Occurrence Patterns of Dead Wood and Wood-dependent Lichens in Managed Boreal Forest Landscapes

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Cover: A clear-cut in a managed boreal forest landscape. Vänsjö, Hälsingland, Sweden (photo: Måns Svensson 2012).

Occurrence of dead wood and wood-dependent lichens in managed boreal forest landscapes

Abstract

Dead wood is a key resource for biodiversity, on which thousands of forest organisms are dependent. Because of current forest management, there has been a large-scale change in dead wood amounts and qualities, and consequently, many wood-dependent species are threatened. The general aim of this thesis is to increase our understanding of habitat requirements and occurrence patterns of wood-dependent lichens in managed, boreal forest landscapes. We surveyed dead wood and wood-dependent lichens in three study landscapes of managed boreal forest in southern Sweden. The observed occurrence patterns of dead wood in the studied landscapes are to a large extent attributable to management practices, with clear-felling as the main driver of dead wood input. Harvesting forest biomass for bio-fuel production will cause wood-dependent lichens species to decline. Coarse woody debris is important for wood-dependent lichens, but stumps, snags and logs host different species assemblages. Snags are rare in managed forest landscapes and increasing the landscape-scale amount of them would benefit wood-dependent lichens. The previously neglected dead wood type of dead branches on living trees make up a large portion of all dead wood available to wood-dependent species in managed boreal forests. Fine woody debris, including both branches on the ground and dead branches attached to living trees, was, however, found to have a low relative importance for wood-dependent lichens. We modeled species abundance in relation to characteristics of dead wood objects and forest stands, and estimated the landscape-scale abundance of wood-dependent lichens. Young managed forests <60 years of age held the largest populations of these species, because such stands contain more coarse woody debris per hectare than older forests or forested mires, and they occupy a much larger total area. Keeping parts of the landscape outside the forestry system is probably necessary to maintain the landscape-scale persistence of dead wood types that are rarely created within standard management regimes. To conserve the most threatened wood-dependent species, it is necessary to find ways to create and maintain dead wood types and qualities that are currently rare in managed boreal forest landscapes.

Keywords: biodiversity, bio-fuel harvest, coarse woody debris, fine woody debris, habitat requirements, lignicolous, mycobiont, photobiont, saproxylic

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Dedication

Till Lovisa och Alfred

Då han förstod hur lite ved som fanns, så förvandlades inför hans syn Smålands alla stubbar till ved. Han önskade att han haft tio armar och kunnat cykla på tio cyklar och vara på tio stubbåkrar samtidigt. Han ställde sig alltså och bröt stubbar. Han klöv dem, lade upp dem i kastar, körde och sålde stubbarna som ved. (...) Han var öppen för allt som kunde bli ved. Åkerstubb, roddbåtar, logar, lador, stugor där väder och vind hade hus. Han hade en väldig begåvning för allt som kunde bli ved. Mest var det som sagt stubbar. Under krigsåren var han stubbakung och sov på kuddar som var stoppade med sedlar.

Sune Jonsson, Minnesbok över den svenske bonden (1973)

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I   Svensson, M., Dahlberg, A., Ranius, T. & Thor, G. (2013). Occurrence patterns of lichens on stumps in young managed forests. *PLoS ONE* 8(4): e62825.

II   Svensson, M., Dahlberg, A., Ranius, T. & Thor, G. (2013). Dead branches on living trees constitute a large part of the dead wood in managed boreal forests, but are not important for wood-dependent lichens. *Journal of Vegetation Science* (in press).

III Svensson, M., Johansson, V., Dahlberg, A., Frisch, A., Thor, G. & Ranius, T. The relative importance of different forest and dead wood types as habitat for wood-dependent lichens in managed boreal forest landscapes (manuscript).

IV   Svensson, M., Caruso, A., Thor, G. & Snäll, T. Combined observational and experimental data provide no support for facilitation in lichens (manuscript).

Papers I–II are reproduced with the permission of the publishers.

The contribution of Måns Svensson to the papers included in this thesis was as follows:

I   Main author, field work and analysis. Developed research questions and design and wrote the paper together with AD, TR and GT.

II Main author, field work and analysis. Developed research questions and design and wrote the paper together with AD, TR and GT.

III Main author, field work (with AF) and co-responsible for analysis (with VJ and TR). Developed research questions and design together with AD, TR and GT. Wrote the paper with assistance from VJ, AD, AF, GT and TR.

IV Main author, analysis and part of the field work. Developed research questions and design and wrote the paper together with AC, GT and TS.

1 Introduction

1.1 Boreal forests

Boreal forest is the largest forest biome in the world, constituting about 30% of the global forested area (Hansen *et al.*, 2010). In Fennoscandia, which largely lies within the boreal zone, the conifers Norway spruce *Picea abies* (L.) H. Karst. and Scots pine *Pinus sylvestris* L. are the dominating tree species (Esseen *et al.*, 1997; Engelmark & Hytteborn, 1999). Intermixed with these, there are deciduous trees such as silver birch *Betula pendula* Roth, downy birch *Betula pubescens* Ehrh., aspen *Populus tremula* L. and goat willow *Salix caprea* L. (Esseen *et al.*, 1997; Engelmark & Hytteborn, 1999).

1.1.1 Succession and disturbance

Natural dynamics of boreal forest ecosystems are mainly driven by two kinds of processes: disturbances and successions (Esseen *et al.*, 1997; Kuuluvainen, 2009; Shorohova *et al.*, 2009). In boreal Fennoscandian forests, major stand-replacing disturbances in the past have been forest fires, pathogen outbreaks and storms. These disturbances interact with other small-scale processes, such as gap-dynamics driven by tree-mortality (Engelmark & Hytteborn, 1999; Kuuluvainen, 2009). Together, these processes create and maintain spatial and temporal heterogeneity in forest ecosystems, and thus also affect the biodiversity found in these systems (Esseen *et al.*, 1997; Kuuluvainen, 2002; Brūmelis *et al.*, 2011).

1.1.2 The impact of forest management

The establishment of modern forestry during the 19th and 20th centuries has introduced a new set of disturbances and stand-altering processes in Fennoscandian boreal forests, notably routine clear-cutting and thinning, while natural disturbances such as fire have largely been suppressed (Östlund *et al*., 1997). This has resulted in a homogeneous forest landscape characterized by even-aged, well-delineated stands and a large proportion of young forest (Esseen *et al*., 1997; Bengtsson *et al*., 2000; Löfman & Kouki, 2001). The challenge for species in managed boreal forests is thus to find a place in a drastically altered landscape, with changed proportions of available substrate and fragmented distributions of them. These changes have diverging impacts on different species. Specialist species could be hypothesized to show a higher risk of local extinction, since the chance that their niche is represented in the remaining fragments should be smaller than for generalists (Henle *et al*., 2004). A major challenge for biodiversity management in managed forest landscapes is therefore to maintain viable populations of specialist species (Kuuluvainen, 2002).

1.1.3 Dead wood

A key resource in natural boreal forest ecosystems is dead wood, on which thousands of forest organisms are dependent (Siitonen, 2001; Stokland *et al*., 2012). As natural disturbances to a large extent have been suppressed or replaced in managed forests, the single most important driver of dead wood input in such forests is management practices, such as routine clear-felling or thinning (Esseen *et al*., 1997; Stokland *et al*., 2012). This large-scale change of forest systems has led to extensive changes in amounts and qualities of dead wood. Although low-diameter wood might be more common today than before (Dahlberg *et al*., 2011), there has generally been a sharp decrease in the amounts of dead wood in managed boreal forests during the 20th century (Fridman & Wahlheim, 2000; Siitonen, 2001; Brassard & Chen, 2006; Stokland *et al*., 2012). This is both because forestry operations remove trees that would eventually have become dead wood, and because managed forests are usually cut well before tree mortality has started to accumulate substantial dead wood amounts (Fig. 1). Further, forest management brings about changes in the distribution of different decay stages as well as sizes and types of dead wood (Siitonen, 2001; Storanuet *et al*., 2005; Stokland *et al*., 2012). For example, large-diameter logs and snags are rare in managed forests, while dead wood types created by management practices, such as cut stumps, have

increased. The general picture though, is one of a decreasing diversity of dead wood types (Stokland *et al.*, 2012). As a consequence of this large-scale change in dead wood amounts and qualities, roughly half of the red-listed forest species in Fennoscandia are wood-dependent species (Tikkanen *et al.*, 2006; Gärdenfors, 2010; Kålås *et al.*, 2010; Rassi *et al.*, 2010; Stokland *et al.*, 2012).
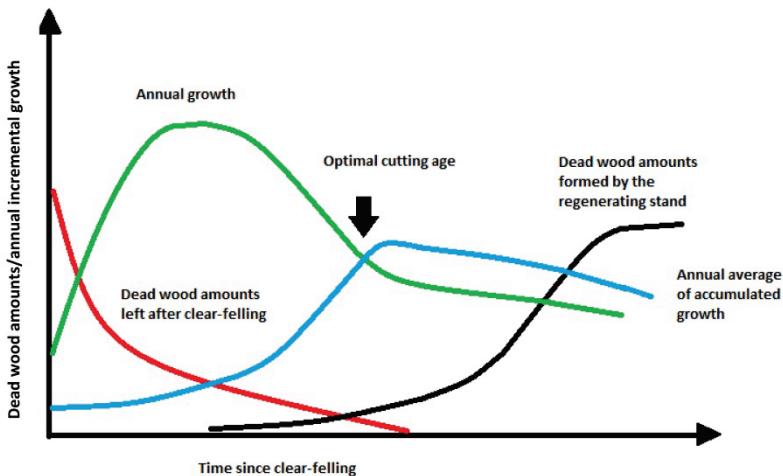

Figure 1. Conceptual model of the relations between dead wood amounts and optimal cutting age in relation to time since clear-felling. The optimal cutting age occurs before substantial amounts of dead wood have been formed by the regenerating stand. Actual timing and quantities may vary between different forest types (based on Stokland *et al.*, 2012, p. 306).

1.1.4 Conservation measures and biofuel harvest

Since large-scale clear-felling was introduced in Fennoscandia in the 1950's, the standard practice has been to extract the stems of trees, while tops, branches and stumps are left in the forest. With the realisation that forest management causes a decrease in available substrate for wood-dependent organisms, various measures to counteract this deficit have been proposed. Currently, the main ways to increase or maintain dead wood amounts include leaving forests unmanaged, green tree retention and leaving dead wood (e.g. as high stumps) at clear-felling (Jonsson *et al.*, 2005; Gustafsson *et al.*, 2012). An

alternative that yet has to see large-scale implementation is the use of alternative management systems, such as prolonged rotation periods (Jonsson *et al.*, 2005; Stokland *et al.*, 2012). As a counterweight to such conservation efforts, there has been an increasing interest in harvesting wood residues for bio-fuel production (Björheden, 2006; Gan & Smith, 2011) (Fig. 2). Their extraction will inevitably further decrease the landscape-scale amount of dead wood, with likely impacts on wood-dependent species (Walmsley & Godbold, 2010). However, it is currently difficult to predict how forest biodiversity would respond to large-scale biofuel harvest, especially in the long-term (Riffell *et al.*, 2011).

Figure 2. Biofuel harvest removes substrate for wood-dependent organisms. A pile of stumps from a clear-cut, Rejmyre, Östergötland (photo Måns Svensson).

1.1.5 Habitat and habitat availability

Habitat can be defined as the conditions and resources present in an area that enables an organism to survive and reproduce (Hall *et al.*, 1997; Dennis *et al.*,

2003). For some wood-dependent species, a wooden object displaying appropriate characteristics (e.g., regarding tree species, degree of decay, exposure to light, etc.) is sufficient to meet its habitat requirements, regardless of where the wooden object is situated. Other species have more specific demands regarding the surroundings, e.g. requirements for high humidity. A common distinction in studies of dead wood is between coarse woody debris (CWD, defined as wood with a diameter >10 cm in thickest end) and fine woody debris (FWD, wood with a diameter <10 cm in the thickest end). There are wood-dependent species that are specialized on either CWD or FWD (e.g., Kruys & Jonsson, 1999; Nordén *et al*., 2004; Stokland *et al*., 2012). The landscape-scale distribution of different dead wood types, i.e. the habitat availability for wood-dependent species, is influenced both by forest management practices and by conservation efforts.

1.2 Lichens

1.2.1 Lichens as symbiotic associations

Lichens are symbiotic associations composed of a fungus, referred to as the mycobiont, and a photosynthesizing alga or cyanobacterium, referred to as the photobiont (e.g., Nash, 2008). Possibly, bacterial communities are also an integrated component of the lichen symbiosis (Bates *et al*., 2011). Because of the composite nature of lichens, there is strictly speaking no such thing as a "lichen species". However, the term is commonly used in the scientific literature. It is usually taken to mean "a species of fungus that is lichenized (i.e. associated with a species of algae and/or a species of cyanobacterium)", thus emphasizing the mycobiont. This is also the way in which "lichen species" is used in this thesis. The Latin binomial that denotes the "lichen species" refers to the mycobiont only.

1.2.2 Lichens on dead wood

Numerous lichen species grow on dead wood, but most of these are substrate generalists, which means that they are also able to grow on other substrates (e.g., bark, rocks or soil). They are thus not dependent on dead wood (Spribille *et al*., 2008). Such substrate generalists are referred to as generalists in this thesis, while species that are strictly confined to wood are regarded as

specialists. Studies of lichens on dead wood often use total lichen species richness or lichen species composition as response variables. From a conservational standpoint, the value of such a study may be limited, since the effect is reflecting responses of generalist species, while the response of the specialized species may be obscured. Partly this praxis has arisen because of the lack of reliable classifications of lichens into relevant guilds. Recently however, Spribille *et al.* (2008), in their thorough survey of lichen species on wood, listed 378 Fennoscandian lichen species known to occur on wood, of which 97 were classified as wood-dependent. According to their definition, a wood-dependent lichen species should have >99% of its occurrences on wood, and this definition has been adopted for this thesis. Thus, several lichen species that may have substantial parts of their populations on wood are not treated as wood-dependent lichens in this thesis.

1.2.3 Lichens and biotic interactions

Understanding biotic interactions is important when trying to predict species' responses to changes in management. Competition with other organisms may affect the occurrence patterns of wood-dependent lichens. Facilitation (i.e. positive interactions between species) has also been suggested to be an important driver of community assembly of lichens (e.g., Fedrowitz *et al.*, 2012). Lichens disperse sexually (mycobiont only) or vegetatively (both mycobiont and photobiont), and for successful establishment of sexually dispersed species the fungal spores need to encounter algal cells for producing a new lichen thallus. One way of obtaining algae could be to get them from other lichens; thus, lichens already present on a substrate could facilitate the colonization of lichens with the same photobiont. As the majority of wood-dependent lichens are sexually dispersed (Spribille *et al.*, 2008), facilitation could be hypothesized to be an important factor in explaining their establishment success (or lack thereof).

2 Thesis aims

The general aim of this thesis is to increase our understanding of habitat requirements and occurrence patterns of wood-dependent lichens in managed, boreal forest landscapes. Such knowledge is an important step in the direction of understanding how management practices (e.g., clear-felling or biofuel harvest) drive habitat availability for these species. This, in turn, is required knowledge when designing efficient conservation measures. The specific questions for each paper were:

I How does the habitat requirements of generalist and wood-dependent lichens growing on Norway spruce stumps in young managed forest differ? What factors drive their occurrence and species richness patterns?

II How much dead wood in the form of dead branches attached to living trees is present in managed boreal forest compared to other types of dead wood? What is the importance of this substrate for wood-dependent lichens?

III What is the relative importance of different stand ages of managed forest for wood-dependent lichens? How does forested, unmanaged mires affect the abundance of wood-dependent lichens at a landscape-level? What is the relative importance of different dead wood types for wood-dependent lichens?

IV Is facilitation a driver of community assembly in metapopulations of wood-dependent lichens?

3 Methods

3.1 Study landscapes

In papers I, II and III, we used two areas in southern Sweden as study landscapes, each covering ca. 150 km^2. The northern landscape is located in the provinces of Dalarna and Västmanland in the middle-boreal vegetation zone (Sjörs, 1999), 60°05'N, 14°05'E, elevation 300–400 m.a.s.l.; the southern landscape is in Östergötland in the boreonemoral zone, 58°48'N, 15°41'E, 60–70 m.a.s.l. (Fig. 3). The forested land in these areas is mainly composed of monocultures or mixed stands of *Picea abies* and *Pinus sylvestris*, with some deciduous trees, mainly *Betula pendula*, *B. pubescens* and *Populus tremula*. The forests are managed according to standard Fennoscandian forestry practice: stands are routinely thinned 1–2 times during their life-span and they are typically clear-felled after 80–100 years. Both landscapes have a long history of forestry and old-growth stands are rare. The proportion of different age classes is similar to the Swedish average (Swedish Forest Agency, 2012), which means that forests below 60 years of age constitute 60–70% of the area, while forests over 110 years are rare (<6%). The most common type of unmanaged land in both areas is forested mire (17% and 7% in the northern and southern study landscape, respectively). They support open *Pinus sylvestris* stands with an annual productivity <1 m^3/ha and are by law exempted from forest production (Jasiniski & Ulizka, 1998; Swedish Forest Agency 2012).
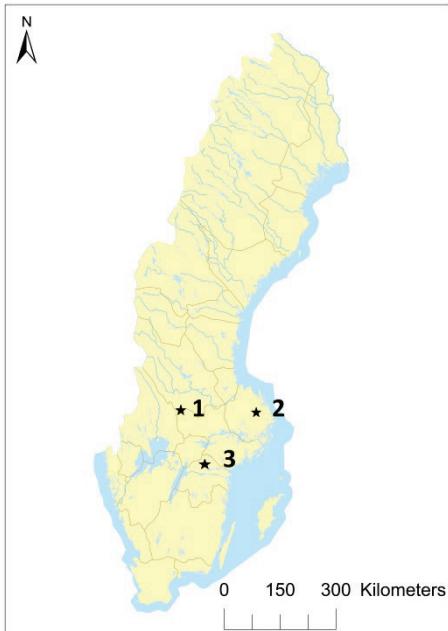
Figure 3. The locations for the three study landscapes in southern Sweden. 1= Dalarna/Västmanland (Papers I–III); 2= Östergötland (Papers I–III); 3= Uppland (Paper IV).

For paper IV, we chose an area in the boreonemoral zone (Sjörs, 1999) in the province of Uppland, south Sweden (59º43'N, 17º30'E; Fig. 3). The study landscape (1700 km^2) is similar to the two study landscapes used for papers I–III and is, like them, to a large extent composed of managed mixed coniferous forests of different successional stages.

3.2   Data collection

For all four papers, data was collected using stratified sampling and line transects. We used chronosequences (Walker *et al*., 2010), which were constructed by dividing forest stands into age classes. In papers I and IV, forests below 20 years of age were divided into two and four age classes, respectively (Table 1). In papers II and III, we divided the forested land into five classes: four age classes of productive forests and one consisting of forested mires (of unknown age) (Table 1). The reason for choosing stratification as opposed to random sampling from the whole forest database was that some classes of forests, for example forests >110 years or forested mires, could be hypothesized to have a disproportionate importance for wood-dependent species due to, for example, presence of rare dead wood qualities.

Transects were randomly placed in forest stands using GIS. Dead wood and lichens were surveyed along these transects, and explanatory variables recorded for individual dead wood objects. In papers I and II, only presence/absence of lichen species were noted. In papers III and IV, abundance of lichens species was estimated, in both cases by noting number of occurrences in a grid net on each wooden object.

Table 1. Stratification used in papers I–IV. The ages refer to the number of years since the stand was established.

Paper	Stratification used				
I	3–7 years	16–19 years			
II	0–20 years	21–60 years	61–110 years	>110 years	Forested mires
III	0–20 years	21–60 years	61–110 years	>110 years	Forested mires
IV	4–5 years	8–9 years	12–13 years	16–18 years	

Species interactions were studied in paper IV, using both observational data and a field experiment. We used *Cladonia botrytes* and *Xylographa parallela* as focal species, and investigated whether the occurrence of lichen species with the same photobionts would increase their colonization probabilities. The observational data was acquired by twice surveying lichen species on 293 cut stumps, thus giving us data that enabled us to analyze factors influencing the colonization probabilities of the focal species. For the field experiment in paper IV, we removed the cut surface of 56 cut stumps with a chain saw. The new cut surface on each stump was divided into four plots, which we treated with different algal pastes (i.e. facilitators). We then monitored lichen colonizations over three years.

Lichen species were mainly determined in the field, except in paper II, for which all branches were collected and lichens subsequently determined at the lab. Species not possible to reliably determine in the field were collected for later identification using light microscopy and/or thin layer chromatography (HPTLC, Arup *et al*., 1993). Many wood-dependent lichens display similarities in their life-history traits, e.g., poorly developed thalli and sexual reproduction in minute (<0.4mm in diam.) fruitbodies (Spribille *et al*., 2008). Specimens displaying these traits were routinely collected for identification. Since several species encountered (e.g., *Lecidea apochroeella* and *Puttea caesia*) are poorly known and the published descriptions often are old, identifications were

sometimes based on careful comparisons with herbarium specimens kept at the Evolutionary Museum in Uppsala (herbarium UPS). Nomenclature for lichens follows Nordin *et al.* (2013).

Table 2. *Wood-dependent lichens found in papers I–IV. In total, 112 lichen species were found.*

Species	Papers	Species	Papers
Absconditella delutula	I	*Lecidea apochroeella*	III
Absconditella lignicola	I, III, IV	*Micarea anterior*	III
Calicium trabinellum	I, III	*Micarea denigrata*	I–IV
Catillaria erysiboides	I	*Micarea misella*	I–III
Chaenotheca brunneola	I, III	*Mycocalicium subtile***	I–IV
Chaenotheca xyloxena	III	*Puttea caesia****	I–IV
Cladonia botrytes*	I, III, IV	*Puttea exsequens*	I
Cladonia macilenta	I, III, IV	*Pycnora sorophora*	III, IV
Hertelidea botryosa	III	*Trapeliopsis glaucolepidea*	III
Hypocenomyce friesii	III	*Xylographa parallela*	I, III, IV
Lecanora anopta	III	*Xylographa truncigena*	III
Lecanora saligna	I, IV	*Xylographa vitiligo*	I, III

**C. botrytes* was not treated as wood-dependent lichen in Papers I and III, as it has been shown to be facultatively lignicolous, especially in Northern Sweden (Bogomazova, 2012). In paper IV, it is treated as a species assumed to have the majority of its occurrences on wood, but not >99% as the classification of wood-dependent species of Spribille *et al.* (2008) requires.
***M. subtile* is not lichenized, but belongs to a group of lichen-like fungi that traditionally has been treated by lichenologists.
****P. caesia* was treated as *Lecidea symmictella* by Spribille *et al.* (2008), but was revised and transferred to *Puttea* by Svensson & Spribille in Dillman *et al.* (2012).

3.3   Statistical analysis

We used several different statistical methods in the papers of this thesis. In papers I and IV, we used generalized linear mixed models (GLMM, Bolker *et al.*, 2009) under the information theoretic framework (Burnham & Anderson, 2010). In paper II, we mainly used multivariate statistics, specifically non-metric multidimensional scaling (NMDS, Minchin, 1987; Peck, 2010) and detrended correspondence analysis (DCA, Peck, 2010). For paper III, we used hierarchical Bayesian models (Gelman *et al.*, 2004).

In papers I and IV, we evaluated the importance of various explanatory variables for species richness, occurrence probabilities or colonization probabilities of lichens using GLMM:s. We used the information theoretic framework of Burnham & Anderson (2010), which is recognized as a way to overcome problems of null hypothesis testing, for example arbitrary significance tresholds and *a priori* false null hypotheses (Nakagawa & Schielzeth, 2007; Grueber *et al*., 2011). It also avoids some of the problems associated with stepwise model selection (Whittingham *et al*., 2006, but see Murtaugh, 2009). For each response variable, we tested all possible combinations of explanatory variables and ranked these models using Akaike's Information Criterion (AIC). Inferences were then based on model averaging (i.e. weighted support from several models), thus taking model selection uncertainty into account (Burnham & Anderson 2010, Grueber *et al*., 2011).

In paper II, we used NMDS to analyze variation in lichen species composition. NMDS is an ordination technique that is suitable for analyzing community data, with no assumptions of normal or linear species' responses to underlying complex-gradients (Peck, 2010). Differences in species composition were tested for significance using permutational MANOVA (Anderson, 2001). To ensure that the main gradient structure of the data had been found by the NMDS, we performed a parallel Detrended Correspondence Analysis (DCA), as recommended by Økland (1996). We then ensured that the corresponding axes of the NMDSs and the DCAs were correlated using Kendall's rank correlation coefficients (Sokal & Rohlf, 1995).

Finally, in paper III, we used hierarchical Bayesian models, where model parameters are estimated using the Markov Chain Monte Carlo (MCMC) method, to model abundance of three wood-dependent lichen species (*Micarea misella*, *Mycocalicium subtile* and *Xylographa parallela*) in relation to stand and dead wood characteristics. The parameter estimates from these models were then used to predict the landscape-scale abundance of these three species. These predictions include parameter uncertainty, as Bayesian methods provide probability distributions of model parameters (posterior distributions), which is an important difference compared to frequentist methods that only provide point estimates of model parameters. Another reason for choosing the Bayesian framework in this study was its flexibility in handling data sets with hierarchical structure (Gelman and Hill, 2007). The hierarchical Bayesian framework enables the utilization of explanatory variables measured at the stand level (i.e. at the higher hierarchical level), as we use them to model the stand-specific intercepts (which cannot be done with frequentist methods).

Bayesian methods also differ from frequentist methods in the possibility of including prior information of parameters. In paper III, however, we used flat (or "uninformative") priors, resulting in posterior modes (peaks of the posterior distributions) close to the point estimates that would have been obtained using frequentist estimation (Ellison, 2004). As in paper I and IV, model selection was based on an information criterion: the Deviance Information Criterion (DIC; Spiegelhalter *et al*., 2002). All response variables had an excessive number of zeros compared to that assumed by a regular Poisson distribution, which means that parameter estimates will be biased and that models will have trouble converging if such a distribution is used. Therefore, we used zero-inflated Poisson models, which includes a binomial sub-model for occurrence probability and a count sub-model for abundance (Martin *et al*., 2005; Zuur *et al*., 2012).

The statistics software R (R Development Core Team 2013) was used for the information theoretic multimodel inference in papers I and IV and for the multivariate analyses in paper II. The Bayesian analysis in paper III was performed using OpenBUGS 3.0.2 (Thomas *et al*., 2006).

4 Results and Discussion

4.1 Relative importance of dead wood types for wood-dependent lichens

CWD is important for wood-dependent lichens, but stumps, snags and logs host different species assemblages. In paper III, snags appeared as the preferred substrate for one species (*Mycocalicium subtile*; Fig. 4), while two other study species (*Micarea misella* and *Xylographa parallela*; Fig. 5) hardly occurred on this substrate. Among the additional 17 wood-dependent lichen species that were found in this study, several species apparently also prefer snags and never or rarely occurred on other substrate types. Other studies have also pointed to the special properties of snags as a substrate for lichens (e.g., Lõhmus & Lõhmus, 2001; Humphrey *et al.*, 2002; Svensson *et al.*, 2005). Stumps and logs seem to be interchangeable for wood-dependent lichen species (Paper I, II, III). This indicates that both stumps and logs on the one hand and snags on the other hand are needed to maintain the diversity of wood-dependent lichens. Wood of smaller dimensions (FWD) has received less attention than CWD in studies of forest biodiversity, but could potentially be an important substrate type because of the large amounts present in managed forests. We found however, that branches on the ground were only utilized by the five most common wood-dependent lichen species, and these species had most of their total abundances on snags, stumps or logs (Paper III). Further, dead branches still attached to living trees were found to be dominated by generalist lichen species, both in terms of abundance and species richness, while wood-dependent lichen species were almost absent (Paper II). We conclude that FWD in general has a low relative importance for wood-dependent lichens in managed boreal forests.

Figure 4. The minute, needle-like fruitbodies of *Mycocalicium subtile* are mostly found on snags. (Uppland, photo Måns Svensson).

Figure 5. The wood-dependent lichen *Xylographa parallela* (the light brown, elongated fruitbodies in the middle of the picture) has the majority of its landscape-scale abundance in forests below 20 years of age. (Uppland, photo Måns Svensson).

A type of dead wood that has been neglected in previous studies of biodiversity of boreal forests is dead branches still attached to trees. We show that the surface area of this substrate is of the same magnitude as that of all other wood types combined in managed forests (Paper II; Fig. 6). As discussed above,

however, we conclude that this substrate has low relative importance for wood-dependent lichens in managed boreal forests. Still, our results show that the amount of dead branches may be large, and consequently, the importance of this substrate for other boreal forest organisms deserves to be evaluated. It should, however, be noted that the relative amounts of dead branches as compared to other types of dead wood will be lower if volumes are compared rather than surface areas. For organisms that are dependent on dead wood volume (e.g., many beetles or wood-degrading fungi), the relative importance of dead branches on living trees in managed forests may thus be modest.
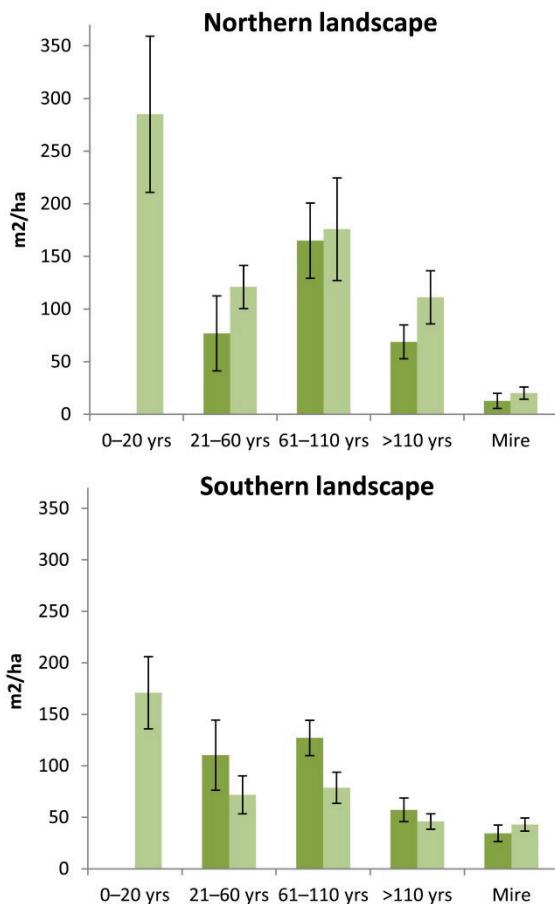
Figure 6. Wooden surface areas (mean ±SE) of attached dead branches (dark green) and other types of dead wood (light green) in productive stands of four age classes and forested mires in the two study landscapes. Attached branches are extremely few in 0–20-year old stands and were therefore not surveyed (adapted from Paper II).

Figure 7. Dead wood in a 60-year old Norway spruce forest. Logs and stumps are regularly recorded in surveys of dead wood, but dead branches attached to trees have largely been ignored. Gälbo, Östergötland (photo Måns Svensson).

4.2 Relative importance of stand types for wood-dependent lichens

Forests up to 60 years old hold the largest populations of the modelled wood-dependent lichens (*Micarea misella*, *Mycocalicium subtile* and *Xylographa parallela*) in managed boreal forest landscapes (Paper III; Fig. 8). This is both because such stands contain more coarse dead wood per hectare than older forests or forested mires, and because they occupy a much larger total area. We

were only able to statistically analyze the three most abundant species. All of them also occur in older forests (>60years; Fig. 9) and in forested mires, but these stand types only harbour a small proportion of the total population. It is likely that other wood-dependent lichens found in this study that occur in all or most forest types will also have the main proportion of their abundances, at the landscape-scale, in young to middle-aged forests.
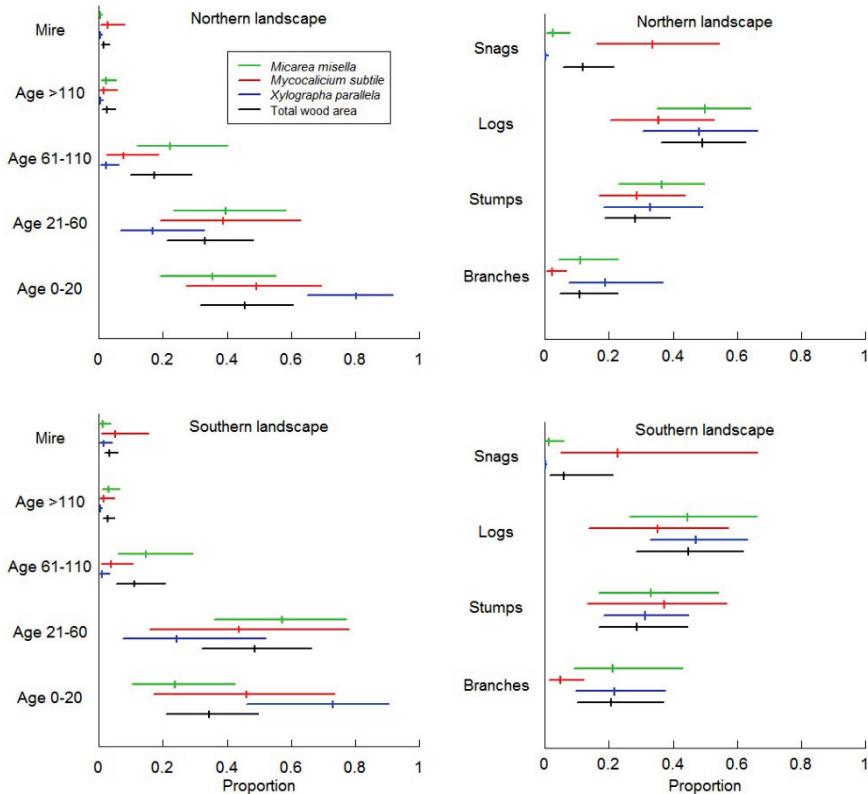
Figure 8. The proportion of the total abundance of three wood-dependent lichens in different forest types and on different main types of dead wood based on predictions of occurrence and abundance on all dead wood objects in two simulated areas based on field data from two study landscapes in Sweden. Mean (short vertical line) and 95% confidence limits (horizontal line) are shown (adapted from Paper III).

Forested mires have recevied little attention in studies of boreal biodiversity, but such land is probably the most common unmanaged forest land in many managed forest landscapes in Fennoscandia (e.g., Rydin *et al*., 1999; Swedish Environmental Protection Agency & Swedish Forest Agency, 2012). Since

forestry is not practiced on these mires, they could be hypothesized to serve as important habitats for wood-dependent lichens that are adapted to more stable conditions than those of the prevailing short-rotation system. A few wood-dependent species recorded (e.g., *Pycnora sorophora*, Paper III), probably have the main part of their populations in forested mires in managed forest landscapes, but generally, species found on mires also occurred in managed forest stands. Thus, we conclude that forested mires are not a major habitat for wood-dependent lichens, mainly because of the small amounts of dead wood present in them (Paper II, III). One explanation for the low quantities of dead wood in these areas may be their low productivity. However, it is also possible that it is low compared to more natural conditions, since forested mires have been extensively used for woodfuel and hay production in the past (Emanuelsson, 2009; Rydin & Jeglum, 2013).

Figure 9. Forests older than 110 years cover too small an area to harbour a large proportion of the total population of three modelled wood-dependent lichens. Kampberget, Dalarna (photo Måns Svensson).

4.3 Implications for conservation

Keeping parts of the landscape outside the forestry system is probably necessary to maintain the landscape-scale persistence of dead wood types that are rare and only to a small extent created within standard management regimes. Apart from the comparatively small areas of legally protected forest (e.g. nature reserves), such unmanaged areas already exist in the form of low-productivity areas, e.g. forested mires. Due to the very low volumes of dead wood found at forested mires, it is, however, improbable that these areas can replace more productive dead wood-rich stands with limited influence of forestry. It is therefore probable that protecting productive forest will remain important for the conservation of wood-dependent species. We found that snags are uncommon but probably preferred by several wood-dependent lichen species (Paper III; Fig. 9). The only snag-generating management practice today is leaving high-stumps after clear-felling as a conservation measure. To improve intensively managed forest landscapes for biodiversity enhancement, increased artificial creation of snags could thus be an option (Fig. 10). To allow these snags to persist, an alternative is to locate them in low-productivity land such as unmanaged, forested mires, perhaps by depositing dead wood or by killing trees growing there. However, such a procedure will be more justified if not only lichens benefit from it: designing conservation measures that target several organism groups need careful consideration, as their response to these measures differs (e.g., Lõhmus *et al*., 2007; Djupström *et al*., 2010).

Harvesting forest biomass for bio-fuel production decreases the amount of dead wood present. As wood-dependent lichen species currently to a large extent utilize dead wood generated by clear-felling, they will likely decline with increased outtake of residues. Some species, such as *Micarea misella*, which mainly occur in middle-aged to mature forests (21–60 and 61–110 years), will be less affected as long as residues from thinning are not extracted. It would in general be worthwhile to consider how thinning procedures could be brought to the service of conservation of wood-dependent species (cf. Fuller 2013). In view of the rather large proportion of populations of the three modelled species present on stumps (13–57%) and branches on the ground (0–53%) (Fig. 8), further, large-scale removal of stumps and FWD will cause wood-dependent lichens to decline. Stump harvest will probably have a greater negative effect on wood-dependent lichens than removal of FWD, since most wood-dependent lichens found in our study utilize stumps, whereas FWD is of low relative importance (see above). The decline of wood-dependent lichens caused by stump removal must, however, be seen from the perspective that

many of the wood-dependent lichens on them may in fact be favoured by, or at least tolerant of, the management system as it is currently practiced. For the most threatened wood-dependent lichens, the most pressing question is unlikely to be how large outtakes for bio-fuel are, but rather how to create and maintain other dead wood qualitites that are currently rare in managed boreal forest landscapes.

Figure 10. Increasing the amount of snags is beneficial for wood-dependent lichens. Trollkäringgölen, Östergötland (photo Måns Svensson).

4.4   Factors influencing lichen communities on wood

Lichen assemblages on dead wood in managed forests are generally dominated by generalist species, while wood-dependent lichens are comparatively rare (Paper I–IV, see also Caruso *et al.*, 2008; Spribille *et al.*, 2008). The major changes in forest landscapes during the 20th century might have shifted the landscape-scale balance between species with different life-history traits. As suggested by Berglund *et al.* (2011) for wood-degrading fungi, generalist species may have acquired a competitive advantage over more specialized

species with the introduction of modern forestry. Species that colonize a broad range of dead wood types should be able to maintain a high propagule pressure both locally and regionally, and could perhaps qualify as "native invaders" (e.g., Carey *et al*., 2012). Thus, even if dead wood objects of rare types are present, they are more likely to be colonized by generalist species (e.g., Nordén *et al*., 2013). When the generalist species are already established, they could suppress colonization of other species, including specialists (e.g. Holmer & Stenlid, 1993). Generalist lichens species are able to grow on an even broader range of substrates than generalist wood-degrading fungi, and some are very common on soil and rocks on clear-cuts. Other organism groups also compete with lichens on wood. For example, bryophyte cover generally has a negative effect on lichens (Paper I), and increased propagule pressure from bryophytes may therefore also play a role in shaping communities on dead wood. Thus, different management regimes and landscapes could give rise to different balances between species, with consequences for conservation. Landscape context has been shown to affect restoration success (e.g., Kouki *et al*., 2012), but such studies usually focus on the specialist species and their colonization of restored parts of the landscape. Propagule pressure from generalist species could further aggravate the situation for dispersal-limited, specialist species and consequently also affect the success of conservation efforts.

Apart from competition with generalist species, positive interactions may also affect the occurrence patterns of wood-dependent lichens. We tested for the existence of facilitation both by analyzing colonizations over time and by a manipulative field experiment. The observational and experimental parts of this study showed conflicting results, as the colonization probabilities on stumps increased when the hypothesized facilitators were present, but no such effect was seen when facilitators were added experimentally. It is possible that the apparent effect of facilitation in the observational part result from some unmeasured environmental variable, that positively affects both the presence of the facilitators and the colonization probabilities of the focal species. Our results illustrate the importance of combining modelling of observational data with experiments when studying interactions between species.

The biogeography and distribution patterns of Fennoscandian lichens are generally poorly known. Interestingly, the species richness on wooden objects were always higher in the northern study area (Papers I and II). Although the data do not allow for sorting out the separate effects of, e.g., climate, forest history and differences in management, it is possible that lichen species richness is partly driven by large-scale climatic factors. Studies from Central

Europe have established that local factors (dead wood amounts, diversity of tree species etc.) are more important drivers of forest cryptogam diversity than large-scale factors such as climate (Moning *et al*., 2009; Raabe *et al*., 2010). However, the rather limited geographical span of these studies makes it doubtful whether they can be applied to Fennoscandia, an area spanning six vegetation zones (Sjörs, 1999). Disentangling the multiple, landscape-scale drivers of lichen occurrence patterns and diversity remains a challenge and requires consideration of air pollution regimes in addition to the influence of climate (Ellis & Coppins, 2010). A better understanding of the large-scale distribution patterns of wood-dependent lichens would be useful for conservation planning.

4.5 Future directions

The rarity of wood-dependent lichens presents a challenge for data collection. In paper III, despite great sampling effort, we could only analyze the three most abundant species. The possibilities to draw inferences for conservation purposes are thus limited, as species that utilize types of dead wood that occur abundantly even in managed forests are not likely to be under threat (Stokland *et al*., 2012). The most threatened wood-dependent species may have become so rare, that obtaining adequate sample sizes by the use of stratified random sampling is difficult (Berglund *et al*., 2005; Framstad *et al*., 2009; Stokland *et al*., 2012). To further our understanding of the ecology of rare and threatened wood-dependent lichens, it is therefore necessary to employ alternative sampling strategies. One possibility would be to systematically sample key microhabitats (e.g. Newmaster *et al*., 2005), which in the case of wood-dependent lichens would be, e.g., coarse and weathered snags or burnt wood.

Data on dispersal abilities are essential when predicting species' response to habitat fragmentation. For most of the wood-dependent lichens found during this study, a reasonable hypothesis is that they are not dispersal limited, but are able to disperse to the dead wood available in the landscape. If this is the case, then it would have implications for conservation, as these species would then be able to disperse to their substrates even if landscape-scale dead wood amounts would decrease because of bio-fuel harvest. This hypothesis would be worth testing using molecular methods (e.g., Werth, 2010).

In studies of lichens on wood, it has been a common practice to analyze factors driving total lichen species richness (e.g., Humphrey *et al*., 2002; Caruso *et al*., 2008; Nascimbene *et al*., 2008; Hautala *et al*., 2011; Dittrich *et al*., 2013). As

these factors are not necessarily the same as those driving species richness of wood-dependent lichens, the value of this kind of analysis for conservation of wood-dependent species could be questioned. However, on Norway spruce stumps in young managed forests, we found that both total species richness and richness of wood-dependent lichens are explained by the same factors (Paper I). Lichen species growing on such stumps may be pioneer species with similar ecological requirements, whether they are wood-dependent or not. The diversity of wood qualities and micro-climates in young managed forests is low. It is possible that if wood in more heterogeneous habitats (e.g. old-growth forests) would be sampled, wood-dependent species with very specific requirements would be found, and those species probably rarely occur in young managed forest stands. In such a case, the response of total lichen species richness and species richness of wood-dependent lichens could show more marked differences. Generally, future studies that seek to understand the requirements of wood-dependent lichens should consider the use of other response variables than total lichen species richness.

Taxonomic knowledge is fundamental for credible biological research (Wheeler, 2004). Ecological studies of lichens are often hampered by unclear taxonomy and by the fact the many of the available species descriptions are old. The knowledge gap concerning lichen species on wood is illustrated by a number of records of lichen species made during the course of this work. For example, one species, *Arthonia coronata*, found on Norway spruce stumps was reported as new to Fennoscandia (Paper I, Svensson & Westberg, 2010) and a probably undescribed species of the genus *Bacidina* was also recorded on such stumps (Paper I). Other examples include *Catillaria ameibospora* (Paper I) and *Lecidea apochroeella* (Paper III), for which the reports in the present work represent the first findings in >100 years from southern Sweden (Arup & Hultengren, 2000; Nordin *et al*., 2013). Rather than representing finds of extremely rare species, this is probably just as much a sign of our lack of knowledge of crustose lichens and the impenetrable nature of the available literature concerning them (for example, *C. ameibospora* and *L. apochroeella* were last treated scientifically in 1892 and 1934, respectively, both times in Latin). There is thus an urgent need for taxonomic revisions and improved identification guides, something that in general would greatly facilitate ecological studies of wood-dependent species.

5   Conclusions

Forest management has altered the conditions for biodiversity over large areas. Current and future management will affect habitat availability for wood-dependent species. The observed occurrence patterns of dead wood in the studied landscapes are to a large extent attributable to management practices, with clear-felling as the main driver of dead wood input.

CWD is important for wood-dependent lichens, but cut low stumps, snags and logs host different species assemblages. Snags are preferred by some wood-dependent lichen species, while others rarely occur on them. Stumps and logs seem to be more or less interchangeable for wood-dependent lichen species. This indicates that both stumps and logs on the one hand and snags on the other hand are needed to maintain the diversity of wood-dependent lichens. This study, however, shows that snags are rare in managed forest landscapes. Increasing the landscape-scale amount of snags would therefore benefit wood-dependent lichens. FWD occurs in great numbers, but we found that branches on the ground were only utilized by the five most common wood-dependent lichen species, and these species had most of their abundances on snags, stumps or logs. We have also shown that the previously neglected dead wood type of dead branches of living trees occurs in amounts of the same magnitude as all other dead wood types combined, and that they thus make up a large portion of all substrate available to organisms living on dead wood surfaces in managed boreal forests. However, wood-dependent lichens were almost absent from this substrate. We conclude that FWD in general has a low relative importance for wood-dependent lichens in managed boreal forests.

Young managed forests up to 60 years old held the largest populations of the three modelled wood-dependent lichens at the landscape level. This is both because such stands contain more CWD per hectare than older forests and forested mires, and because they occupy a much larger total area than other forest types. All of these three species also occur in older forests (>60years) and in forested mires, but these stand types only harbour a small proportion of the total population. This general pattern is probably applicable to several other wood-dependent lichens found during this work.

Apart from the comparatively small areas of legally protected forest, unmanaged areas are probably necessary to maintain the landscape-scale persistence of dead wood types that are rarely created within standard management regimes. Such areas currently occur mainly in the form of low-productivity areas, such as forested mires. We show, however, that forested mires contain very low volumes of dead wood. To enhance biodiversity in intensively managed forest landscapes, increased artificial creation of dead wood is an option. One option would be to locate this dead wood to unmanaged, low-productivity land. However, it is probable that protecting more productive forest will remain important for the conservation of wood-dependent species.

Harvesting forest biomass for bio-fuel production will cause some wood-dependent lichens species to decline. Stump harvest will probably have a greater negative effect on wood-dependent lichens than harvest of FWD, since more wood-dependent species grow on stumps. To conserve the most threatened wood-dependent species, it is probably necessary to find ways to create and maintain dead wood types and qualities that are currently rare in managed boreal forest landscapes.

Understanding biotic interactions is important when trying to predict species' response to changes in management. In several studies, it has been found that the specialist wood-dependent lichens are affected by the presence of generalist lichen species on dead wood. Competition with generalists may explain the relative rarity of wood-dependent lichens on the dead wood substrates of managed boreal forests. Apart from competition, facilitation could also be an important driver of community assembly of wood-dependent lichens. We could, however, not find any support for such facilitation. Our results show the importance of combining observational data with experimental data when studying species interactions.

Wood-dependent lichens are comparatively rare, which makes them difficult to sample. To study rare and threatened wood-dependent lichens, alternative sampling strategies has to be devised. Systematic sampling of microhabitats (e.g., coarse and weathered snags or burnt wood) is a promising possibility.

6 Acknowledgements

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