

Lichen Diversity on Stems, Slash and Stumps in Managed Boreal Forests

Impact of Whole-tree Harvest

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Doctoral thesis
Swedish University of Agricultural Sciences
Uppsala 2008

Acta Universitatis agriculturae Sueciae

2008:3

Cover: A 12 year old Norway spruce *Picea abies* stump with the cut surface colonised predominantly by lichens

(photo: J. Rudolphi)

ISSN 1652-6880

ISBN 978-91-85913-36-7

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Lichen Diversity on Stems, Slash and Stumps in Managed Boreal Forests. Impact of Whole-tree Harvest

Abstract

The shortage and low diversity of coarse dead wood in managed forests are major threats to wood living organisms. Increasing harvest of slash and stumps for biofuel may further decrease the amounts of dead wood. The aim of this thesis was to predict the impact of forest fuel harvest on lichen diversity in a managed forest landscape. First, lichen diversity was compared between the stem and slash fractions within living mature trees. Comparisons were also made between slash and stumps created at final felling. The effects of local factors on the species composition and richness of lichens and bryophytes on stumps were analyzed. Finally, colonization and extinction dynamics of epixylic lichens on stumps were examined.

Lichen species composition differed between the stem and the slash fractions, indicating that slash harvest removes lichen communities other than those removed with stems. The lichen flora on slash changed from freshly created slash with bark to decorticated slash. There were compositional differences between decorticated slash and stumps created at final felling. The majority of species found on both substrates were more frequent on stumps, on which eight rare species were found. Lichen richness on stumps increased with presence of irregularities on the cut surface. Metapopulation processes structure the local epixylic lichen community. Connectivity and stump quality affected the probability of stump colonization by epixylic lichens. The extinction risk of local populations was mainly explained by variables describing patch quality.

The effects of slash harvest are probably of minor importance to the overall lichen diversity in the study area. However, stumps may be important since 1) the majority of the epixylic lichens found have a preference for less shaded environments, 2) we found eight rare lichen species on the cut surface, and 3) stumps constitute the major part of coarse dead wood in these kinds of stands. The relative importance of stumps to the regional persistence of species in managed forests will depend on the availability of other types of coarse dead wood which depends on, e.g. geographic region, present and past land use, and forest type.

Keywords: biofuel, composition, dead wood, epixylic, metapopulation, richness

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Dedication

To Daniel

Pappa åbbaj daton (= daddy works at the computer).

Daniel Caruso, December 2007

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List of publications

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

- I 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, *Scandinavian journal of forest research*, 22, pp. 219-230. (<http://www.informaworld.com>)
- II 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*, *Biological Conservation*, 141, pp. 47-55.
- III Caruso, A. & Rudolphi, J. Influence of stand successional stage and substrate quality on species diversity of lichens and bryophytes on stumps. (submitted manuscript).
- IV Caruso, A., Thor, G. & Snäll, T. Colonization-extinction dynamics of epixylic lichens among their dynamic stump patches. (manuscript).

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I contributed with major parts of study set up, field work, data analysis, and preparing of the papers I and II. In paper III, I did most of the data analysis and preparation of the paper, both authors contributed to the study set up and field work. In paper IV, I contributed with major parts of study set up, field work and data analysis, GT helped determine and classify species, and provided helpful comments on the text, whereas TS suggested the study, and both AC and TS contributed equally to the writing process.

Abbreviations

Slash	Logging residues consisting of branches, twigs and tops
CWD	Coarse woody debris, diameter >10 cm
FWD	Fine woody debris, diameter <10 cm

1 Introduction

Not much of the natural forests remain in the boreal vegetation zone of Scandinavia (Lloyd, 1999; Lofman & Kouki, 2001). Tree harvest for timber and pulp has dramatically changed the forest ecosystem on the expense of some of the organisms inhabiting the forest landscape (Dahlberg & Stokland, 2004; Gärdenfors, 2005; Siitonen, 2001). In addition, the search for more CO₂ neutral fuels during the last decades has lead to further exploitation of this natural resource by the extraction of slash (branches, twigs and tops, also termed FWD = diameter <10 cm) and stumps, i.e. tree fractions previously left in the stand after final felling. This extraction has the potential to increase, yet the knowledge of the diversity of organisms on slash and stumps is poor.

The shortage and low diversity of coarse dead wood (CWD = diameter >10 cm) in managed forests are considered the biggest contemporary threats to the diversity of forest dwelling organisms (Berg *et al.*, 1994; Gärdenfors, 2005; Samuelsson *et al.*, 1994). Of the 25 000 species in Swedish forests, 5 000–7 000 are depending on dead wood (Dahlberg & Stokland, 2004), and of these about 1 000 are on the Red List (Gärdenfors, 2005). Many species may face extinction since species responses to changes and disturbances generally are slow (Hanski, 2000; Hanski & Ovaskainen, 2002).

Due to the low amounts of “natural” dead wood in managed forests stumps and slash may constitute an important part of the habitat patches available for the forest biota in these forests. However, this has been poorly investigated. It is therefore of great importance to describe the species communities inhabiting these tree fractions. In addition, the metapopulation concept, which is widely used in fragmented landscapes, provides an important theoretical basis for examining the mechanisms behind the regional distribution patterns of species, and hence the structure of local communities.

2 Thesis aims

The general aim of this thesis was to examine lichen diversity on tree fractions generally overlooked in diversity studies. More specifically, my objective was to assess the relative importance of slash and stumps created at final felling to overall lichen diversity in a managed forest landscape.

This was done by comparing lichen species richness and composition between fractions of mature trees (paper I), and between stumps and slash created at final felling (paper II). To get a picture of the available substrate amounts, the volume and surface area of stumps and slash were estimated (paper II). Important substrate quality variables to the diversity of lichens and bryophytes growing on stumps were also identified (paper III). Finally, metapopulation dynamics of epixylic lichens were explored by examining colonization-extinction dynamics of lichens on stumps (paper IV).

Specific questions discussed in the respective papers were:

- I. Does lichen species diversity differ between tree fractions conventionally harvested (stem) and those extracted for fuel (slash)?
- II. Does lichen species diversity and substrate amounts differ between stumps and slash in young managed forests?
- III. How does stand successional stage and substrate variability influence species diversity of lichens and bryophytes on stumps?
- IV. Can the dynamics of epixylic lichen species be generalized using the metapopulation concept?

In the thesis, “managed forests” are defined as regenerated after clear-cutting or by planting on former arable land, with subsequent cleaning and thinning operations. “Epiphytic” species are defined as growing on other plants, but not parasitic. However, in the thesis it is used consistently for species inhabiting bark. “Epixylic” is used for species on decorticated dead wood.

3 Boreal forests

3.1 Natural vs. managed

The Fennoscandian (Sweden, Norway and Finland) boreal forest is dominated by Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*, and with birch *Betula* spp. (*B. pendula* and *B. pubescens*), aspen *Populus tremula*, goat willow *Salix caprea*, and rowan *Sorbus aucuparia* as the most common deciduous tree species. The forest of today is to a great extent architected by human activities (Lloyd, 1999; Lofman & Kouki, 2001; Östlund *et al.*, 1997). Large scale harvest of trees for timber, pulp and fuel have turned the structurally diverse and multi-aged natural forest ecosystem into a forest comprised of monospecific, evenaged forest stands with short rotation periods (Axelsson, 2001; Östlund *et al.*, 1997). The heterogeneity of natural forests is maintained by wildfires, windstorms, insect and fungi outbreaks (Kuuluvainen, 2002; Niklasson & Granström, 2000; Sernander, 1936; Syrjänen *et al.*, 1994), on both large and small scales. These natural disturbance regimes are heavily controlled in the managed forest, which as a consequence, lacks the mosaic of multilayered forests of various successional stages.

The intensively managed boreal forest also lacks the large quantities and diverse types of dead wood, which are key features of a natural forest (Jonsson, 2000; Kirby *et al.*, 1998; Siitonen, 2001). Dead wood in managed Fennoscandian forests is mainly created through silvicultural measures such as final felling, cleaning and thinning. Managed forest of today contain only 2-10% (<10 m³/ha) of CWD compared to natural forests (Fridman & Walheim, 2000; Gibb *et al.*, 2005; Jonsson *et al.*, 2005; Linder, Elfving & Zackrisson, 1997; Siitonen, 2001), stumps excluded. Natural forests also have a greater diversity of dead wood substrates such as standing dead trees

(snags), fallen logs, FWD and stumps, all of which of different decay stages, tree species, dimensions and surface texture.

However, contrary to the decreased amounts of CWD in managed forests, rough calculations of the inflow of FWD during the 20th century in Sweden reveal an increase of FWD by 75% since since the 1920'ies (Thor, pers. comm.).

3.2 Threats to the forest biodiversity

Two major causes for the high number of red-listed species in the forest landscape are habitat destruction and fragmentation caused by modern forestry (Davies *et al.*, 2000; Gärdenfors, 2005; Saunders *et al.*, 1991). A large part of these species are in various ways dependent on dead wood (Dahlberg & Stokland, 2004; Esseen *et al.*, 1997; Gärdenfors, 2005; Harmon *et al.*, 1986; Jonsson *et al.*, 2005; Samuelsson, Gustafsson & Ingelög, 1994). The low density and diversity of, mainly, CWD in the modern boreal forest have drastically increased the isolation of the few, often small, forest fragments with high conservational value, to which the red-listed dead wood dependent species are confined. Only about 1% (i.e. 300 000 ha) of the productive forest landscape (the mountain region excluded) in Sweden is formally protected (Anonymous, 2007a). If the approximately 80 000 woodland key habitats (WKH) are added to the calculations, the figure increases to less than 2% of the Swedish forestland (Anonymous, 2007b). Consequently, many species may face extinction even if habitat destruction and fragmentation ceases (Hanski, 2000). Creating new reserves is not the single solution to stop the degradation of forest biodiversity. Restoration efforts to improve the quality of the managed forest landscape are also much needed (Hanski, 2000; Mönkkönen, 1999; Nilsson, 1997).

3.3 Harvest of slash and stumps for biofuel

During recent decades, the increasing demand for more CO₂-neutral energy sources has lead to an increased interest in the post-harvest extraction of logging residues (i.e. slash and stumps) for bioenergy (Berglund, 2006; Egnell *et al.*, 2001; Hofsten, 2006). Between 2003 and 2006 in Sweden, the total area of forest stands where forest fuel (of which slash constitute the major part) was reported to be extracted almost doubled, i.e. from 47 000 ha to 84 000 ha (Anonymous, 2007a). Generally, about 70% (or 10 m³/ha) of the slash created at final felling is removed from stands subjected to bioenergy extraction (Anonymous, 1994; Rudolphi & Gustafsson, 2005).

Further, an estimated 20–70 m³/ha of wood from conifer stumps can be extracted depending on latitude, and of this, 10–25 m³/ha are made up of the above ground parts of the stumps (Hofsten, 2006). Thus, the extraction of slash and stumps may dramatically reduce the amount of substrate available for dead wood dependent species in managed forests.

Whereas the importance of CWD for forest biodiversity has been well documented for various organism groups (Bader *et al.*, 1995; Crites & Dale, 1998; Humphrey *et al.*, 2002; Kruys *et al.*, 1999), few studies have been made on the contribution of FWD and stumps to the diversity of forest organisms. In the already dead wood poor forests, FWD has shown to host a higher number of lichen, fungi and bryophyte species on equal volumes of FWD and CWD (Kruys & Jonsson, 1999; Nordén *et al.*, 2004). Slash may also function as an important breeding substrate for insects (Edmonds & Eglitis, 1989; Jonsell, Weslien & Ehnström, 1998), and provide shelter for both small mammals and desiccation-sensitive bryophytes (Ecke, Löfgren & Sörlin, 2002; Åström *et al.*, 2005). Owing to the extraction of slash, the alteration of microhabitat complexity decreased both the diversity and abundance of beetles in boreal forests in Sweden (Gunnarsson *et al.*, 2004), and is also suggested to cause shifts in dominance from more specialized forest species to generalists (Nittérus, Åström & Gunnarsson, 2007).

Several studies have stressed the conservation value of high stumps (height of 4–5 m) in managed forests (Jonsell, Nittérus & Stighäll, 2004; Jonsell & Weslien, 2003; Lindhe & Lindelöw, 2004), whereas little effort has been spent on the importance of low stumps (usually <0.5 m) created at final felling to the diversity of dead wood inhabiting organisms. Nevertheless, after logging in a Tasmanian wet forest, stumps acted as hotspots of lichen diversity in the young forest (Kantvilas & Jarman, 2006). Similarly, in planted and semi-natural forests in Britain, early successional stands were the richest in lichens, with stumps being especially important for *Calicium* and *Cladonia* species (Humphrey *et al.*, 2002).

Clear-felled areas and the subsequent regenerated young forests are man-made habitats, and no species can be considered primarily adapted to slash and stumps in these environments. High stumps and logs in open or newly burned forests are probably the most comparable substrate types in natural forest landscapes to stumps, whereas branches and twigs on freshly felled trees after large scale fires, storms and insect and fungi attacks are so to slash in newly felled areas. However, since such environments and qualities of dead wood are rare in the managed forest landscape (Berg *et al.*, 1994), there is a need to assess the importance of slash and man-made stumps to the diversity of forest organisms.

4 Study organisms

Lichens are defined by their biology, i.e. the relationship between a photosynthetic green alga and/or cyanobacteria (photobiont) and a heterotrophic fungus (mycobiont). They reproduce asexually by fragmentation or by the production of special propagules (e.g. soredia and isidia) containing both the mycobiont and the photobiont. The mycobiont may also reproduce sexually by the production of spores, which form new lichens when they germinate and come into contact with an appropriate photobiont.

Bryophytes are classified among the basal land plants. Their vegetative reproduction comprises the production of special propagules (e.g. gemmae), fragmentation, and progressive growth, i.e. older parts of the individual die off as new emerges. Sexual reproduction is by the formation of spores.

Lichens and bryophytes are known to be among the first organisms to colonise pioneer terrestrial habitats (Longton, 1992), and thus contribute to e.g. soil formation. They also play a significant role for the nutrient cycling in forests. In addition, many animals utilize lichens as food, shelter, or nesting material (Gilbert, 2000), and lichens and bryophytes should be considered an important structural component for the maintenance of biodiversity in forested areas (Gunnarsson, Nittérus & Wirdenäs, 2004; Longton, 1992; Pettersson, 1996; Pettersson *et al.*, 1995). However, the symbiotic life style and the lack of mechanisms to regulate water uptake and loss, makes them vulnerable to drastic changes in their environment, such as forestry.

There are approximately 2 000 lichens and 1 000 bryophytes in Sweden, and of these, 800 and 300, respectively, are mainly found in forests (Hallingbäck, 1995; Hallingbäck, 1996; Hallingbäck, 2007). One of the biggest threats to lichens and bryophytes in Fennoscandian forests is the low amounts and diversity of CWD (Berg *et al.*, 1994; Gårdenfors, 2005).

5 Diversity of epiphytic and epixylic communities

5.1 Populations and communities at different spatial scales

Depending on the scale of interest, species organization can be discussed within populations, metapopulations, communities and metacommunities. Populations contain all individuals of a single species within a habitat patch. A patch is a discrete (local) area of habitat. A metapopulation is formed by a set of local populations of a single species that are linked by dispersal (Hanski & Gilpin, 1991). Similarly, a community consists of the individuals of all species that potentially interact within a single patch, whereas a metacommunity is defined as a set of local communities that are linked by dispersal of multiple interacting species (Hanski & Gilpin, 1991; Wilson, 1992).

The patterns of distribution, abundance and interactions of species occur at different spatial scales, and are influenced by ecological processes also operating at multiple scales (Chase & Leibold, 2002; Levin, 1992; Ricklefs, 1987; Wiens, 1989). At the local scale, community diversity is mainly determined by e.g. niche differentiation, resource heterogeneity, and the interactions between competing species. Regional scale processes include species interactions affecting colonization and extinction dynamics among local communities. The metacommunity concept has been proposed as an important framework for linking different spatial scales in community ecological issues (Leibold *et al.*, 2004). However, up to date there are no empirical data supporting the concept.

5.2 Influence of local factors and processes

5.2.1 Epiphytic communities

At the tree level, the composition of the epiphytic lichen flora is strongly influenced by the variation of microclimate, which not only vary vertically along the trunk, but also between tree fractions, such as trunk and branches (Barkman, 1958; Coxson & Coyle, 2003; Kermit & Gauslaa, 2001; Legrand, Asta & Goudard, 1996). Microclimate is determined by the interactions between regional climate, tree architecture and bark properties, such as chemistry, texture and moisture holding capacity (Campbell & Coxson, 2001; Coxson & Coyle, 2003; Halonen, Hyvärinen & Kauppi, 1991; Lowman & Rinker, 2004).

The bark in upper part of the trunk is generally smoother than the bark on the tree base. Light intensity and exposure to desiccating wind increase with height in the canopy while humidity, water holding capacity and rate of water absorption of the bark generally decrease in the same direction. The directional trend of a trunk's vertical bark pH gradient depends, among other things, on soil properties and element concentrations in stemflow which is highly influenced by atmospheric input and tree species. Both increases (Legrand, Asta & Goudard, 1996) and decreases (Bates, 1992; Kershaw, 1964) of trunk pH with height above ground have been reported. The greater interception of rain by branches often results in a higher pH on trunks than on branches due to the continuous enrichment of precipitation with H⁺ during its descent through the canopy (Hauck & Meissner, 2002). This further means that branches in the lower canopy often are more acidic than the ones higher up (Kermit & Gauslaa, 2001).

Several studies have ruled out the importance of interspecific interactions on the diversity of epiphytic communities since they rarely lead to exclusion of species (Hawksworth & Chater, 1979; Kimmerer & Driscoll, 2000; Löbel, Snäll & Rydin, 2006; Ojala, Mönkkönen & Inkeröinen, 2000; Rydin, 1997; Uliczka & Angelstam, 1999). However, the colonization of the sexually dispersed lichen *Xanthoria parietina* is highly facilitated by the presence of other species from which the germinating fungal spore can “steal” the photobiont, and eventually overgrow (Ott, 1987). In addition, other studies have proposed both facilitation and competition as important processes during lichen species succession on tree trunks (Rogers, 1988), branches (Hilmo, 1994; Stone, 1989) and on shrubs (Ruchty, Rosso & McCune, 2001). For a review of studies suggesting that individual lichen species can be excluded from a substratum as a result of competition see Armstrong & Welch (2007).

5.2.2 Epixylic communities

Decorticate wood, such as logs, snags, stumps and branches host many specialized, often crustose, lichens (Crites & Dale, 1998; Humphrey *et al.*, 2002; Lõhmus & Lõhmus, 2001; Söderström, 1988a). Generally, snags are more favorable to lichens than logs because they receive a higher amount of light and are drier than logs, which in turn are favored by bryophytes (Laaka, 1995; Lõhmus & Lõhmus, 2001; Svensson, Johansson & Thor, 2005). In planted and semi-natural forests in Britain decorticate snags had the highest lichen diversity while bryophyte richness on logs increased with diameter and decay (Humphrey *et al.*, 2002). Compared to living tree trunks, which show a gradient in bark pH from acid to around neutral (depending on tree species) dead wood is generally an acid environment (Lõhmus & Lõhmus, 2001). Decay stage, microclimatic conditions and wood dimensions are important local factors determining the species composition of wood-inhabiting lichens and bryophytes (McCollough, 1948; Muhle & LeBlanc, 1975; Söderström, 1988a; Söderström, 1988b).

Lichen species can often be coupled to a particular decay stage (Daniels, 1983, 1993; Söderström, 1988). In general, lichen diversity tends to peak at intermediate to late decay classes, whereas bryophytes often dominate the latest stages of decay (Humphrey *et al.*, 2002; Kruijs *et al.*, 1999). However, species on particular decay stages can differ between forests of different ages indicating that both time and structural attributes are important in determining species composition (Crites & Dale, 1998).

Species richness is often positively correlated to log diameter. CWD is considered more diverse than FWD if comparisons are made on a pieces basis (Bader *et al.*, 1995; Kruijs *et al.*, 1999; Siitonen, 2001; Söderström, 1988b). A larger log has a longer life time and offers a more stable substrate with more niches. In addition, the break down of FWD is more rapid and smaller logs are also more rapidly overgrown by ground vegetation. However, some recent studies have pointed out the problem of comparing equal number of pieces of CWD and FWD since the results can be quite different if instead equal surface area or volume is compared (Heilmann-Clausen & Christensen, 2004; Kruijs & Jonsson, 1999; Nordén *et al.*, 2004).

Biotic interactions are probably also important in structuring epixylic communities, although it has been questioned if competition can lead to exclusion of species (McAlister, 1995). However, on individual logs, the availability of space may be a crucial local factor for the dynamics of species since establishment in closed communities is difficult (Kimmerer, 1993, 1994; Kimmerer & Young, 1996). In addition, lichens can inhibit the establishment of vascular plants (Deines *et al.*, 2007; Zamfir, 2000).

5.3 Influence of regional processes: the exchange of colonists

By only taking into consideration factors and species interactions on a local scale when exploring the structure of a community, it is assumed that local communities are closed and isolated. However, species interactions also occur on larger scales where they might affect colonization probabilities and extinction patterns in a network of local communities (Levin, 1992; Wiens, 1989). These aspects are highlighted in the metacommunity concept (Leibold *et al.*, 2004). In this perspective, the supply of colonists for the local communities comes from the regional species pool, which is affected by e.g. macroclimate, landscape history and disturbance regimes operating at larger scales. A successful colonization process includes dispersal, attachment to the substrate and germination of the dispersed propagule. The inherent biological differences between species regarding e.g. dispersal capacity, germination and competitive ability are thus likely to have a strong influence on community structure. However, the relative importance of the trade-offs among species traits, such as dispersal and competitive ability, depends on the conceptual model imposed on the system in question (Leibold *et al.*, 2004). The neutral perspective (Hubbell, 2001) assumes no variation in ecological traits, and consequently no covariation either. With this perspective, single species metapopulation dynamics can be summed to assess community dynamics (Hanski & Gyllenberg, 1997). In the patch-dynamic models, species exhibit sufficient variation in competitive ability, and a trade-off with dispersal permits regional coexistence. Two other metacommunity models, mass-effect and species-sorting, assume trade-offs in the abilities of species to perform well under different habitat conditions.

However, in a bigger perspective the evolution of the species pool may strongly affect the dynamics of metacommunities (Amarasekare, 2003; Shurin *et al.*, 2000). Together with biogeographic processes it will determine the distribution of traits among species in the regional species pool (Leibold *et al.*, 2004), which sets the basic assumptions for some of the models mentioned above.

There are no empirical metapopulation studies of epixylic lichens and bryophytes, and there are only a few studies of metapopulation processes of single epiphytic lichen and bryophyte species (e.g. Snäll, Ehrlen & Rydin, 2005; Snäll *et al.*, 2005; Snäll, Ribeiro & Rydin, 2003).

6 Study areas

All studies were conducted in the province of Uppland (Fig. 1), South Central Sweden ($59^{\circ}43'N$, $17^{\circ}30'E$), within the hemiboreal vegetation zone (Ahti, Hämet-Ahti & Jalas, 1968). The mean temperatures in February (the coldest month) and July (the warmest month) are about $-4^{\circ}C$ and $+17^{\circ}C$, respectively. Annual precipitation averages 600 mm and the mean number of frost free days per year is 120. The climatic values are mean values for the years 1961 - 1990 (Raab & Vedin, 2004).



Figure 1. Study area located within the hemiboreal vegetation zone in the province of Uppland, Sweden.

The forest stands within the study area are mostly regenerated after clear-cutting of the previous generation or by planting on former arable land, and with subsequent cleaning and thinning operations (i.e. managed forests). The area is mainly composed of managed mixed coniferous forests of contrasting successional stages, covering the entire rotation period of about 70–100 years. It has a long history of logging, and, therefore, old-growth stands (>130 years) are rare. The most common tree species are Norway spruce *Picea abies*, Scots pine *Pinus sylvestris* and birch *Betula* spp. (*B. pendula* and *B.*

pubescens). Aspen *Populus tremula* shows a patchy distribution in the landscape.

In all four papers, the selected stands were dominated by Norway spruce ($\geq 60\%$ basal area) and had a site index of G26–28, which means that a 100 year old (=mature) Norway spruce tree reaches the height of 26–28 m. The ground flora was composed mainly of either grasses such as *Deschampsia cespitosa*, *Melica nutans* and *Milium effusum* or herbs such as *Anemone hepatica*, *A. nemorosa*, *Gymnocarpium dryopteris* and *Oxalis acetosella*. *Vaccinium myrtillus* was the most common dwarf shrub.

The size of the 10 mature stands in paper I varied from 0.9 to 9.2 ha, with an average of 3.6 ha (SE = 0.9). Stand age ranged from 71 to 96 years, which corresponded to the average rotation period in the study area, and the canopy was evenaged.

Papers II–IV: Based on field observations, the colonization of the cut surface of stumps by lichens became visible in four year old stands, in which also most of the slash was decorticated, whereas in stands older than eighteen years most stumps and slash were highly decayed and often completely covered in ground living bryophytes. Based on this, and of available stands in the forest owners' stand databases, four age classes were defined: 1 = 4–5, 2 = 8–9, 3 = 12–13 and 4 = 16–18 year old stands. By this definition, we obtained equally long intervals between age classes, and the highest possible number of samples from the stand databases.

The aim was to select eight stands of each age class, but only six stands of age class 4 that contained stumps were found. This was probably due to the fact that the majority of the 16–18 years old stands were planted on former agricultural land and/or that the harvest of the previous stand generation included stump removal. Average stand sizes (\pm sd) were 7.4 (2.4), 9.0 (6.9), 10.5 (6.6), and 5.0 (1.9) ha for the four age classes, respectively.

7 Summary of papers

7.1 I. Lichen species diversity differs between living stems and slash

Since epiphytic lichen surveys usually are done on the parts of trunks and branches that can easily be reached from the ground, the knowledge of canopy lichen diversity is poor. Owing to the vertical variation in microclimate, it is, however, likely that there are differences in lichen species composition between tree fractions. The harvest of tops, branches and twigs (i.e. slash) for biofuel may pose a threat to epiphytic lichen diversity in managed forests.

Thus, in this paper we aimed to compare lichen species richness, density and composition between these fractions and the stem of mature trees in managed forests.

In each of 10 Norway spruce *Picea abies* dominated stands, we felled two mature (70-100 years) individuals of both Norway spruce (Fig. 2) and aspen *Populus tremula*. We defined the top as the part of the trunk with a diameter <10 cm, branches were defined as attached to the trunk and twigs as attached to branches.



Figure 2. Lichen survey of a felled spruce.

The comparisons between fractions were made separately for the two tree species, and we also compared the stem with the slash fractions pooled together.

In total, we found 30 lichen species on 19 Norway spruce trees and 46 on 17 aspens. We found no significant differences in species richness or species density between fractions of Norway spruce, whereas aspen tops were significantly less species rich and species dense than the other fractions. Moreover, the lichen species composition of the stems clearly differed from that of the tops, branches and twigs in both tree species (Fig. 3).

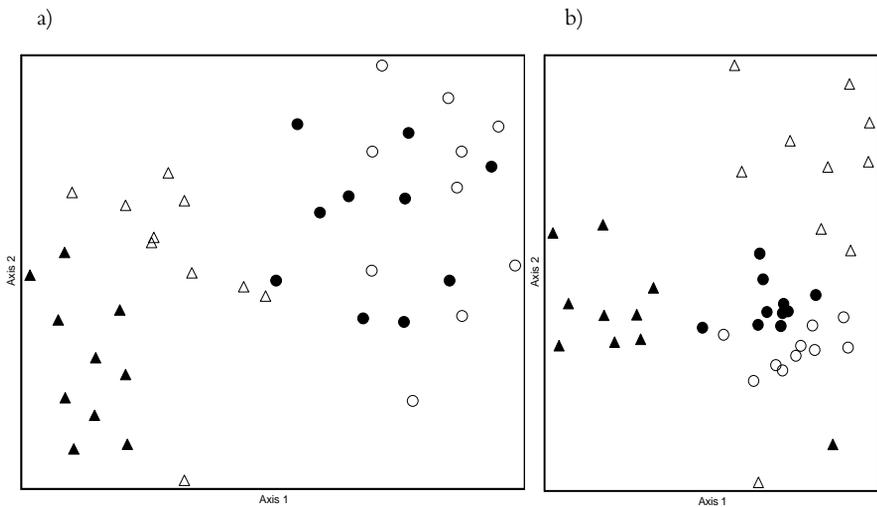


Figure 3. Non-metric multidimensional scaling (NMS) graphs showing differences/similarities in species composition between the four fractions (▲ stem, △ top, ● branch, ○ twig) of a) Norway spruce and b) aspen.

Thus, lichen communities other than those removed with stems by conventional forestry are removed from the stands owing to slash harvest. The potential of slash to act as a propagule source for epiphytic lichens is not covered by this study. A disturbance like final felling means a drastic change in substrate quality as the slash starts to decay and eventually lose the bark, and subsequently also the lichens growing on the bark. Until then, the lichens probably act as a propagule source.

Since the species in this study are all rather common and widespread in Sweden, we concluded that the impact of slash harvest on the epiphytic lichen flora may be of minor importance in forests established after clear-cutting or on former arable land.

7.2 II. Lichen species composition differs between stumps and slash

In the first paper we described the lichen flora of slash fractions with bark on mature trees in managed forests. This flora is likely to change as the slash becomes decorticated, but this succession is poorly described. Thus, in paper II we followed the slash through the decomposition process in the young stand. In addition to slash, stumps created at final felling constitute a major component of dead wood in young managed forests (Fig. 4), but have been poorly studied in terms of lichen diversity. Both substrates are big potential sources of more CO₂-neutral energy sources. This harvest may, however, have a negative effect on dead wood dependent species.

The aim of paper II was to compare lichen species diversity (richness and composition) between slash and stumps, and also to estimate the amounts of these substrates in young managed forests.

We surveyed the lateral surface of 1 025 slash objects and the cut surface of 449 stumps of Norway spruce in 30 planted forest stands of four age classes; 4-5, 8-9, 12-13, and 16-18 years. We also estimated the amounts of the two substrates, and discriminated between slash with bark and decorticated slash.



Figure 4. A young stand of age class 2 (8-9 years old), where the major part of the downed dead wood is made up of stumps and slash.

In total we found 60 lichen taxa, of which 41 occurred on the lateral surface of slash and 52 on the cut surface of stumps, whereas 33 species were found on both substrates. There were no differences in species number per surface area, but slash had more species when equal volumes were compared. We found compositional differences between slash and stumps throughout the decay process (Fig. 5). The majority of species found on both substrates were more frequent on stumps, which also had a higher number of unique species, and eight species in the literature indicated as nationally rare or uncommon.

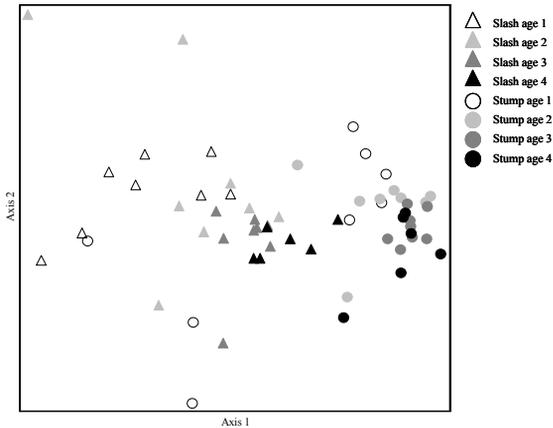


Figure 5. Non-metric multidimensional scaling (NMS) graph comparing lichen species composition between slash (Δ) and stumps (\circ). Proportions of objects with species presence in each stand were used in the calculations. Age classes: 1 = 4-5, 2 = 8-9, 3 = 12-13 and 4 = 16-18 year old stands. The final solution was rotated 24° so that axis 1 explained most of the variance in the data, 73.9%, whereas axis 2 accounted for 13.4%.

The volume per hectare of stumps was ten times greater than that of slash but conversely, the lateral surface area of slash was five times greater than the cut surface area of stumps.

One consequence of stump harvest is the removal of lichen communities other than those removed with stems by conventional forestry (Paper I) or by slash harvest. Few dead wood specialist lichen species were, however, strictly associated with slash. Stumps (Fig. 6) offer a more heterogeneous environment and may provide important habitats for many lichens in the managed forest landscape. Thus, if stumps are left after final felling, the effects on lichens of slash harvest are probably of minor importance.



Figure 6. A 12 year old stump with the cut surface colonized predominantly by lichens. (Photo J. Rudolphi)

7.3 III. Lichens and bryophytes respond differently to stand successional stage and substrate quality

In the study area stumps persist as a woody substrate for about 20 years before they are decomposed. What determines the diversity of organisms inhabiting stumps during this time is, however, poorly investigated.

Lichens and bryophytes are known to be among the first organisms to colonize pioneer terrestrial habitats, and also to respond differently to both time and measurable qualities of their substrate. In this paper the aim was to study the importance of stand age and substrate variability for the diversity of lichens and bryophytes on stumps. For this purpose we used the same chronosequence of forest stands as in paper II, i.e. four age classes; 4-5, 8-9, 12-13, and 16-18 year old stands.

We surveyed both the cut surface and peripheral wood ("chair", Fig. 7). In total, we found 53 lichens and 35 bryophytes on 449 Norway spruce stumps.



Figure 7. Some stumps had wood still attached to their periphery, i.e. "chair".

The average number of species per stump was 6.1 ($se = 0.2$) and 3.1 ($se = 0.1$) of lichens and bryophytes, respectively. Lichen species richness was higher for age classes 2-4 compared to age class 1, whereas bryophyte richness differed between age classes 3-4 and 1 (Fig. 8).

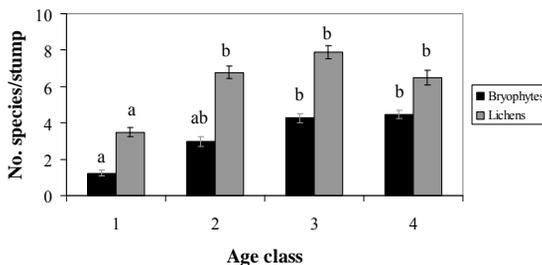


Figure 8. Average lichen and bryophyte species richness per stump ($\pm se$) for each age class. Age classes with same letters do not differ in species richness of lichens and bryophytes, respectively.

Lichen richness increased with increasing stump height and the presence of surface structural components (Table 1), such as chairs (Fig. 7) and level

differences, which together with decay also influenced lichen species composition. Conversely, stump height and the presence of levels decreased bryophyte richness (Table 1), which instead increased with increasing decay, surface area, and number of surrounding trees and bushes. Only decay explained differences in bryophyte species composition.

The different response of lichens and bryophytes to age and substrate variables indicates the importance of including several organism groups in species diversity studies of dead wood.

Further, stumps in this region seem more important to overall lichen than to bryophyte diversity, since there were on average more lichen species per stump and we only found common bryophytes but several uncommon dead wood specialist lichens.

Table 1. Score statistics from a type 3 GEE analysis ($DF = 1$ if not stated otherwise) of the effects of substrate and environmental variables on total number of lichens and bryophytes per stump. No estimate is given for 'Age class' because it is a categorical variable.

Source	Lichens		Bryophytes	
	Estimate	p	Estimate	p
Cut surface area (dm ²)	1.00	0.604	1.04	<0.001
Height (dm)	1.10	<0.001	0.89	<0.001
Decay	1.03	0.484	1.39	<0.001
Chair (% frequency)	1.46	<0.001	0.79	0.102
Level (% frequency)	1.27	<0.001	0.81	0.017
Tot. no. of bushes	1.00	0.990	1.04	0.048
No. of deciduous bushes	1.00	0.902	0.97	0.092
Hole (% frequency)	-	-	1.04	0.600
Age class, $DF = 3$		0.025		0.041

An estimate of 1.5 corresponds to a 50% increase in species number per unit increase in the predictor variable, whereas an estimate of 0.5 corresponds to a 50% reduction in species number.

7.4 IV. Lichen communities on stumps are structured by metapopulation processes of multiple species

Metapopulation models are often used for predicting species dynamics in altered landscapes. Several models have been proposed depending on e.g. the relative importance of patch dynamics on the metapopulation dynamics. There are no empirical studies of metapopulation dynamics of epixylic lichens.

We studied colonizations and extinctions of lichens on stumps by re-surveying stumps of the first three age classes of the chronosequence used in

paper II. In total we re-surveyed 104, 89, and 100 stumps in age classes 1, 2, and 3, respectively. Of the 45 lichen species found in the two surveys, eight are confined to stumps in these kinds of stands. The observed number of colonization and extinction events allowed us to investigate the effect of environmental variables and connectivity on the probability of local (stump) colonization and extinction for four of the eight species: *Cladonia botrytes*, *Lecidea turgidula*, *Micarea denigrata* coll. (including *M. misella*), and *Xylographa parallela*. The four other species confined to stumps were *Absoconditella lignicola*, *Lecidea gibberosa*, *Mycocalicium subtile*, and *Xylographa vitiligo*, for which we reported colonization and extinction rates.

We found evidence for importance of metapopulation processes in structuring the local epixylic lichen community. For two of the species, connectivity affected the probability of local colonization. Patch quality was important for four species (Table 2). The extinction risk of local populations was mainly explained by variables describing patch quality (Table 3). Moreover, the role of deterministic extinctions, caused by patch destruction, increased with patch age (Fig. 9). Our results suggest that the dynamics of lichens on stumps in this managed forest landscape can be characterized by the habitat-tracking metapopulation model.

Several of the species examined are light preferring, indicating the importance of exposed stumps to epixylic lichen diversity in managed forest landscapes with low amounts of other types of coarse dead wood.

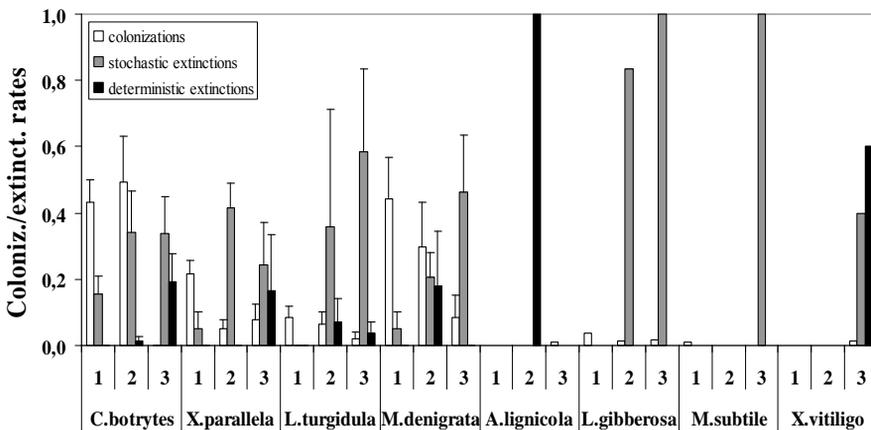


Figure 9. Colonization and extinction rates for epixylic lichen species expressed as probabilities of colonization, of stochastic extinction, and of deterministic extinction due to patch destruction. Means among stands 4–5 (1), 8–9 (2), and 12–13 (3) years old (+se).

Table 2. Parameter estimations of the effect of single variables on colonization probabilities of lichen species. Number of colonizations of each species is given. *DF* = Degrees of freedom.

	<i>Cladonia botrytes</i> (38)			<i>Xylographa parallela</i> (27)			<i>Lecidea turgidula</i> (15)			<i>Micarea denigrata</i> coll. (42)		
	Estimate	DF	Pr>F	Estimate	DF	Pr>F	Estimate	DF	Pr>F	Estimate	DF	Pr>F
Intercept	-0.761	15.6	0.043	-2.298	63.2	<0.001	-3.461	167.6	<0.001	-3.359	48.9	<0.001
Density of occupied patches										0.279	18.3	0.042
Number of occupied patches	0.256	13.7	0.008									
Decay	-0.435	95	0.057	-0.806	75.9	0.003	1.803	252	0.165			
Decay ²							-0.835	252	0.072			
Presence of level differences							1.353	17.8	0.031	1.025	180	0.033
Stump height				0.347	233	0.005				0.252	180	0.030

Table 3. Parameter estimations of the effect of single variables on extinction probabilities of lichen species. Number of extinctions of each species is given. *DF* = Degrees of freedom.

	<i>Cladonia botrytes</i> (37)			<i>Xylographa parallela</i> (15)			<i>Micarea denigrata</i> coll. (17)		
	Estimate	DF	Pr>F	Estimate	DF	Pr>F	Estimate	DF	Pr>F
Intercept	0.450	150	0.542	-2.293	50	0.223	-3.009	19.0	<0.001
Decay				-0.038	50	0.966	0.791	13.1	0.036
Stump height	-0.448	150	0.021						
No. deciduous stems				-0.515	50	0.161			
Decay* No. deciduous stems				0.555	50	0.022			

8 Discussion

This thesis deals with the predictions of the impact of forest fuel harvest on the overall diversity of lichen species in managed forest landscapes. The focus has been on the youngest successional stages of heavily managed forests, and of tree fractions highly neglected in diversity studies. More specifically, I studied the effects of local factors and regional processes on the diversity of lichens on stump and slash at two spatial scales, i.e. the stand and patch (substrate) level. The study set up also allowed for comparisons of the lichen flora between stumps and slash through their duration as a dead wood substrate.

Owing to differences in e.g. chemistry, texture and water holding capacity of the substrates, the lichen communities of decorticated slash and stumps created at final felling differed from the epiphytic community in the study area (paper I, II). The differences in species composition between stumps and slash (paper II) could be explained by the more heterogeneous environment offered by the cut surface of stumps, which also is bigger than the colonisable lateral surface of one single branch or top. This is in line with one of the hypotheses of the mechanism behind the universally accepted species-area curve: large areas have more species than small ones because of their greater range of habitats. In fact, not only differences in species frequencies between stumps and slash explained the compositional differences, but also the fact that several species present on stumps were missing on slash. The presence of chairs (Fig. 7) and level differences on the cut surface increased lichen species richness by contributing to a greater diversity of microhabitats (paper III). The higher turnover of slash, partly as a result of the higher probability of dead wood of small dimensions to be overgrown, may explain the low number of lichen dead wood specialists found on slash.

Paper IV provides the first empirical evidence for importance of metapopulation processes in structuring the local (patch) community of epixylic lichen species. Decreasing decay and increasing height increased the colonization probabilities of stumps by three and two epixylic lichens, respectively. The probability of extinction increased with increasing patch deterioration, as measured by stump decay, and probably reflects a decrease in local population size. Decreasing height also increased local extinction probabilities. The effects of decay and height on both colonization and extinction probably reflect unfavorable local conditions caused by, e.g. the slower snow-melting process on lower stumps, and alteration of moisture or surface area conditions on both highly decayed and lower stumps. In addition, bryophyte richness increased with increasing decay and decreasing stump height, whereas the latter decreased the number of lichens. Bryophyte dominance over lichens in the latest stages of decay of dead wood has been shown in other studies (Humphrey *et al.*, 2002; Kruys *et al.*, 1999; Rambo, 2001). This suggests that lichen colonization on highly decayed stumps is hindered by bryophytes, which also may cause lichen extinctions. The replacement of lichen communities by bryophytes has been shown on highly decayed wood (Humphrey *et al.*, 2002; Kruys *et al.*, 1999).

Moreover, since increasing stump height increased the species richness of lichens the relative importance of competition among lichen species on extinction probabilities is suggested to increase with increasing height. It has been shown that lichens can inhibit the establishment of vascular plants (Deines *et al.*, 2007; Zamfir, 2000). Hence, the assumption of neutral relations among species may overestimate the importance of abiotic factors in structuring epixylic lichen communities. However, since species abundances were not recorded, the effects of competition could not be significantly stated or quantified. Exclusion experiments are needed to explicitly study species interactions.

9 Conclusions and implications

A consequence of the harvest of slash and stumps is the removal of lichen communities other than those removed with stems by conventional forestry. For the epiphytic lichen flora in the study area, this “extra” disturbance is probably of minor importance, since the species found on living branches, twigs and tops in paper I were all rather common and widespread in Sweden. However, there are some rare lichens associated to slash fractions of Norway spruce and aspen in Sweden. The ecology of these lichens is poorly known but their absence from our studied forest stands might indicate that they require particular conditions (e.g. high moisture) and/or that they are strictly associated to continuity forests, i.e. forest that have never gone through a clear-cutting phase. The time required for the majority of newly created slash to lose its bark is about 10% of the rotation period (paper II), indicating that even though slash with bark may still function as a source of epiphytic lichens, this extra time is short compared to the rotation period of the stands (70–100 years). Thus, final felling, regardless of slash harvest, has the greatest impact on the epiphytic slash flora.

Whereas the amounts of CWD (stumps excluded) in the boreal forest has decreased to 2–10% of the amounts in natural forests (Fridman & Walheim, 2000; Jonsson *et al.*, 2005; Linder *et al.*, 1997; Siitonen, 2001), FWD has increased by 75% since 1920 in Sweden (Thor, pers. comm.). However, as indicated by paper II, slash is less likely to support viable populations of strictly epixylic lichens in the study area.

Epixylic lichens in managed forest landscapes have experienced a high degree of habitat loss and isolation of habitat patches. Their regional long-term persistence requires a colonization rate of the artificially created dead wood that compensates for the rate of stochastic and deterministic population extinctions. The early successional stages of the rotation period hold the greatest amounts of all fractions of dead wood in managed forest

landscapes. Stumps created at final felling are not included in the estimations of CWD volumes, but increase these amounts by 200–700% (Hofsten, 2006: paper II), indicating their importance as patches for epixylic species. That we found eight lichen species described as nationally rare or uncommon (paper II) further underlines the potential of stumps as important lichen substrates in managed forests. In addition, seven of the eight epixylic lichens in paper IV have a preference for less shaded environments, which indicates the importance of coarse dead wood in the open early stages of the rotation period to epixylic lichen species diversity. Thus, stumps in young forest stands may be important to the maintenance of viable epixylic lichen populations since they constitute the major part of coarse dead wood in these kinds of stands.

However, the relative importance of stumps to the regional persistence of epixylic species is likely to vary depending on the contribution of other types of CWD to the regional dead wood pool, and may thus depend on, e.g. geographic region, present and past land use, forest type, and stand characteristics. In addition, conservation measures derived from the study of one single organism group should not be applied on other groups due to inherent ecological differences among groups.

10 Acknowledgements

I thank Holmenskog, Korsnäs and Stora Enso for the access to their databases and forest stands. Anders Dahlberg, Lena Gustafsson, Karin Perhans and Göran Thor provided valuable comments on the thesis manuscript. The studies in the thesis were partly financed by The Swedish Energy Agency (Energimyndigheten) and The Royal Swedish Academy of Agriculture and Forestry (Kungliga Skogs- och Lantbruksakademien, KSLA).

References

- Ahmadjian, V. 1993. *The Lichen Symbiosis*. John Wiley & Sons. New York.
- Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968. Vegetation zones and their sections in Northwestern Europe. *Annales Botanici Fennici* 5, 169-211.
- Amarasekare, P. 2003. Competitive coexistence in spatially structured environments: a synthesis. *Ecology Letters* 6, 1109-1122.
- Anonymous. 1994. *Amount of tree residues following harvesting of wood fuel*. Projekt Skogkraft. Vattenfall report 20 U(B) 1993/28. Vällingby. (In Swedish with English summary).
- Anonymous. 2007a. *Skogsstatistisk årsbok 2006. Swedish statistical yearbook of forestry 2007*. Skogsvårdsorganisationens förlag. Jönköping. (in Swedish with English summary).
- Anonymous. 2007b. *Skogsstyrelsens inventering av nyckelbiotoper – resultat till och med 2006*. The Swedish Forest Agency. Jönköping, Sweden, (in Swedish).
- Armstrong, R.A. & Welch, A.R. 2007. Competition in lichen communities. *Symbiosis* 43, 1-12.
- Axelsson, A-L. 2001. *Forest landscape change in Boreal Sweden 1850-2000 – a multi-scale approach*. Doctoral thesis in Forest Vegetation Ecology 183. Swedish University of Agricultural Sciences, Umeå, Sweden.
- Bader, P., Jansson, S. & Jonsson, B.G. 1995. Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. *Biological Conservation* 72, 355-362.
- Barkman, J.J. 1958. *Phytosociology and ecology of cryptogamic epiphytes*. Van Gorcum. Assen (Netherlands). 628 pp.
- Bates, J.W. 1992. Influence of Chemical and Physical Factors on *Quercus* and *Fraxinus* Epiphytes at Loch Sunart, Western Scotland - a Multivariate-Analysis. *Journal of Ecology* 80, 163-179.

- Berg, Å., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M. & Weslien, J. 1994. Threatened plant, animal, and fungus species in Swedish forests – distribution and habitat associations. *Conservation Biology* 8, 718–731.
- Berglund, H. 2006. *Helträdsutnyttjande – konsekvenser för klimat och biologisk mångfald*. Swedish Environmental Protection Agency report 5562. Stockholm. (In Swedish with English summary).
- Brakenhielm, S. & Liu, Q. 1998. Long-term effects of clear-felling on vegetation dynamics and species diversity in a boreal pine forest. *Biodiversity and Conservation* 7, 207–220.
- Campbell, J. & Coxson, D.S. 2001. Canopy microclimate and arboreal lichen loading in subalpine spruce-fir forest. *Canadian Journal of Botany-Revue Canadienne De Botanique* 79, 537–555.
- Chase, J.M. & Leibold, M.A. 2002. Spatial scale dictates the productivity-biodiversity relationship. *Nature* 416, 427–430.
- Coxson, D.S. & Coyle, M. 2003. Niche partitioning and photosynthetic response of alectoroid lichens from subalpine spruce-fir forest in north-central British Columbia, Canada: the role of canopy microclimate gradients. *Lichenologist* 35, 157–175.
- Crites, S. & Dale, M.R.T. 1998. Diversity and abundance of bryophytes, lichens, and fungi in relation to woody substrate and successional stage in aspen mixedwood boreal forests. *Canadian Journal of Botany* 76, 641–651.
- Dahlberg, A. & Stokland, J.N. 2004. *Vedlevande arters krav på substrat – sammanställning och analys av 3600 arter*. Rapport 2004:7. The Swedish Forest Agency, Jönköping, Sweden (in Swedish with English summary).
- Daniels, F.J.A. 1983. Lichen communities on stumps of *Pinus sylvestris* L. in the Netherlands. *Phytocoenologia* 11, 431–444.
- Daniels, F.J.A. 1993. Succession in lichen vegetation on Scots pine stumps. *Phytocoenologia* 23, 619–623.
- Davies, K.E., Margules, C.R. & Lawrence, J.E. 2000. Which traits of species predict population declines in experimental forest fragments? *Ecology* 81, 1450–1461.
- Deines, L., Rosentreter, R., Eldridge, D.J. & Serpe, M.D. 2007. Germination and seedling establishment of two annual grasses on lichen-dominated biological soil crusts. *Plant and Soil* 295, 23–35.
- Ecke, F., Löfgren, O. & Sörlin, D. 2002. Population dynamics of small mammals in relation to forest age and structural habitat factors in northern Sweden. *Journal of Applied Ecology* 39, 781–792.

- Edmonds, R.L. & Eglitis, A. 1989. The role of the Douglas-fir beetle and wood borers in the decomposition of and nutrient release from Douglas-fir logs. *Canadian Journal of Forest Research* 19, 853-859.
- Egnell, G., Liedholm, H. & Lönnell, N. 2001. *Skogsbränsle, hot eller möjlighet? [Forest fuel, threat or possibility?]*. Skogsstyrelsen. Jönköping. (In Swedish).
- Esseen, P.-A., Ehnström, B., Ericson, L. & Sjöberg, K. 1997. Boreal forests. *Ecological Bulletins* 46, 16-47.
- Fridman, J. & Walheim, M. 2000. Amount, structure, and dynamics of dead wood on managed forestland in Sweden. *Forest Ecology and Management* 131, 23-36.
- Gärdenfors, U. 2005. *The 2005 Red List of Swedish Species*. Swedish Species Information Centre, SLU, Uppsala, Sweden.
- Gibb, H., Ball, J.P., Johansson, T., Atlegrim, O., Hjalten, J. & Danell, K. 2005. Effects of management on coarse woody debris volume and composition in boreal forests in northern Sweden. *Scandinavian Journal Of Forest Research* 20, 213-222.
- Gilbert, O. 2000. *Lichens (New Naturalist)*. Trafalgar Square.
- Gunnarsson, B., Nittérus, K. & Wirdenäs, P. 2004. Effects of logging residue removal on ground-active beetles in temperate forests. *Forest Ecology and Management* 201, 229-239.
- Hallingbäck, T. 1995. *Ekologisk katalog över lavar. [The lichens of Sweden and their ecology]* SNV Rapport 4411. ArtDatabanken. Uppsala.
- Hallingbäck, T. 1996. *Ekologisk katalog över mossor. [The bryophytes of Sweden and their ecology.] Rapport 4558.* ArtDatabanken och Naturvårdsverket. Uppsala.
- Hallingbäck, T. 2007. Working with Swedish cryptogam conservation. *Biological Conservation* 135, 334-340.
- Halonen, P., Hyvärinen, M. & Kauppi, M. 1991. The Epiphytic Lichen Flora on Conifers in Relation to Climate in the Finnish Middle Boreal Subzone. *Lichenologist* 23, 61-72.
- Hanski, I. & Gilpin, M. 1991. Metapopulation Dynamics - Brief-History and Conceptual Domain. *Biological Journal of the Linnean Society* 42, 3-16.
- Hanski, I. & Gyllenberg, M. 1997. Uniting two general patterns in the distribution of species. *Science* 275, 397-400.
- Hanski, I. & Ovaskainen, O. 2002. Extinction debt at extinction threshold. *Conservation Biology* 16, 666-673.
- Hanski, I. 2000. Extinction debt and species credit in boreal forests: modelling the consequences of different approaches to biodiversity conservation. *Annales Zoologici Fennici* 37, 271-280.

- Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkamper, G.W., Cromack, K. Jr. & Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15, 133-302.
- Hauck, M. & Meissner, T. 2002. Epiphytic lichen abundance on branches and trunks of *Abies balsamea* on Whiteface Mountain, New York. *Lichenologist* 34, 443-446.
- Hawksworth, D.L. & Chater, A.O. 1979. Dynamism and Equilibrium in a Saxicolous Lichen Mosaic. *Lichenologist* 11, 75-80.
- Heilmann-Clausen, J. & Christensen, M. 2004. Does size matter? On the importance of various dead wood fractions for fungal diversity in Danish beech forests. *Forest Ecology and Management* 201, 105-117.
- Hilmo, O. 1994. Distribution and Succession of Epiphytic Lichens on *Picea-Abies* Branches in a Boreal Forest, Central Norway. *Lichenologist* 26, 149-169.
- Hofsten, H. v. 2006. *Maskinell upptagning av stubbar - möjligheter och problem*. Arbetsrapport från Skogforsk 621. (In Swedish).
- Hubbell, S.P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, NJ.
- 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 deadwood. *Biological Conservation* 107, 165-180.
- Jonsell, M. & Weslien, J. 2003. Felled or standing retained wood – it makes a difference for saproxylic beetles. *Forest Ecology and Management* 175, 425-435.
- Jonsell, M., Nittérus, K. & Stighäll, K. 2004. Saproxylic beetles in natural and man-made deciduous high stumps retained for conservation. *Biological Conservation* 118, 163-173.
- Jonsell, M., Weslien, J. & Ehnström, B. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodiversity and Conservation* 7, 749-764.
- Jonsson, B.G. 2000. Availability of coarse woody debris in a boreal old-growth *Picea abies* forest. *Journal of Vegetation Science* 11, 51-56.
- Jonsson, B.G., Kruys, N. & Ranius, T. 2005. Ecology of species living on dead wood – lessons for dead wood management. *Silva Fennica* 39, 289-309.
- Kantvilas, G. & Jarman, S.J. 2006. Recovery of lichens after logging: preliminary results from Tasmania's wet forests. *Lichenologist* 38, 383-394.

- Kermit, T. & Gauslaa, Y. 2001. The vertical gradient of bark pH of twigs and macrolichens in a *Picea abies* canopy not affected by acid rain. *Lichenologist* 33, 353-359.
- Kershaw, K.A. 1964. Preliminary observations on the distribution and ecology of epiphytic lichens in Wales. *Lichenologist* 2, 263-276.
- Kimmerer, R.W. & Driscoll, M.J.L. 2000. Bryophyte species richness on insular boulder habitats: The effect of area, isolation, and microsite diversity. *Bryologist* 103, 748-756.
- Kimmerer, R.W. & Young, C.C. 1996. Effect of gap size and regeneration niche on species coexistence in bryophyte communities. *Bulletin of the Torrey Botanical Club* 123, 16-24.
- Kimmerer, R.W. 1993. Disturbance and dominance in *Tetraxis pellucida*: A model of disturbance frequency and reproductive mode. *The Bryologist* 96, 73-79.
- Kimmerer, R.W. 1994. Ecological consequences of sexual versus asexual reproduction in *Dicranum flagellare* and *Tetraxis pellucida*. *The Bryologist* 97, 20-25.
- Kirby, K.J., Ried, C.M., Thomas, R.C. & Goldsmith, F.B. 1998. Preliminary estimates of fallen dead wood and standing dead trees in managed and unmanaged forests in Britain. *Journal of Applied Ecology* 35, 48-55.
- Krok, T. & Almquist, S. 2001. *Svensk flora*. 28. edition. Liber utbildning. Stockholm.
- Kruys, N. & Jonsson, B.G. 1999. Fine woody debris is important for species richness on logs in managed boreal spruce forests of northern Sweden. *Canadian Journal of Forest Research* 29, 1295-1299.
- Kruys, N., Fries, C., Jonsson, B.G., Lämås, T. & Stål, G. 1999. Wood-inhabiting cryptogams on dead Norway spruce (*Picea abies*) trees in managed Swedish boreal forests. *Canadian Journal of Forest Research* 29, 178-186.
- Kuuluvainen, T. 2002. Natural variability of forests as a reference for restoring and managing biological diversity in Boreal Fennoscandia. *Silvia Fennica* 36, 97-125.
- Laaka, S. 1995. Epixylic lichens on conifer logs in four natural forests in Finland. *Graphis scripta* 7, 25-31.
- Legrand, I., Asta, J. & Goudard, Y. 1996. Variations in bark acidity and conductivity over the trunk length of silver fir and Norway spruce. *Trees-Structure And Function* 11, 54-58.
- Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M. & Gonzalez, A. 2004. The metacommunity concept: a

- framework for multi-scale community ecology. *Ecology Letters* 7, 601-613.
- Levin, S.A. 1992. The Problem of Pattern and Scale in Ecology. *Ecology* 73, 1943-1967.
- Linder, P., Elfving, B. & Zackrisson, O. 1997. Stand structure and successional trends in virgin boreal forest reserves in Sweden. *Forest Ecology and Management* 98, 17-33.
- Lindhe, A. & Lindelöw, Å. 2004. Cut high stumps of spruce, birch, aspen and oak as breeding substrates for saproxylic beetles. *Forest Ecology and Management* 203, 1-20.
- Lloyd, S. 1999. *The last of the last: the old-growth forests of boreal Europe*. Taiga Rescue Network, International Coordination Centre, Jokkmokk, Sweden.
- Löbel, S., Snäll, T. & Rydin, H. 2006. Species richness patterns and metapopulation processes - evidence from epiphyte communities in boreo-nemoral forests. *Ecography* 29, 169-182.
- Lofman, S. & Kouki, J. 2001. Fifty years of landscape transformation in managed forests of Southern Finland. *Scandinavian Journal of Forest Research* 16, 44-53.
- Lõhmus, P. & Lõhmus, A. 2001. Snags, and their lichen flora in old Estonian peatland forests. *Annales Botanici Fennici* 38, 265-280.
- Longton, R.E. 1992. The role of bryophytes and lichens in terrestrial vegetation. In: Bryophytes and lichens in a changing environment. In. Eds. J.W. Bates & A.M. Farmer. Clarendon Press. Oxford. pp. 32-76.
- Lowman, M.D. & Rinker, H.B. 2004. *Forest canopies*. Second edition. Elsevier Academic Press. Amsterdam. 517 pp.
- McAlister, S. 1995. Species Interactions and Substrate-Specificity among Log-Inhabiting Bryophyte Species. *Ecology* 76, 2184-2195.
- McCullough, H.A. 1948. Plant Succession on Fallen Logs in a Virgin Spruce-Fir Forest. *Ecology* 29, 508-513.
- Mönkkönen, M. 1999. Managing Nordic boreal forest landscapes for biodiversity: ecological and economic perspectives. *Biodiversity and Conservation* 8, 85-99.
- Muhle, H. & LeBlanc, F. 1975. Bryophyte and lichen succession on decaying logs. I. Analysis along an evaporational gradient in eastern Canada. *Journal of the Hattori Botanical Laboratory* 39, 1-33.
- Niklasson, N., & Granström, A. 2000. Numbers and sizes of fires: long-term spatially explicit fire history in a Swedish boreal landscape. *Ecology* 81, 1484-1499.

- Nilsson, S.G. 1997. Forests in the temperate-boreal transition: natural and man-made features. *Ecological Bulletins* 46, 61-71.
- Nittérus, K., Åström, M. & Gunnarsson, B. 2007. Commercial harvest of logging residue in clear-cuts affects the diversity and community composition of ground beetles (Coleoptera: Carabidae). *Scandinavian Journal of Forest Research* 22, 231-240.
- 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. *Biological Conservation* 117, 1-10.
- Ojala, E., Mönkkönen, M. & Inkeröinen, J. 2000. Epiphytic bryophytes on European aspen *Populus tremula* in old-growth forests in northeastern Finland and in adjacent sites in Russia. *Canadian Journal of Botany-Revue Canadienne De Botanique* 78, 529-536.
- Ott, S. 1987. Sexual Reproduction and Developmental Adaptations in *Xanthoria- Parietina*. *Nordic Journal of Botany* 7, 219-228.
- Pettersson, R.B. 1996. Effect of forestry on the abundance and diversity of arboreal spiders in the boreal spruce forest. *Ecography* 19, 221-228.
- Pettersson, R.B., Ball, J.P., Renhorn, K.E., Esseen, P.A. & Sjöberg, K. 1995. Invertebrate Communities in Boreal Forest Canopies as Influenced by Forestry and Lichens with Implications for Passerine Birds. *Biological Conservation* 74, 57-63.
- Raab, B. & Vedin, H. 2004. *National atlas of Sweden. Climate, lakes and rivers*. SNA. Stockholm.
- Ricklefs, R.E. 1987. Community Diversity - Relative Roles of Local and Regional Processes. *Science* 235, 167-171.
- Rogers, R.W. 1988. Succession and Survival Strategies in Lichen Populations on a Palm Trunk. *Journal of Ecology* 76, 759-776.
- Rogers, R.W. 1990. Ecological Strategies of Lichens. *Lichenologist* 22, 149-162.
- Ruchty, A., Rosso, A.L. & McCune, B. 2001. Changes in epiphyte communities as the shrub, *Acer circinatum*, develops and ages. *Bryologist* 104, 274-281.
- Rudolphi, J. & Gustafsson, L. 2005. Effects of forest-fuel harvesting on the amount of deadwood on clear-cuts. *Scandinavian Journal of Forest Research* 20, 235-242.
- Rydin, H. 1997. Competition between Sphagnum species under controlled conditions. *Bryologist* 100, 302-307.
- Samuelsson, J., Gustafsson, L. & Ingelög, T. 1994. *Dying and dead trees – a review of their importance for biodiversity*. Swedish Threatened Species Unit, Uppsala.

- Saunders, D.A., Hobbs, R.J. & Margules, C.R. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5, 18-32.
- Sernander, R. 1936. A study of the part played by storm-gaps and dwarf trees in the regeneration of the Swedish spruce forest. *Acta Phytogeographica Suecica VIII*, 1-232. (in Swedish with English summary).
- Shurin, J.B., Havel, J.E., Leibold, M.A. & Pinel-Alloul, B. 2000. Local and regional zooplankton species richness: A scale-independent test for saturation. *Ecology* 81, 3062-3073.
- Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins* 49, 11-41.
- Snäll, T., Ehrlén, J. & Rydin, H. 2005. Colonization-extinction dynamics of an epiphyte metapopulation in a dynamic landscape. *Ecology* 86, 106-115.
- Snäll, T., Pennanen, J., Kivisto, L. & Hanski, I. 2005. Modelling epiphyte metapopulation dynamics in a dynamic forest landscape. *Oikos* 109, 209-222.
- Snäll, T., Ribeiro, P.J. & Rydin, H. 2003. Spatial occurrence and colonisations in patch-tracking metapopulations: local conditions versus dispersal. *Oikos* 103, 566-578.
- Söderström, L. 1988a. The Occurrence of Epixylic Bryophyte and Lichen Species in an Old Natural and a Managed Forest Stand in Northeast Sweden. *Biological Conservation* 45, 169-178.
- Söderström, L. 1988b. Sequence of Bryophytes and Lichens in Relation to Substrate Variables of Decaying Coniferous Wood in Northern Sweden. *Nordic Journal of Botany* 8, 89-97.
- Stone, D.F. 1989. Epiphyte Succession On *Quercus-Garryana* Branches In The Willamette Valley Of Western Oregon. *Bryologist* 92, 81-94.
- Svensson, M., Johansson, P. & Thor, G. 2005. Lichens of wooden barns and *Pinus sylvestris* snags in Dalarna, Sweden. *Annales Botanici Fennici* 42, 351-363.
- Syrjänen, K., Kalliola, R., Puolsamaa, A. & Mattsson, J. 1994. Landscape structure and forest dynamics in subcontinental Russian European taiga. *Annales Zoologici Fennici* 31, 19-34.
- Uliczka, H. & Angelstam, P. 1999. Occurrence of epiphytic macrolichens in relation to tree species and age in managed boreal forest. *Ecography* 22, 396-405.
- Wiens, J.A. 1989. Spatial Scaling in Ecology. *Functional Ecology* 3, 385-397.

- Wilson, D.S. 1992. Complex Interactions in Metacommunities, with Implications for Biodiversity and Higher Levels of Selection. *Ecology* 73, 1984-2000.
- Zamfir, M. 2000. Effects of bryophytes and lichens on seedling emergence of alvar plants: evidence from greenhouse experiments. *Oikos* 88, 603-611.
- Åström, M., Dynesius, M., Hylander, K. & Nilsson, C. 2005. Effects of slash harvest on bryophytes and vascular plants in southern boreal forest clear-cuts. *Journal of Applied Ecology* 42, 1194-1202.
- Östlund, L., Zackrisson, O. & Axelsson, A-L. 1997. The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Canadian Journal of Forest Research* 27, 1198-1206.

Tack

Jag skulle inte sitta här med ”boken” i handen idag utan den uppbackning jag fått av en rad personer. För att inte glömma någon vill jag därför tacka alla kollegor på Naturicum och den nya ekologiinstitutionen som på ett eller annat sätt bidragit till att avhandlingen till slut gått i tryck. Några personer har givetvis haft en lite tyngre roll i mina forskarstudier och förtjänar därför ett speciellt tack.

Först ut blir Göran som gav mig chansen att prova på vad forskningsstudier går ut på. Tack för att du alltid har tagit dig tid för att läsa alla manuskript samt att hjälpa till såväl i fält som vid mikroskopet. Ett stort tack också för det förtroende du har visat för mig vad det gäller undervisning. Ser fram emot att färdigställa manus 5, dock efter en lång semester. Tack Lena för din tillgänglighet under doktorandtiden. Snabba kommentarer och synpunkter på manus har betytt mycket. Tack Anders för alla dina förslag på vinklingar av studier och frågeställningar. Det tvingade mig att tänka till på saker jag annars skulle ha missat.

Tack Jörgen för alla mer eller mindre vetenskapliga diskussioner vi har haft genom åren, samt för den goda stämningen i rummet. Nu kör vi vidare på det här med stubbar, va? Tack Tord för en intensivkurs i metapopulationsdynamik. Det var stressigt den sista månaden men också väldigt kul och lärorikt. Tack alla fältassistenter för insamlande av data: Gry Benediktsson, Mattias Lif, Måns Svensson och Liv Lötberg. Stort tack till Tobias för sista minuten hjälp med SAS-syntax.

Tack alla gamla doktorandkollegor på NVB som ”lät” mig ta hem vandringspriset efter tre segrar i NVB-games, och tack Bosse för din förmåga att välja de rätta grenarna. Förresten, fick inte du ett begrepp uppkallat efter dig? Tack alla med- och motspelare på fredagsinnebandyn för uppiggande aktivitet mitt i allt stillasittande. Tack Weronika för alla glada inbjudningar till fika, även om jag var ganska dålig på att följa med. Mot slutet av

studierna fick jag ny inspiration och drivkraft tack vare att grabbar som Buffon, Cannavaro, Grosso, Zambrotta, Gattuso, Pirlo, Perrotta, Camoranesi, Toni, Del Piero, Totti och inte minst Materazzi med sin vassa tunga, lät mig uppleva ett andra välförtjänat och rättvist guld.

Sist men definitivt inte minst vill jag speciellt tacka alla familjemedlemmar. Allra först är jag hjärtligt tacksam för att Mamma och Pappa hela tiden har uppmuntrat vidare studier, och att de har trott på sin son. Tack Lia som har tagit hand om "gamlingarna" när jag inte varit på plats. Tack Daniels mormor och morfar för all hjälp med underhåll av huset.

De allra sista raderna tillägnas de viktigaste familjemedlemmarna. Daniel, nu ska du inte behöva stå utanför en stängd dörr på helgerna och konstatera att "pappa åbbaj daton". Nu ska vi busa. Störst tack till Jenny, för stöd och uppbackning både i fält och hemma. Utan dig hade jag inte fått ihop det.