarily from photosynthesis and nutrients from air or water on the wood surface. Some lichens are such organisms. They are fungi that live in symbiosis with one or more photobionts (Stenroos *et al.* 2011). The photobiont provides sugars by photosynthesis, and the fungi (mycobiont) can protect the photobiont from drying and provide water and inorganic nutrients from the air or rainwater. Lichens are often classified into crustose, foliose, or fruticose lichens based on their growth form. Most lichen species are crustose – they are tightly attached to their growth surface and can even live inside plants or rocks. On the contrary, the thallus of foliose and fruticose lichens has leave-like or shrubby form. Foliose and fruticose lichens are usually visible to eye whereas crustose lichens often need magnification for detection and especially for identification. Thus, in contrast to crustose lichens, foliose and fruticose lichens are often called macrolichens. Macrolichens can be used as indicators of the total lichen diversity at least in some temperate forests (Bergamini *et al.* 2007). However, their indicator value for threatened crustose lichens richness is poor.

Dead wood is an essential substrate for 10 % of the epiphytic lichen diversity (Spribille *et al.* 2008). It is a special substrate because it can change in time rather radically. For example, loss of bark changes the lichen species composition on dead wood (Caruso & Thor 2007), and decorticated snags may host numerous species unique to the substrate (Lõhmus & Lõhmus 2001). For some species, dead wood is the only surface they can grow on; these are thus obligate epixylic species (Stokland *et al.* 2012). In Fennoscandia there are 378 saproxylic lichen species known, of which 97 cannot grow on any other substrate (Spribille *et al.* 2008). Most of the obligate saproxylic lichens are crustose lichens such as calicioid (i.e. “pin” lichens), and all obligate macrolichens are members of the *Cladonia*-genus.

The most species-rich dead wood substrates are stumps, logs, and snags (Spribille *et al.* 2008). The importance of snags in particular for lichen diversity is addressed in many studies (Lõhmus & Lõhmus 2001, Humphrey *et al.* 2002, Svensson 2013). The lichen species compositions on stumps and logs resemble each other (Svensson 2013). Therefore, on clear-cuts where logs are scarce, stumps can act as an alternative substrate for lichens. Stumps can offer more diverse microhabitats than FWD and thus are more likely to host rare species not found on other logging residues, although the majority of the lichen species on spruce stumps are generalists (Caruso *et al.* 2008, Svensson *et al.* 2013). Stumps are especially important for *Calicium* and *Cladonia* species (Humphrey *et al.* 2002). The height of the stump matters: lichen species richness increases with increasing stump height (Caruso & Rudolphi 2009, Svensson *et al.* 2013). Species richness tends to grow also with increasing stand age and light availability (Humphrey *et al.* 2002). According to recent studies, FWD has only a minor importance for lichens (Caruso *et al.* 2008, Svensson 2013). However, when comparing equal surface areas of dead wood, FWD can be as species rich as stumps (Caruso *et al.* 2008). Even though most of the species on FWD are common generalists, few cannot grow on any other substrate (Caruso *et al.* 2008).

1.5. Study questions and hypotheses

The aim of this study is to explore the effects of forest-fuel harvesting on the diversity of dead wood and epixylic lichens on clear-cuts. The specific research questions and hypotheses are:

1. **How does forest-fuel harvesting (FFH) affect the amount, characteristics, and diversity of dead wood on clear-cuts?** The question includes the volume and surface area of dead wood, the characteristics (epixyle cover, moisture, etc.) of the remaining dead wood, the distribution of different kind of dead wood categories (branches, stumps, etc.) and size classes (FWD, CWD, stumps), and the diversity when it comes to different characteristics and size of the dead wood. I hypothesize that the heavy harvesting machinery affects such characteristics as size, moisture, distance from the ground, and possibly the epixyle cover by tramping dead wood into the ground and destroying it (Hautala *et al.* 2004, Bouget *et al.* 2012). By focusing on two dead wood categories: branches and stumps, I hypothesize, that FFH decreases their amounts and changes the distribution of different dead wood categories (Eräjää *et al.* 2010). That way FFH would be expected to decrease also the diversity of dead wood.
2. **How does forest-fuel harvesting (FFH) affect the richness and diversity of epixylic macrolichens on clear-cuts?** I hypothesize that based on the theory of species area relationship (Arrhenius 1921, Connor & McCoy 1979, Rosenzweig 1995) the lichen species richness will decrease due to the decreased amount of growth surface. In addition, if FFH reduces the variability of different kinds of dead wood resources, it would then also decrease the lichen species richness, based on the theory of habitat heterogeneity and species richness (Williams 1964, MacArthur & Wilson 1967, Lack 1969). Based on previous studies, I hypothesize, that the effects will be more severe on the lichen diversity on stumps compared to the fine woody debris (Caruso *et al.* 2008, Svensson 2013).

2. MATERIALS AND METHODS

2.1. Study sites and experimental plots

This study was conducted in the southern boreal zone (Ahti *et al.* 1968). There were 12 study sites. Most of the sites were located in the Central Finland region in Jyväskylä (2), Toivakka (2), Jämsä (4), and Saarijärvi (2). In addition, 2 sites were in Suonenjoki, Northern Savonia, close to the border of Central Finland (Appendix 1). The study sites were dominated by Norway spruce (*Picea abies*) and clear-cut between years 2006–2008. Clear-cuts of that age have had time for lichen colonization but the dead wood on the sites has not decayed too much and has not been covered completely by bryophytes (Caruso *et al.* 2008). The sites were classified as forest-fuel harvested (FFH) and control sites according to the human activity after the clear-cut, and will also be treated as different treatments in this thesis. There were 7 FFH sites. From 5 of these sites most branches, tops, and stumps had been collected after the clear-cuts, and from 2 of them, only branches and tops had been collected. There were 5 control sites where the residues had not been collected. Each FFH site had a control site as a pair in the same region. An exception was one site in Jyväskylä. It was revealed after the data collection, that from a presumable control clear-cut, Saanila, branches and tops had been collected contrary to the expectations. In the present case the impact of the missing branches and tops on biodiversity was evaluated to be larger than the impact of the existent stumps (which were scarce) and therefore Saanila was categorized as a FFH site. Because of the status change of this site, there was an unequal number of FFH and control sites. Another exception was a FFH site in Jämsä, called Perälä, where the stumps had not been harvested contrary to the expectations (Appendix 2). All sites were either owned by the Biofore Company UPM or owned by private forest owners but harvested by UPM.

At each of the sites, 3 experimental plots with the size of 10 m x 5 m were founded (Fig. 1). First, the approximate center of the site was determined and marked. Then the northeast corner of the first plot was positioned by walking 10 m into a randomized compass direction. The second plot was positioned according to a similar procedure except that now the distance to the centre was 20 m and for the third plot 30 m. If the plot was going to be positioned partly outside the clear-cut or within a 2-meter distance to the border of the site, a new direction was taken. The first corner was marked to be able to find the plot again. If there was anything unusual – such as a road going through the plot – the first corner was transformed to be a southeast corner, southwest corner, or a northwest corner respectively as long as an undisturbed plot was found. In few cases a new compass direction had to be taken.

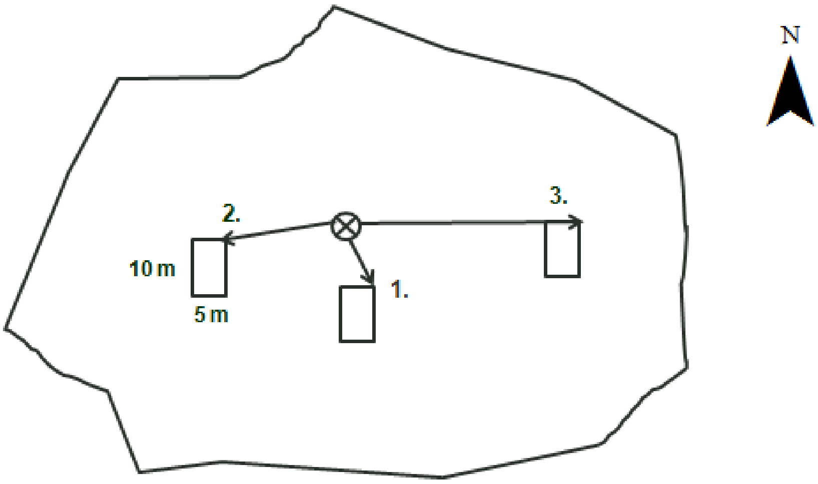


Figure 1. An example illustration of the experimental design on a clear-cut. The approximate centre of the plot was estimated (circle with a cross). Three random compass directions (arrows) were taken and then used for positioning the northeast corner of the experimental plots, which were the size of 10 x 5 m. The other corners were in southeast, southwest and northwest. The distance between the centre and the northeast corner was 10 m for the first (1.), 20 m for the second (2.), and 30 m for the third (3.) plot.

2.2. Data collection

The fieldwork was conducted between 9.6. –16.7.2015. All dead wood pieces that had their basal end inside the plot were examined except the ones that were less than 20 cm long or less than 2 cm in diameter. If a stump was on the border, and more than half of it was inside, it was included in the study. Dead wood that was completely under the ground or a thick layer of humus was ignored because of practical reasons and because it was not relevant for lichens. If a dead wood piece was partly underground or under humus, the aboveground part was taken under investigation if it met the above requirements for the minimum length and diameter. Only the aboveground part of dead wood was considered in the analyses. Therefore, the study can describe the dead wood diversity of only the aboveground dead wood on clear-cuts.

The pieces of dead wood were classified into categories of logs, stumps, pieces of stumps, uprooted stumps, roots, branches, and snags. Length and diameter from both ends were measured to calculate the volume and area of the pieces. In cases of stumps the length was measured from the cutting surface to the ground, and the diameter was measured only from the cutting surface. Uprooted stumps' length was measured starting from the cutting surface and ending to the tip of the biggest root. The volume for logs, branches, roots, snags, pieces of stumps, and uprooted stumps was calculated using the formula for a truncated cone volume (Table 1). The area was based on the formula for the mantle of the truncated cone area. The gained area was then divided by 2 because that is the approximate proportion that could have been colonized by lichens when the other half was facing the ground (see Caruso *et al.* 2008). Stump volume and area were calculated using the formula for cylinder volume and area (Table 1). There were a few pieces that were in the shape of a board, and the volume and area for those pieces were calculated using the formula for rectangular cuboid (Table 1). Also in these cases the original area was divided by 2.

Table 1. Formulas for volume (V) and area (A) calculations for different dead wood categories.

Dead wood category	**Shape**	**Formula**	**Variables**
Logs, branches, roots, snags, pieces of stumps, uprooted stumps	Truncated cone	$V = \frac{\pi h}{3}(r_1^2 + r_1 r_2 + r_2^2)$ $A = (\pi(r_1 + r_2)\sqrt{(r^2 + h^2)})/2$	h = height, r_1 = radius of the narrower end, r_2 = radius of the wider end
Stumps	Cylinder	$V = \pi r^2 h$ $A = h2\pi r$	r = radius, h = height
Board shaped logs	Rectangular cuboid	$V = abc$ $A = (2(ab + bc + ac))/2$	a = length, b = width, c = height

The tree species of the studied dead wood was identified if possible. Distance to the ground was measured with a measuring tape from the central point of the dead wood piece. The degrees of bark and epixyle cover (organism living **on** dead wood: bryophytes and lichens) were estimated by eye in percentages. Moisture of the dead wood was measured with a 2 pin probe digital mini moisture meter and thermometer, and temperature of the dead wood was measured with a Biltema, Art. 17-236, Infrared Thermometer IRT 260. The measurements were taken from 4 different places on the dead wood for calculating an average for the piece: on top of the wider end, on top of the middle, on the side of the middle and on top of the narrower end. In cases of stumps, the measurements were taken from the cutting surface, one side of the stump, the upper surface of the biggest root (if aboveground) and one side of the biggest root. If the stump was uprooted, the first measurements were taken from the upper surface and other measurements from the biggest root as previously.

The decay stage was measured following a scale from 1 to 5 (Hautala *et al*. 2004, Lõhmus & Kraut 2010), 1 being fresh dead wood and 5 fully decayed. Dead wood pieces belonging to decay stage 5 were not considered since measuring the above mentioned characteristics of them would have been impossible.

At few sites, a thinning-cut had occurred shortly before the fieldwork (Appendix 2). At these plots we removed the fresh dead wood from the plots by hand to keep the conditions as similar as possible compared to the other sites.

All macrolichen species were identified from all of the studied dead wood pieces on the plots. Crustose lichens were ignored. An exception was *Hypocenomyce scalaris* because of its easy detectability and identification. Specimens were taken in all uncertain cases using a knife. Dried samples were identified by using microscopy, chemicals, and UV-light during the autumn of 2015. The identifications were on a species-level when possible and otherwise on a genus-level. Only species-level identifications were used in the analyses, together with genus-level identifications for genera that did not occur in the data at the species level.

2.3. Statistical methods

The total volume of dead wood was compared between forest-fuel harvested (FFH) and control sites with independent two-sample t-test. To examine the volumes in different size classes, the dead wood data was divided by size into fine and coarse woody debris (FWD and CWD, respectively) and stumps (stumps of all sizes except the uprooted ones). Large dead wood pieces (diameter ≥ 10 cm and length ≥ 130 cm) which were not stumps, were categorized as CWD and the rest as FWD (see Gibb *et al.* 2005, Eräjää *et al.* 2010). The volume of stumps, FWD, and CWD was compared separately between treatments with independent two-sample t-test and Mann-Whitney U-test. The t-test was used for FWD and Mann-Whitney U-test for CWD and stumps. The surface area of dead wood was also compared between treatments in all classes, and the classes combined, using independent two-sample t-test, except for the surface area of FWD for which an independent sample Mann-Whitney U-test was used. In addition, the dead wood distribution was examined by looking for differences in the volume and surface area of different dead wood categories between treatments. Independent two-sample t-test was used for branches, pieces of stumps, roots, and stump areas, and independent sample Mann-Whitney U-test was conducted for logs, stump volumes, and uprooted stumps. The volume and area of snags was not compared because snags occurred only on 3 sites. All the volumes and areas were transformed into cubic and square meters per hectare based on the investigated areas on the clear-cuts.

The characteristics of the sampled dead wood were compared between FFH and control sites with independent two-sample t-test. The tested characteristics were the basal diameter, distance to the ground, epixyle cover, bark cover, temperature, moisture, and decay stage.

Diversity indices were created for dead wood on each site. The following variables were used in the diversity index calculation because they represent the general variation in the dead wood quality: tree species, dead wood category (logs, stumps, etc.), diameter (≤ 10 cm, > 10 cm), decay stage (2, 3, 4), distance to the ground (0, $0 < x \leq 10$, > 10 cm), and bark cover (0, $0 < x \leq 50$, > 50 %). Epixyle cover was excluded because it included lichens and thus could not have been compared with lichen diversity. The number of different dead wood types was then constituted from the number of different combinations of the above variables. The used index was the exponential Shannon diversity index (H'):

$$H' = \exp(-\sum_{i=1}^{S} p_i \ln p_i)$$

Where p_i stands for the proportion of individuals belonging to the i:th species (or the proportion of the dead wood pieces belonging to the i:th dead wood type) and S for the species richness (or the number of different dead wood types) (Shannon 1948). An exponential form was used in order to convert indices into effective numbers of species or "true diversities" (Jost 2006). This index was chosen because it best describes the heterogeneity of the dead wood and species richness (Haines-Young & Chopping 1996, Nagendra 2002). The created diversity indices for each site were compared between treatments with independent sample Mann-Whitney U-test.

When investigating the effects of FFH on epixylic lichens, first the number of lichen species was compared between treatments with an independent two-sample t-test. After comparing the species richness between treatments, lichen diversity indices were created for each site using the above exponential Shannon diversity index. Each site's total species record was used in the indices. The exponential Shannon diversity indices were then compared between treatments with an independent two-sample t-test. The number of lichen species in different dead wood categories was compared between treatments with the same t-test. The only category that was not tested was snags because they occurred only on few sites.

Finally, the relationship between lichen and dead wood diversity was examined. Analyses of covariance (ANCOVA) were executed using a measure of lichen diversity as a dependent variable and a measure of dead wood diversity as a covariate. Treatment was a fixed factor. First, the indices of lichen and dead wood diversity were compared. The lichen species richness was also compared with dead wood diversity to study the relationship between habitat heterogeneity and species richness. Then, to study the relationship of area and species richness, the total number of lichen species was compared with the total surface area. To set apart the effects of different dead wood classes, the area – species richness comparison was conducted also separately for FWD, CWD, and stumps using ANCOVA. All the statistical tests were conducted with IBM SPSS Statistics 22.0 (IBM Corp. 2013). Diversity indices were calculated with EstimateS 9.1.0 (Colwell 2013).

3. RESULTS

3.1. The amount of dead wood

In total, 1 297 pieces of dead wood were measured. The total volume of dead wood was not statistically different between treatments (mean total volume at control sites: 46.7 $m^3 ha^{-1}$, and at forest-fuel harvested (FFH) sites: 31.7 $m^3 ha^{-1}$) ($t_{10} = 1.20$, $p = 0.26$) (Fig. 2A).

Most of the dead wood pieces were fine woody debris (FWD) (89 %) of which 69 % was branches. The proportion of coarse woody debris (CWD) was only 3 % of all the studied pieces, and 7 % of the pieces were stumps. Although a minority of all pieces were CWD, almost half of the total dead wood volume consisted of it (48 %). FWD and stumps contributed equally to the remaining volume. There were no statistical differences in the dead wood volume of any of the classes between treatments (FWD: $t_{10} = 0.41$, $p = 0.69$; CWD: $U_{12} = 12.00$, $W = 40.00$, $p = 0.43$; stumps: $U_{12} = 7.00$, $W = 35.00$, $p = 0.11$) (Fig. 2A).

The total dead wood surface area tended to be larger on control than on FFH sites ($t_{10} = 2.03$, $p = 0.07$), but when the data was divided into the three size classes the differences could not be detected (FWD: $U_{12} = 12.00$, $W = 40.00$, $p = 0.43$; CWD: $t_{10} = 0.67$, $p = 0.52$; stumps: $t_{10} = 1.43$, $p = 0.18$) (Fig. 2B).

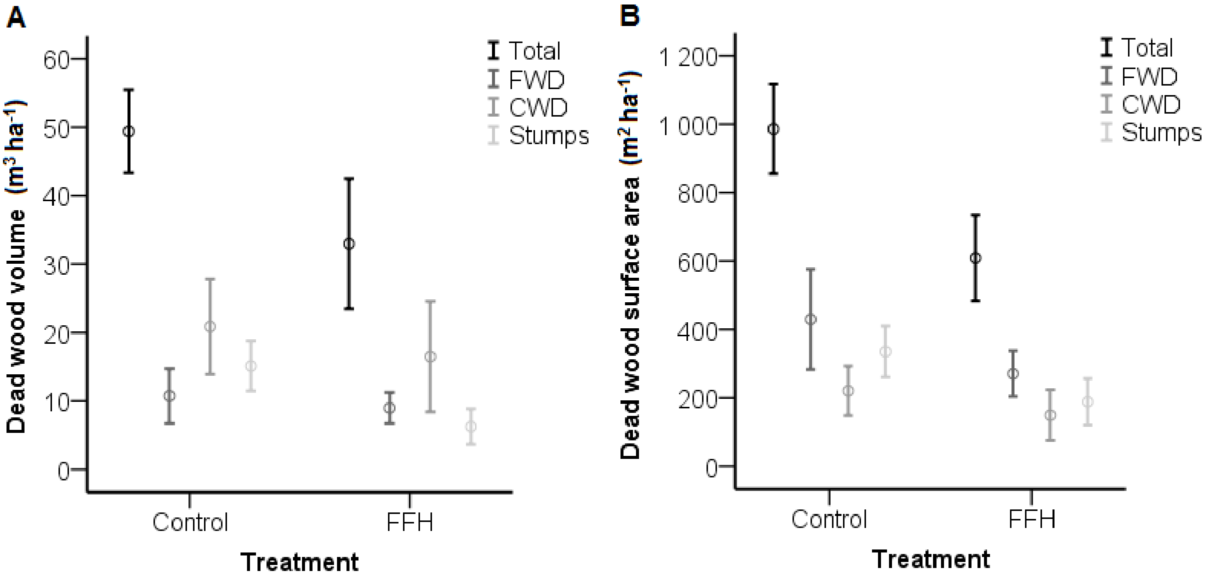


Figure 2. The volume and surface area of the dead wood in forest-fuel harvested (FFH) and control sites (mean ± standard error): (A) the total dead wood, fine woody debris (FWD), coarse woody debris (CWD), and stump volume ($m^3 ha^{-1}$), (B) the surface area of all dead wood, FWD, CWD, and stumps ($m^2 ha^{-1}$).

The volume and area of different dead wood categories did not differ significantly between treatments. Yet the volumes of roots and uprooted stumps seemed to be larger on FFH sites than on control sites. The surface area of roots tended to be larger on FFH sites as well. In addition, the volumes of logs and stumps tended to be larger on control sites than on FFH sites (Table 2) (Fig. 3).

Table 2. The comparison of the volume and surface area of different dead wood categories on forest-fuel harvested (FFH) and control sites. The test statistics that refer to either independent two-sample t-test (t_x) or independent samples Mann-Whitney U-test (U_x & W) and statistical significances (P) are presented.

Dead wood category	Volume/ Area	Test statistics	P
Branches	Volume	$t_{4.2}$ = 1.52	0.20
	Area	$t_{4.2}$ = 1.49	0.20
Logs	Volume	U_{12} = 6.00, W = 34.00	0.07
	Area	U_{12} = 9.00, W = 37.00	0.20
Stumps	Volume	U_{12} = 7.00, W = 35.00	0.11
	Area	t_{10} = 1.43	0.18
Uprooted stumps	Volume	U_{12} = 29.00, W = 57.00	0.07
	Area	U_{12} = 27.00, W = 55.00	0.15
Pieces of stumps	Volume	t_{10} = -1.30	0.22
	Area	t_{10} = -1.37	0.20
Roots	Volume	t_{10} = -2.17	0.056
	Area	t_{10} = -1.94	0.08

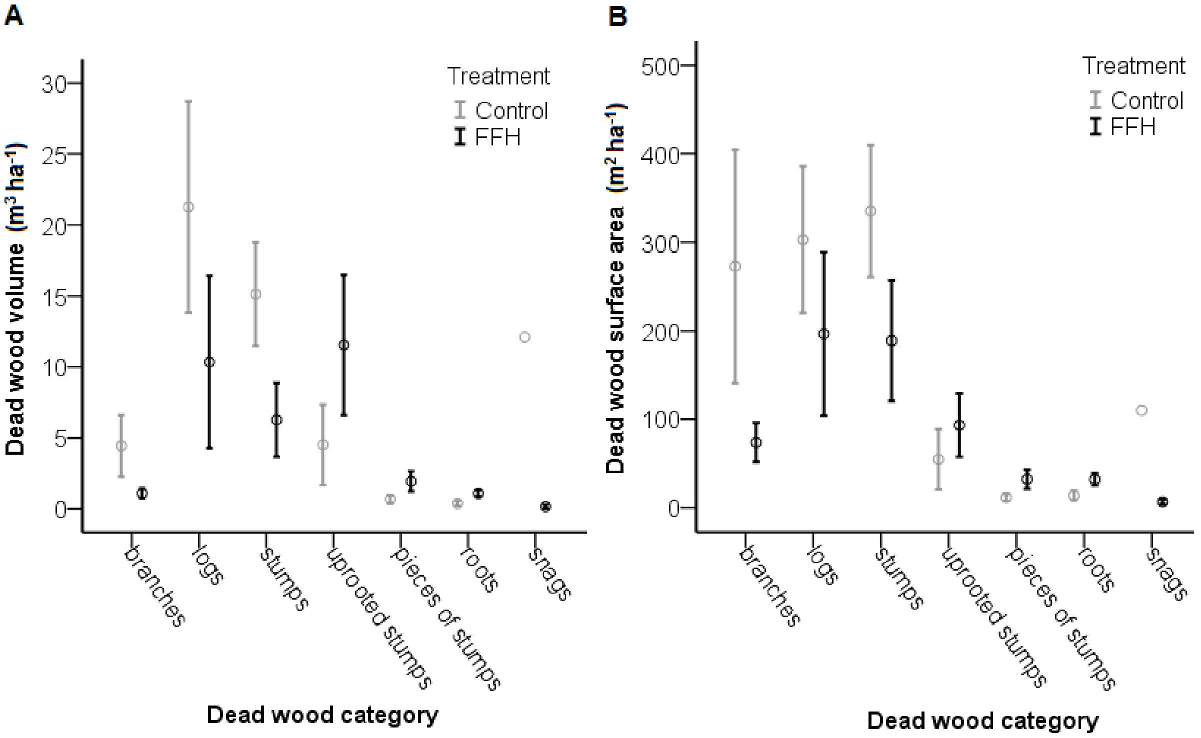


Figure 3. (A) The volume (m^{3}ha^{-1}) and (B) surface area (m^2 ha^{-1}) of branches, logs, stumps, uprooted stumps, pieces of stumps, roots, and snags in control and forest-fuel harvested (FFH) clear-cuts (mean ± SE).

3.2. Dead wood characteristics and diversity

Most of the measured characteristics of dead wood did not differ significantly between treatments (Table 3) (Fig. 4). The only significant difference was found in the epixyle cover (Table 3): the dead wood on FFH sites had on average more epixyle cover than dead wood on control sites (Fig. 4G). The temperature of the dead wood, instead, tended to be higher on control sites (Fig. 4D).

The diversity of dead wood (measured by the exponential Shannon diversity index) was not significantly different between treatments ($U_{12} = 27.00$, $W = 55.00$, $p = 0.15$) (Fig. 4H).

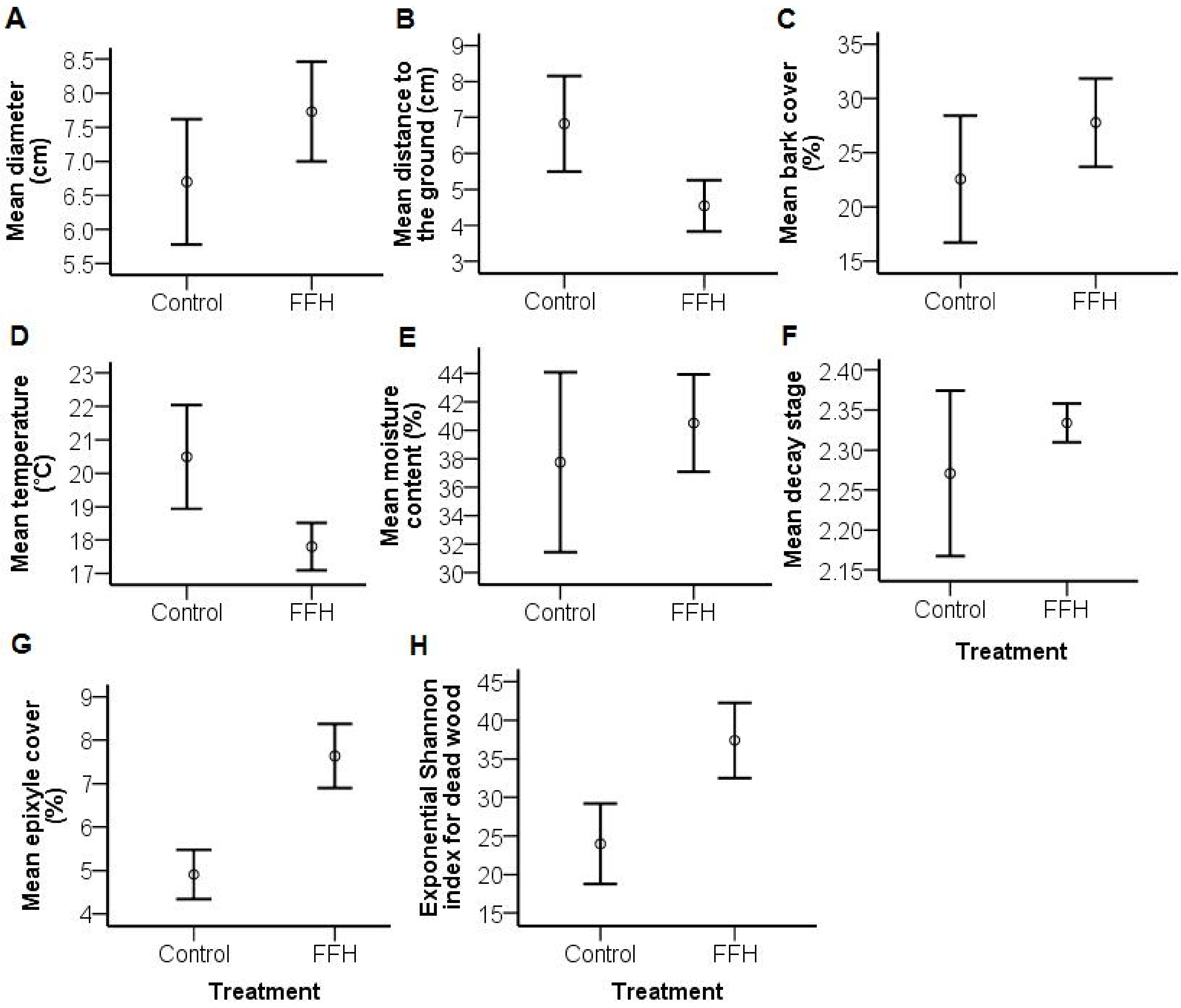


Figure 4. The measured characteristics of dead wood in control and forest-fuel harvested (FFH) sites (mean ± standard error): (A) mean diameter (cm), (B) mean distance to the ground (cm), (C) mean bark cover (%), (D) mean temperature (˚C), (E) mean moisture content (%), (F) mean decay stage (1–5), and (G) mean epixyle cover (%). (H) In addition, some of the variables (tree species, dead wood category, diameter, decay stage, distance to the ground, and bark cover) are combined in the Exponential Shannon diversity index for dead wood in control and FFH sites (mean ± standard error).

Table 3. The results for the comparison of the measured characteristics of dead wood between treatments with independent two-sample t-test. T-values, degrees of freedom (df), and statistical significances (P) are presented in different columns.

Dead wood charasteristic	**t**	**df**	**P**
Diameter (cm)	-0.89	10	0.40
Distance to the ground (cm)	1.63	10	0.13
Bark cover (%)	-0.76	10	0.47
Temperature (˚C)	1.74	10	0.11
Moisture content (%)	-0.42	10	0.69
Decay stage	-0.59	4.4	0.58
Epixyle cover (%)	2.73	10	0.02

(*) significant difference when $p < 0.05$

3.3. Lichen species richness and diversity

In total, there were 2 858 macrolichen observations. Of all observations, 2 220 were identified on species level, 570 on genus level, and 68 were uncertain identifications. In the analyses, a data of 2 252 identifications (species-level and exclusive genus-level observations) was used of which 1 251 identifications were observed on control sites (Appendix 3) and 1 001 on forest-fuel harvested sites (Appendix 4). This accounted for 31 lichen species on control sites and 35 on forest-fuel harvested sites. 1 nearly threatened (NT) species, *Cladonia norvegica*, was found on 2 FFH sites and 1 control site in Toivakka, Suonenjoki, and Saarijärvi, respectively. All other species were of least concern (LC) (Jääskeläinen *et al.* 2010).

There was no statistical difference in either the total number of lichen species ($t_{10} = -1.17$, $p = 0.27$) (Fig. 5A) nor the lichen diversity between treatments ($t_{10} = -0.21$, $p = 0.84$) (Fig. 5B).

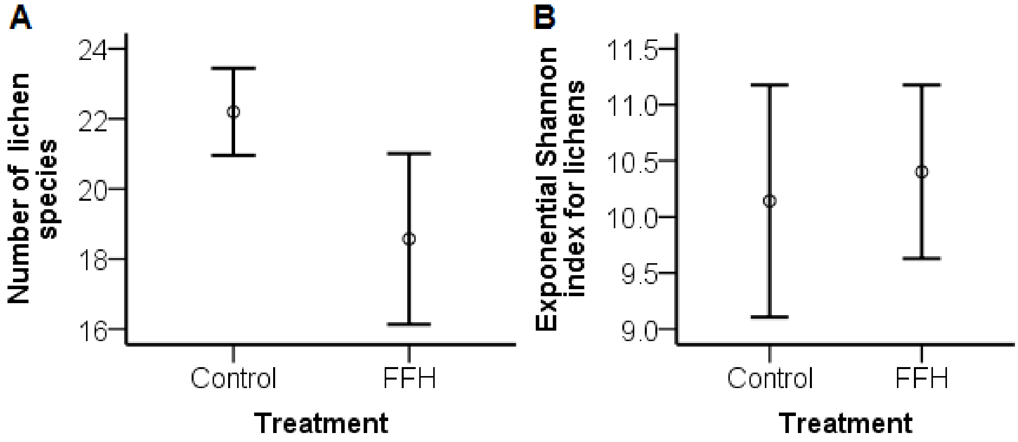


Figure 5. (A) The total number of lichen species and (B) lichen diversity measured by the exponential Shannon index on control and forest-fuel harvested (FFH) sites (mean ± SE).

However, when comparing the species richness on different dead wood categories, there were more species on the branches of control sites than on the branches of FFH sites. Species richness of the other dead wood categories did not significantly differ between treatments (Table 4) (Fig. 6). Although, there tended to be more species on the stumps of control sites than of FFH sites.

Table 4. The results from the independent two-sample t-test comparing lichen species richness between forest-fuel harvested (FFH) and control sites. The number of lichen species was compared within each dead wood category. T-values, degrees of freedom (df), and statistical significances (P) are presented in different columns.

Dead wood category	**t**	**df**	**P**
Branches	3.13	10	0.01*
Logs	1.06	10	0.31
Stumps	1.76	10	0.11
Uprooted stumps	-1.57	10	0.15
Pieces of stumps	-0.72	10	0.49
Roots	0.39	10	0.71

(*) significant difference when $p < 0.05$

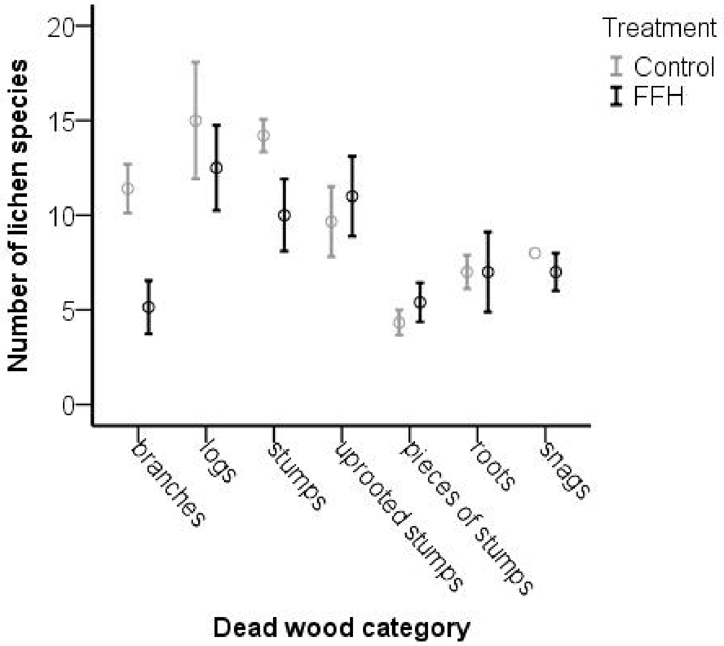


Figure 6. The number of lichen species on different dead wood categories on control and forest-fuel harvested (FFH) sites (mean ± SE).

3.4. Relationship between dead wood and lichen diversity

Neither the dead wood diversity ($F_1 = 1.39$, $p = 0.27$) nor the treatment explained lichen diversity ($F_1 = 0.17$, $p = 0.69$) (measured by the exponential Shannon index) (Fig. 7A). Dead wood diversity did not explain the number of lichen species either ($F_1 = 0.04$, $p = 0.85$, treatment: $F_1 = 1.13$, $p = 0.32$) (Fig. 7B). However, the total surface area of dead wood on the sites did explain the number of lichen species ($F_1 = 7.29$, $p = 0.02$), but treatment did not ($F_1 = 0.04$, $p = 0.84$) (Fig. 7C). When comparing the surface area of different dead wood classes separately, it was found that CWD was the only dead wood class that the lichen richness reacted to (FWD: $F_1 = 1.32$, $p = 0.28$, treatment: $F_1 = 0.56$, $p = 0.47$; CWD: $F_1 = 15.93$, $p = 0.003$, treatment: $F_1 = 0.97$, $p = 0.35$; stumps: $F_1 = 0.16$, $p = 0.70$, treatment: $F_1 = 1.40$, $p = 0.27$).

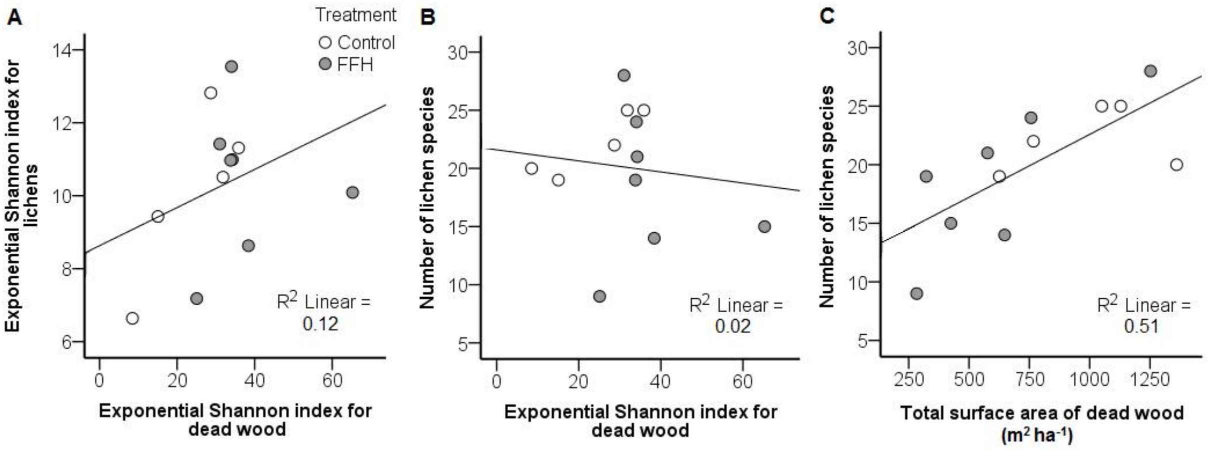


Figure 7. (A) The relation of lichen diversity and dead wood diversity measured by the exponential Shannon diversity index, (B) the relationship of lichen richness and dead wood diversity, and (C) the total number of lichen species compared with the total dead wood area (m^2 ha^{-1}). Each dot represents one site and is labelled by the treatment (white = control, grey = FFH = forest-fuel harvested).

4. DISCUSSION

4.1. The effects of FFH on the volume of dead wood

The overall volume of dead wood was not lower on forest-fuel harvested (FFH) sites than on control sites. The result is contradictory because the function of FFH is to take dead wood away from clear-cuts. However, in a similar study by Eräjää *et al.* (2010) the difference of the total dead wood volume between treatments was not significantly different either. The reason for not detecting a difference in the present study might be in the large variability of the sites and a rather small sampling. More explanations are found from the below- and aboveground aspect: FFH does not only reduce the amount of the dead wood but it also moves dead wood from underground to the surface, for example by uprooting stumps. In this study, this was realised as a seemingly larger volume of uprooted stumps and roots on FFH sites compared to the controls. One other reason could be in the sites themselves. There were 2 FFH sites in this study where only branches had been collected and stumps left behind. The treatment was therefore not identical for all of the FFH sites, which might have confused the results. On one hand, the average volume of FFH sites should have been smaller if stumps would have been collected from all FFH sites. On the other hand, the effect is hard to predict because there would also have been more exposed uprooted stumps and roots left behind.

The total volume of dead wood on both FFH and control clear-cuts was slightly higher than found in a study where dead wood of the same criteria was measured (Eräjää *et al.* 2010). There were small differences in the methods. Eräjää *et al.* (2010) excluded the pieces of dead wood that were partly under the ground, whereas in the present study also those pieces were measured and the aboveground part of them was added to the final volume. The observed dead wood volume is strongly affected by the method of the volume measurements and thus the volumes in different studies cannot often be directly compared (Eräjää *et al.* 2010).

Half of the dead wood volume consisted of CWD and half of FWD and stumps. Logs took the largest share of the total dead wood volume as it also did in Eräjää *et al.* (2010). Since FFH targets mainly FWD (branches and tops) and stumps, half of the dead wood volume in clear-cuts is threatened by the FFH practice according to my results. Although in the present study, no significant difference in the FWD volume between the treatments was found, it has been reported that FFH can reduce the amount of FWD with as much as 70 %

(Rudolphi & Gustafsson 2005). The proportions of FWD, CWD, and stumps varied greatly among clear-cuts, which was most likely the reason for not detecting differences in their volumes between treatments. At a few sites, large trunks had their basal end on the experimental plots, and therefore contributed for most of the dead wood volume on those plots. On the other hand, there were plots where large trunks or other CWD were extremely scarce or even non-existent and FWD and stumps contributed for most of the dead wood volume. Still, about one quarter of the dead wood volume consisting of FWD is a considerable proportion of the total volume and has been recognised in other studies as well (Rudolphi & Gustafsson 2005, Caruso *et al.* 2008, Eräjää *et al.* 2010). However, the number of studies observing the FWD volumes on clear-cuts is still low as the focus in previous dead wood research has been on CWD (Fridman & Walheim 2000, Siitonen 2001, Gibb *et al.* 2005). This is unfortunate as by doing so, these studies have ignored as much as half of the dead wood volume in clear-cuts along with all the saproxylic species – not only lichens – that use stumps and FWD as their resource.

When the dead wood volume was observed from different dead wood categories' perspective, the volume of roots and uprooted stumps seemed to be higher on FFH than on control sites thus being in line with Eräjää *et al.* (2010). The result is not surprising knowing that stump harvesting lifts stumps up from the ground and can break stumps and their roots in the process. The volume of logs seemed to be lower on FFH sites than on the control sites. This might be a consequence of increased traffic by FFH machinery, which may have caused the dead wood to break into smaller pieces and get stamped into the ground (Hautala *et al.* 2004, Bouget *et al.* 2012). Already, a major part of CWD, retained on the stands as dead wood originated before cuttings, or as retention trees, is destroyed by soil scarification (Hautala *et al.* 2004). It has been observed that a notable proportion of old dead wood logs can also be removed during FFH (Rudophi & Gustafsson 2005), although recommendations for good practices of FFH advise retaining all old dead wood (Äijälä *et al.* 2010). However, because of the small size of the present study and the discussed uncertainties with the volume of logs, it can be concluded that more studies are needed to get a reliable picture about this question.

Surprisingly, neither the volume of branches nor pieces of stumps differed significantly between treatments. The volume of stumps, instead, tended to be larger on control sites than on FFH sites. The volume of the pieces of stumps was low in general, which might explain the lack of difference between treatments. What comes to branches, the pattern of the volume in different treatments was relatively clear and variation between sites very high. Therefore, it is highly likely that with a larger sample size the observed difference in both stump and branch volume between treatments would have been significant. Previously, it has been noted that the volume of stumps can decrease with as much as 80 % on FFH sites (Eräjää e*t al.* 2010).

4.2. The effects of FFH on the characteristics and diversity of dead wood

The only significant difference regarding dead wood characteristics between the treatments was the epixyle cover on dead wood. Dead wood on FFH sites had more epixyle cover than on the control sites. Even though the epixyle cover included both lichen and bryophyte cover, most of the cover was bryophytes. The difference between treatments may be explained by more deciduous tree saplings, especially of birch, growing on FFH sites than on control sites. Stump harvesting disturbs soil more than conventional soil preparation and can facilitate the regeneration of especially deciduous trees (Saksa 2013). In the present study, there were 3 sites (Saanila, Perämaa, and Lehtosalo) that had seemingly more deciduous tree saplings than others and where thus more shaded, based on my field observations. All of these sites had been FFH, which is in line with the findings of Saksa (2013). This might be the reason for the difference in the epixyle cover between treatments, because the deciduous tree saplings would also logically support a more humid microclimate and consequently a larger bryophyte cover. Bryophytes compete with lichens on wood and can outcompete them especially in shaded environments (Rose 1993, Stokland *et al.* 2012).

Dead wood's mean distance to the ground was not significantly larger at control sites than at FFH sites. The result does not support the hypothesis of the harvesting machinery tramping dead wood into the ground. Temperature of the dead wood, however, tended to be higher on control than on FFH sites. This could be explained by the effect of stump harvesting on the regeneration of deciduous trees (Saksa 2013). By having more deciduous tree saplings, FFH sites were more shadowy. This is likely to be the reason for detecting lower dead wood temperatures on the FFH sites than on the more open control sites. According to my hypothesis more elevated dead wood on control sites would have been more likely to face the sun directly which would have led to higher dead wood temperatures on control than on FFH sites. Since no difference in the elevation could have been documented, this hypothesis was not supported. The weather conditions varied a lot during the 6-week long data collection period, and the temperature and moisture measurements of dead wood seemed to reflect the weather. Therefore, the reliability of these measurements is questionable.

The diameter of dead wood was not found to differ between treatments, which suggests that FFH does not skew the dead wood diameter distribution into either direction. This is a logical result since FFH targets both large diameter dead wood (stumps) and FWD. However, the harvesting machinery could have been predicted to reduce the average size of dead wood by breaking it into smaller pieces (Hautala *et al.* 2004, Bouget *et al.* 2012). The bark cover of dead wood did not differ between treatments. The way that FFH could have affected the bark cover of dead wood was either by removing the remaining dead wood's bark mechanically during the harvesting process or by affecting the age distribution of the dead wood (decortication by age). The decay stage was not affected by FFH either. Most of the dead wood pieces were in decay stages 2 and 3, and there was not much variation beyond that. The uniformity in decay stage is probably a consequence of all the sites being clear-cut approximately the same time.

The diversity of dead wood did not differ between treatments, and thus the hypothesis of FFH reducing the diversity of dead wood was not supported. The control sites could have been more diverse than FFH sites because of the selective removal of dead wood in FFH. Alternatively, the FFH could have been more diverse due to the more diverse set of dead wood resources on FFH sites caused by the adding of uprooted stumps.

4.3. Lichen diversity in relation to dead wood surface area and diversity

The lichen species richness correlated positively with the dead wood area on a clear-cut. This result can be explained by the theory of species-area relationship (SAR) (Arrhenius 1921, Rosenzweig 1995) and supports the hypothesis of decreasing dead wood area leading to reduced species richness. If the phenomenon had been due to habitat heterogeneity, lichen richness would have been expected to correlate with dead wood diversity. However, the hypothesis of FFH reducing lichen species richness through a decreased dead wood heterogeneity was not supported. Since it was not, the relationship of lichens and dead wood area could have been due to the random placement hypothesis and area *per se* (Arrhenius 1921, Connor & McCoy 1979). According to the hypothesis, in a larger area, there was space for more lichen individuals and there was thus more likely to be more species. This is logical also because lichens use dead wood only as a growth surface, not as a source of nutrition (Stokland *et al.* 2012). Therefore, many of them are able to utilize different kinds of dead wood or even other surfaces. Most of the species found in the present study were generalists that can grow on different kinds of woody substrates and often even on rocks or humus

(Stenroos *et al.* 2011) and were thus not affected by the heterogeneity of the dead wood substrate. The hypothesis based on the theory of island biogeography (MacArthur & Wilson 1967) could not have been tested by this study arrangement because there were no repeated measures that could have grasped the immigration and extinction aspect.

When looking at the species-area relationship in more detail, it was found that the lichen species richness grew with increasing CWD area and did not react to FWD or stumps. This result suggests that the epixylic macrolichen richness on spruce dominated clear-cuts would not be threatened by the harvesting of FWD or stumps. Indeed, FWD has not been seen as an important substrate for saproxylic lichens since it hosts mostly generalist species (Caruso *et al.* 2008, Svensson 2013). Other reasons can be found from the large amount of FWD. FWD took the largest share of all the dead wood pieces found in the present study, and most of the FWD was branches. A large proportion of FWD did not have any lichens on it, and hence there was a lot of variation in the number of species on FWD. Therefore, to increase the lichen species richness, large amounts dead wood area was needed, and this is why the species-area relationship might have been hard to observe. Additionally, the other dead wood categories which were present in FWD, roots and pieces of stumps, seem not to be especially good substrates for lichens based on the species richness on them. Although there tended to be more root volume and area on the FFH sites, there were no more lichen species on the roots of FFH than of control sites. The large variation between sites in the surface area and quality of FWD and a small sample size most likely affected the results as well.

FFH affected neither the total species richness nor the diversity of epixylic macrolichens directly. This result is not surprising in the light of the ecology of the observed species. As mentioned above, most of the found species were generalists that are not dependent on dead wood as a substrate (Stenroos *et al.* 2011). However, when observing the effects on different dead wood categories separately, the species richness on branches was found to be lower on FFH than on control sites. This was observed, even though the volume or area of the branches did not statistically differ between treatments. Logically, this was due to the fact that there were more branches and more surface area for lichens on control, sites even though the difference between treatments was not significant. Another reason could be the in the larger epixyle cover on dead wood in the FFH sites. Since the epixyle cover consisted mostly of bryophytes, which compete with lichens for space (Rose 1993, Stokland *et al.* 2012), it could be assumed that the larger epixyle cover might have affected the lichen diversity negatively at the FFH sites.

It was surprising that there was no correlation between stump area and species richness. Even though no correlation was found, the stumps on control sites tended to have more species than stumps on FFH sites. Stumps are indeed a species rich substrate for many lichens (Caruso *et al.* 2008, Sbribille *et al.* 2008, Walmsley & Godbold 2009, Hämäläinen *et al.* 2015), especially for *Calicium* and *Cladonia* genera (Humphrey *et al.* 2002). Stumps can host also rare species, which was demonstrated in the present study by finding a nearly threatened species, *Cladonia norvegica*, on stumps (as well as logs). A positive correlation between individual stump surface areas and lichen richness has also been found (Svensson *et al.* 2013). One reason for not finding strong responses for the lichens on stumps in the present study can be in the scope of the study. By excluding crustose lichens, most of the lichen species diversity was overlooked (Stenroos *et al.* 2011).

Variation between clear-cuts probably also affected the species-area result for both FWD and stumps. In addition, it was not controlled whether the species were relics of the forest community before the clear-cut, or had colonized the dead wood since then. Even though most of the observed dead wood surface was decorticated, it was not documented how many lichen observations where on bark and how many on bare wood. If only the lichen species on bare wood would have been included in the study, it would have been certain that the lichens had colonized the surface after the decortication, which most likely would have happened after the clear-cutting. Disturbances such as logging may have negative effects on epiphytic lichen persistence, (Johansson 2008), and therefore, an increased disturbance could have affected the persistence of the relict species as well. Growth rates and colonization rates of at least most foliose lichens, however, do not seem to be affected by disturbances (Johansson 2008), which could explain part of the weak responses of the lichens to the added FFH disturbance.

The CWD in the present study consisted mainly of logs and uprooted stumps. Logs are known to be an important substrate for lichens (Spribille *et al.* 2008). Uprooted stumps instead are a new resource that is created by FFH, which contrasts with the overall influence of FFH decreasing the amount of dead wood on clear-cuts. Therefore, even though the overall dead wood volume decreases, uprooted stumps may increase the structural diversity of the dead wood. This could benefit lichens either due to area *per se* or due to the substrate's beneficial properties. Uprooted stumps may have positively affected the total lichen diversity as well. Uprooted stumps are usually largely decorticated and rather elevated. It may be that uprooted stumps could even be compared to high stumps because of their shared characteristics and microclimate since lichens favour both high stumps and decorticated dead wood (Lõhmus & Lõhmus 2001, Caruso & Rudolphi 2009, Svensson *et al.* 2013). It would be interesting to compare the species richness on stumps and uprooted stumps. Although this study cannot directly demonstrate that lichens would have favoured uprooted stumps, it cannot be excluded either, since lichen richness did react to the increasing area of CWD which was dominated by uprooted stumps along with logs. The observed lichen species richness on uprooted stumps was also rather high compared to the other substrates.

4.4. Conclusions

Forest-fuel harvesting (FFH) reduces the amount of stumps and fine woody debris (FWD) (Rudolphi & Gustafsson 2005, Eräjää *et al.* 2010) but at the same time, it increases the aboveground volume of uprooted stumps and roots. Therefore, the effects of FFH on the total aboveground volume of dead wood are not straightforward, as demonstrated in the present study. No significant difference in the volume or surface area between treatments was found in any size class or dead wood category. Even so, the effect of FFH on especially the amount of stumps and FWD is clear. FFH can reduce as much as 80 % of the stump volume (Eräjää *et al.* 2010) and 70 % of the FWD volume on clear-cuts (Rudolphi & Gustafsson 2005).

FFH affected epixylic macrolichen richness clearly only on the branches of the clear-cuts. However, the species richness on stumps also tended to be lower on FFH sites. Even though the reduction of branches or stumps was not documented by this study, it is the main function of FFH. Therefore, by reducing the amount of branches and stumps, it seems that FFH decreases the epixylic macrolichen richness on clear-cuts. Nevertheless, since no difference in the total species richness or diversity was found, it may be that the availability of the other substrates was enough to ensure the presence of the common epixylic macrolichen community. This can be assumed because a majority of the species found in the present study were generalists that can grow on other substrates than dead wood as well (Stenroos *et al.* 2010). However, the results of the present study address only epixylic macrolichens which are only a small part of the whole lichen diversity. In order to get a full picture of the effects of FFH on lichens, more studies, including also crustose lichens, are needed. When the species richness of different dead wood substrates on clear-cuts has been studied, the importance of especially stumps for lichen diversity has arisen (Caruso *et al.* 2008, Hämäläinen *et al.* 2015). The role of uprooted stumps as a new resource for lichens and other saproxylic species has not been studied to my knowledge. There is a possibility that it could act as a new kind of substitutive dead wood resource on clear-cuts. However, the effects of stump harvesting on biodiversity on a wider perspective have to be taken into consideration as well.

Although, in the light of the present study, the effects of FFH on the diversity of lichens do not seem severe, FFH does decrease the amount of dead wood, and thus the effects on other saproxylic species need to be studied further. The extent of FFH increases rapidly in the future, and more information about its effects on biodiversity is needed quickly. The new information can be used when forming guidelines for ecologically sustainable FFH practises.

ACKNOWLEDGEMENTS

I would like to express my gratitude especially towards my supervisors Panu Halme and Jenna Purhonen. Thank you for the very interesting and timely topic. Thank you also for being so flexible and for answering rapidly even when you have had hectic schedules. And thank you for all your valuable comments and encouraging feedback that really helped me forward. I am extremely grateful for Annina Launis who guided me into the beginning in my lichen identification and patiently helped me even with the most difficult and tiny *Cladonias*. Without you I would have been in big trouble with my identification. I would also like to thank Sandra Savinen and Meeri Väätäinen for being excellent field assistants. Additionally, I would like to thank Martin Chilman for commenting my work and moral support. Finally, I would like to thank Kuopion Luonnon Ystäväin Yhdistys, Suomen Biologian Seura Vanamo, and Societas pro Fauna et Flora Fennica for funding this thesis as well as the Natural History Museum of Central Finland for providing space for microscopy.

REFERENCES

Ahti T., Hämet-Ahti L. & Jalas J. 1968. Vegetation zones and their sections in northwestern Europe. *Ann. Bot. Fenn.* 5(3): 169–211.

Allmér J., Vasiliauskas R., Ihrmark K., Stenlid J. & Dahlberg A. 2006. Wood-inhabiting fungal communities in woody debris of Norway spruce (*Picea abies* (L.) Karst.), as refected by sporocarps, mycelial isolations and T-RFLP identification. *FEMS Microbiol. Ecol.* 55: 57–67.

Arrhenius O., 1921. Species and area. *J. Ecol.* 9(1): 95–99.

Asikainen A., Ilvesniemi H. & Hynynen J. 2013. Bioenergiaa metsistä kestävästi ja kilpailukykyisesti. In: Asikainen A., Ilvesniemi H. & Muhonen T. (eds.), *Bioenergiaa metsistä — Tutkimus- ja kehittämisohjelman keskeiset tulokset*, Metlan työraportteja 289, 10–12.

Báldi A. 2008. Habitat heterogeneity overrides the species-area relationship. *J. Biogeogr.* 35: 675–681.

Bengtsson J., Nilsson S.G., Franc A. & Menozzi P. 2000. Biodiversity, disturbances, ecosystem function and management of European forests. *Forest Ecol. Manag.* 132: 39–50.

Bergamini A., Stofer S., Bolliger J. & Scheidegger C. 2007. Evaluating macrolichens and environmental variables as predictors of the diversity of epiphytic microlichens. *Lichenologist* 39(5): 475–489.

Bergeron Y. & Fenton N.J. 2012. Boreal forests of eastern Canada revisited: old growth, nonfire disturbances, forest succession, and biodiversity. *Botany* 90: 509–523.

Björheden R. 2006. Drivers behind the development of forest energy in Sweden. *Biomass Bioenerg.* 30: 289–295.

Boddy L., Frankland J.C. & van West P. (eds.). 2008. *Ecology of Saprotrophic Basidiomycetes.* Elsevier, London.

Bouget C., Lassauce A. & Jonsell M. 2012. Effects of fuelwood harvesting on biodiversity – a review focused on the situation in Europe. *Can. J. For. Res.* 42: 1421–1432.

Brin A, Bouget C., Brustel H. & Jactel H. 2011. Diameter of downed woody debris does matter for saproxylic beetle assemblages in temperate oak and pine forests. *J. Insect Conserv*. 15: 653–669.

Cain M.L., Bowman W.D. & Hacker S.D. 2011. *Ecology*, 2nd edition. Sinauer Associates, Inc., Sunderland, Massachusetts.

Caruso A. & Thor G. 2007. Importance of different tree fractions for epiphytic lichen diversity on *Picea abies* and *Populus tremula* in mature managed boreonemoral Swedish forests. *Scand. J. Forest Res.* 22: 219–230.

Caruso A. & Rudolphi J. 2009. Influence of substrate age and quality on species diversity of lichens and bryophytes on stumps. *Bryologist* 112: 520–531.

Caruso A., Rudolphi J. & Thor G. 2008. Lichen species diversity and substrate amounts in young planted boreal forests: A comparison between slash and stumps of *Picea abies*. *Biol. Conserv.* 141: 47–55.

Colwell R. K. 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Version 9.1.0. User's Guide and application published at: http://purl.oclc.org/estimates.

Connor E.F. & McCoy E.D. 1979. The statistics and biology of the species-area relationship. *The American Naturalist* 113(6): 791–833.

Engelmark O. 1999. Boreal forest disturbances. In: Walker L.R. (eds.), *Ecosystems of disturbed ground*, Elsevier, New York. pp. 161–186.

Ericsson K., Huttunen S., Nilsson L.J. & Svenningsson P. 2004. Bioenergy policy and market development in Finland and Sweden. *Energ. Policy* 32: 1707–1721.

Eräjää S., Halme P., Kotiaho J.S., Markkanen A. & Toivanen T. 2010. The volume and composition of dead wood on traditional and forest fuel harvested clear-cuts. *Silva Fenn.* 44(2): 203–211.

European Commission.2014. Communication from the commission to the European parliament, the council, the European economic and social committee and the committee of the regions. A policy framework for climate and energy in the period from 2020 to 2030. Available from: http://ec.europa.eu/smart-regulation/impact/ia_carried_out/docs/ia_2014/swd_2014_0015_en.pdf

Evans K.L., Warren P.H. & Gaston K.J. 2005. Species-energy relationships at the macroecological scale: a review of the mechanisms. *Biol. Rev.* 80: 1–25.

Foit J. 2010. Distribution of early-arriving saproxylic beetles on standing dead Scots pine trees. *Agr. Forest Entomol.* 12: 133–141.

Foley J.A., DeFries R., Asner G.P., Barford C., Bonan G., Carpenter S.R., Chapin F.S., Coe M.T., Daily G.C, Gibbs H.K., Helkowski J.H., Holloway T., Howard E.A., Kucharik C.J., Monfreda C., Patz J.A., Prentice I.C., Ramankutty N. & Snyder P.K. 2005. Global consequences of land use. *Science* 309: 570–574.

Fridman J. & Walheim M. 2000. Amount, structure, and dynamics of dead wood on managed forestland in Sweden. *Forest Ecol. Manag.* 131: 23–36.

Gaston K.J., editor. 1996. *Biodiversity. A biology of numbers and difference.* Blackwell, Oxford, UK.

Gibb H., Ball J.P., Johansson T., Atlegrim O., Hjältén J. & Danell K. 2005. Effects of management on coarse woody debris volume and composition in boreal forests in northern Sweden. *Scand. J. Forest Res.* 20: 213–222.

Gleason H.A. 1922. On the relation between species and area. *Ecology* 3(2): 158–162.

Greaves H. 1971. The bacterial factor in wood decay. *Wood Sci. Technol.* 5: 6–16.

Gromtsev A. 2002. Natural disturbance dynamics in the boreal forests of European Russia: a review. *Silva Fenn.* 36(1): 41–55.

Haines-Young R. & Chopping M. 1996. Quantifying landscape structure: a review of landscape indices and their application to forested landscapes. *Prog. Phys. Geog.* 20(4): 418–445.

Hakkila P. 2006. Factors driving the development of forest energy in Finland. *Biomass Bioenerg.* 30: 281–288.

Halme P., Vartija N., Salmela J., Penttinen J. & Norros V. 2013. High within- and between-trunk variation in the nematoceran (Diptera) community and its physical environment in decaying aspen trunks. *Insect Conserv. Diver.* 6: 502–512.

Hanski I. 2000. Extinction debt and species credit in boreal forests: modelling the consequences of different approaches to biodiversity conservation. *Ann. Zool. Fennici* 37: 271–280.

Harmon M.E., Franklin J.F., Swanson F.W., Sollins P., Gregory S.V., Lattin J.D., Anderson N.H., Cline S.P., Aumen N.G., Sedell J.R., Lienkaemper G.W., Cromack K.Jr. & Cummins K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* 15: 133–302.

Hautala H., Jalonen J., Laaka-Lindberg S. & Vanha-Majamaa I. 2004. Impacts of retention felling on coarse woody debris (CWD) in mature boreal spruce forests in Finland. *Biodivers. Conserv.* 13: 1541–1554.

Hawkins B.A., Field R., Cornell H.V., Currie D.J., Guégan J-F., Kaufman D.M. Kerr J.T., Mittelbach G.G., Oberdorff T., O'Brien E.M., Porter E.E. & Turner J.R.G. 2003. Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84(12): 3105–3117.

Helmisaari H-S., Kaarakka L. & Olsson B.A. 2014. Increased utilization of different tree parts for energy purposes in the Nordic countries. *Scand. J. Forest Res.* 29: 312–322.

Honkanen M., Roberge J-M., Rajasärkkä A. & Mönkkönen M. 2010. Disentangling the effects of area, energy and habitat heterogeneity on boreal forest bird species richness in protected areas. *Global Ecol. Biogeogr.* 19: 61–71.

Hooper D.U., Chapin F.S., Ewel J.J., Hector A., Inchausti P., Lavorel S., Lawton J.H., Lodge D.M., Loreau M., Naeem S., Schmid B., Setälä H., Symstad A.J., Vandermeer J. & Wardle D.A. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.* 75(1): 3–35.

Hottola J. 2009. *Communities of wood-inhabiting fungi: Ecological requirements and responses to forest management and fragmentation.* Department of Biological and Environmental Sciences, University of Helsinki, 23 p.

Humphrey J.W., Davey S., Peace A.J., Ferris R. & Harding K. 2002. Lichens and bryophyte communities of planted and semi-natural forests in Britain: the influence of site type, stand structure and dead wood. *Biol. Conserv.* 107: 165–180.

Hämäläinen A., Kouki J. & Lõhmus P. 2015. Potential biodiversity impacts of forest biofuel harvest: lichen assemblages on stumps and slash of Scots pine. *Can. J. For. Res.* 45: 1239–1247.

IBM Corp. Released 2013. IBM SPSS Statistics for Windows, Version 22.0. Armonk, NY: IBM Corp.

Johansson P. 2008. Consequences of disturbance on epiphytic lichens in boreal and near boreal forests. *Biol. Conserv.* 141: 1933–1944.

Jonsell M. & Hanson J. 2011. Logs and stumps in clearcuts support similar saproxylic beetle diversity: Implications for bioenergy harvest. *Silva Fenn.* 45(5): 1053–1064.

Jonsell M., Weslien J. & Ehnström B. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodivers. Conserv.* 7: 749–764.

Jonsson B.G., Kruys N. & Ranius T. 2005. Ecology of species living on dead wood – lessons for dead wood management. *Silva Fenn.* 39(2): 289–309.

Jost L. 2006. Entropy and diversity. *Oikos* 113(2): 363–375.

Jüriado I., Suija A. & Liira J. 2006. Biogeographical determinants of lichen species diversity on islets in the West-Estonian Archipelago. *J. Veg. Sci.* 17: 125–134.

Juutilainen K., Halme P., Kotiranta H. & Mönkkönen M. 2011. Size matters in studies of dead wood and wood-inhabiting fungi. *Fungal Ecol.* 4: 342–349.

Juutilainen K., Mönkkönen M., Kotiranta H. & Halme P. 2014. The effects of forest management on wood-inhabiting fungi occupying dead wood of different diameter fractions. *Forest Ecol. Manag.* 313: 283–291.

Juutinen A., Mönkkönen M. & Sippola A-L. 2006. Cost-efficiency of decaying wood as a surrogate for overall species richness in boreal forests. *Conserv. Biol.* 20(1): 74–84.

Jääskeläinen K., Pykälä J., Rämä H., Vitikainen O., Haikonen V., Högnabba F., Lommi S. & Puolasmaa A. 2010. Lichens. In: Rassi P., Hyvärinen E., Juslén A. & Mannerkoski I. (eds.), *The 2010 Red List of Finnish Species*, Ympäristöministeriö & Suomen ympäristökeskus, Helsinki, p. 278–310.

Kallimanis A.S., Mazaris A.D., Tzanopoulos J., Halley J.M., Pantis J.D. & Sgardelis S.P. 2008. How does habitat diversity affect the species–area relationship? *Global Ecol. Biogeogr.* 17: 532–538.

Kataja-aho S., Saari E., Fritze H. & Haimi J. 2011. Effects of stump removal on soil decomposer communities in undisturbed patches of the forest floor. *Scand. J. Forest Res.* 26: 221–231.

Kataja-aho S., Smolander A., Fritze H., Norrgård S. & Haimi J. 2012. Responses of soil carbon and nitrogen transformations to stump removal. *Silva Fenn.* 46(2): 169–179.

Kruys N. & Jonsson B.G. 1999. Fine woody depris is important for species richness on logs in managed boreal spruce forests of northern Sweden. *Can. J. For. Res.* 29: 1295–1299.

Kruys N., Fries C., Jonsson B.G., Lämås T. & Ståhl G. 1999. Wood-inhabiting cryptogams on dead Norway spruce (*Picea abies*) trees in managed Swedish boreal forests. *Can. J. For. Res.* 29: 178–186.

Kuuluvainen T. 1994. Gap disturbance, ground microtopography, and the regeneration dynamics of boreal coniferous forests in Finland: a review. *Ann. Zool. Fennici* 31: 35–51.

Lack D. 1969. The numbers of bird species on islands. *Bird Study* 16: 193–209.

Lassauce A., Paillet Y., Jactel H. & Bouget C. 2011. Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecol. Indic.* 11: 1027–1039.

Lindhe A., Lindelöw Å. & Åsenblad N. 2005. Saproxylic beetles in standing dead wood density in relation to substrate sun-exposure and diameter. *Biodivers. Conserv.* 14: 3033–3053.

Lõhmus P. & Lõhmus A. 2001. Snags and their lichen flora in old Estonian peatland forests. *Ann. Bot. Fennici.* 38: 265–280.

Lõhmus, A. & Kraut, A., 2010. Stand structure of hemiboreal old-growth forests: Characteristic features, variation among site types, and a comparison with FSC-certified mature stands in Estonia. *Forest Ecol. Manag.* 260: 155–165.

Mac Nally R. & Watson D.M. 1997. Distinguishing area and habitat heterogeneity effects on species richness: birds in Victorian buloke remnants. *Aust. J. Ecol.* 22: 227–232.

MacArthur R.H. & MacArthur J.W. 1961. On bird species diversity. *Ecology* 42(3): 594–598.

MacArthur R.H. & Wilson E.O. 1967. *The theory of island biogeography.* Princeton University Press, Princeton, New Jersey.

Nagendra H. 2002. Opposite trends in response for the Shannon and Simpson indices of landscape diversity. *Appl.Geogr.* 22: 175–186.

Niemelä J. 1999. Management in relation to disturbance in the boreal forest. *Forest Ecol. Manag.* 115: 127–134.

Nilsson S.G., Bengtsson J. & Ås S. 1988. Habitat diversity or area *per se*? Species richness of woody plants, carabid beetles and land snails on islands. *J. Anim. Ecol.* 57(2): 685–704.

Nilsson S.G., Hedin J. & Niklasson M. 2001. Biodiversity and its assessment in boreal and nemoral forests. *Scand. J. Forest Res.* 3: 10–26.

Nordén B., Ryberg M., Götmark F. & Olausson B. 2004. Relative importance of coarse and fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests. *Biol. Conserv.* 117: 1–10.

Nordén J., Penttilä R., Siitonen J., Tomppo E. & Ovaskainen O. 2013. Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. *J. Ecol.* 101: 701–712.

Purvis A. & Hector A. 2000. Getting the measure of biodiversity. *Nature* 405: 212–219.

Rose F. 1993. Ancient british woodlands and their epiphytes. *British Wildlife* 5: 83–93.

Rosenzweig M.L. 1995. *Species diversity in space and time.* Cambridge University Press, Cambridge.

Rudolphi J. & Gustafsson L. 2005. Effects of forest-fuel harvesting on the amount of dead wood on clear-cuts. *Scand. J. Forest Res.* 20: 235–242.

Saksa T. 2013. Regeneration after stump harvesting in southern Finland. *Forest Ecol. Manag.* 290: 79–82.

Samuelsson J., Gustafsson L. & Ingelög T. 1994. *Dying and dead trees – a review of their impact for biodiversity*. Swedish Environmental Protection Agency, Uppsala.

Schmit J.P. 2005. Species richness of tropical wood-inhabiting macrofungi provides support for species-energy theory. *Mycologia.* 97(4): 751–761.

Schoener T.W. 2010. The MacArthur-Wilson equilibrium model – A chronicle of what it said and how it was tested. In: MacArthur R.H., Ricklefs R.E., Losos J.B. (eds.), *The theory of island biogeography revisited*, Princeton University Press, Princeton and Oxford, 52–87.

Shannon C.E. 1948. A mathematical theory of communication. *Bell. Syst. Tech. J.* 27: 379–423.

Shen G., Yu M., Hu X-S., Mi X., Ren H., Sun I-F. & Ma K. 2009. Species–area relationships explained by the joint effects of dispersal limitation and habitat heterogeneity. *Ecology* 90(11): 3033–3041.

Siitonen J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecol. Bull.* 49: 11–41.

Siitonen J., Martikainen P., Punttila P. & Rauh J. 2000. Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. *Forest Ecol. Manag.* 128: 211–225.

Spribille T., Thor G., Bunnell F.L., Goward T. & Björk C.R. 2008. Lichens on dead wood: species-substrate relationships in the epiphytic lichen floras of the Pacific Northwest and Fennoscandia. *Ecography.* 31: 741–750.

Stenroos S., Ahti T., Lohtander K. & Myllys L. (eds.). 2011. *Suomen jäkäläopas*. Luonnontieteellisen keskusmuseon kasvimuseo, Helsinki.

Stokland J.N., Siitonen J. & Jonsson B.G. (eds.). 2012. *Biodiversity in dead wood*. Cambridge University Press, Cambridge.

Svensson M. 2013. *Occurrence patterns of dead wood and wood-dependent lichens in managed boreal forest landscapes.* Department of Ecology, Swedish University of Agricultural Sciences. 84: 1–50.

Svensson M., Dahlberg A., Ranius T. & Thor G. 2013. Occurrence patterns of lichens on stumps in young managed forests. *Plos One* 8(6): 1–8.

Tews J., Brose U., Grimm V., Tielbörger K., Wichmann M.C., Schwager M. & Jeltsch F. 2004. Animal species diversity driven by habitat heterogeneity/ diversity: the importance of keystone structures. *J. Biogeogr.* 31: 79–92.

Toivanen T., Markkanen A., Kotiaho J.S. & Halme P. 2012. The effect of forest fuel harvesting on the fungal diversity of clear-cuts. *Biomass Bioenerg.* 39: 84–93.

Toljander Y.K., Lindahl B.D., Holmer L. & Högberg N.O.S. 2006. Environmental fluctuations facilitate species co-existence and increase decomposition in communities of wood decay fungi. *Oecologia* 148: 625–631.

Turner M.G., Baker W.L., Peterson C.J. & Peet R.K. 1998. Factors influencing succession: Lessons from large, infrequent natural disturbances. *Ecosystems* 1: 511–523.

Ulyshen M.D. 2016. Wood decomposition as influenced by invertebrates. *Biol. Rev.* 91: 70–85.

Valtioneuvosto. 2008. *Pitkän aikavälin ilmasto- ja energiastrategia – Valtioneuvoston selonteko eduskunnalle 6. päivänä marraskuuta 2008*. TEM, Energiaosasto, Helsinki.

Vanha-Majamaa I., Lilja S., Ryömä R., Kotiaho J.S., Laaka-Lindberg S., Lindberg H., Puttonen P., Tamminen P., Toivanen T. & Kuuluvainen T. 2007. Rehabilitating boreal forest structure and species composition in Finland through logging, dead wood creation and fire: the EVO experiment. *Forest Ecol. Manag.* 250: 77–88.

Verkerk P.J., Lindner M., Zanchi G. & Zudin S. 2011. Assessing impacts of intensified biomass removal on dead wood in European forests. *Ecol. Indic.* 11: 27–35.

Vitousek P.M., Mooney H.A., Lubchenco J. & Melillo J.M. 1997. Human domination of Earth's ecosystems. *Science* 277: 494–499.

Walmsley J.D. & Godbold D.L. 2009. Stump harvesting for bioenergy – a review of the environmental impacts. *Forestry* 83(1): 17–38.

Whittaker R.J. & Fernández-Palacios J.M. 2007. *Island biogeography: ecology, evolution, and conservation,* 2nd edition. Oxford University Press, Oxford.

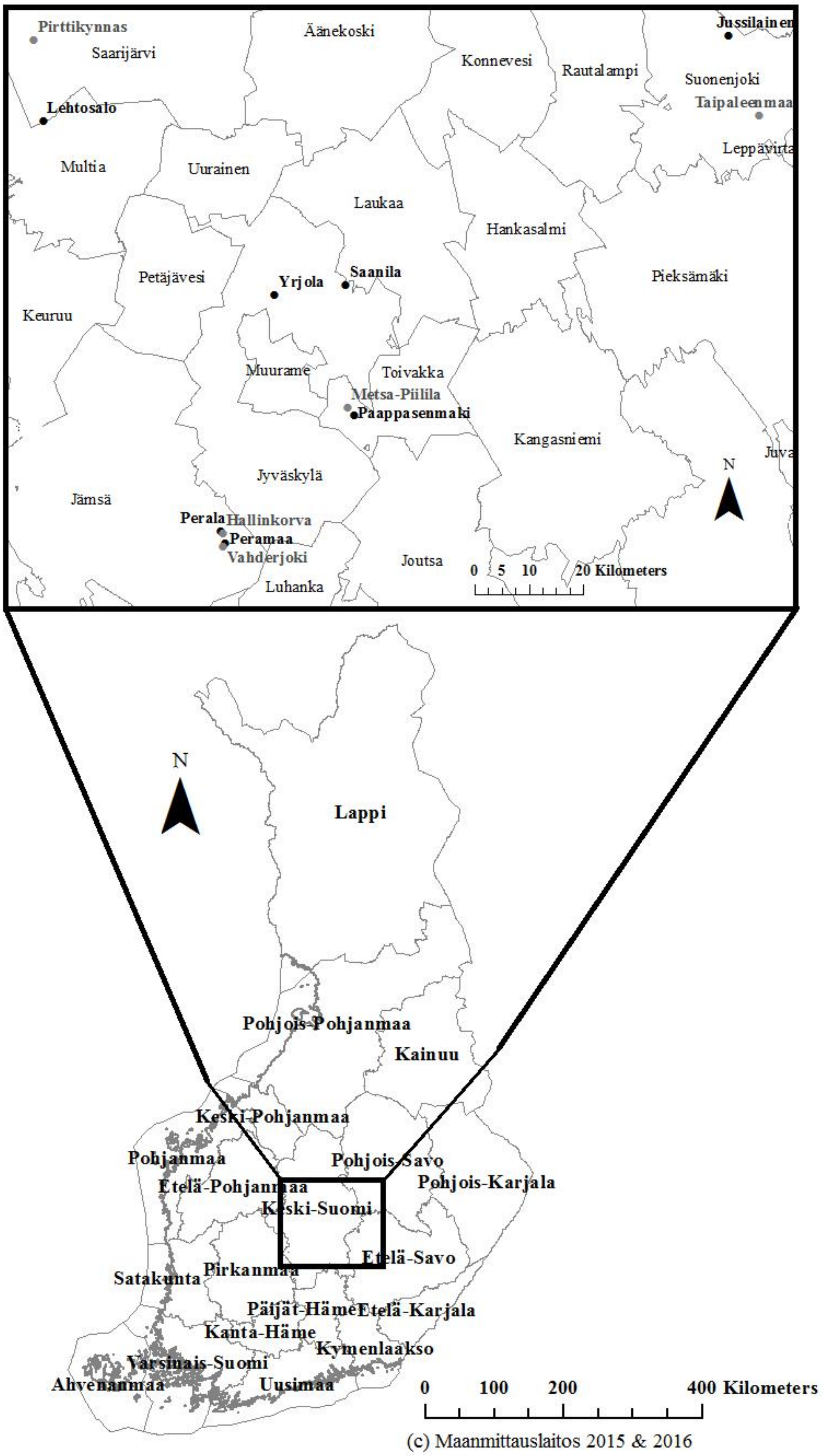
Williams C.B. 1964. *Patterns in the balance of nature.* Academic Press, London.

Wright D.H. 1983. Species–energy theory: an extension of species–area theory. *Oikos*. 41: 496–506.

Äijälä O., Kuusinen M. & Koistinen A. 2010. *Hyvän metsänhoidon suosituksen energiapuun korjuuseen ja kasvatukseen*. Metsätalouden kehittämiskeskus Tapion julkaisuja, Helsinki.

APPENDIXES

Appendix 1. The map shows the locations of the study. The map below shows the regions of Finland and the map above shows municipalities and the clear-cut locations. Grey dots represent control sites and black dots FFH sites. (Keski-Suomi = Central Finland, Pohjois-Savo = Northern Savonia)



(c) Maanmittauslaitos 2015 & 2016

Appendix 2. A list of all the study sites and their municipality, region (CF = Central Finland, NS = Northern Savonia), identification number, treatment (FFH = forest-fuel harvested), and special notifications.

Site name	**Municipality& region**	**Identification number**	**Treatment**	**Notifications**
Saanila	Jyväskylä, CF	1	FFH	Stumps not collected, a lot of deciduous tree saplings
Metsä-Piililä	Toivakka, CF	2	Control	
Hallinkorva	Jämsä, CF	3	Control	
Vahderjoki	Jämsä, CF	4	Control	Thinning-cut conducted
Pirttikynnäs	Saarijärvi, CF	5	Control	
Taipaleenmaa	Suonenjoki, NS	6	Control	
Yrjölä	Jyväskylä, CF	7	FFH	Thinning-cut conducted
Paappasenmäki	Toivakka, CF	8	FFH	
Perämaa	Jämsä, CF	9	FFH	A lot of deciduous tree saplings
Perälä	Jämsä, CF	10	FFH	Stumps not collected
Lehtosalo	Saarijärvi, CF	11	FFH	A lot of deciduous tree saplings
Jussilainen	Suonenjoki, NS	12	FFH	

Appendix 3. A list of the lichen species and genera that were used in the analyses and found from the control sites (N = 31). The species are in the alphabetical order according to the scientific name. Red-listed status is in brackets. The number of observations of each species is under each site. In addition, the total number of observations on each site and of each species is included. The naming follows Stenroos *et al.* (2011).

	Site					
Species	**2**	**3**	**4**	**5**	**6**	**Total**
Bryoria sp.	5	1	2	2	4	14
Cetraria sepincola	3	1	1	3	5	13
Cladonia arbuscula	10	7	4	6	16	43
Cladonia bacilliformis	2	–	–	2	6	10
Cladonia botrytes	40	10	10	15	38	113
Cladonia carneola	2	–	1	2	4	9
Cladonia cenotea	3	1	2	6	8	20
Cladonia chlorophaea	4	3	2	1	–	10
Cladonia coniocraea	15	15	14	11	20	75
Cladonia decorticata	–	–	–	–	1	1
Cladonia digitata	2	–	2	5	1	10
Cladonia fimbriata	2	12	11	1	6	32
Cladonia gracilis	–	–	1	–	1	2
Cladonia grayi	8	3	–	4	8	23
Cladonia merochlorophaea	–	–	–	1	–	1
Cladonia mitis	3	–	–	–	6	9
Cladonia norvegica (NT)	–	–	–	1	–	1
Cladonia pyxidata	–	–	1	–	–	1
Cladonia rangiferina	22	7	6	11	26	72
Hypogymnia physodes	36	8	51	8	12	115
Hypogymnia tubulosa	6	2	1	1	2	12
Imshaugia aleurites	2	–	–	–	–	2
Parmelia sulcata	2	–	–	1	2	5
Parmeliopsis ambicua	67	19	41	30	60	217
Parmeliopsis hyperopta	11	1	1	7	9	29
Peltigera sp.	–	2	–	–	–	2
Platismatia glauca	3	1	1	–	1	6
Pseudevernia furfuracea	4	–	–	–	1	5
Tuckermannopsis chlorophylla	2	2	6	2	3	15
Usnea sp.	1	–	–	–	2	3
Vulpicida pinastri	103	47	112	27	92	381
Total	358	142	270	147	334	1251

Appendix 4. A list of the lichen species and genera that were used in the analyses and found from the forest-fuel harvested sites (N = 35). The species are in the alphabetical order according to the scientific name. Possible red-listed status is in brackets. The number of observations of each species is under each site. In addition, the total number of observations on each site and of each species is included. The naming follows Stenroos *et al.* (2011).

	Site							
Species	**1**	**7**	**8**	**9**	**10**	**11**	**12**	**Total**
Bryoria sp.	–	–	3	–	–	–	5	8
Cetraria sepincola	–	–	11	–	–	1	3	15
Cladonia arbuscula	3	5	17	4	–	7	2	38
Cladonia bacilliformis	–	–	3	–	1	1	5	10
Cladonia botrytes	5	15	55	8	1	10	13	107
Cladonia carneola	–	–	–	–	–	–	1	1
Cladonia cenotea	2	4	3	–	3	2	10	24
Cladonia chlorophaea	1	1	2	1	–	1	–	6
Cladonia coniocraea	9	14	33	7	9	11	8	91
Cladonia deformis	–	–	–	–	–	–	3	3
Cladonia digitata	–	3	2	–	5	2	4	16
Cladonia fimbriata	4	8	6	4	2	2	4	30
Cladonia gracilis	–	–	–	–	–	2	–	2
Cladonia grayi	5	5	12	–	3	3	4	32
Cladonia macilenta	–	–	–	–	–	–	1	1
Cladonia merochlorophaea	1	2	1	–	–	1	–	5
Cladonia mitis	–	2	7	–	–	–	–	9
Cladonia norvegica (NT)	–	–	2	–	–	–	1	3
Cladonia pyxidata	–	1	2	–	–	–	–	3
Cladonia rangiferina	3	8	31	3	1	8	6	60
Cladonia squamosa	–	–	1	–	–	–	–	1
Cladonia stygia	–	1	–	–	–	–	–	1
Hypocenomyce scalaris	–	–	–	–	–	–	1	1
Hypogymnia physodes	–	5	16	1	1	4	14	43
Hypogymnia tubulosa	–	–	1	–	–	–	1	2
Imshaugia aleurites	–	–	1	–	–	–	–	1
Parmelia sulcata	–	1	2	–	–	–	–	4
Parmeliopsis ambicua	–	18	71	1	4	17	29	144
Parmeliopsis hyperopta	–	4	17	–	2	4	11	40
Peltigera sp.	–	1	–	–	2	–	3	6
Platismatia glauca	–	3	5	–	1	–	1	10
Pseudevernia furfuracea	–	–	1	–	–	–	–	1
Tuckermannopsis chlorophylla	–	1	2	–	–	2	5	11
Usnea sp.	–	–	3	–	–	–	–	3
Vulpicida pinastri	–	47	111	6	18	26	43	269
Total	61	149	421	35	53	104	178	1001