

Bryophytes, Lichens and Dead Wood in Young Managed Boreal Forests

JÖRGEN RUDOLPHI

*Faculty of Natural Resources and Agricultural Sciences
Department of Ecology
Uppsala*

**Doctoral thesis
Swedish University of Agricultural Sciences
Uppsala 2007**

Acta Universitatis Agriculturae Sueciae

2007: 88

ISSN 1652-6880

ISBN 978-91-576-7387-9

© 2007 Jörgen Rudolphi, Uppsala

Tryck: SLU Service/Repro, Uppsala 2007

Abstract

Rudolphi, J. 2007. Bryophytes, lichens and dead wood in young managed boreal forests. Doctor's dissertation.

ISSN 1652-6880, ISBN 978-91-576-7387-9

The decrease in old-growth forests threatens the diversity of a range of organisms. Only a small portion of the forested area in Sweden is formally protected and the majority of unprotected forests are young (<70 years). The objective of this thesis is to provide a deeper understanding of the production forest landscape, with special focus on young forests and to increase the knowledge about man-made substrates. Moreover, this thesis investigates the long-term survival chances of forest bryophytes and lichens, and gives insight into the dispersal biology of bryophytes.

After clear-cutting, the remaining dead wood consists of logging residues (slash), logs, snags and man-made high and low stumps. Results from this thesis show that the effect on dead wood supply of harvesting slash for biofuel is most significant for slash and logs. Sixty-five percent of the lying dead wood volume left after clear-cutting was piled for extraction. In addition, 36 % of the remaining dead wood was removed, including a significant volume of coarse dead wood.

On stumps in different age classes, bryophytes showed a tendency to increase in richness over time, whereas lichens colonized stands in early succession more rapidly and had an earlier peak in species richness. As a dispersal mechanism for bryophytes living on stumps, ants inhabiting the same substrates were shown to passively carry bryophyte diaspores for a significant period of time. This result sheds light on the complexity of species dispersal.

In adjoining young and old forest stands, red-listed bryophytes and lichens were more abundant in the old stands. This difference disappeared when the amount of substrate available was taken into account. When the young stands were positioned north of the old, the bryophytes were equally frequent in both forest stages, indicating that the aspect of a clearcut matters.

In conclusion, young forests have the potential to host a high diversity of species. Research on young natural and managed forests is needed to formulate science-based conservation strategies in managed forest landscapes.

Keywords: boreal forests, bryophytes, dead wood, dispersal, diversity, lichens, recovery, slash, succession, young forests

Author's address: Jörgen Rudolphi, Department of Ecology, Swedish University of Agricultural Sciences, Box 7002, SE-750 07 Uppsala, Sweden.

E-mail: Jorgen.Rudolphi@ekol.slu.se

"Den sista tallen var tre fot och en tum i brösthöjd, den fick vara, den stod sedan som ett landmärke i nära hundra år. Under den tallen lade Elis i Lillåberg ifrån sig redskapen. Det var vid middagstid en av de sista dagarna i maj, solskenet var starkt. Han grep tag med båda armarna om tallen och klöste och slet och drog tills han stod upprätt. Sedan gjorde han detta som han inte unnat sig på hela vintern: han släppte blicken fri utåt och bortåt. Ingen hade gjort det före honom: han såg världen från toppen av Klåvaberget. Ingenting som skymde, han såg Ormberget och Rävaberget och Storgransberget och berg som han aldrig hört talas om, Gruslidtjärn och Kattjärn och Långsmalträsket och Blåholmsjön, i söder såg han Vindelälven och i norr Skellefteälven, ja, det var hela Västerbotten, den blå randen längst bort var antagligen havet. Och ingen dimma. Allt detta hade ändå legat under stordimman, han hade insett och vetat det, hela skapelsen. Det var inte förgäves som han kalthuggit Klåvaberget, ingenting är förgäves, tvåhundra-trettio hektar urskog!"

Torgny Lindgren ur "I Brokiga Blads vatten"

*Till min familj!
Frida, Alva & Hjalmar*

Contents

Introduction, 7

Thesis aims and questions, 7

Succession, 8

Silviculture and dead wood, 9

Study organisms, 11

Summary of papers, 12

Study areas, 12

Effects of slash removal (Paper I), 12

Succession of bryophytes and lichens on stumps (Paper II), 14

Bryophyte dispersal (Paper III), 15

Old-growth species in young managed forests (Paper IV), 17

Conclusion, 18

Implications for conservation, 22

Acknowledgements, 23

References, 23

Svensk populärvetenskaplig sammanfattning, 30

Tack, 32

List of Appendices

Papers I-IV

This thesis is based on the following papers, which will be referred to by their Roman numerals:

- I. Rudolphi J. & Gustafsson L. 2005. Effects of forest-fuel harvesting on the amount of dead wood on clear-cuts. *Scandinavian Journal of Forest Research* 20, 235-242.
- II. Caruso A. & Rudolphi J. Influence of stand successional stage and substrate variability on diversity of lichens and bryophytes growing on stumps. *Manuscript*.
- III. Rudolphi J. Ant-mediated dispersal of asexual moss propagules. *Submitted manuscript*.
- IV. Rudolphi J., Gustafsson L. & Berglund T. Old-growth forest bryophytes and lichens in young boreal production forests. *Manuscript*.

Paper I is reproduced with permission from Taylor & Francis.

My contributions to the four studies included in this thesis:

(I) In collaboration with LG, I designed the field work. I conducted the field work in one of the two sub-studies and was responsible for the data analyses. I did most of the writing, with significant contribution by LG.

(II) Equal amounts of planning and data collection were conducted by the two authors of this manuscript. AC was responsible for the lichens and I for the bryophytes. Together, we planned and conducted the data analyses. The two authors contributed equally to the writing of the manuscript.

(III) I planned the field work, collected and analyzed the data, and wrote the manuscript.

(IV) LG planned most of the study. TB collected the lichen data and I the data on bryophytes, deciduous trees and dead wood. I planned and performed most of the analyses. LG and I contributed equally to the writing of the manuscript.



Introduction

For contemporary ecology, one of the great tasks is to understand the determinants of biological diversity (Rosenzweig, 1995). Conservation efforts are underway in all biomes, although less than 12 % of the Earth's land surface stands under any formal protection (UNEP-WCPA, 2007). The vast majority of the Earth's land area lacks any legal conservation status. Changes in land use activities during the last decades have led to a severe loss of biodiversity worldwide (Foley *et al.*, 2005). In Scandinavia, these changes are exemplified by the intensification of forestry, where the natural forest landscape has been replaced by young, single-aged and evenly-sized monocultures (Axelsson, 2001). As a result, an increasing number of species are becoming threatened with extinction, or even going extinct (Berg *et al.*, 1995; Gärdenfors, 2005). Today, less than one percent of the forested area below the mountainous region is protected in Sweden (Anonymous, 2006).

Thesis aims and questions

The objective of this thesis is to provide a deeper understanding of the production forest landscape, with special focus on the young forests and to increase the knowledge about man-made substrates. Moreover, this thesis investigates the long-term survival chances of forest species, especially bryophytes and lichens, and gives insight into the dispersal biology of bryophytes.

This thesis and the papers it includes deal with (I) the prerequisites, (II) the course, (III) a mechanism and (IV) one possible outcome of succession and recovery of an ecosystem following disturbance by forestry. The focus is on young managed forests in the boreal and hemi-boreal regions of Sweden, which belong to a biogeographic zone that reaches from the Urals in the east to the coast of Norway in the west.

More specifically, this thesis aims to increase the knowledge about the diversity of bryophytes and lichens in young forests regenerated after clear-cutting. This was done mainly by focusing on dead wood, as it is one of the most important substrates for forest biodiversity (Siitonen, 2001). The question asked in the first study, was how the supply of dead wood is affected by the extraction of logging residues for biofuel. In the second, a dead wood substrate was studied that, although wide-spread, has received very little attention in the literature: man-made stumps created at final felling. The question in this study was how substrate age and variability affect the diversity of bryophytes and lichens. In the third, one possible mechanism for the dispersal of bryophytes living on dead wood was studied, asking if *Aulacomnium androgynum* (Hedw.) Schwägr. dispersal may be mediated by the ant species *Lasius platythorax* (L.) Seifert, which occupies the same substrate. Finally, the fourth study was performed on rare and declining species in young forest stands adjoining old stands, with special emphasis on the effects of substrate availability, stand age and present and historic environmental factors in the surroundings.

Succession

Natural forested landscapes are shaped by disturbances like fires and wind-storms. In present-day boreal forests, naturally occurring disturbances are much less frequent due mainly to successful fire-prevention. In the Nordic countries and in many other parts of the world, artificial disturbances are today more common since a large proportion of forested landscapes is managed for the purpose of biomass extraction. The structure of the post-harvest forest succession differs significantly from that after a natural disturbance, because there are few above-ground structures left after logging, in contrast to after most natural disturbances (Franklin *et al.*, 2002).

Even before modern forestry, humans have had a profound impact on the disturbance of forests. For example, hunters and gatherers induced fires to increase the yield of plant and animal species. It was essential for them to be able to predict what happens after a disturbance. Although humans have long been aware of community succession, it has only been a subject for scientific research for little over 100 years. One of the pioneers in succession research was Henry C. Cowles, who in the late nineteenth century studied the sand dune vegetation along the shores of Lake Michigan (Cowles, 1899). However, the first comprehensive theory of plant succession was developed by Clements (Clements, 1904; Clements, 1916). He presented a view of plant succession as an orderly and predictable process in which vegetation changes were likened to the life history of an individual organism. A central point in Clements' theory was that communities progress towards a stable climax state, defined solely by the regional climate. The thoughts of Clements came to dominate the field for the first half of the twentieth century. Early critique came from Gleason (1926), who stressed the role of chance events and Tansley (1935), who criticised Clements' climax assumptions. Whittaker (1953) synthesized these thoughts on the climax state as constantly changing across a continuously varying landscape.

In the 1960s, Odum and Margalef formulated new theories on succession, suggesting that communities develop either towards greater complexity with more trophic layers (Margalef, 1963), or up to a maximum biomass and diversity given the physical limits of the environment (Odum, 1969). From the early 1970s, the field broadened considerably and many mutually non-exclusive hypotheses developed, that may all apply in varying degrees to succession (Glenn Lewin, Peet & Veblen, 1992).

After an ecosystem suffers from a disturbance, the renewal cycle theory, devised by Holling *et al.* (1995), holds that a phase of reorganisation follows, succeeded by recolonization. The result of this process is largely determined by the ecological memory of the ecosystem (Bengtsson *et al.*, 2003). One of several constituents to ecological memory is the internal, or within-patch memory, which is the biological structures and species that survive or are left on a disturbed area. The structures may be logs or snags after a fire or storm. The species could be ones that survive either above-ground or even below-ground in the seed or diaspore bank. This idea is equivalent to what has been called “biological legacies” in recent literature (e.g. Keeton & Franklin, 2005; Ledger *et al.*, 2006). Another important part of the ecological memory though, is external memory, which is species from the surroundings that may contribute to the recolonization of a disturbed area. Metapopulation theory and landscape ecology have both emphasized the importance of the spatial configuration of habitat patches for single species persistence. Recently, Löbel, Snäll and Rydin (2006) showed that spatial aggregations may also affect community species richness.

Succession theory forms one of the foundations of modern ecology and in conservation biology, it is crucial for the understanding of how an ecosystem responds to human impacts, as well as of the patterns and processes linked to restoration. Succession is intimately associated with the fundamental processes of species dispersal, colonization and establishment.

Silviculture and dead wood

Forest management has altered forest ecosystems in at least three ways: 1) the size, configuration and spatial distribution of different forest stand types has changed (Mladenoff *et al.*, 1993); 2) the structural features of different forest types and the transition zones between them have changed (Angelstam, 1992); and 3) particular microhabitats, e.g. snags and decaying wood, have been lost (Esseen *et al.*, 1992). Clear-cutting has large effects on a variety of organisms (Pawson *et al.*, 2006). The surrounding forest communities often suffer from steep gradients between stands with different micro-climatic conditions and other edge effects (Chen *et al.*, 1999). The loss of natural forests threatens the long-term persistence of many species that are confined to these habitats (Fahrig, 2003 and references therein).

In Sweden, modern silviculture, which involves clear-cutting, cleaning and thinning, developed in the 1950s (Fries & Lämås, 2000). It has caused a dramatic decrease in the amount of dead wood in managed forests (Linder & Östlund, 1998) reducing important substrate availability for many forest-living species (Berg *et al.*, 1994; Siitonen, 2001). The single most important factor governing the

supply of dead wood in productive forests today, is intensive management (Söderström, 1988a; Nilsson *et al.*, 2002; Ranius *et al.*, 2003).

Dead wood is a key factor for biodiversity in boreal forests as it hosts a large number of polypores and other decomposing fungi, bryophytes, lichens and invertebrates (Siitonen, 2001). Large amounts of dead wood are also characteristic of old-growth boreal forests (Lämås & Fries, 1995; Ohlson *et al.*, 1997; Linder & Östlund, 1998). The amount of dead wood is sometimes considered to be the main difference between managed and natural forests (Samuelsson & Ingelög, 1996). The estimated average volume of dead wood on managed productive forest land in Central Sweden is $5.3 \text{ m}^3 \text{ ha}^{-1}$ (Anonymous, 2006), which is only between two and 30 % of the quantity in unmanaged forests (Fridman & Walheim, 2000; Siitonen, 2001). In Sweden, the managed forests with the largest amounts of dead wood are the oldest stands, which are mature for harvest (Siitonen, 2001). Following harvest, the amount of dead wood decreases significantly. Models suggest that the amount of dead wood decreases to 30 % of the preharvest amounts at the end of the first 100-year rotation and to six percent after the second (Spies & Cline 1988 in Hansen *et al.*, 1991). In natural boreal forests, the amount of dead wood is greatest immediately following disturbances such as fires or windstorms (Uotila *et al.*, 2001; Pedlar *et al.*, 2002). Along with this is a high species diversity (Junninen *et al.*, 2006). Although there are still forests in some parts of Sweden that have not been subjected to clear-cutting, most managed forests have little or no chances of developing into forests that resemble old-growth forests because repeated clear-cut rotations successively decrease the amounts of dead wood.

By the early 1990s, efforts to mimic the post-disturbance structures of natural forests by retaining dead and living trees on logging sites became standard practice in Fennoscandian silviculture (Vanha-Majamaa & Jalonen, 2001; Lindhe, Åsenblad & Toresson, 2004). Today, a wide variety of structures are retained in clearcuts: e.g. single trees, tree groups and logs. High stumps are artificially created by cutting some live trees at a height of three to four metres. In 2000, the Swedish parliament implemented 15 environmental quality objectives (Anonymous, 2001). One of these objectives concerns forested land and states that the amount of hard dead wood in our managed forests is to be increased by 40 % by the year 2010. This has led to an increased effort to integrate dead wood into forestry planning (e.g. Jonsson, Kruys & Ranius, 2005).

At the same time as more dead wood is being created and left in clearcuts, a new forestry practice is arising in Sweden and elsewhere, in which logging residues (slash) as well as cut stumps are being removed for biofuel. This is done with the aim of reducing the dependence on fossil fuels (Egnell, Liedholm & Lönnell, 2001). Most studies on biodiversity associated with dead wood have focused on coarse woody debris (diameter >20 cm) (Siitonen, 2001). An increasing number of studies have, however, showed that fine woody debris (diameter <10 cm) may support as many or more species as coarser debris when the same volumes are compared (Kruys & Jonsson, 1999; Nordén *et al.*, 2004). Twigs and branches may be an important breeding substrate for saproxylic insects, likely because they become warmer earlier in the season and thereby promote insect activity (Edmonds & Eglitis, 1989; Jonsell, Weslien & Ehnström, 1998).

On newly clear-cut sites, slash reduces wind velocity and affects temperature fluctuations both below and above ground (Proe, Griffiths & McKay, 2001). Slash contributes to structural heterogeneity at the stand level and, in doing so, may have both short- and long-term effects on the species richness and composition of ground-living beetles (Nittérus & Gunnarsson, 2006; Nittérus, Åström & Gunnarsson, 2007). Slash has also been shown to provide shelter for both small mammals and desiccation-sensitive bryophytes (Ecke, Löfgren & Sörlin, 2002; Åström *et al.*, 2005).

Study organisms

The focus in this thesis has been on bryophytes and lichens (lichenized fungi). The reasons for this are manifold. Bryophytes and lichens are important components of boreal and temperate forests and constitute a significant proportion of the biological diversity (Longton, 1992). In Sweden, approximately 1000 bryophyte and 2000 lichen species have been found (Hallingbäck, 2007), and of these approximately 800 lichens and 300 bryophytes are mainly found in forests (Hallingbäck, 1995; Hallingbäck, 1996). Since both groups are poikilohydric, i.e. they lack effective mechanisms for regulating the uptake and loss of water (Proctor, 1990), they are sensitive to alterations in their environment and therefore forestry (Lesica *et al.*, 1991; Esseen *et al.*, 1997). Many of them are also considered to be confined to old-growth forests in the boreal and hemi-boreal zones (McCune, 1993; Kuusinen & Siitonen, 1998; Vellak & Paal, 1999). Lichens and bryophytes are used widely as biodiversity indicators. Several studies have found higher diversity and abundance of bryophytes and lichens in old-growth forests compared to managed forests (Söderström, 1988a; Andersson & Hytteborn, 1991; Crites & Dale, 1998; Rambo & Muir, 1998; Kruys *et al.*, 1999; Sillett *et al.*, 2000; Botting & Fredeen, 2006). The lower abundance of these species in managed forests could either be due to inefficient dispersal (Esseen *et al.*, 1997; Sillett & McCune, 1998; Pharo & Zartman, 2007), to unfavourable microclimates, or to lack of substrate (Frisvoll & Presto, 1997), or a combination of these factors. Successful transplantations of species classified as old-growth forest lichens into young forests indicate that these species can survive there and are limited primarily by dispersal (Hilmo & Sâstad, 2001). This result is supported by Dettki *et al.* (2000), who showed a decline in abundance among epiphytic lichen species occurring in young stands with increasing distance from old forest stands. The difference in available substrates between old-growth and managed forests has been pointed out in many studies (Siitonen, 2001). This difference has been suggested as one explanation for why many forest species have become rare or threatened (Berg *et al.*, 1994; Gärdenfors, 2005).

Succession of bryophytes and lichens has been studied indirectly by comparing the species composition on dead wood of different decay stages (Muhle & LeBlanc, 1975; Nakamura, 1987; Söderström, 1988b; Heilmann-Clausen, Aude & Christensen, 2005). The conclusion from those studies is that there is a clear change in the composition of bryophyte and lichen vegetation during the decay of trees. It is not clear what determines this succession, but differences in substrate

and micro-habitat requirements among species along with dispersal limitations could affect the order in which the species occur.

Summary of papers

Study areas

The boreal and hemi-boreal zones are the largest terrestrial biomes in the world. They stretch from Fennoscandia, through Siberia to Alaska and Canada. The studies in this thesis were conducted in central Sweden (Fig. 1), either in the province of Uppland (I, II and III), which lies within the hemi-boreal vegetation zone, or in the province of Hälsingland (IV), which lies in the transition between the southern and middle boreal vegetation zones (Ahti, Hämet-Ahti & Jalas, 1968). Uppland has an average annual precipitation of 600 mm, with February as the coldest month (- 4°C) and July as the warmest (+ 16°C). Hälsingland is slightly wetter and colder with 700-800 mm of precipitation, - 7°C in February and + 15°C in July (Raab & Vedin, 1995). Few old-growth forest stands (i.e. > 130 years old) can be found in either province. Most of the forested area is young managed forest stands (Anonymous, 2006). They are mainly composed of managed mixed coniferous stands that cover an entire rotation. A rotation, from clear-cutting to mature stand, takes about 100 years in this part of Sweden. The dominating tree species are either Norway spruce (*Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris* L.), or less commonly European weeping birch (*Betula pendula* Roth.) and Common white birch (*Betula pubescens* Ehrh.).

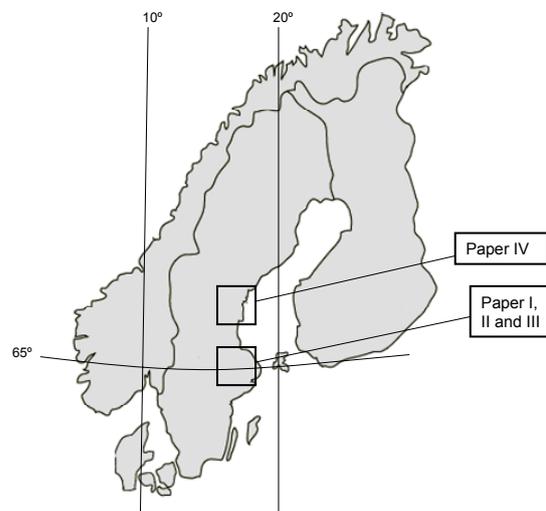


Fig. 1. A map showing the study areas used for this thesis. Data for papers I, II and III were collected in the hemi-boreal zone and for paper IV in the boreal zone (sensu Ahti, Hämet-Ahti & Jalas, 1968).

Effects of slash removal (Paper I)

Due to increased awareness of climate change and the need to use renewable energy sources, the interest in biofuel extraction from forests has increased. The extraction of slash (branches and tops) is currently very common in Swedish forestry. After being piled in clearcuts, the slash is transported to thermal power

plants where it is incinerated for energy production (Fig. 2). There is a fear that damage done to the remaining substrates as a result of the additional driving involved in slash extraction, combined with increased dead wood removal may have an adverse effect on biodiversity (Samuelsson & Ingelög, 1996; Esseen *et al.*, 1997; Larsson, 1998).



Fig. 2. Piles of forest residue left after clear-cutting.

Two studies were performed on newly clear-cut sites. The stands investigated were all dominated by Norway spruce. The aim was to quantify the amount of dead wood remaining on the clearcut after slash extraction and compare it with the amount that was removed. Statistical comparisons of the number of logs, total volumes and surface areas were performed using a mixed-model analysis of variance (ANOVA).

In the first part of the study, four piles (to be removed as biofuel) and 15 circular plots between piles (to remain on the clear-cut) on eight sites were surveyed for the abundance and sizes of branches and tops. There were, on average, 25,000 pieces ha^{-1} of slash on the clear-cuts, in and outside piles. The majority (85 %) of the dead wood pieces were branches. Stem pieces summed up to 155 pieces ha^{-1} and tops 454 pieces ha^{-1} . Of the total number of branches, stem parts and tops, 15, 62 and 41 %, respectively, were found outside the piles. Thirty-five percent of the total dead wood volume was found outside the piles. This corresponded to approximately 121 m^2 surface area of slash that would remain in the stands. Stem parts and tops contributed almost 20 % of the total surface area. In piles to be extracted, 2.5 $\text{m}^3 \text{ha}^{-1}$ of coarse woody debris (diameter >10cm at the thickest end) were found.

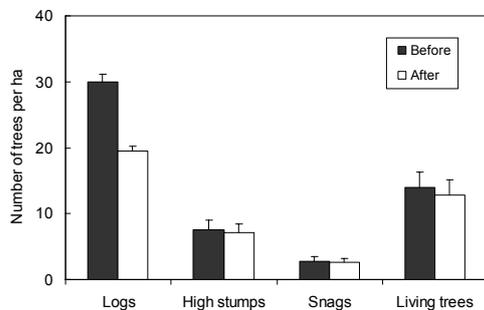


Fig. 3. The number of retained living and dead tree objects before and after extraction of logging residue on 23 clear-cuts (slash piles excluded). Bars indicate standard error.

In the second part of this study, all living and dead trees were mapped and measured both before and after pile extraction on 23 clear-cuts. The results showed that, in addition to the dead wood in piles, dead wood outside the piles was also extracted. Of the number of lying dead trees outside piles, 36 % were removed (Fig. 3). The majority had a diameter of <15 cm at the thickest end and most of them were stem parts left after logging. Additionally, approximately one out of six (17 %) of the naturally fallen logs with a diameter >15 cm at the thickest end were extracted per hectare.

Succession of bryophytes and lichens on stumps (Paper II)

Man-made stumps (Fig. 4) constitute a major part of the dead wood available in young managed forests, and also in the production forest landscape as a whole in Sweden. There is an emerging interest for extracting stumps for biofuel purposes in Sweden, but so far there are very few studies on species associated with stumps. The aim of this study was to examine the influence of stand succession and substrate variability on the species richness and composition of lichens and bryophytes that grow on the cut surface of stumps.



Fig. 4. Man-made stumps of Norway spruce (*Picea abies* (L) Karst.). The picture on the left shows a stump four years after the tree was cut, and on the right a stump 13 years after cutting.

We studied the succession of lichens and bryophytes on spruce stumps created during clear-cutting, using a chronosequence approach in stands dominated by Norway spruce. The stands were selected within four age classes: 1 = 4-5, 2 = 8-9, 3 = 12-13 and 4 = 16-18 years old. This age span was selected because the cut surfaces of spruce stumps in stands younger than four years have very little lichen or bryophyte colonization, while stumps older than 18 years are highly decayed and often completely covered by ground living bryophytes.

The total richness and composition of species were analyzed. Analyses were also done using species functional groups. These functional groups were categorised with respect to dispersal mode, life-strategy and substrate preference. A log-linear regression model with a Poisson distribution of residuals was used to analyze the influence of environmental factors and time since cutting on species richness. Species composition patterns were analyzed using Redundancy Analysis (RDA), a constrained ordination method.

The study showed that factors affecting colonization differ between bryophytes and lichens. Among lichens, structures on the cut surface that offers a heterogenic micro-habitat together with the age of the substrate significantly explained both species richness and species composition. Bryophytes were primarily affected by stump surface area and the degree of decay.

Whereas lichens colonized young stumps more rapidly, bryophyte colonization was slower, with a tendency for an increase in species richness throughout a stump's "life-span" (Fig. 5).

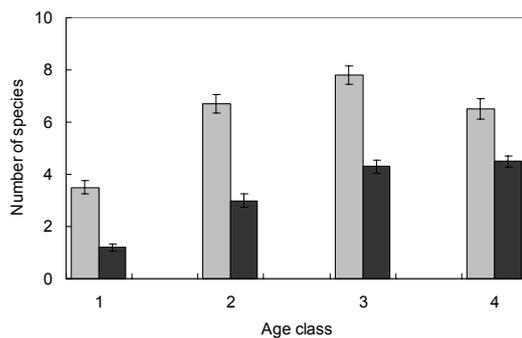


Fig. 5. Average species richness of lichens (grey) and bryophytes (black) per stump in each age class. Error bars indicate standard error; n = 8 for age classes 1, 2 and 3 and n = 6 for age class 4.

Contrary to the total species richness of the two groups, neither bryophyte colonists, nor lichens that disperse via spores increased in richness over time. This result indicates that these two functional groups disperse readily and may establish on suitable stumps, regardless of age class.

The species turnover rate of lichens decreased over time while, simultaneously, lichen species richness increased. This opposed pattern could indicate increasing stability in community assemblage over time. There was, however, no clear pattern in the species turnover rate of bryophytes across stand age classes.

Bryophyte dispersal (Paper III)

The ability to disperse is vital for all organisms, especially for those that inhabit transient habitats. The prevailing view for bryophytes has been that species disperse by wind or water. Only rarely, have studies shown other modes of dispersal among bryophytes (e.g. Kimmerer & Young, 1995; e.g. Heinken *et al.*, 2001). In this study, the potential of the small bryophyte species *Aulacomnium androgynum* (Fig. 6) to be dispersed by the ant species *Lasius platythorax* was studied. The moss is widespread on dead wood in forests in Central and Western Europe. It rarely produces spores; instead, *A. androgynum* disperses via vegetative propagation, with so called gemmae. In Central and Southern Sweden, *A. androgynum* is commonly found on man-made stumps in young managed forests, a substrate on which *L. platythorax* is also common.



Fig. 6. Photograph of *Aulacomnium androgynum* (Hedw.) Schwägr. with clusters of gemmae (photo by Tomas Hallingbäck).

Two experiments were performed; one in which ants were allowed to move across a moss tuft and another where gemmae were attached manually to the abdomen of the ants. In the first experiment, eight petri dishes were used on which tufts of moss bearing gemmae were placed. One ant was released in each petri dish for at least 30 seconds. The experiment was repeated eight times and clearly showed that gemmae adhered to the body of the ants as they moved freely over the moss tuft (Fig. 7). In total, gemmae adhered to 33 % of the ants within less than two minutes of exposure to the moss.



Fig. 7. A *Lasius platythorax* (L.) Seifert individual with two gemmae (encircled) adhered to its dorsal abdomen (photo by Tomas Hallingbäck).

The second experiment was conducted to determine how long the gemmae stayed adhered. This was done by attaching two gemmae each on the dorsal abdomen of 36 ants. The ants were released one by one into empty petri dishes. The dishes were divided into four groups and after one, two, four or eight hours, respectively, they were put in a freezer for subsequent investigation. This experiment revealed that under laboratory conditions half of the gemmae stayed attached for approximately four hours before falling off (Fig. 8). The results indicate that dispersal of this asexual bryophyte species may be mediated by ants as animal vectors.

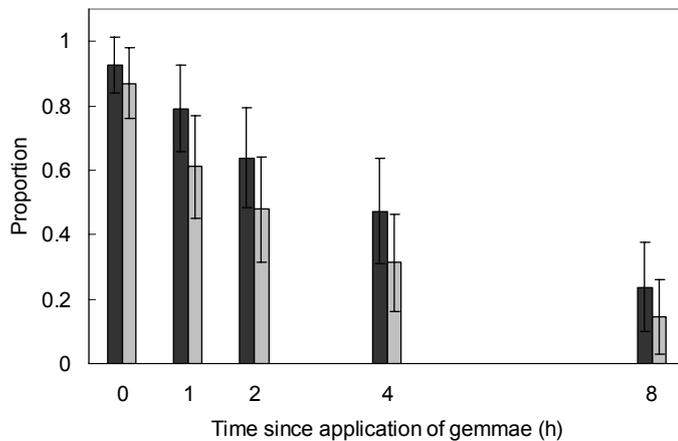


Fig. 8. The proportion of ants with gemmae still remaining after specified time periods since application (black bars) and the proportion of gemmae remaining on the ants after specified times since application (grey bars). Error bars are 95 % confidence intervals.

Old-growth forest species in young managed forests (Paper IV)

Clear-cutting has dominated Swedish silviculture during the last 50-60 years, resulting in a depletion of old-growth forests. Today, young managed stands (i.e. <70 years old) constitute most of the forested area below timberline in Sweden. Young managed stands also dominate production forest landscapes in other countries. The aim of this paper was to compare, between young and old forest stands, the richness and abundance of red-listed species, most of which are presumed to be old-growth specialists. The intention was also to identify the causes for possible differences, with special emphasis on substrate amounts and distance to possible dispersal sources. The survey was conducted in 19 adjoining stands of young (30-70 years) and old (>95 years) Norway spruce forests situated within the northern part of the county of Gävleborg (Fig. 1) in the transition zone between the southern and middle boreal vegetation regions (Ahti, Hämet-Ahti & Jalas, 1968). The young stands were all previously clear-cut, while the old stands were most likely selectively cut repeatedly during the last few decades and also subjected to thinnings.

A 100 x 100 m plot was positioned on either side of the border between the young and old forest stands, and each plot was subdivided into 10 x 10 m subplots. In each subplot, the presence and abundance of red-listed bryophyte and lichen species were registered. Amounts of logs and living deciduous trees were recorded. The area of old forest and other environmental factors in the surrounding landscape were assessed from satellite imagery and digitized maps. The differences in species richness and abundance, as well as in the amount of available substrate between young and old stands was analyzed using Wilcoxon signed rank tests. Edge effects and influence of the surrounding landscape were analyzed using log-linear regression, with species richness and abundance as

response variables and environmental factors as independent variables. Since the response variables were counts, a Poisson distribution was used with a logarithmic link function. Where response variables showed signs of over-dispersion, we used a negative binomial distribution of residuals.

Red-listed lichen and bryophyte species were richer and more abundant in old forest stands compared to young stands. No difference was found when species data were standardised against substrate amounts. In contrast to lichens, the difference between old and young forests was significant only when young stands were positioned south, but not north, of the old stands (Fig. 9).

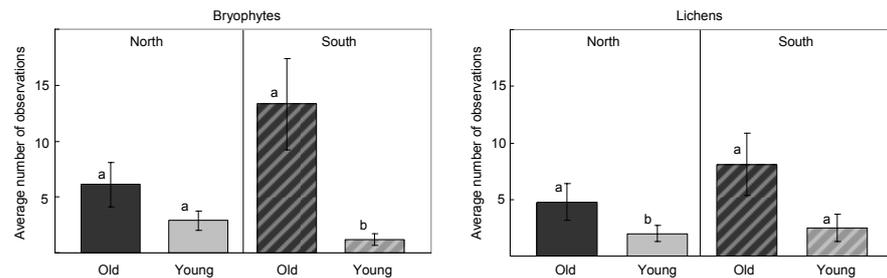


Fig. 9. Average number of observations of red-listed species in young stands positioned north and south, respectively, of the old stands for bryophytes and lichens (excluding *Bryoria nadvornikiana* (Gyeln.) Brodo & D. Hawksw.) in the 100 x 100 m plots. Bars with the same letter do not differ significantly according to Wilcoxon signed rank test (n.b. the comparisons are only within the same cardinal groups). The error bars indicate standard error.

The richness of red-listed bryophyte species and the abundance of both red-listed bryophytes and lichens in the young stands was explained by the area of old forests during the last decades within 9-25 ha of the young plot. Also, bryophyte abundance in the adjoining old stands together with the area of wetlands in the surrounding landscape affected bryophyte abundance in young forest stands. One lichen species that grew on Norway spruce, *Bryoria nadvornikiana* (Gyeln.) Brodo & D. Hawksw., was more common in young stands, indicating that this species has a high dispersal and colonization capacity.

At the spatial and temporal scale of the study, no edge effects were found on species richness or abundance in either the young, or the old stands. Edge effects may have been evident earlier in the succession, but, if so, time has erased them. A distance of 100 m may not be enough to distinguish edge effects after times up to 70 years.

Conclusion

This thesis has focused on young stands in the forest successions of managed forest landscapes. Parallel early stages of succession exist in natural unmanaged forest landscapes, but these have not been studied here. Succession following a natural disturbance differs significantly from succession in a forest after clear-

cutting. But there are similarities as well. The processes by which the species recover are the same, even though the prerequisites differ. Many factors influence the recovery of stand-level bryophyte and lichen diversity following a disturbance (Fig. 10). Some of them have been touched upon in this thesis, but they require further study and many more factors remain to be investigated as well. The internal memory of a forest stand, which consists of species surviving *in situ* after a clear-cut, is poorly described and understood. After a forest is cut down, the living and dead trees that are retained may function as temporal stepping-stones from the clear-cut phase into the forest regeneration phase (Vanha-Majamaa & Jalonen, 2001). Species that live on these trees may survive the inhospitable period of strong winds and intense sunlight. Structural legacies, in the form of retained trees, have been shown to provide habitat for both epiphytic bryophytes and lichens (Peck & McCune, 1997; Hazell & Gustafsson, 1999). Micro-climate variables, such as wind-velocity and irradiation increase desiccation in clear-cuts (Chen, Franklin & Spies, 1993). This in turn affects the local performance of species on the site. Micro-climate effects are stronger at south-facing clear-cut edges than north-facing edges (Hylander, 2005). Slope aspect has also been shown to modify a species' responses to clear-cutting (Åström *et al.*, 2007).

The external memory of a site, which is the regional species pool, obviously affects its diversity after disturbance. Stand connectivity in both the present-day and historical landscape has also been shown to explain the occurrence of species at the local scale (Snäll *et al.*, 2004; Paltto *et al.*, 2006).

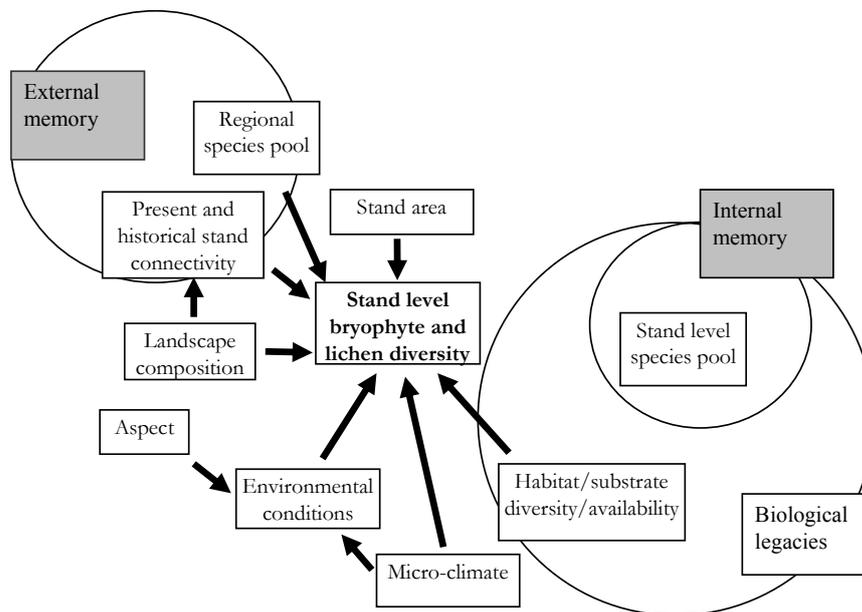


Fig. 10. Factors influencing the stand level species diversity of bryophytes and lichens following a disturbance.

Whereas a natural forest contains large quantities of dead wood following a disturbance, a managed forest, where most logging residues are harvested, may suffer from long-term losses in the diversity of forest species because of reductions in downed dead wood. The practice of harvesting branches and tops may not endanger the rare species since they often are connected to more specialized substrates, but removing larger logs from the forest floor may impact future biodiversity. Very little new dead wood is created in young forest stands and the temporal gap in substrate supply may be too long for lichens, bryophytes and other dead wood-dependant organisms to survive locally. The dead wood left on the forest floor following clear-cutting consists mainly of man-made stumps. Whether or not these stumps can function as “life-boats” for dead wood-dependent species over the period where other dead wood-substrates are scarce is uncertain.

The species found on stumps are mainly common ones and not dead wood specialists. But, more studies have to be conducted before it is possible to rule out stumps as hosts for rare and threatened species. There might be certain stump types, with a particular trees species, microhabitat, decomposition pattern or geographic location, that have a higher value to biodiversity than the ones studied in this thesis. The distance to sources of dead wood species is of crucial importance for the future succession of species living on a stump. A recent review by Pharo and Zartman (2007) concludes that, given the dispersal limitations shown by bryophytes in many studies, the spatial configuration of forests with intact bryophyte flora is essential for conservation efforts. Since the “life-time” of a stump is relatively short, the distance to species pools that can colonize the stump must be also be short. Studies on the stump flora in the vicinity of forests with large amounts of dead wood and with a high richness of dead wood species including rare ones are needed. In addition, experimental transplantations of species onto stumps may reveal whether or not stumps can substitute for other dead wood substrates.

Studies on individual species’ ability to disperse and colonize are needed to be able to distinguish between two vital concepts in community and population ecology: habitat versus dispersal limitations. The question of whether species are limited by dispersal or substrate remains un-answered and can only be addressed by single-species approaches. In biodiversity conservation, much attention has been paid to rare and declining species (e.g. Gustafsson *et al.*, 2004) and habitat qualities (Ohlson *et al.*, 1997). Studying common species, however, can help clarify the differences between rare and common species and hence lead to an understanding about what makes rare species rare. Species, especially long-lived ones, may persist in habitats that are suboptimal. Perhaps they cease to reproduce and when all individuals die, they are not replaced by others and the species are doomed to extinction (Hanski, 2000). The species studied in paper III, *Aulacomnium androgynum*, is one that shares many characteristics with rare species. It is dioecious and rarely produces sporophytes. It is also most commonly found on dead wood; a substrate that has decreased dramatically during the last decades. However, *A. androgynum* is still common throughout most of its natural range. The results from this study reveal that species that seem at first to be dispersal-limited may in fact, be target-oriented dispersers that use animal vectors.

Some parts of the boreal and, to a lesser extent, hemi-boreal forests have yet to be clear-cut, having only previously been selectively cut. These forests have retained some of the old-growth forest characteristics, e.g. the presence of dead wood in different decay stages and old deciduous trees. The young stands in Paper IV belong to the first regeneration following clear-cutting. Their history is likely going to be different from the young forests created today, since they have been surrounded by old forests with natural characteristics. Due to the increased fragmentation of old forests, the distance from regenerating forests to the closest old forest has increased. There is little chance that the young stands of today will develop into forests with natural characteristics.

Hansen *et al.* (1991) emphasized the importance of young natural forests for the preservation of biodiversity. Many studies agree that such young forests should be incorporated into reserve networks (Similä *et al.*, 2002; Simons, Schwab & Otto, 2002; Lorimer & White, 2003; Uotila & Kouki, 2005; Hyvärinen, 2006; Junninen, 2007). In Fennoscandia, very few young natural forests exist. More knowledge on the ecology of both natural and managed young forests is needed, and their relation to later successional stages.

One key-question that needs further research is to what extent the species mostly found in old-growth forests today are in fact limited by substrate, dispersal and micro-climate. Translocation of substrates with species present from old-forests to young may provide answers, together with transplantation experiments. These techniques have been used, but much more can be done. Including several species groups in these studies is essential since different organisms respond differently. To evaluate young forests as potential habitat for species, documenting species survival in these forests is important. However, to be able to determine the quality of these young forests as habitats, measures of the species condition is needed. Species may be able to disperse and establish in inhospitable environments, but if they do not reproduce the young forests will merely function as sinks.

The field of animal vector-mediated dispersal of cryptogams is wide and vastly unexplored. Experimental approaches including field experiments with capture-release-recapture methods may be one way to address this topic. Molecular techniques to distinguish relationships between clones of animals and cryptogams is another. Clearcuts with man-made stumps can in this sense be viewed as experimental fields with discrete patches of substrates of known age and a long array of both cryptogams and potential insect vectors utilizing the same substrates. Studying insect-cryptogam interactions may potentially unravel interactions arisen from co-evolution among these very old species groups.

As opposed to human-induced disturbance in the form of clearcutting, natural disturbances vary in intensity. Modern forestry practices are in some sense trying to mimic these natural disturbances. In research comparisons between young naturally disturbed forests and young experimentally disturbed forests are still lacking. If it would be possible to create stands shaped by disturbances of different intensities, e.g. through selective logging and inducing fire, this would increase the understanding of the response of species to these disturbances. Only by such increased knowledge, efficient and relevant conservation actions can be formulated.

Implications for conservation

Young managed forests do possess potential for biodiversity. This potential is, however, not unconditional. Promoting the conditions that are necessary for the long-term survival of sensitive species can increase the conservation value of the young managed forests. Such conservation actions might also benefit biodiversity in subsequent stages in the forest succession.

Extraction of logging residue for bioenergy reduces the on-site supply of dead wood, including coarse woody debris, which is important for many organisms. The aim of biofuel extraction is to decrease the dependence on fossil fuels and to combat climate change. This aim is praiseworthy and the ecological drawbacks of biofuel extraction can be mitigated. Guidelines for the operators of slash forwarders should include not removing logs left to benefit biodiversity. Damage to logs during driving operations should also be avoided because it may speed up decay, resulting in a deficit in dead wood later in the succession. This is especially important with old decaying logs that remain from before clear-cutting. Succession of species has already started on these logs and disturbance of this process may have negative effects for late-succession species. Application of these guidelines together with creation of new dead wood may partially mitigate the negative consequences of clear-cutting and slash harvest.

Stump removal for bioenergy is not yet as widespread as slash harvest, but it is beginning to be practiced. As indicated in this thesis, no red-listed species were found on stumps in managed forests. However, the results revealed that, at least for lichens, stumps can provide a previously unknown and species rich-flora. Although no species are adapted to this novel and man-made substrate *per se*, it may still be important to species that are dependent on dead wood when other dead wood substrates are lacking. Further studies are needed before it is possible to state for certain that stumps are a substitute to logs and snags for dead wood-dependent species in young forests.

Leaving dead wood and old living trees in young stands is the first step to provide managed forests with the prerequisites for biodiversity recovery. Still, it is uncertain what these trees resemble in natural forests. Dead wood created naturally in virgin forests differs vastly from the fresh dead wood created for biodiversity purposes by humans in clearcuts. Many studies remain to be conducted before the effects of these conservation efforts are revealed. Unfortunately, the fragmentation in some areas has left gaps that are hard for some species to bridge. This is a much harder task for foresters and conservationists to solve. Creating networks so that stands of all different ages are in close contact is one way, but it will inevitably take time before diversity is re-established in areas that have been isolated for a long time. Results from this thesis suggest, however, that the micro-climate in young stands need not be inhospitable to so-called old-growth species and that red-listed species may survive in young production forests. At least for bryophytes, the effect of clear-cutting is stronger in young stands to the south of intact forests. Focusing the nature concern in this parts of cut stands, so as not to entirely remove tree cover and leave dead trees, is probably the most effective measure to speed up the re-colonization of species.

As concluded from this and numerous earlier studies, one way to maintain a rich diversity of species in the boreal forest is to retain old deciduous trees and dead wood of different decay stages on clear-cuts. The negative effects of large logs being removed from the clear-cut sites together with slash for biofuel, may be counteracted by strict guidelines to operators of the slash forwarders.

Acknowledgements

I would like to thank Lena Gustafsson, Bengt Gunnar Jonsson and Karin Perhans for valuable comments on this thesis. Tomas Hallingbäck is thanked for assistance with photographs. Thanks also to Holmen Skog, Mellanskog, Sveaskog and Sydved Energileveranser for providing sites and data. The studies in this thesis were in part financed by The Swedish Energy Agency (Energimyndigheten), The Forestry Research Institute of Sweden (SkogForsk), The Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (Formas) and The Royal Swedish Academy of Agriculture and Forestry (Kungliga Skogs- och Lantbruksakademien, KSLA).

References

- Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968. Vegetation zones and their sections in Northwestern Europe. *Annales Botanici Fennici* 5, 169-211.
- Andersson, L.I. & Hytteborn, H. 1991. Bryophytes and decaying wood - a comparison between managed and natural forest. *Holarctic Ecology* 14, 121-130.
- Angelstam, P. 1992. Conservation of communities - The importance of edges, surroundings and landscape mosaic structure. In: *Ecological principles of nature conservation*. (Ed. L. Hansson). Elsevier Science Publishers. Amsterdam. pp. 9-70.
- Anonymous 2001. *The Swedish environmental objectives. Interim targets and action strategies. Gov. bill 2000/01:130*. Ministry of Environment. Stockholm, Sweden. 78 pp.
- Anonymous 2006. *Skogsstatistisk årsbok 2006. Swedish Statistical Yearbook of Forestry 2006*. Skogsvårdsorganisationens förlag. Jönköping. In Swedish with English summary.
- Axelsson, A.L. (2001). *Forest landscape change in boreal Sweden 1950-2000*. Ph.D. thesis, Department of Forest Vegetation Ecology, Swedish University of Agricultural Sciences, Umeå, Sweden.
- Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F. & Nystrom, M. 2003. Reserves, resilience and dynamic landscapes. *Ambio* 32, 389-396.
- Berg, A., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M. & Weslien, J. 1995. Threat levels and threats to red-listed species in Swedish forests. *Conservation Biology* 9, 1629-1633.
- 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.
- Botting, R.S. & Fredeen, A.L. 2006. Contrasting terrestrial lichen, liverwort, and moss diversity between old-growth and young second-growth forest on two soil

- textures in central British Columbia. *Canadian Journal of Botany-Revue Canadienne De Botanique* 84, 120-132.
- Chen, J.Q., Franklin, J.F. & Spies, T.A. 1993. Contrasting microclimates among clear-cut, edge, and interior of old-growth Douglas-fir forest. *Agricultural and Forest Meteorology* 63, 219-237.
- Chen, J.Q., Saunders, S.C., Crow, T.R., Naiman, R.J., Brososke, K.D., Mroz, G.D., Brookshire, B.L. & Franklin, J.F. 1999. Microclimate in forest ecosystem and landscape ecology - Variations in local climate can be used to monitor and compare the effects of different management regimes. *Bioscience* 49, 288-297.
- Clements, F., E. 1904. *The development and structure of vegetation*. Lincoln, Nebraska.
- Clements, F.E. 1916. *Plant succession*. Carnegie Institute Washington Publication 242. Washington D.C.
- Cowles, H.C. 1899. The ecological relations of vegetation on the sand dunes of Lake Michigan. *Botanical Gazette* 27, 95-117, 167-202, 281-308, 361-391.
- 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-Revue Canadienne De Botanique* 76, 641-651.
- Dettki, H., Klintberg, P. & Esseen, P.A. 2000. Are epiphytic lichens in young forests limited by local dispersal? *Ecoscience* 7, 317-325.
- 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. 1992. Boreal forests - The focal habitats of Fennoscandia. In: *Ecological principles of nature conservation*. (Ed. L. Hansson). Elsevier Science Publishers. Amsterdam. pp. 252-325.
- Esseen, P.-A., Ehnström, B., Sjöberg, K. & Ericson, L. 1997. Boreal forests. *Ecological Bulletin* 46, 16-47.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics* 34, 487-515.
- Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. 2005. Global consequences of land use. *Science* 309, 570-574.
- Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K. & Chen, J.Q. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management* 155, 399-423.
- Fridman, J. & Walheim, M. 2000. Amount, structure, and dynamics of dead wood on managed forestland in Sweden. *Forest Ecology and Management* 131, 23-36.
- Fries, C. & Lämås, T. 2000. Different management regimes in a boreal forest landscape: ecological and economical effects. *Studia Forestalia Suecica*. 1-25.

- Frisvoll, A.A. & Presto, T. 1997. Spruce forest bryophytes in central Norway and their relationship to environmental factors including modern forestry. *Ecography* 20, 3-18.
- Gleason, H.A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53, 7-26.
- Glenn Lewin, D.C., Peet, R.K. & Veblen, T.T. (Eds.) 1992. *Plant succession - theory and prediction*. Chapman & Hall. London.
- Gustafsson, L., Appelgren, L., Jonsson, F., Nordin, U., Persson, A. & Weslien, J.O. 2004. High occurrence of red-listed bryophytes and lichens in mature managed forests in boreal Sweden. *Basic and Applied Ecology* 5, 123-129.
- Gärdenfors, U. 2005. *Rödlistade arter i Sverige 2005. (The 2005 red list of Swedish species)*. ArtDatabanken, SLU. Uppsala.
- 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.
- Hansen, A.J., Spies, T.A., Swanson, F.J. & Ohmann, J.L. 1991. Conserving biodiversity in managed forests - lessons from natural forests. *Bioscience* 41, 382-392.
- 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.
- Hazell, P. & Gustafsson, L. 1999. Retention of trees at final harvest - evaluation of a conservation technique using epiphytic bryophyte and lichen transplants. *Biological Conservation* 90, 133-142.
- Heilmann-Clausen, J., Aude, E. & Christensen, M. 2005. Cryptogam communities on decaying deciduous wood - does tree species diversity matter? *Biodiversity and Conservation* 14, 2061-2078.
- Heinken, T., Lees, R., Raudnitschka, D. & Runge, S. 2001. Epizoochorous dispersal of bryophyte stem fragments by roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*). *Journal of Bryology* 23, 293-300.
- Hilmo, O. & Såstad, S.M. 2001. Colonization of old-forest lichens in a young and an old boreal *Picea abies* forest: an experimental approach. *Biological Conservation* 102, 251-259.
- Holling, C.S., Schindler, D.W., Walker, B.W. & Ruogharden, J. 1995. Biodiversity in the functioning of ecosystems. In: *Biodiversity loss - economic and ecological issues*. Eds. C. Perrings, K.-G. Mäler, C. Folke, C.S. Holling & B.-O. Jansson). Cambridge University Press. Cambridge.
- Hylander, K. 2005. Aspect modifies the magnitude of edge effects on bryophyte growth in boreal forests. *Journal of Applied Ecology* 42, 518-525.
- Hyvärinen, E. (2006). *Green-tree retention and controlled burning in restoration and conservation of beetle diversity in boreal forests*. Ph.D. thesis, Faculty of Forest Sciences, University of Joensuu, Finland.
- 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., Krüys, N. & Ranius, T. 2005. Ecology of species living on dead wood - Lessons for dead wood management. *Silva Fennica* 39, 289-309.

- Junninen, K. (2007). *Conservation of polypore diversity in managed forests of boreal Fennoscandia*. Ph.D. thesis, Faculty of Forest Sciences, University of Joensuu, Finland.
- Junninen, K., Simila, M., Kouki, J. & Kotiranta, H. 2006. Assemblages of wood-inhabiting fungi along the gradients of succession and naturalness in boreal pine-dominated forests in Fennoscandia. *Ecography* 29, 75-83.
- Keeton, W.S. & Franklin, J.F. 2005. Do remnant old-growth trees accelerate rates of succession in mature Douglas-fir forests? *Ecological Monographs* 75, 103-118.
- Kimmerer, R.W. & Young, C.C. 1995. The role of slugs in dispersal of the asexual propagules of *Dicranum flagellare*. *The Bryologist* 98, 149-153.
- 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.
- 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.
- Kuusinen, M. & Siitonen, J. 1998. Epiphytic lichen diversity in old-growth and managed *Picea abies* stands in southern Finland. *Journal of Vegetation Science* 9, 283-292.
- Larsson, P. 1998. Biobrånslé och mångfald - på kollisionskurs i skogen? *Naturskyddsföreningen*. 28. ISSN Rapport 9417/98.
- Ledger, M.E., Harris, R.M.L., Milner, A.M. & Armitage, P.D. 2006. Disturbance, biological legacies and community development in stream mesocosms. *Oecologia* 148, 682-691.
- Lesica, P., McCune, B., Cooper, S.V. & Hong, W.S. 1991. Differences in lichen and bryophyte communities between old-growth and managed 2nd-growth forests in the Swan Valley, Montana. *Canadian Journal of Botany-Revue Canadienne De Botanique* 69, 1745-1755.
- Linder, P. & Östlund, L. 1998. Structural changes in three mid-boreal Swedish forest landscapes, 1885-1996. *Biological Conservation* 85, 9-19.
- Lindhe, A., Åsenblad, N. & Toresson, H.G. 2004. Cut logs and high stumps of spruce, birch, aspen and oak - nine years of saproxylic fungi succession. *Biological Conservation* 119, 443-454.
- Longton, R.E. 1992. The role of bryophytes and lichens in terrestrial vegetation. In: *Bryophytes and lichens in a changing environment*. Eds. J.W. Bates & A.M. Farmer). Clarendon Press. Oxford. pp. 32-76.
- Lorimer, C.G. & White, A.S. 2003. Scale and frequency of natural disturbances in the northeastern US: implications for early successional forest habitats and regional age distributions. *Forest Ecology and Management* 185, 41-64.
- Lämås, T. & Fries, C. 1995. An integrated forest inventory in a managed North-Swedish forest landscape for eliminating growing stock and coarse woody debris. In: *The Monte Verità Conference on Forest Survey Designs - "Simplicity versus Efficiency" and Assessment of Non-Timber Resources*. Eds. M. Köhl, P. Bachman, P. Brassel & G. Preto). Swiss Federal Institute for Forest, Snow and Landscape Research (WSL/FNP). Zürich, Swiss Federal Institute of Technology (ETH), Section of Forest Inventory and Planning. Birmensdorf. pp. 296-311.
- Margalef, R. 1963. On certain unifying principles in ecology. *The American Naturalist* 97, 357-374.

- McCune, B. 1993. Gradients in epiphyte biomass in 3 *Pseudotsuga-Tsuga* forests of different ages in Western Oregon and Washington. *The Bryologist* 96, 405-411.
- Mladenoff, D.J., White, M.A., Pastor, J. & Crow, T.R. 1993. Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. *Ecological Applications* 3, 294-306.
- 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.
- Nakamura, T. 1987. Bryophyte and lichen succession on fallen logs and seedling establishment in *Tsuga-Abies* forests of central Japan. *Symposia Biologica Hungaria* 35, 485-495.
- Nilsson, S.G., Niklasson, M., Hedin, J., Aronsson, G., Gutowski, J.M., Linder, P., Ljungberg, H., Mikusinski, G. & Ranius, T. 2002. Densities of large living and dead trees in old-growth temperate and boreal forests. *Forest Ecology and Management* 161, 189-204.
- Nittérus, K. & Gunnarsson, B. 2006. Effect of microhabitat complexity on the local distribution of arthropods in clear-cuts. *Environmental Entomology* 35, 1324-1333.
- 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.
- Odum, E.P. 1969. The strategy of ecosystem development. *Science* 164, 262-270.
- Ohlson, M., Söderström, L., Hörnberg, G., Zackrisson, O. & Hermansson, J. 1997. Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old-growth swamp forests. *Biological Conservation* 81, 221-231.
- Paltto, H., Norden, B., Götmark, F. & Franc, N. 2006. At which spatial and temporal scales does landscape context affect local density of Red Data Book and Indicator species? *Biological Conservation* 133, 442-454.
- Pawson, S.M., Brockerhoff, E.G., Norton, D.A. & Didham, R.K. 2006. Clear-fell harvest impacts on biodiversity: past research and the search for harvest size thresholds. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 36, 1035-1046.
- Peck, J.E. & McCune, B. 1997. Remnant trees and canopy lichen communities in western Oregon: A retrospective approach. *Ecological Applications* 7, 1181-1187.
- Pedlar, J.H., Pearce, J.L., Venier, L.A. & McKenney, D.W. 2002. Coarse woody debris in relation to disturbance and forest type in boreal Canada. *Forest Ecology and Management* 158, 189-194.
- Pharo, E.J. & Zartman, C.E. 2007. Bryophytes in a changing landscape: The hierarchical effects of habitat fragmentation on ecological and evolutionary processes. *Biological Conservation* 135, 315-325.
- Proctor, M.C.F. 1990. The physiological basis of bryophyte production. *Botanical Journal of the Linnean Society* 104, 61-77.
- Proe, M.F., Griffiths, J.H. & McKay, H.M. 2001. Effect of whole-tree harvesting on microclimate during establishment of second rotation forestry. *Agricultural and Forest Meteorology* 110, 141-154.

- Raab, B. & Vedin, H. (Eds.) 1995. *Sveriges nationalatlas. Klimat, sjöar och vattendrag*. Sveriges nationalatlas. Vällingby. (In Swedish).
- Rambo, T.R. & Muir, P.S. 1998. Bryophyte species associations with coarse woody debris and stand ages in Oregon. *The Bryologist* 101, 366-376.
- Ranius, T., Kindvall, O., Kruys, N. & Jonsson, B.G. 2003. Modelling dead wood in Norway spruce stands subject to different management regimes. *Forest Ecology and Management* 182, 13-29.
- Rosenzweig, M. 1995. *Species diversity in space and time*. Cambridge University Press. Cambridge.
- Samuelsson, J. & Ingelög, T. 1996. *Den levande döda veden - bevarande och nyskapande i naturen*. ArtDatabanken, SLU. Uppsala. 89 pp pp.
- Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological bulletins* 49, 11-41.
- Sillett, S.C. & McCune, B. 1998. Survival and growth of cyanolichen transplants in douglas-fir forest canopies. *The Bryologist* 101, 20-31.
- Sillett, S.C., McCune, B., Peck, J.E., Rambo, T.R. & Ruchty, A. 2000. Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. *Ecological Applications* 10, 789-799.
- Similä, M., Kouki, J., Martikainen, P. & Uotila, A. 2002. Conservation of beetles in boreal pine forests: the effects of forest age and naturalness on species assemblages. *Biological Conservation* 106, 19-27.
- Simons, N.P.P., Schwab, F.E. & Otto, R.D. 2002. Songbird abundance in clear-cut and burned stands: a comparison of natural disturbance and forest management. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 32, 1343-1350.
- Snäll, T., Hagström, A., Rudolphi, J. & Rydin, H. 2004. Distribution pattern of the epiphyte *Neckera pennata* on three spatial scales - importance of past landscape structure, connectivity and local conditions. *Ecography* 27, 757-766.
- 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.
- Tansley, A.G. 1935. The use and abuse of vegetational concepts and terms. *Ecology* 16, 284-307.
- UNEP-WCPA 2007. <http://www.iucn.org/themes/wcpa/>. Accessed 6 August 2007.
- Uotila, A. & Kouki, J. 2005. Understorey vegetation in spruce-dominated forests in eastern Finland and Russian Karelia: Successional patterns after anthropogenic and natural disturbances. *Forest Ecology and Management* 215, 113-137.
- Uotila, A., Maltamo, M., Uuttera, J. & Isomäki, A. 2001. Stand structure in semi-natural and managed forests in eastern Finland and Russian Karelia. *Ecological bulletins* 49, 149-158.
- Vanha-Majamaa, I. & Jalonen, J. 2001. Green tree retention in Fennoscandian forestry. *Scandinavian Journal of Forest Research*, 79-90.
- Vellak, K. & Paal, J. 1999. Diversity of bryophyte vegetation in some forest types in Estonia: a comparison of old unmanaged and managed forests. *Biodiversity and Conservation* 8, 1595-1620.

- Whittaker, R.H. 1953. A consideration of climax theory: the climax as a population and pattern. *Ecological Monographs* 23, 41-78.
- 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.
- Åström, M., Dynesius, M., Hylander, K. & Nilsson, C. 2007. Slope aspect modifies community responses to clear-cutting in Boreal forests. *Ecology* 88, 749-758.

Svensk populärvetenskaplig sammanfattning

Mossor, lavar och död ved i unga boreala produktionsskogar

I en naturlig skog i Sverige (dvs en som inte har påverkats av människan) skulle granarna och tallarna bli flera hundra år gamla. I den allra största delen av de svenska skogarna, där skogsbruk bedrivs, avverkas träden efter 70-100 år, vilket har lett till att de flesta skogar är unga idag. Endast en bråkdel är skyddade, till exempel som naturreservat. Att skogarna blivit allt yngre samtidigt som många företeelser som hör hemma i den naturliga skogen försvunnit, har skapat ett hot mot många arter som är anpassade till just en naturlig skog. Dessa företeelser kan vara t.ex. döda eller gamla träd som numera endast finns i större mängder i de få kvarvarande gamla skogarna och i reservaten.

Den här avhandlingen, som baseras på fyra undersökningar, handlar om döda träd, mossor, lavar och svenskt skogsbruk. Döda träd är mycket viktiga för den biologiska mångfalden eftersom en rad arter är beroende av att sådana finns i skogarna. Mossor och lavar har ofta mycket speciella krav på sin miljö och reagerar därför snabbt på miljöförändringar. Avhandlingen handlar också om något som man kallar ekologiskt minne och biologiska arv. Dessa två termer betecknar funktioner i skogsekosystemet som verkar för att återställa systemet efter en störning, t.ex. en avverkning. Arter som överlever avverkningen eller som finns i det omgivande landskapet utgör det ekologiska minnet, medan t.ex. döda såväl som levande träd som finns kvar utgör det biologiska arvet. Arter som är beroende av träd av en viss ålder eller av döda träd har minskat drastiskt under de senaste hundra åren. Om skogsbruket lämnar levande och döda träd vid avverkning kan dessa fungera som viktiga levnadsmiljöer för en del känsliga arter. Då kan också återhämtningen ske snabbare efter störningen.

Efterfrågan på förnyelsebar energi har ökat de senaste årtiondena, i syfte att minska beroendet av fossila bränslen. Detta har lett till att man har försökt hitta fler sätt att få ut energi på även från skogen. Ett sådant sätt är att efter avverkning ta ut grenar och toppar (GROT), som sedan flisas och bränns. Ett av arbetena i avhandlingen visar att uttag av GROT minskar mängden död ved mer än man tidigare trott. Vid GROT-uttag läggs först grenar och toppar i högar så att den maskinförare som kommer och hämtar veden bara behöver ta högarna. Studien visar att det inte bara är högarna som hämtas ut utan även ved som ligger utanför högarna. Om denna i stället fått ligga kvar är det möjligt att den hade kunnat fungera som ett biologiskt arv till den nya skogsgeneration som växer upp efter avverkningen.

En typ av död ved som det än så länge finns väldigt gott om är vanliga avverkningsstubbar. Även stubbar har dock blivit intressanta för energiutvinning och försök pågår att ta ut dem för flisning. En studie i avhandlingen handlar om hur mossor och lavar koloniserar dessa stubbar efter en avverkning. Det visar sig att lavar vandrar in på stubbarna tidigare än mossor och att olika faktorer styr när dessa två olika artgrupper börjar växa på stubbarna. Lavarna är mer beroende av stubbens ålder och utformningen på snittytan, medan mossorna styrs mer av hur stor och förmultnad stubben är. Lavarna är talrika på höga stubbar, medan mossorna är färre. Att lavar och mossor skiljer sig åt i sina krav på levnadsmiljön

är något som avspeglas i denna studie. Lavarna verkar trivas bättre på torra och solbelysta växtplatser, medan mossorna tycks trivas bäst i fuktiga och skuggiga miljöer. I studien hittades framförallt arter som är vanliga i skogarna i den undersökta regionen. Några lavar som förmodas vara ovanliga hittades, men det är emellertid osäkert om de verkligen är så ovanliga eller om det är så att de växer på ställen som inte undersökts i någon större utsträckning, som t.ex. stubbar.

Mossor och lavar kan använda sig av två sätt att sprida sig. Dels genom spridningskroppar som uppkommit genom könlig förökning (sporer), dels genom avknoppning av delar av mossan eller laven. Det senare kallas vegetativ förökning och innebär att den del som sprider sig redan bär på lite energi så att den snabbt kan växa till. Problemet med detta sätt är att det inte sker en genetisk blandning med en annan växtindivid som är fallet vid den sexuella förökningen. En annan nackdel är att de vegetativa spridningskropparna ofta är större än sporer och att de därmed, via vatten och vind, bara kan transporteras väldigt korta avstånd och hamna alldeles i närheten av moderplantan. Genom att sprida sig med hjälp av ett djur ökar möjligheterna att komma till nya platser längre bort. Avhandlingens tredje arbete är ett experiment i växthus med en mossart och en myrart som båda finns i stubbar i vanliga skogar. Experimentet visade att när en myra går på mossan som bär på vegetativa förökningskroppar fastnar dessa på myran och kan sitta kvar i flera timmar. Om detta sker i naturen skulle det kunna förklara varför just den här mossarten så snabbt kan kolonisera stubbar i ungskog när den samtidigt i princip aldrig sprids med hjälp av sporer.

Den fjärde och sista studien utfördes i Hälsingland i södra Norrland. Den visade att det finns fler rödlistade mossor och lavar (d.v.s. arter som är hotade eller minskar i antal) i gamla skogar än i angränsande unga skogar. Detta är inte så konstigt, med tanke på att dessa arter är utvalda just för att de tillhör en grupp som påverkas negativt av framförallt skogsbruket. Inte oväntat fanns även betydligt mer döda träd och gamla lövträd i de gamla skogarna än i de unga. Dessa träd utgör viktiga levnadsmiljöer för många rödlistade arter och det intressanta var att om man tog hänsyn till mängden sådana träd så suddades skillnaderna ut mellan åldersstadierna. Det visade sig också att mossorna var lika vanliga i de unga skogarna som i de gamla om de unga låg norr om de gamla. Detta var inte fallet för lavar. Förklaringen är åter igen sannolikt att mossor i högre utsträckning trivs i skuggiga och fuktiga miljöer, medan lavar gynnas av ljusare omgivningar. Rikedomen på både mossor och lavar var störst i de områden som hade haft mest gammal skog i omgivningarna under de senaste decennierna.

De praktiska slutsatser som kan dras från avhandlingen är att unga skogar kan hysa sällsynta arter, men att det krävs att det finns en hel del gamla och döda träd kvar som biologiska arv från den gamla skogen. Vidare är det viktigt att de unga skogarna inte befinner sig på alltför stort avstånd från skogar där arterna redan finns. En förutsättning för att känsliga arter och biologiska arv ska finnas kvar i framtiden är att naturvården beaktas då skogsbruk bedrivs, t.ex. genom att hänsyn visas vid slutavverkning, inklusive bioenergiutvinning i form av GROT- och stubbskörd.

Tack...

Ibland har den här avhandlingen känts som Klåvaberget, men många skillnader finns mellan mig och Torgny Lindgrens Elis i Lillåberg. Den största är nog att jag fått så mycket hjälp av många fantastiska människor på vägen. Det finns många att tacka. För att inte utelämna någon av misstag vill jag kollektivt tacka alla kollegor vid institutionen för ekologi, men även alla andra som på olika sätt bidragit till mitt avhandlingsarbete. Jag kan dock inte låta bli att nämna några som varit särskilt viktiga för mig under de senaste åren.

Till Lena Gustafsson – Du har alltid funnits till hands när jag behövt det. Det har gått att nå dig med ett mejl eller sms oavsett var i världen du befunnit dig. Din osvikliga raskhet i att läsa och konstruktivt kommentera manus har flera gånger imponerat på mig. Jag har fått uppmuntran i svackor och ivriga hejarop när det rullat på. Ett stort tack till dig!

Till Janne Weslien – Med dina handfasta råd har det varit lätt att hålla sig till de viktiga frågorna när jag försökt dra iväg åt något mindre genomtänkt håll.

Till Bengt Gunnar Jonsson – Du är en vetenskaplig förebild för mig och jag bannar mig själv ibland för att jag inte nyttjat din stora kunskap mer under min doktorandtid.

Till Tomas Hallingbäck – Utan din artkunskap och artkänsla hade jag aldrig vågat ge mig ut för att inventera artrikedom och sällsynta mossor. Du har alltid funnit tid att kontrollbestämma några kollektioner eller att hjälpa till med fotografering av mossor eller myror.

Till Toni Berglund – din noggrannhet gjorde det lätt för mig, både i fält och framför datorn, när jag förberedde och skrev det sista manuset i avhandlingen.

Till Sandro Caruso – De sista månaderna har varit hemskt effektiva, men jag kan med bästa vilja i världen inte säga att de har varit lika roliga som innan du gick på föräldraledighet.

Till alla mina andra vänner, inte minst ni som finns utanför den akademiska världen för mycket glädje och stöd.

Till Mamma, pappa och Tomas – er har jag att tacka för så mycket! Jag har alltid känt ert stöd för mina studier under åren som gått. Bärplockningen på Kärringberget och fisketurerna i Rödingträsket har nu bärgat en lite annorlunda skörd.

Till mina underbara barn, Alva och Hjalmar. Nu är boken äntligen klar. Tack för att ni varje dag påminner mig om min mest betydelsefulla uppgift här i livet: att vara pappa, sångstundskompare och klätterträd!

Till Frida. Inte ens ”störstorden” räcker till. Det hade verkligen aldrig fungerat utan dig. TACK!