Impact of tree retention on wood production, biodiversity conservation and carbon stock changes in boreal pine forest

Francesca Santaniello

Faculty of Forest Sciences Department of Ecology Uppsala

Doctoral thesis Swedish University of Agricultural Sciences Uppsala 2017 Acta Universitatis Agriculturae Sueciae 2017:63

Cover: Pine forest

(Illustration: Francesca Santaniello)

ISSN 1652-6880 ISBN (print version) 978-91-7760-016-9 ISBN (electronic version) 978-91-7760-017-6 © 2017 Francesca Santaniello, Uppsala Print: SLU Service/Repro, Uppsala 2017

Impact of tree retention on wood production, biodiversity conservation and carbon stock changes in boreal pine forest

Abstract

Tree retention at forest harvesting aims at promoting biodiversity by increasing structural diversity in managed forests. For this thesis, I have investigated the influence of tree retention on delivery of ecosystem services (wood production and carbon storage) and dead wood (as a proxy for biodiversity). Furthermore, habitat requirements of lichens dependent on dead wood were investigated. The investigation was conducted in 15 Scots pine forest stands with five tree retention levels, in which four categories of trees were retained at similar proportions: green living trees, girdled trees, high-cut stumps and cut trees left on the ground. Three control stands were left untouched. This thesis consists of three studies. In the first, we investigated how tree retention influences the amount and diversity of dead wood, logging productivity during harvest and both present and future income loss for the landowner (given as discounted opportunity costs). In the second, we simulated outputs of merchantable wood, dead wood and carbon stock during a 100-year forest rotation period at stand and landscape scales. At landscape scale, we simulated dead wood volumes and carbon stock under the constraint that landscape size and merchantable wood production were kept constant among scenarios, while retention level and area set aside for conservation varied. In the third study, we investigated how dead wood types (low stumps, snags, logs), wood hardness, wood age and occurrence of fire scars influence the occurrence of dead wood dependent lichens. We found that logging productivity and net incomes from harvest decreased with increasing retention levels, but also that volumes and diversity of dead wood and proportion of undamaged old dead wood increased. Furthermore, at the stand scale, increased retention level increased total carbon storage above and below ground. At the landscape scale, differences in carbon stock and dead wood input were generally small between the scenarios with varying retention levels and set-aside forest area. The lichen species composition differed significantly among the investigated substrates. Many species were highly associated with old and hard wood. Such wood is formed in fire-affected pine forests, but is rare in managed forest. The findings of this thesis could be used to guide future forest management and conservation.

Keywords: carbon; dead wood; habitat requirement; lichen; pine; species richness; tree growth; tree mortality

Author's address: Francesca Santaniello, SLU, Department of Ecology, Box 7044, 75007 Uppsala, Sweden

Effekten av att naturhänsyn vid avverkning på virkesproduktion, biologisk mångfald, och kolförråd i boreal tallskog

Sammanfattning

Syftet med att lämna levande träd och att skapa död ved vid avverkning är gynna biologisk mångfald genom att öka den strukturella variationen i brukad skog. I den här avhandlingen har jag undersökt hur naturhänsyn vid avverkning påverkar ekosystemtiänster (lagring av kol och virkesproduktion) och död ved (som är en indikator på biologisk mångfald). Studien genomfördes i 15 tallbestånd med olika hänsynsnivåer och med fyra kategorier av träd lämnade i lika stora proportioner: levande träd, ringbarkade träd, högstubbar (dvs. träd kapade ca. 3 meter över marken) och fällda träd som lämnades på marken. Tre kontrollbestånd lämnades orörda. Denna avhandling består av tre studier. I den första undersökte vi hur naturhänsynen påverkade mängden och diversiteten av död ved, produktiviteten under avverkning samt intäktsförluster för markägaren nu och i framtiden. I den andra studien simulerade vi virkesproduktion (massaved och sågtimmer), död ved och kolförråd under en hundraårig omloppstid på både bestånds- och landskapsnivå. På landskapsnivå simulerade vi volymen av död ved och kolförråd där landskapets areal och volym producerat virke konstanta i alla scenarier, medan hänsynsnivå och areal skog avsatt för fri utveckling varierade. I den tredje studien undersökte vi hur typen av död ved (stubbar, torrakor, lågor), vedens hårdhet och ålder, samt eventuella spår av brand (vedytan förkolnad) påverkar förekomst av lavar. Vi fann att produktiviteten under avverkningen minskade och intäktsförlusten ökade med stigande hänsynsnivåer men samtidigt ökade volymen och diversiteten av död ved samt andelen oskadad äldre död ved. På beståndsnivå ökade kolförrådet (totalt ovan och under mark) med ökad hänsynsnivå vid avverkningen. På landskapsnivå, när virkesproduktion hölls konstant och andelen avsatt skog och hänsynsnivå varierades så var skillnaderna i kolförråd och dödvedsproduktion små mellan de olika scenarierna. Artsammansättningen bland lavar skilde sig signifikant mellan de undersökta substraten. Många arter var starkt associerade med gammal och hård ved som bildas i tallskogar som utsatts för brand, men som sällan bildas i dagens brukade skogar. Resultaten som presenteras i denna avhandling kan användas för att vägleda framtida skogsskötsel och naturvård.

Nyckelord: artrikedom; död ved; habitatkrav; kol; lav; tall; trädtillväxt

Författarens adress: Francesca Santaniello, SLU, Institutionen för ekologi, Box 7044, 75007 Uppsala, Sverige

Dedication

To the freedom of all creatures

Contents

Li	List of publications			
A	Abbreviations			
1	Introduction	13		
	1.1 Natural condition in boreal forest	13		
	1.2 Forest management	15		
	1.3 Adaptation of forestry to natural conditions	16		
	1.3.1 Tree retention	16		
	1.3.2 Land sharing/land sparing	17		
	1.4 Study system	18		
	1.4.1 Scots pine	19		
	1.4.2 Tree retention studies	20		
	1.5 Response variables	21		
	1.5.1 Dead wood	21		
	1.5.2 Carbon	22		
	1.5.3 Stand growth and merchantable wood production	23		
	1.5.4 Costs and revenues	24		
	1.5.5 Forest operations	25		
	1.5.6 Dead wood dependent lichens	26		
2	Aims	27		
	2.1 Aims of the papers	27		
3	Study area	28		
	3.1 Experimental design	29		
4	Data collection	31		
	4.1 Green trees and dead wood	31		
	4.2 Harvesting operations	32		
5	Data analysis	34		
	5.1 Data analysis	34		
	5.2 Forest model - Heureka	35		
	5.3 Merchantable wood production, cost and revenues	36		

	5.4	Dead wood	36	
	5.5	Carbon stock	37	
	5.6	Landscape scenarios	38	
	5.7	Dead wood dependent lichens	39	
6	Re	esults and discussion	42	
	6.1	Effects of tree retention	42	
	6.2	Stand level outcome	43	
	6.2	2.1 Merchantable wood production, costs, and reve	nues43	
	6.2	2.2 Dead wood	44	
	6.2	2.3 Carbon stock	47	
	6.3	Landscape level outcome	48	
	6.4	Dead wood dependent lichens	50	
7	Co	onclusions	54	
8	Future prospects			
R	References			
Popular science summary				
A	cknov	wledgements	73	

List of publications

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

- I Santaniello, F., Djupström, B. L., Ranius, T., Rudolphi, J., Widenfalk, O., Weslien, J. (2016). Effects of partial cutting on logging productivity, economic returns and dead wood in boreal pine forest. *Forest Ecology* and Management, 365, 152–158.
- II Santaniello, F., Djupström, L. B., Ranius, T., Weslien, J., Rudolphi, J., Sonesson, J. (2017). Simulated long-term effects of varying tree retention on wood production, dead wood and carbon stock changes. *Journal of Environmental Management*, 201, 37–44.
- III Santaniello, F., Djupström, L. B., Ranius, T., Weslien, J., Rudolphi, J., Thor, G. (2017). Large proportion of wood dependent lichens in boreal pine forest are confined to old hard wood. *Biodiversity and Conservation*, 26, 1295–1310.

All the papers are reproduced with the permission of the publishers.

The contribution of Francesca Santaniello to the papers included in this thesis was as follows:

- I Field work and data processing, statistical analysis, interpretation of the results and writing, under the supervision of all the co-authors.
- II Field work and research planning, data processing, interpretation of the results and writing, under the supervision of all the co-authors.
- III Part of the field work, research planning, data processing, statistical analysis, interpretation of the results and writing, under the supervision of all the co-authors.

Abbreviations

CO_2	Carbon dioxide
CWD	Coarse woody debris
FSC	Forest Stewardship Council
Sub	Solid wood under bark

1 Introduction

The 4th of June 1732 Carl Linnaeus, visiting the parish forest of the Swedish village of Lycksele, stated: "*The large forests are desolate and wasteful, because no-one needs the timber, which falls down and decays*" (Agnoletti & Anderson, 2000). These types of forests are now rare in Swedish forest landscapes, which are instead dominated by even-aged stands used for wood production. As a consequence of the fragmentation of the old growth forests, many species dependent on natural forest attributes, such as old dead wood, have declined (Kouki et al., 2001). If forest management does not implement measures to promote natural dynamics, biodiversity will inevitably continue to decline (Kuuluvainen, 2009). This multidisciplinary thesis aims to fill some of the knowledge gaps relating to the sustainable management of boreal pine forest, focusing on the promotion of biodiversity by increasing structural diversity.

1.1 Natural condition in boreal forest

The boreal forest is one of the largest biomes on the planet, constituting 22% of the global forested area (Keenan et al., 2015). It is characterized by a mosaic of coniferous and deciduous forests, dominated by cold-tolerant trees (Brandt, 2009).

Unmanaged boreal forests are much affected by natural disturbances, such as windstorms, pest outbreaks and fire (Esseen et al., 1997), the extent of which ranges from minor events affecting individual trees to stand replacement (Angelstam & Kuuluvainen, 2004). Fire is considered to be the most important natural disturbance in boreal forest (Johnson, 1992). Fire intensity varies greatly, from stand-replacing crown fires to slowly burning ground fires with low tree mortality. This, together with fire frequency, largely determined the structure of the primeval forest landscape with regard to the successional stages, age distribution and size of the forest stands (Niklasson & Granström, 2000). Boreal forests are often considered to be slow systems with long-lasting vegetational successions, which disturbances can quickly alter, thus promoting species adapted to early-successional stages (Kuuluvainen, 2009).

Fire intervals of 30-40 years have been documented in Scandinavian pine stands over the last few centuries, but during the last 100 years fire intervals have increased greatly due to the implementation of measures for fire suppression (Engelmark et al., 1994; Linder et al., 1997; Niklasson & Granström, 2000; Zackrisson, 1977, 1980). Fire frequency nevertheless differs between forest types. The fire frequency of boreal pine forests is higher than that of boreal spruce forests (Larsen, 1997), mainly because pines typically grow on drier sites than spruce (Carleton & Maycock, 1978). Pine is more resistant to fire than spruce and birch, due to a thicker bark and a deep root system (Gromtsev, 2002). Scots pine also tends to increase production of resin at fire scars, making it more resistant to pathogens and thus more long-lived (Engelmark, 1999). After a disturbance, the greater light availability initially promotes species favoured by sun-exposed conditions. Subsequently, forest-interior species may return. The stand dynamics post-disturbance are related to the socalled external and internal "ecological memory" (Bengtsson et al., 2003). The external memory is the species pool in the surrounding area, which affects the recolonization of the disturbed site, while the internal memory is the source of surviving species and structural legacies remaining from the forest before the disturbance (Lundberg & Moberg, 2003).

1.2 Forest management

In boreal forests, forest management for timber production is the predominant anthropogenic disturbance regime. Forestry has typically aimed at minimizing the effect of natural disturbances, since these cause trees to die that otherwise could have been harvested. However, more recently attempts have been made to emulate the natural disturbance regime, for example by retaining some living trees and dead wood on the clear-cuts (Franklin et al. 1997; Koivula et al. 2014).

Before the late 19th century, the prevailing cutting method in European forests was selective cutting (Lowenthal, 1956). With increasing timber demand, clearfelling was introduced, being a more efficient management method (Lundmark et al., 2013). Today, in northern Europe, the most common management practice is based on the establishment of even-aged and homogeneous stands with a rotation period of ca. 100 years. After clearfelling, a new even-aged stand is regenerated by soil scarification and planting. Stands are thinned and sometimes fertilized. In Sweden today, most of the seedlings used are containerized and genetically enhanced through selection, with the main aim of increasing growth rate, although genetic variation, vitality, wood quality, resistance to damage, and adaptability to climate change are also considered (Frumerie, 1997; The Royal Swedish Academy of Agriculture and Forestry, 2015). Since 1923, when the first forest inventory in Sweden was conducted, the total standing volume has increased by more than 80% (3.1 billion m³), of which 39% presently consists of Scots pine, 42% Norway spruce and 12% birch (Swedish Forest Agency, 2014). On productive forest land, the average annual growth is 5.4 m³ per hectare. Total annual growth is 120 million m³, while annual felling is around 80 million m³ (Swedish Forest Agency, 2014).

Forest management is often supported by planning tools aimed at producing forecasts associated to alternative forest management strategies. Due to the increased demand for wood and other products and services, and to the concern about global changes and nature conservation, forest models able to simultaneously predict the response of different variables (for example wood production and biodiversity conservation) to specific treatments, are largely required (Kimmins et al., 1999). Some models predicting habitat availability (Felton et al., 2017a) and ecosystem services provisioning (Triviño et al., 2015) are already available.

1.3 Adaptation of forestry to natural conditions

Forests frequently affected by large-scale natural disturbances are often characterized by an uneven age distribution within the stands, and large amounts of dead wood (Kuuluvainen & Aakala, 2011). By contrast, forestry under clearfelling management generates even-aged stands, and small amounts of dead wood (Bergeron et al., 1999). During the past two decades, interest in developing forest management strategies aimed at emulating the natural disturbance dynamics has increased (Bergeron et al., 2004). The type, frequency, spatial extent, and severity of natural disturbances can be emulated. This is done by controlled burning, creation of dead wood, and tree retention.

1.3.1 Tree retention

The primary aim of tree retention is to promote biodiversity by increasing structural diversity on the clear-cuts (Lindenmayer & Franklin, 2003) and in the future forest stands (Kruys et al., 2013). This is done by retaining living trees (green tree retention), either spatially aggregated or dispersed, and retaining and creating dead wood (Gustafsson et al., 2010). Other aims are the maintenance of forest productivity, nitrogen retention (Gustafsson et al., 2010), improving aesthetical value (Tönnes et al., 2004) and protecting the integrity of aquatic systems by retaining riparian buffer zones (Clinton, 2011).

Retention increases the amount of dead wood in the forest in three principal ways. First, dead wood may be artificially created at forest cut. Second, the input of coarse dead wood from tree mortality becomes higher since living retained trees die (Lõhmus et al., 2013). Third, the destruction of old dead wood by machinery during logging is reduced (Hautala et al., 2004). Retention incurs income losses for landowners, due to reduction both of harvested timber volumes and of the land area available for future forest production (LeDoux & Whitman, 2006; Ranius et al., 2005). Jonsson et al. (2010) found that in Sweden it is more expensive to retain Scots pine trees than other boreal tree species due to their high timber value. The land area available for future forest production decreases due to the fact that retained trees hamper the growth of the new growing stand (Elfving & Jakobsson 2006; Jakobsson & Elfving 2004; Zenner et al., 1998). In addition, retention increases harvesting time per unit volume, due to reduced number

of harvested trees per processing patch (Eliasson et al., 1999) and increased driving distances within stands because of obstruction by retained trees. However, the magnitude of such productivity losses relative to levels of tree retention and dead wood creation has not been evaluated. Hence one of the aims of this thesis is to assess economic costs and revenues associated with different tree retention levels, using field surveys.

1.3.2 Land sharing/land sparing

Land sharing and land sparing represent two alternative approaches to combine production with conservation. Land sparing means that production and conservation are separated into different stand types, which is consistent with traditional conservation in forests, where areas are set aside as reserves. Land sharing means reduced management intensity or setting aside some smaller unmanaged areas within the production area (Kremen, 2015). Thus, tree retention can be considered as a kind of land sharing. The relative advantages and disadvantages of land sharing versus land sparing have mostly been discussed in relation to agricultural landscapes (e.g. Fischer et al., 2014; Phalan et al., 2011); but some consideration has been given to forests (see Edwards et al., 2014). In forest landscapes, a combination of both strategies is usually applied. In Sweden and Finland, land sharing plays a comparatively large role (Box 1). This has however changed over time; protection of forests started earlier than the introduction of retention forestry (Simonsson et al., 2015). One reason for this is that there are few large forest areas of high conservation quality to protect outside the existing reserves. This approach has been criticized, because if conservation efforts are evenly distributed over all forest land, there is a risk that for sensitive species there will be insufficient contiguous habitat anywhere. With a greater emphasis on land sparing, it is more likely that there will be a large enough habitat at least somewhere (Hanski, 2000). Thus, increased land sparing may promote the survival of threatened species (Ranius & Roberge, 2011).

Box 1. Biodiversity conservation in Swedish forest lands

In Sweden, forest owners are responsible for biodiversity conservation efforts at small and medium scale, while the state is responsible for largescale efforts, such as establishing reserves. Currently, 3.6% of forest land is protected as national parks or nature reserves (Swedish Forestry Agency, 2014). Due to their spatially fragmented occurrence and proportionally small area, reserves alone are not sufficient to support forest biodiversity (Lindenmayer & Franklin, 2002). To complement national parks and nature reserves, habitat protection areas (Svedlund & Löfgren, 2003) and woodland key-habitats have also been established. Land owners also voluntarily set aside land (4.7% of the productive forest land; Swedish Forest Agency, 2014) as part of certification agreements. Sweden was one of the first countries where certification agreements were introduced (Simonsson et al., 2015). Another way to conserve biodiversity is represented by Natura 2000 sites, which commonly consist of areas dedicated to the conservation of sites important for particular species (for example migratory birds). Furthermore, green tree retention is applied at almost all clear-cuts, as a result of environmental conservation policies, who find their foundation in the Swedish Forestry Act guidelines (SFS, 1974; 1979; 1993) (Simonsson et al., 2015). Nowadays, according to the national Forest Stewardship Council (FSC) standard, the minimum number of living trees to be retained per hectare is ten (FSC, 2010). Moreover, logs and snags should be left and about three living trees per hectare should be high-cut or girdled.

1.4 Study system

This thesis is based on a field experiment that took place in 2013, in a boreal pine-dominated forest in Sweden. The main aim has been to study the effects of varying tree retention level on biodiversity, wood production and climate change mitigation through carbon storage. Further information about the experiment can be found in chapter 3.1.

1.4.1 Scots pine

The experiment was conducted in Scots pine forests. Scots pine (*Pinus sylvestris* L.) is, together with Norway spruce (*Picea abies* (L.), H. Karst), the predominant tree species in European boreal forests (Sundseth, 2006). In boreal pine forest, many species of lichens, fungi and insects are associated with burnt wood, or are favoured by the high volumes and diversity of sun-exposed dead and dying trees on burned areas (Esseen et al., 1997). Many such species are considered rare or threatened (Tikkanen et al., 2006). Cohort dynamics, defined as scattered surviving trees in new generation stands after fire, are naturally much more frequent in pine forests than in spruce forests (Kuuluvainen & Aakala, 2011). In today's protected forests, fires are rare, and therefore even set-aside forests tend to diverge from the natural state (Hedwall & Mikusiński, 2015). However, through retention forestry management and prescribed burning (i.e. land sharing instead of land sparing), natural disturbances may be better emulated.



Figure 1. Prescribed burning experiment. Effaråsen, Dalarna, Sweden. Photo: Line B. Djupström.

1.4.2 Tree retention studies

Tree retention has been studied especially in Northern Europe and Northern America, but sometimes also in the Southern hemisphere (Gustafsson et al., 2012). The effect of tree retention on biodiversity has mostly been studied at the stand level and over a short time scale (see Fedrowitz et al., 2014; Gustafsson et al., 2010, 2016; Rosenvald & Lõhmus, 2008).

In Fennoscandia, Norway spruce and aspen have been the most investigated species, while there have been few studies on Scots pine. For example, in a review by Gustafsson et al. (2016), comparing retained dead wood on clearcuts with dead wood inside closed forests, not a single study among the 26 reviewed papers on biodiversity had investigated pine forests. Independent on tree species, few analyses have been made on the effect of retention forestry on carbon fluxes, and these have mainly focused on short-term effects. Nunery & Keeton (2010) found that post-harvest retention positively affects carbon sequestration. Klockow et al. (2013) investigated the impact of slash and live-tree retention on biomass and nutrient cycles, and found that slash retention was the primary factor influencing the carbon stock.

Since the 1990s, more than 40 experiments have been set up in North America and Europe to study how cutting can mimic natural disturbances e.g. by tree retention and prescribed burning (see Koivula et. al 2014). For instance, in the US, the DEMO (Demonstration of Ecosystem Management Options) experiment has assessed the effects of varying level of tree retention on flora, fauna, hydrology and social perception (Aubry et al., 2009). Also in the EMEND (Ecosystem Management Emulating Natural Disturbance) experiment in Canada (Work et al., 2004), and in two Finnish projects, FIRE (Hämäläinen et al., 2014) and DISTDYN (Forest management inspired by natural disturbance dynamics) (Koivula et al., 2014), the effects of tree retention and fire on flora and fauna have been studied.

1.5 Response variables

Forests provide a wide range of functions. Those of benefit to human wellbeing are defined as ecosystem services. These can be divided in three main categories: provisioning services, such as timber; regulating services, such as global climate regulation; and cultural services, such as recreation (Carpenter et al., 2009). Some of these ecosystem services are relatively easy to measure and, like timber, often have a market price. On the contrary, biodiversity is more difficult both to measure and to price. (Stenger et al., 2009).

In this thesis, I have studied a few key measures that are important indicators of biodiversity conservation, climate regulation and provisioning of merchantable wood. These are all fundamental aspects of multifunctional forests. The aim of multifunctional forest management is to achieve a balanced production of different goods and services (Gustafsson et al., 2012). The response variables used in this thesis are described below.

1.5.1 Dead wood

In forests, dead wood is a habitat for many species groups, such as lichens, bryophytes, fungi and insects (Harmon et al., 1986). In boreal forest, about 25% of species are dependent on dead wood (Siitonen, 2001), and as result of the decrease in dead wood amounts, many dead wood dependent organisms are now threatened. Dead wood dependent species are not only dependent on the quantity but also the quality of dead wood (Lonsdale et al., 2008; Similä et al., 2003; Svensson et al., 2016). Created wood may have different characteristics in comparison to naturally occurring dead wood, but is nevertheless utilized by large numbers of species. For instance, artificially created high stumps (Lindhe et al., 2005) and burnt girdled trees (Toivanen & Kotiaho, 2010) have been found to harbour a species-rich fauna of beetles, and stumps are used by many dead wood dependent lichens (Svensson et al., 2016).

In old-growth boreal forests, dead wood is mainly created by self-thinning, pathogens and disturbances such as storms, fire, and insect outbreaks (Esseen et al., 1997; Niklasson & Granström, 2000; Stokland et al., 2012).



Figure 2. Dead wood rich Scots pine dominated forest. Suobbatjaure nature reserve, Sweden. Photo: Francesca Santaniello.

By contrast, in managed forests trees are typically harvested before natural processes creating larger quantities of dead wood take effect. Furthermore, since in today's managed forest landscapes fire is usually suppressed and salvage logging carried out after large disturbances, the accumulation of dead wood is restricted. As a result, the volume of dead wood with a diameter > 10 cm in managed boreal forests has been estimated to be only 2-10% of the amount in natural forests (Siitonen, 2001). However, during the last ten years, due to tree retention (Kruys et al., 2013) the amount of dead wood in Swedish production forests has doubled, from 4 to 8 m³ ha⁻¹ (Skogsdata, 2017). In pine-dominated old-growth forests in Fennoscandia, the volumes of CWD vary from 60 to 120 m³ ha⁻¹ in the middle and southern zones to 20 m³ ha⁻¹ in the northern zone (Siitonen, 2001).

1.5.2 Carbon

Since the industrial revolution, the emission of CO_2 into the atmosphere caused by the combustion of fossil fuels and changes in land cover (Houghton et al., 2012) has increased (Canadell et al., 2007). This increase in CO_2 contributes to global warming (Barnola et al., 1991).

Forests play a key role in the global carbon cycle (Pan et al., 2011), both by sequestrating CO_2 from the atmosphere through photosynthesis and by releasing CO_2 through decay of dead wood and soil respiration (Hadden, 2017). The carbon pool of a forest depends on different factors, such as climatic conditions, stand age (Hyvönen et al., 2007), and forest management (Johnson, 1992; Schlamadinger & Marland, 1996).

Forest management (growth rate, rotation period, and amount of wood extracted) affects how much carbon is stored in soil and vegetation and how much is released into the atmosphere (Brown et al., 1996). After clearfelling and regeneration, the soil carbon pool decreases for a number of years until the new stand is established. Then both stand and soil carbon increases (Schulze et al., 2000). Management practices that enhance tree growth, like damage control, genetic improvement, rotations optimized for tree growth, and fertilization have a positive impact on carbon sequestration.

To reduce the emissions of CO₂ and other greenhouse gases to the atmosphere, three main forestry-related strategies are often considered. First, carbon can be stored in soil and vegetation (Lal, 2005). Second, carbon can be stored in long-lasting wood products, such as wooden houses (Pingoud et al., 2001). Finally, fossil-based energy and products can be replaced with bioenergy and bio-based products, such as wood (Marland & Schlamadinger, 1997). While the efficiency of the first two strategies is recognized, the efficiency of the latter is still under debate, because its magnitude depends on the use of the harvested wood (Lundmark et al., 2014), and also because to substitute fossil fuels more bioenergy needs to be produced over the same land area (i.e. under spatial restrictions).

1.5.3 Stand growth and merchantable wood production

A forest stand is considered as a portion of land where vegetation of similar structure grows under similar site conditions (Oliver & Larson, 1990). Forest growth is affected by tree growth efficiency, which differs according to species, light interception capacity (Linder, 1987), site fertility, stand characteristics, and climate.

After the establishment of a forest, the net primary production increases rapidly until the canopy closes (Ryan et al. 2004). Subsequently, competition between trees increases (Gadow et al., 2012) and some start to

die due to self-thinning (Yoda et al. 1963). Tree mortality is higher in dense stands than in stands with a lower tree density (Lloyd & Harms, 1986). The death of some trees increases structural diversity in the forest canopy, and consequently affects the microclimatic conditions that influence the net primary production (Vesala et al. 2005).

Forest management tends to hamper the natural dynamics of the stands, since management typically aims at promoting the wood quality and the growth of the trees. Examples of such practices are thinning (Nilsson et al., 2010), optimization of the rotation length (Newman, 2002), and fertilization (Pettersson & Högbom, 2004; Jacobson & Pettersson, 2010). Fertilization may increase growth over the short or the long term, influencing the merchantable wood production, whether it operates on seedling growth or on the growth of older trees (Nilsson & Allen, 2003). Increase in production can also be obtained through genetic improvement (Zobel & Talbert, 1984). The effect of green tree retention on the growth of new seedlings and consequently on the production of merchantable wood has been investigated in a few studies (see for example Elfving & Jakobsson, 2006), but poor is the knowledge about long-term observations covering the whole rotation period, due to the limited availability of empirical studies.

1.5.4 Costs and revenues

In forest economy, it is important to define the boundaries for the calculation of costs and revenues. Often (as in this thesis), only the costs and revenues at the stand level are considered, i.e. costs from seed to stump including harvest and forwarding to the forest roadside. In this context, costs include the amount of money that needs to be paid for silvicultural measures, i.e. scarification, regeneration, cleaning, thinning, fertilization and finally the logging, which also includes conservation measures (e.g. high cutting and girdling). Revenues are the price paid for the cut and forwarded pulpwood and timber at roadside before transport to the industry.

In forest conservation and production, cost-efficiency is important (Eriksson, 2016), which means that costs should be minimized and conservation/production maximized under given restrictions. Maximizing production involves silvicultural regimes at the stand level as well as bucking of the individual trees as raw material, such as for paper or lumber. Since the late nineteenth century, economic costs have been calculated and

separated into, for example, labour costs and investment costs (e.g. Williams, 1908). More recently, other aspects have been taken into account such as the economic cost of conservation measures (Naidoo et al., 2006). The interest in reducing the impact of forest operations on biodiversity, soil erosion and water pollution has increased (Lämås, 1996). This has resulted in a multitude of studies aimed at optimizing the cost-efficiency while also considering environmental aspects (e.g. Mönkkönen et al., 2014; Ranius et al., 2005).

Financial estimations of forestry investments are typically based on a collection of actual and future values associated with various aspects, which in some cases are not easy to evaluate (Duku-Kaakyire & Nanang, 2004). Oscillations of the market price lists are good examples. Among the collection of valid financial estimates, net present value, land expectation value and opportunity cost are often used. The net present value is the economic value of a forest assuming a defined future management regime at a specific interest rate (in Swedish forestry often 2-4%, see Felton et al., 2017b) and is calculated by subtracting total discounted costs from the discounted revenues. The net present value of the land without trees subjected to an eternal sequence of identical forest rotations (Faustmann, 1849). The opportunity cost in this context is the difference in net present values between two management regimes (Nghiem & Tran, 2016).

1.5.5 Forest operations

In Europe, logging is generally done using two machines: the single grip harvester that fells, delimbs and bucks the trees into logs, and the forwarder that transports the wood to the road side (Ringdahl, 2011). The predominant Nordic harvesting technique is the cut-to-length method where tree stems are cut into smaller logs at the harvesting site (Nurminen et al., 2006). The productivity (time consumption per m³ of harvested or transported wood) of the machinery is influenced by several factors. According to Eliasson (1998) these factors can be divided into three main groups: 1) stand-related (e.g. terrain conditions, stem density, tree size); 2) work-related (e.g. machine type and worker experience); and 3) policy related (e.g. legislation and environmental policies). Both the harvester and the forwarder productivity is influenced by terrain and climatic characteristics (Samset, 1990), type of harvesting (i.e. final harvesting or thinning; Axelsson & Eriksson, 1986; Eriksson & Lindroos, 2014) and machinery characteristics (such as size and motor type). Among treerelated factors, harvester productivity is mainly influenced by the mean harvested stem volume at final felling (Brunberg, 2007; Eriksson & Lindroos, 2014) and by a combination of number of harvested stems, number of retained stems, and mean stem volume at thinning (Brunberg, 1997; Eliasson, 1998). Forwarder productivity is mostly influenced by the mean extraction distance to roadside both at final felling and thinning, but also by load capacity and mean stem volume (Brunberg, 2004; Eriksson & Lindroos, 2014). Given the multiplicity of factors influencing logging productivity, it is essential that factors other than those of specific interest (in this thesis number of retained trees) are controlled for, e.g. by using the same drivers and same machines across the study sites.

1.5.6 Dead wood dependent lichens

In boreal forest, lichens are a species rich group, being found on bark (corticolous lichens), soil (terricolous lichens), rocks (saxicolous lichens), and decorticated dead wood (lignicolous lichens) (Boch et al., 2013). In forest research, lichens are one of the most commonly used biomonitors, since many of them are long-lived and have a high habitat specificity (Nimis et al., 2002) and thus are sensitive to habitat changes (McCune, 2000).

In Fennoscandia, about 400 lichen species may occur on wood (Spribille et al., 2008). Out of these, about 100 are found only on dead wood, and are therefore called "obligately lignicolous" (Spribille et al., 2008). Forestry is considered to be the most serious threat to this group of lichens (Thor, 1997), owing to the fact that the amount of old living and dead trees decreased as modern forestry methods developed during the 20th century (Berg et al., 1994). Some species of dead wood dependent lichens occur in high abundances on stumps, snags, and to some extent logs, while dead branches are colonized by only a few species (Svensson et al., 2016). The decay stage of dead wood also affects lichen species richness and composition (Botting & DeLong, 2009; Caruso & Rudolphi, 2009; Nascimbene et al., 2008; Svensson et al., 2013).

2 Aims

The general aim of this thesis is to increase knowledge about the impact of different levels of tree retention on production of merchantable wood, costs and revenues, dead wood amounts and qualities and carbon stock; and to investigate the habitat requirements of dead wood dependent lichens. Due to the short time interval between the forest cut and the lichen inventory, it was not possible to investigate the specific effect of tree retention on lichen diversity. Therefore, the focus was on the identification of the substrates they utilized, the availability of which can be promoted through the creation and conservation of dead wood. My experimental approach was to vary the level of green trees and dead wood retained, including levels far higher than those typical in Fennoscandia today. This enabled the evaluation of different response variables along a tree retention gradient.

2.1 Aims of the papers

I To assess economic costs, revenues and structural diversity (i.e. dead wood amount and diversity) in relation to different tree retention levels using field surveys.

II To compare the production of merchantable wood, amount of dead wood input and carbon storage over the whole rotation period in stands with different tree retention levels.

III To compare the composition and density of dead wood dependent lichen on different substrates.

3 Study area

The data were collected in an area around Effaråsen (60° 58'29'' N, 14° 01' 55'' E), located in the province of Dalarna, in the southern boreal vegetation zone (Ahti et al., 1968) of Sweden. The study area comprised 140 ha of relatively homogenous forest dominated by Scots pine with an age range of 120-140 years, but including some much older trees. Other tree species present in the area are Norway spruce and birch. The ground vegetation is dominated by dwarf shrubs (*Vaccinium vitis-idaea* L. and *Vaccinium myrtillus* L.) and lichens (among fruticose species, mainly *Cladonia* spp.). The stands were naturally regenerated after a large forest fire in 1888 and have been managed for wood production, including thinning during the second half of the 1900s and fertilization in the 1990s.



Figure 3. Location of the study area. Effaråsen forest, Dalarna.

3.1 Experimental design

Fifteen stands, with a mean area of 5 ha, were randomly allotted to different levels of partial cutting (from very low to total tree retention). In each stand, we retained four categories of trees: 1) green trees, 2) girdled trees 3) high-cut stumps and 4) cut trees left on the ground, so that each category represented about 25% of the total number of retained trees in each stand. However, within our study plots, the numbers differ between the categories due to the random location of the plots within the stands (see chapter 4 for further information). In three stands, all trees were retained, and treated as described above. Three additional stands (control stands) were left untouched. Prior to harvest, single trees and outer boundaries of tree groups (typically including 15–20 trees) were marked, to prevent their cutting. The spaces between tree groups varied between stands in accordance with the allotted cutting regimes. If possible, tree groups were selected in patches containing old living trees or large diameter logs, indicating high conservation value. In each of these groups, half of the trees were left intact and half were girdled. Corresponding numbers of cut trees left on the ground and high-cut stumps were created outside the groups' boundaries by cutting trees at ca. 3 m above ground. Cut trees left on the ground were often moved into the retention patches to reduce destruction by logging machines.



Figure 4. Tree retention experiment, Effaråsen forest. Green living trees, girdled trees, high-cut stumps and cut trees left on the ground. Photo: Francesca Santaniello, July 2013.



Figure 5. Stand types and retention categories in Effaråsen forest. Examples of: 1) control stand, where the forest has been left intact; 2) retention treatments, with various proportions of retained green trees and dead wood, from total retention to very low retention (the light grey represents the area dedicated to merchantable wood production); 3) the four tree retention categories. The number of trees retained per ha varied from 5 in the lowest retention stand, to 714 in the denser control stand. The volume of retained dead wood varied from 1.6 m³ ha⁻¹ in the lowest retention stand, to 40.9 m³ ha⁻¹ in the denser high retention stand. Illustration: Francesca Santaniello.

4 Data collection

4.1 Green trees and dead wood

During the summers of 2013 and 2014, green trees and dead wood were inventoried along one transect consisting of ten 100 m² circular plots in each of 12 retention stands (from very low to high retention, figures 5 and 7, table 1); and in 1-ha square plots within these 12 stands, plus 3 control stands. In the circular plots, we inventoried all green trees of >10 cm diameter at breast height and dead wood of >1 cm diameter (paper I). In the 1-ha square plots the minimum diameter of deadwood was 10 cm. We divided deadwood items into categories according to tree species, diameter, position (standing or lying), bark cover, age, and decomposition stage. These characteristics have been identified as important predictors for the occurrence of species confined to dead wood (Berglund et al., 2011; Ranius et al., 2015). We also collected qualitative data on vegetation and soil type. The total number of retained standing trees in each stand was counted and their canopy projection area was estimated using aerial photos taken from a camera drone



Figure 6. Forest stand with the 1-ha square plot and the transect with ten 100 m^2 circular plots, each randomly positioned in the stand. Illustration: Francesca Santaniello.

4.2 Harvesting operations

Logging productivity was measured as time consumption per unit cut and forwarded timber volume in 8 stands ranging from very low to high retention. (paper I). We used the on-board computers of the harvester and the forwarder to collect information on logging times and volumes. For each stand, data on harvester processing times and driving times, forwarder total times, forwarder mean driving distances (while empty or fully loaded), and harvested stem numbers and volumes were extracted. For the time estimates, we used "G15 time", which includes machine stops shorter than 15 minutes (Anon., 1987). Since harvester processing time is sensitive to variations in stem volume, the processing performance was normalized to a mean stem volume of 0.2 m³ sub per stand, according to functions by Brunberg (2007). Since forwarding performance is sensitive to variations in forwarding distance, we used only terminal/landing times, calculated by subtracting the modelled time for transport at full and empty loads (derived from Brunberg, 2004) from the total time.



Figure 7. Effaråsen stands. VL= very low retention stands; L= low retention stands: M= mid retention stands; H= high retention stands; T= total retention stands; C=control stands. The unmarked stands belong to the experiment, but they were not included in this study.

5 Data analysis

5.1 Data analysis

In paper I and II, I tested the effect of retention levels on a range of response variables, while in paper III I tested the effect of dead wood types on dead wood dependent lichens (table 1).

Table 1. Focus of the studies and type of stands investigated. *= Dead wood dependent lichens were inventoried in the same stands used in the retention experiment, but tree retention gradient was not considered for the purposes of this study.

Studies			II	III
	Merchantable wood	\checkmark	\checkmark	
of ies	Costs and revenues	\checkmark		
stud	Dead wood	\checkmark	\checkmark	
Fo the	Carbon stock		\checkmark	
	Dead wood dependent lichens			\checkmark
ated	From very low to high retention	\checkmark	\checkmark	*
stiga tands	Total retention			*
Inve	Control		\checkmark	
۲ŗ.	Circular plots	\checkmark		\checkmark
'ento type	Square plots	\checkmark	\checkmark	
Inv	Stands	\checkmark	\checkmark	

5.2 Forest model - Heureka

The forest development over the following 100 years was predicted in 15 study stands (from very low to high retention stands and control stands; figures 5 and 7) using Heureka (paper II). Heureka is a decision support system for forest managers in Sweden (Wikström et al., 2011). Except for the various levels of tree retention, all harvested stands were assumed to be exposed to the same management regime, consistent with conventional pine management in Sweden. The following setting was assumed: 2300 containerized seedlings (improved with 10% gain in growth) planted per hectare after soil scarification; cleaning at year 25 (leaving 2000 stems/ha with 90% pine and 10% birch); thinning at year 55 (with a thinning grade of 40% and leaving small trees (diameter <10 cm) intact; and final felling (clear cut) at year 100. The productive areas and the retention areas were simulated separately in Heureka for every stand. Both these areas were assumed to be covered by even-aged growing forest. The area occupied by retention trees and designated as a competition zone was estimated assuming a radius of 4 m from the central point of single trees and trees in small groups. This is because height growth of young trees of Scots pine has been found to be reduced within a zone of 8 m radius around single retention trees (Elfving & Jakobsson, 2006) and Erefur (2010) found competition zones that reached 7-8 m into a logged gap from a forest edge. We assumed that the closest 4 m was completely affected by competition while there was no effect over the following 4 m. This is a simplification in comparison to the above cited field studies that revealed a successively decreasing effect of competition within 8 m. Within the competition zone, natural ingrowth but no further planted seedlings was assumed. Outside this zone, regeneration of both planted and natural seedlings was assumed, along with management for wood production. The area dedicated to the growth of new seedlings is the whole area not occupied by tree retention, and was measured using ArcMap 10.3.1. Site productivity varied among stands; half of them had a site index of 19 (dominant height at 100 years of age), and the other half a site index of 21.

In paper II, the total volume of merchantable wood was simulated every 5 years for a total period of 100 years, using growth functions described and validated by Fahlvik et al. (2014). The growth functions as well as functions for tree mortality, biomass and dead wood were all based on empirical data from the Swedish National Forest Inventory. The tree growth was species-specific and determined by tree, stand and site

characteristics. The total wood provisioning resulted from tree growth, tree mortality, and from the planned cleaning and thinning.

5.3 Merchantable wood production, cost and revenues

In paper I, operation costs for the 2012 harvest were calculated based on harvesting, and transportation times for 1 m³ of wood under bark. A twosided t-test was applied to test the differences in logging operation time of stands subjected to the low and high retention level treatments. The cost of retention was calculated as the opportunity cost, defined as the difference between the net present value (sum of harvest net income and soil expectation value) before harvesting with retention or harvesting by clearfelling (Zhang & Pearse, 2011). The silvicultural regime was set and the future harvested volumes calculated by consulting the work package "INGVAR" (www.skogskunskap.se). Soil expectation values were calculated using the work package "Beståndsval" (www.skogskunskap.se) according to Faustmann (1849), assuming a 2% interest rate. Revenues were calculated on the base of the average value of merchantable wood (saw logs and pulpwood) according to the Bergvik Skog AB price list of 2012. Future costs included costs for regeneration and pre-commercial thinning according to Brunberg (2012). Costs and revenues were adjusted for each stand in accordance with to the retained area (i.e. the tree canopy projection area), which was assumed to be set aside in perpetuity. Harvested wood volume was calculated using data from the harvester and forwarder machines (year 0), and by calculated harvested volumes at thinning (in year 58) and final felling (year 103).

5.4 Dead wood

In paper I, the diversity of dead wood and dying trees was estimated using the Shannon diversity index (Magurran & McGill, 2013; Shannon, 1949). The Shannon diversity index indicates the species diversity in a system according to number of species (in our case, types of dead wood) present, and their frequency. Finally, to evaluate the effect of retention level on the conservation of old dead wood (age >120 years), we estimated the damage caused by the logging machines on dead wood (% of wood surface
damaged) and related the proportion of undamaged wood objects to retention level.

In paper II, the dead wood input was simulated using Heureka, employing the mortality model of Elfving (2014). The Elfving model is deterministic and based on a single-tree model, that has higher resolution than previous models and is consequently able to provide a more realistic output. The volume of dead wood artificially created (high-cut stumps, logs and low stumps) at year zero was also assessed, using field data from the square plots.

In paper III, the area of dead wood available for lichen colonization (i.e., lacking mosses and bark) was calculated for every circular plot, using the data collected during the dead wood inventory (paper I). Dead wood was divided into categories reflecting its quality as a potential substrate for lichens.

5.5 Carbon stock

In paper II, the amount of carbon stored in green trees, dead wood, and soil was simulated in the retention and control stands. When estimating the carbon stock, dead wood decomposition was simulated using the function by Harmon et al. (2000) that follows a negative exponential decay rate, and decreases with increasing deadwood diameter (Ortiz et al., 2016). The soil carbon was calculated using a model (Q-model, Rolff & Ågren, 1999) that simulates the decomposition of soil organic matter and is based on the continuous quality theory (Ågren & Bosatta, 1996). According to this theory, soil organic matter (including both naturally created litter and the litter originating from thinning and harvesting) is assumed to change continuously over time due to the activity of decomposers. Two advantages with the Q-model are that it creates a continuum of litter through time and that it is sensitive to different climatic conditions. However, the model provides biomass fractions on the basis of basal areas, while other characteristics of the substrate or the stand are not taken into consideration. For example, long-term effects of changes in soil chemistry (such as nitrogen deposition, which influences decomposers) are not considered. Carbon in living trees was calculated using the biomass functions of Marklund (1988), applicable for stem, bark, branches and needles.

Functions by Petersson and Ståhl (2006) were used to calculate the carbon present in stumps and roots.



Figure 8. Simplistic diagram of the carbon stored and leaving the system (in the form of carbon dioxide, CO_2 , and in harvested wood), according to the Heureka system. Fine woody debris = <10 cm diameter; Coarse woody debris = >10 cm diameter. Illustration: Francesca Santaniello.

5.6 Landscape scenarios

Outputs from the stand-level modelling were used to model different landscape scenarios (paper II). Twelve landscape scenarios were constructed, which were assumed to be located in the same geographical region and thus exposed to the same climatic conditions. Each landscape scenario consisted of a combination of two stand management options in a 100-ha forest area: either cutting with a defined level of retention or leaving as set-aside. In all scenarios, the cut of merchantable wood during the following rotation was fixed to 19000 m³ sub per 100 hectares over 100 years, while the areas harvested and set-aside varied. The volume of 19000 m³ sub resulted from the maximum harvest that can be obtained with the highest tree retention level (165 trees retained per ha) over 100 years. All landscape scenarios were compared in terms of carbon stock and the amount of dead wood input. The harvested stands had the same characteristics as in the stand level simulations while the set-aside areas were simulated based on values extracted from the control stands. In each

landscape scenario, harvested and set-aside stands were paired according to their site index, which was the same for the harvested and for the set-aside stands. The outcomes of the scenarios were expressed as averages per hectare over a 100-year rotation period.



Figure 9. Composition of the landscape in different scenarios. Simulations of forest development in a 100-ha landscape with the same volume of harvested wood (19000 m³ sub) over a 100-year rotation period in all scenarios. The respective areas of the retention and productive parts of managed forests and set-aside forests are shown. The landscape scenarios are divided in two groups, according to their site index, a proxy for site productivity. (Hägglund & Lundmark, 1977).

5.7 Dead wood dependent lichens

In paper III, we compared the species composition among different dead wood substrates using non-metric multidimensional scaling (NMDS). NMDS is an ordination method based on ranked Euclidean distances between samples. The data from the circular plots were pooled for each of the 15 forest stands. All ordination analyses were performed using R (version 3.2.1, and the packages Vegan, MASS, and BiodiversityR; Oksanen et al., 2007). Using the function "adonis" (Anderson, 2001), we

compared the samples by calculating the stress and performing a permutational multivariate analysis of variance using a distance matrix. To compare the species density on the different dead wood substrates, sample-based rarefaction curves were used (Gotelli & Colwell, 2001). The analysis was based on the following comparisons: (1) wood type; (2) wood hardness; (3) wood age; (4) wood hardness and age; and (5) wood type and age. The rarefaction curves were computed using the software EstimateS, version 9.1.0 (Colwell, 2013). In order to compare the number of lichen species on equal areas of available wood, the x-axis was rescaled to represent the cumulative surface area. Calculations were made using the surface area per plot of dead wood without bark or bryophytes.

6 Results and discussion

6.1 Effects of tree retention

At the stand level, increases in tree retention had a negative impact on wood production and on profitability. Conversely, it had a positive impact on the amount, richness, diversity and conservation of dead wood, and on carbon stock. At the landscape level, at fixed constant wood production, the dead wood amount increased and the carbon stock decreased, but only slightly (table 2).

Table 2. Influence of increasing tree retention level on the response variables at the stand and landscape level. The direction of the arrows indicates: decrease (pointing down), increase (pointing up).

Response variables	Stand level	Landscape level
Wood production	Ļ	constant
Dead wood	1	1
Carbon stock	1	ţ
Opportunity cost	1	n.d.
Logging productivity	ţ	n.d.

6.2 Stand level outcome

6.2.1 Merchantable wood production, costs, and revenues

At final harvest, the revenues declined with increased retention level (paper I). Soil expectation values were generally low, reflecting the low productivity of this type of forest, and therefore the differences in opportunity cost were mainly dependent on the loss of income from the harvest. This in turn was due to increased harvesting costs and reduced harvested volumes as retention level increased.

Both harvester and forwarder performance were lower at high than at low retention levels. The economic loss associated with the artificial creation of dead wood can be considered as the cost of creating substrates valuable for biodiversity, which in the case of girdling trees also means creating a continuum of valuable substrates over time (since girdled trees have a range of life expectancies according to the degree of injuries induced by the harvester). It was expected that retaining trees reduces the income due to reduced harvested volumes. Our study emphasizes in addition the increased harvesting costs incurred. The harvester performance was separated in processing and driving times. Both mean processing and driving times increased with retention level, with a relatively greater increase in driving times (ca. 50%) than in processing times (ca. 15%) when comparing low and high retention stands. The relatively larger increase in driving time is probably due to the occurrence of retained trees, which are obstacles to avoid, and fewer trees being processed per machine position. Eliasson et al., (1999) found no difference in processing time between different retention levels. In that study, girdling and high-cutting did not occur. We have no specific data on the time consumption for these measures. However, it seems that girdling is more time consuming and in contrast to high cutting (where the tree top is harvested) no timber is extracted. Thus, the increase in processing time is probably due mainly to tree girdling. Mean forwarding time increased by about 35% between low and high retention stands. The reason for this loss in productivity has not been studied, but can probably be ascribed to smaller timber piles and fewer trees loaded per machine position, as a result the harvester occupying more processing patches per unit area (Brunberg, 2004).

Seen over a whole rotation period, the production of merchantable wood decreased with the number of trees retained and increased with the site

productivity (paper II). Thus, the loss of wood production is related to both the loss of area for production trees in the new forest stand and to its productivity.

6.2.2 Dead wood

The number of dead wood types and dead wood diversity increased linearly from the lowest to highest retention level, in which almost 50% of the trees were retained (paper I). Moreover, old dead wood was not destroyed by forest machines at retention levels above 30%. This result shows that the retention of trees has a direct effect on the conservation of dead wood. Tree retention also reduces the destruction of dead wood during soil scarification (Hautala et al., 2004). Soil scarification had not been carried out when we did our field study, but in a subsequent study within the same stands, Weslien and Westerfelt (2017) reported that the amount of undamaged dead wood outside the retention patches was indeed further reduced by soil scarification.

Seen over a whole rotation, dead wood input increased with increasing retention level (paper II). This was mostly because more dead wood was artificially created in stands with higher retention levels. Consequently, set-aside stands had lower dead wood input, due to the lack of artificially created dead wood. After harvesting, dead wood input was higher in the control stands, but only during the first 90 years, after which the input of dead wood was higher in the lower retention treatments. This can be attributed, to their having the highest standing volume.



Figure 10. Dead wood input over a 100-year forest rotation. The light blue lines represent the dead wood artificially created at year zero.

Old dead wood had a different lichen species composition than young wood, and a higher species density (paper III). Old, hard dead wood was by far the most important category of dead wood for dead wood dependent lichens. All the species observed in this study occurred on this substrate, and over half were exclusive to it. Such wood is referred to as kelo wood (Box 2). The volume of old dead wood is much lower in managed forests in comparison to natural forests (Linder & Östlund, 1998). The lifetime of wooden substrates is always limited due to wood decay, but in managed forest dead wood is also destroyed during forestry operations. To maintain continuous availability of old dead wood, entire forest stands or retention groups should be set aside, since it is difficult for dead wood to become old and hard in managed forests.

Box 2. Kelo

Under certain conditions, which probably include repeated wild fires, dead wood of Scots pine becomes hard and resin-impregnated, and is subsequently very long lasting. In Finland, such old, silver-grey and decorticated trunks of Scots pine are called kelo (Niemelä et al., 2002). Many fungal species are confined to kelo substrates (Niemelä et al., 2002). Formation and decay of kelo trees are very slow processes. Scots pine can become up to 800 years old, and its transformation into kelo trees takes about 40 years after tree death (Sirén, 1961; Leikola, 1969). Kelo trees can remain standing for a further 700 years (Niemelä et al., 2002), and final decay of the fallen stem may take another 200 years (Tarasov & Birdsey, 2001). Formation of kelo trees is unlikely to occur in commercially managed forests with fast growing trees and short rotation cycles.



Figure 11. Kelo tree, Ylikiiminki, Finland. Photo: SeppVei.

6.2.3 Carbon stock

Over the whole rotation, the average carbon stock increased with increasing retention level and site index (paper II). In all treatments, the carbon stock increased over time. The difference in carbon stock between low and high retention treatments was higher early in the rotation, with carbon stock converging across treatments towards the end.



Figure 12. Carbon stock development over a 100-year forest rotation.

At year 0, the control stands were set aside, while the others were harvested with various levels of retention. The unlogged control stands were predicted to keep growing and assimilating carbon during the coming 100 years, indicating that the unmanaged system will not reach a state when the net carbon sequestration approaches zero during that time period, even if the rate levels off. It has been suggested that continued growth of old stands beyond the normal final felling age, i.e. prolonging rotations, can be used to mitigate climate change (Kaipainen et al., 2004; Zanchi et al., 2014). By the same logic, it could be argued that increasing retention levels could be a way to increase carbon stock over time and thus to mitigate climate change (Nunery & Keeton, 2010). However, this is just one part of the overall picture. Increased retention and prolonged rotations reduce overall production of merchantable wood.

Therefore, less will be made available as a substitute for fossil-based energy and fossil-dependent materials like steel or concrete (Lundmark et al., 2014; Nabuurs et al., 2007).

6.3 Landscape level outcome

If production is kept constant, an increasing level of tree retention is associated with a diminishing set-aside area in the landscape scenarios (paper II). Dead wood input increased with increasing retention level, while carbon stock decreased, but in both the cases differences along the retention gradient were small. One explanation for the increased dead wood input is that dead wood is artificially created under tree retention management. The decrease in carbon stock can probably be explained by the fact that, with retention, less space is available for the growth of new trees, whose carbon fixation is more efficient than in older trees (Harmon, 2001). However, which dead wood types were favored by the different management scenarios was not analysed. Simulations taking this into account have suggested that different landscape-level strategies favour different species (Ranius & Roberge, 2011). Setting aside entire stands resulted in lower volumes of dead wood input, but the dead wood from the earlier forest generation is probably better maintained, generating a better continuity of dead wood over time (paper II). This seems to be important for some dead wood dependent species, especially those depending on old growth-forest attributes (Kuuluvainen et al., 2017; Lõhmus & Lõhmus, 2011; Siitonen & Saaristo, 2000; Sverdrup-Thygeson & Lindenmayer, 2003). A substantial proportion of the dead wood input at retention was actively created. Many species, prefer sun-exposed wood, hence the artificially created dead wood at harvesting may be favorable during the period of time before the canopy closes (Djupström B. et al. 2012; Lindhe et al., 2005; Pasanen et al., 2014). Moreover, species that prefer shaded wood during a later phase of decomposition may also be favoured, but to our knowledge no studies have been performed on created dead wood during this later phase of stand development. For many species, the natural accumulation of dead and dving trees in set-asides seems to be necessary since many species are much more frequent there (Djupström B. et al., 2008; Perhans et al., 2007). Thus, to favour different species assemblages, land sharing (with dead wood creation) and land sparing (with continuity) approaches should be combined.

In our landscape-level scenarios we summarized the outcome in a 100-ha area over a rotation period. However, for biodiversity conservation the spatial and temporal distribution of the habitat may also be important. Sverdrup-Thygeson et al. (2014) showed, in a review, that there is a large variation in the response of different dead wood associated species to spatial and temporal habitat patterns. Species adapted to natural large-scale disturbance regimes could be assumed to be generally more dispersed and less dependent on the fine grain landscape structure than species adapted to more stable conditions (cf. Nilsson & Baranowski, 1997). However, empirical studies are needed to test this hypothesis.

6.4 Dead wood dependent lichens

Dead wood dependent lichens occurred on 46 % of all inventoried dead wood objects (paper III). There were 21 species, among which four were red-listed (Near Threatened status, Swedish Species Information Centre, 2015) (figure 13).

1. Carbonicola anthracophila Nyl.



3. Cladonia parasitica Hoffm.

2. Carbonicola myrmecina Ach.



4. Hertelidea Botryosa Fr.



Figure 13. The red-listed species found in Effaråsen. Photos: 1) Mikael Hagström; 2) Jeanette Fahlstad; 3) Jens Johannesson; 4) Billy Lindblom.

Lichen species composition differed significantly among dead wood types (low stumps, snags, logs), wood hardness, wood age and occurrence of fire scars.

Among the studied wood types, snags had the highest species density. This result confirms previous studies on lichens that showed similar patterns (Humphrey et al., 2002; Lõhmus & Lõhmus, 2001; Nascimbene et al., 2008; Svensson et al., 2016). The species composition analyses revealed a significant difference between the three wood types (low stumps, snags, and logs). This may be due to structural differences between dead wood types, but also differences in microclimatic conditions, such as light exposure (Rudolphi & Gustafsson, 2011).

Hard wood had higher species density than softer wood, a difference particularly marked in the hardest wood category. Fourteen species were restricted, entirely or almost entirely, to hard wood, including all four redlisted species. Species density was highest for wood in intermediate decomposition stages. An explanation for this pattern could be that this type of dead wood often provides a wider range of microhabitats than earlier or later decay stages (Caruso & Rudolphi, 2009; Kruys & Jonsson, 1999; Wagner et al., 2014). Moreover, the progressive decrease of substrate stability over time is probably disadvantageous for lichens (Nascimbene et al., 2008).

The species density was about three times higher on old (>120 years) dead wood than on young dead wood. Moreover, species composition was clearly affected by wood age, since more than half of the species, including three of the four red-listed species, were found only on old dead wood. This may be because old dead wood has certain characteristics, such as lower cellulose and lignin content (Stokland et al., 2012) and higher nitrogen content due to fungal mycelia, which are rich in nitrogen (Cowling & Merrill, 1966). Higher frequency of occurrences on older substrate may also be a consequence of lichens having had a longer time for colonization than on more recently formed substrate (Johansson et al., 2012).

Fourteen species were found on burned wood, of which three were found exclusively on this substrate. Species density analyses were not possible in this case, due to the low number of observations on burned wood. Interestingly, both *Carbonicola anthracophila* and *C. myrmecina* have been found to grow on burned wood as much as 300 years after fire (Esseen et al., 1997), indicating that this kind of wood retains its value for biodiversity for a very long time.

All 21 species observed in this study occurred on old and hard wood (kelo wood; Box 2). Eleven species were found only on this type of wood. For red-listed species this type of dead wood was shown to be important, since two of the four red-listed species were not found on any other substrate, and the other two only rarely. Thus, a high proportion of wood dependent lichens depend on kelo wood.

This study adds to the knowledge of dead wood dependent organisms that can be applied in forest management and conservation. To conserve wood dependent lichens, old dead wood should be preserved by tree retention or by setting aside areas, where the wood quality for lichens is most likely higher than in managed forest. Further knowledge is needed on how to sustain the formation of kelo trees. The Effaråsen experiment is ongoing, and may contribute to such knowledge in the future. Our lichen inventory may also serve as a baseline study, to be of use in future assessments of the experimental plots at Effaråsen.

7 Conclusions

In this thesis, I have investigated the synergies and trade-offs between different deliverables from pine forests: dead wood, merchantable wood, and carbon storage, under varying tree retention levels. In addition, I also investigated the habitat requirements of wood dependent lichens. I consider the results collected in this thesis to be representative for most boreal pine forests in Fennoscandia. The outcomes can be used to suggest strategies to sustain such deliverables under economic restriction.

The main outcome of the thesis is that tree retention has an impact on all the investigated variables. The results from paper I showed that increasing the level of tree retention incurs increased costs, not only because of the reduced harvest volumes but also because of the increasing logging costs. For land owners, there is also a reduction of income due to the reduction of area available for regeneration and future forest production, although this loss is comparatively low if "normal" interest rates (2 %) are assumed and the productivity of the land is low.

By increasing the level of retention, the volume of dead wood increased (paper I and II), mainly because the volume of dead wood artificially created was proportional to the level of retention, and because less dead wood was destroyed by machineries. Furthermore, by increasing the level of retention, the number of dead wood types increased with retention level up to the highest level (paper I).

At the stand level, higher level of retention means a slightly higher carbon stock during the rotation, because more trees and dead wood remain postharvest (paper II). To what extent that is a valid argument for more retention depends on which view that is chosen on substitution effects. At the landscape level, with increasing level of retention, carbon stock slightly decreased, probably because set-aside patches store less carbon than productive patches, due to the different carbon fixation capacity associated with tree age.

For lichens dependent on dead wood, old and hard dead wood is the most important type in pine forest. Hence, for lichens it is important to preserve available dead wood by setting aside entire stands or retention groups, since this practice favours the creation of old dead wood, and also by ensuring the creation and conservation of sun exposed substrates. It is not known to what extent it is possible to create such wood, but probably burning of pine forests that have low amount of dead wood present would be useful.

Compensating production loss due to retention by decreasing the area of set-asides at the landscape level produced only small differences in landscape-level dead wood input and in carbon stock. This outcome may however conceal a more varied response among dead wood types and the spatial distribution of dead wood. Today, most forests in Fennoscandia are managed according to a similar strategy, in which both set-asides and tree retention occurs. I believe that increasing diversity in landscapes would be advantageous for biodiversity conservation, since the species richness will be favoured by the simultaneous occurrence of different habitats. Active promotion of specific dead wood substrates, as well as their conservation, may be an attractive complement to the existing management strategies.

8 Future prospects

Tree retention studies are increasing in number, but some aspects are still poorly investigated. Firstly, it would be interesting to study forest carbon dynamics in relation to other aspects, such as the albedo (surface reflectance) and their influence on climate. The albedo exerts a big influence on the earth's climate and its intensity varies among land cover types and tree retention may be counteractive. Secondly, knowledge is needed about the long-term effects of tree retention on both biodiversity and various ecosystem services. Lastly, it would be useful to extend the tree retention studies to forest types not yet investigated.

References

- Agnoletti, M. & Anderson, S., 2000. Methods and Approaches in Forest History. CABI Publishing and the International Union of Forestry Research Organizations, Wallingford, United Kingdom, 281 p.
- Ahti, T., Hämet-Ahti, L. & Jalas, J., 1968. Vegetation zones and their sections in north western Europe. Annales Botanici Fennici, 5: 169-211.
- Anderson, M. J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology, 26: 32-46.
- Angelstam, P. & Kuuluvainen, T., 2004. Boreal forest disturbance regimes, successional dynamics and landscape structures – a European perspective. Ecological Bulletins, 51: 117-136.
- Anon., 1987. Forest Work Study Nomenclature. The Nordic Forest Study Council (NSR), Norwegian Forest Research Institute, Ås, Norway, pp. 83-99.
- Aubry, K. B., Halpern, C. B. & Peterson, C. E., 2009. Variable-retention harvests in the Pacific Northwest: A review of short-term findings from the DEMO study. Forest Ecology and Management, 258: 398-408.
- Axelsson, J. & Eriksson, L. 1986. Estimation of thinning computerized simulation of biological and economic effects due to different thinning methods. Department of Operational Efficiency, Swedish University of Agricultural Sciences, Report 166, 55 p.
- Barnola, J. M., Pimienta, P., Raynaud, D. & Korotkevich, Y. S., 1991. CO2-climate relationship as deduced from the Vostok ice core: a re-examination based on new measurements and on a re-evaluation of the air dating. Tellus B, 43: 83-90.
- Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F. & Nyström, M., 2003. Reserves, resilience and dynamic landscapes. Ambio, 32: 389-396.
- 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.
- Bergeron, Y., Flannigan, M.D., Gauthier, S., Leduc, A. & Lefort, P., 2004. Past, current and future fire frequency in the Canadian boreal forest: implications for sustainable forest management. Ambio, 33: 356-360.

- Bergeron, Y., Harvey, B., Leduc, A. & Gauthier, S., 1999. Forest management guidelines based on natural disturbance dynamics: stand-and forest-level considerations. The Forestry Chronicle, 75: 49-54.
- Berglund, H., Hottola, J., Penttilä, R., & Siitonen, J., 2011. Linking substrate and habitat requirements of wood-inhabiting fungi to their regional extinction vulnerability. Ecography, 34: 864-875.
- Boch, S., Prati, D., Hessenmöller, D., Schulze, E.D. & Fischer, M., 2013. Richness of lichen species, especially of threatened ones, is promoted by management methods furthering stand continuity. PLoS ONE, 8: e55461.
- Botting, R. S. & DeLong, C., 2009. Macrolichen and bryophyte responses to coarse woody debris characteristics in sub-boreal spruce forest. Forest Ecology and Management, 258: 85-94.
- Brandt, J.P., 2009. The extent of the North American boreal zone. Environmental Review Journal, 17: 101-161.
- Brown, S., Sathaje. J., Cannel. M. & Kauppi, P. E., 1996. Mitigation of carbon emissions to the atmosphere by forest management. The Commonwealth Forestry Review, 75: 80-91.
- Brunberg, T., 1997. Basic data for productivity norms for single-grip harvesters in thinning. Redogörelse, 8/1997, Skogforsk (in Swedish with English summary).
- Brunberg, T., 2004. Productivity norm data for forwarders. Redogörelse 3/2004, Skogforsk (in Swedish with English summary).
- Brunberg, T., 2007. Basic data for productivity norms for extra-large single-grip harvesters in final felling. Redogörelse 2/2007, Skogforsk (in Swedish with English summary).
- Brunberg, T., 2012. Forestry costs and revenues 2011 major increase in costs. Redogörelse 6/2012, Skogforsk (in Swedish with English summary).
- Canadell, J. G., Le Quéré, C., Raupach, M. R., Field, C. B., Buitenhuis, E. T., Ciais, P., Conway, T.J., Gillett, N.P., Houghton, R.A. & Marland, G., 2007. Contributions to accelerating atmospheric CO2 growth from economic activity, carbon intensity, and efficiency of natural sinks. Proceedings of the National Academy of Sciences, 104: 18866-18870.
- Carleton, T. J. & Maycock, P. F., 1978. Dynamics of the boreal forest south of James Bay. Canadian Journal of Botany, 56: 1157-1173.
- Carpenter, S. R., Mooney, H. A., Agard, J., Capistrano, D., Defries, R. S., Díaz, S., Dietz, T., Duraiappah, A. K., Oteng-Yeboah, A., Pereira, H. M., Perrings, C., Reid, W. V., Sarukhan, J., Scholes, R. J. & Whyte, A., 2009. Science for managing ecosystem services: beyond the Millennium Ecosystem Assessment. Proceedings of the National Academy of Sciences of the United States of America, 106: 1305-1312.
- Caruso, A. & Rudolphi, J., 2009. Influence of substrate age and quality on species diversity of lichens and bryophytes on stumps. The Bryologist, 112: 520-531.
- Clinton, B. D., 2011. Stream water responses to timber harvest: Riparian buffer width effectiveness. Forest Ecology and Management, 261: 979-988.
- Colwell, R. K., 2013. Estimate S: Statistical Estimation of Species Richness and Shared Species from Samples. Version 9.1.0. and earlier. User's Guide and Application.

- Cowling, E. B. & Merrill, W., 1966. Nitrogen in wood and its role in wood deterioration. Canadian Journal of Botany, 44: 1539-1554.
- Djupström, L. B., Weslien, J. & Schroeder, L. M., 2008. Dead wood and saproxylic beetles in setaside and non set-aside forests in a boreal region. Forest Ecology and Management, 255: 3340-3350.
- Djupström, L. B., Weslien, J., Ten Hoopen, J. & Schroeder, L. M., 2012. Restoration of habitats for a threatened saproxylic beetle species in a boreal landscape by retaining dead wood on clear-cuts. Biological Conservation, 155: 44-49.
- Duku-Kaakyire, A. & Nanang, D. M., 2004. Application of real options theory to forestry investment analysis. Forest Policy and Economics, 6: 539-552.
- Edwards, D. P., Gilroy, J. J., Woodcock, P., Edwards, F. A., Larsen, T. H., Andrews, D. J. R., Derhé, M.A., Docherty, T. D. S., Hsu, W. W., Mitchell, S. L., Ota, T., Williams, L. J., Laurance, W. F., Hamer, K. C. & Wilcove, D. S., 2014. Land-sharing versus land-sparing logging: reconciling timber extraction with biodiversity conservation. Global Change Biology, 20: 183-191.
- Elfving, B., 2014. Modellering av naturlig avgång i Heureka. SLU, inst. för skogens ekologi och skötsel. http://heurekaslu.org/mw/images/f/f4/HeurekaMortality-PM140317.pdf.
- Elfving, B. & Jakobsson, R., 2006. Effects of retained trees on tree growth and field vegetation in Pinus sylvestris stands in Sweden. Scandinavian Journal of Forest Research, 21: 29-36.
- Eliasson, L. 1998. Analyses of single-grip harvester productivity. Doctoral thesis. Swedish University of Agricultural Sciences, Umeå, Sweden.
- Eliasson, L., Bengtsson, J., Cedergren, J. & Lageson, H., 1999. Comparison of single-grip harvester productivity in clear-and shelterwood cutting. Journal of Forest Engineering, 10: 43-48.
- Engelmark, O., 1999. Boreal forest disturbances. In: Walker, L.R. (ed.), Ecosystems of disturbed ground. Ecosystems of the world 16. Elsevier Amsterdam, pp. 161-186.
- Engelmark, O., Kullman, L. & Bergeron, Y., 1994. Fire and age structure of Scots pine and Norway spruce in northern Sweden during the past 700 years. New Phytologist, 126: 163-168.
- Erefur, C., 2010. Regeneration in Continuous Cover Forestry Systems. Doctoral thesis. Swedish University of Agricultural Sciences, Umeå, Sweden.
- Eriksson, M., 2016. Developing client-supplier alignment in Swedish wood supply. Doctoral thesis. Swedish University of Agricultural Sciences, Umeå, Sweden.
- Eriksson, M. & Lindroos, O., 2014. Productivity of harvesters and forwarders in CTL operations in northern Sweden based on large follow-up datasets. International Journal of Forest Engineering, 25: 179-200.
- Esseen, P. A., Ehnström, B., Ericson, L. & Sjöberg, K., 1997. Boreal forests. Ecological Bulletins, 46: 16-47.
- Fahlvik, N., Elfving, B. & Wikström, P., 2014. Evaluation of growth functions used in the Swedish Forest Planning System Heureka. Silva Fennica, 48: 1-17.

- Faustmann, M., 1849. Berechnung des Werthes, welchen Waldboden, sowie noch nicht haubare Holzbestände für die Waldwirthschaft besitzen. Allgemeine Forst und Jagd Zeitung, 20: 441-455.
- Fedrowitz, K., Koricheva, J., Baker, D. C., Lindenmayer, D. B., Palik, B., Rosenvald., R., Beese, W., Franklin, J. F., Kouki, J. & Macdonald, E., 2014. Can retention forestry help conserve biodiversity? A meta-analysis. Journal of Applied Ecology, 51: 1669-1679.
- Felton, A., Ranius, T., Roberge, J. M., Öhman, K., Lämås, T., Hynynen, J., Juutinen, A., Mönkkönen, M., Nilsson, U., Lundmark, T. & Nordin, A., 2017a. Projecting biodiversity and wood production in future forest landscapes: 15 key modeling considerations. Journal of Environmental Management, 197: 404-414.
- Felton, A., Sonesson, J., Nilsson, U., Lämås, T., Lundmark, T., Nordin, A., Ranius, T. & Roberge, J. M., 2017b. Varying rotation lengths in northern production forests: Implications for habitats provided by retention and production trees. Ambio, 46: 324-334.
- Fischer, J., Abson, D. J., Butsic, V., Chappell, M. J., Ekroos, J., Hanspach, J., Kuemmerle, T., Smith, H. G. & von Wehrden, H., 2014. Land sparing versus land sharing: moving forward. Conservation Letters, 7: 149-157.
- Forest Stewardship Council (FSC), 2010. Swedish FSC Standard for Forest Certification including SLIMF indicators. FSC, Uppsala, Sweden.
- Franklin, J. F., Berg, D. R., Thornburgh, D. A. & Tappeiner, J. C., 1997. Alternative silvicultural approaches to timber harvesting: variable retention harvest systems. In: Kohm, K. A., Franklin, J.F. (Eds.), Creating a Forestry for the 21st Century. Island Press, Washington, DC, pp. 111– 140.
- Frumerie, G. (Ed.), 1997. Forestry in Sweden. Skogforsk, 48 p.
- Gadow, K. V., Zhang, C.Y., Wehenkel, C., Pommerening, A., Corral-Rivas, J., Korol, M., Myklush, S., Hui, G.Y., Kiviste, A. & Zhao, X. H., 2012. Forest structure and diversity. In: Pukkala T, Gadow Kv (eds) Continuous cover forestry. Book series managing forest ecosystems, vol 23. Springer, Berlin, pp. 29-84
- Gardner, M., 2013. Pinus sylvestris. In: The IUCN Red List of Threatened Species 2013, 42418/0. Downloaded 25 February 2017.
- Gotelli, N. J. & Colwell, R. K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters, 4: 379-391.
- Gromtsev, A., 2002. Natural disturbance dynamics in the boreal forests of European Russia: a review. Silva Fennica, 36: 41-55.
- Gustafsson, L., Kouki, J. & Sverdrup-Thygeson, A., 2010. Tree retention as a conservation measure in clear-cut forests of northern Europe: a review of ecological consequences. Scandinavian Journal of Forest Research, 25: 295-308.
- Gustafsson, L., Baker, S. C., Bauhus, J., Beese, W. J., Brodie, A., Kouki, J., Lindenmayer, D., B., Lõhmus A., Pastur G. M. & Messier, C., 2012. Retention forestry to maintain multifunctional forests: a world perspective. BioScience, 62: 633-645.

- Gustafsson, L., Weslien, J., Hannerz, M. & Aldentun, Y., 2016. Naturhänsyn vid avverkning en syntes av forskning från Norden och Baltikum. En rapport från forskningsprogrammet Smart Hänsyn. Sveriges Lantbruksuniversitet, Uppsala.
- Hadden, D. G., 2017. Processes controlling carbon fluxes in the soil-vegetation-atmosphere system. Doctoral dissertation. Swedish University of Agricultural Science, Uppsala, Sweden.
- Hägglund, B. & Lundmark, J. E., 1977. Site index estimation by means of site properties of Scots pine and Norway spruce in Sweden. Studia Forestalia Suecica, 138: 1-38.
- Hanski, I., 2000. Extinction debt and species credit in boreal forests: modelling the consequences of different approaches to biodiversity conservation. In Annales Zoologici Fennici. Finnish Zoological and Botanical Publishing Board, pp. 271-280.
- Harmon, M. E., 2001. Carbon sequestration in forests: addressing the scale question. Journal of Forestry, 99: 24-29.
- 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., Lienkaemper, G. W., Cromack, K. & Cummins, K. W., 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research, 15: 133-302.
- Harmon, M. E., Krankina, O. N. & Sexton, J., 2000. Decomposition vectors: a new approach to estimating woody detritus decomposition dynamics. Canadian Journal of Forest Research, 30: 76-84.
- Hautala, H., Jalonen, J., Laaka-Lindberg, S. & Vanha-Majamaa, I., 2004. Impacts of retention felling on coarse woody debris (CWD) in mature boreal spruce forests in Finland. Biodiversity and Conservation, 13: 1541-1554.
- Hämäläinen, A., Kouki, J. & Lõhmus, P., 2014. The value of retained Scots pines and their dead wood legacies for lichen diversity in clear-cut forests: the effects of retention level and prescribed burning. Forest Ecology and Management, 324: 89-100.
- Hedwall, P. O. & Mikusiński, G., 2015. Structural changes in protected forests in Sweden: implications for conservation functionality. Canadian Journal of Forest Research, 45: 1215-1224.
- 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.
- Hyvönen, R., Ågren, G. I., Linder, S., Persson, T., Cotrufo, M. F., Ekblad, A., Freeman, M., Grelle, A., Janssens, I. A., Jarvis, P. G., Kellomäki, S., Lindroth, A., Loustau, D., Lundmark, T., Norby, R. J., Oren, R., Pilegaard, K., Ryan, M. G., Sigurdsson, B. D., Strömgren, M., van Oijen, M. & Wallin, G., 2007. The likely impact of elevated [CO2], nitrogen deposition, increased temperature and management on carbon sequestration in temperate and boreal forest ecosystems: a literature review. New Phytologist, 173: 463-480.
- Houghton, R. A., House, J. I., Pongratz, J., Van Der Werf, G. R., DeFries, R. S., Hansen, M. C., Le Quéré, C. & Ramankutty, N., 2012. Carbon emissions from land use and land-cover change. Biogeosciences, 9: 5125-5142.
- Jacobson, S. & Pettersson, F., 2010. An assessment of different fertilization regimes in three boreal coniferous stands. Silva Fennica, 44: 815-827.

- Jakobsson, R. & Elfving, B., 2004. Development of an 80-year-old mixed stand with retained Pinus sylvestris in Northern Sweden. Forest Ecology and Management, 194: 249-258.
- Johansson, V., Ranius, T. & Snäll, T., 2012. Epiphyte metapopulation dynamics are explained by species traits, connectivity, and patch dynamics. Ecology, 93: 235-241.
- Johnson, E. A., 1992. Fire and vegetation dynamics—studies from the North American boreal forest. Cambridge University Press, Cambridge, United Kingdom, 131 p.
- Jonsson, M., Ranius, T., Ekvall, H. & Bostedt, G., 2010. Cost-effectiveness of silvicultural measures to increase substrate availability for wood-dwelling species: A comparison among boreal tree species. Scandinavian Journal of Forest Research, 25: 46-60.
- Kaipainen, T., Liski, J., Pussinen, A. & Karjalainen, T., 2004. Managing carbon sinks by changing rotation length in European forests. Environmental Science and Policy, 7: 205-219.
- Keenan, R. J., Reams, G. A., Achard, F., de Freitas, J. V., Grainger, A. & Lindquist, E., 2015. Dynamics of global forest area: results from the FAO Global Forest Resources Assessment 2015. Forest Ecology and Management, 352: 9-20.
- Kimmins, J. P., Mailly, D. & Seely, B., 1999. Modelling forest ecosystem net primary production: the hybrid simulation approach used in FORECAST. Ecological Modelling, 122: 195-224.
- Klockow, P. A., D'Amato, A. W. & Bradford, J. B., 2013. Impacts of post-harvest slash and livetree retention on biomass and nutrient stocks in Populus tremuloides Michx-dominated forests, northern Minnesota, USA. Forest Ecology and Management, 291: 278-288.
- Koivula, M., Kuuluvainen, T., Hallman, E., Kouki, J., Siitonen, J. & Valkonen, S., 2014. Forest management inspired by natural disturbance dynamics (DISTDYN) – a long-term research and development project in Finland. Scandinavian Journal of Forest Research, 29: 579-592.
- Kouki, J., Löfman, S., Martikainen, P., Rouvinen, S. & Uotila, A., 2001. Forest fragmentation in Fennoscandia: linking habitat requirements of wood-associated threatened species to landscape and habitat changes. Scandinavian Journal of Forest Research, 16: 27-37.
- Kremen, C., 2015. Reframing the land-sparing/land-sharing debate for biodiversity conservation. Annals of the New York Academy of Sciences, 1355: 52-76.
- 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., Fridman, J., Götmark, F., Simonsson, P. & Gustafsson, L., 2013. Retaining trees for conservation at clearcutting has increased structural diversity in young Swedish production forests. Forest Ecology and Management, 304: 312-321.
- Kuuluvainen, T., 2009. Forest management and biodiversity conservation based on natural ecosystem dynamics in northern Europe: the complexity challenge. Ambio, 38: 309-315.
- Kuuluvainen, T. & Aakala, T., 2011. Natural forest dynamics in boreal Fennoscandia: a review and classification. Silva Fennica, 45: 823-841.
- Kuuluvainen, T., Aakala, T. & Várkonyi, G., 2017. Dead standing pine trees in a boreal forest landscape in the Kalevala National Park, northern Fennoscandia: amount, population characteristics and spatial pattern. Forest Ecosystems, 4: 12.

- Lal, R., 2005. Forest soils and carbon sequestration. Forest Ecology and Management, 220:242-258.
- Lämås, T., 1996. Forest management planning for biodiversity and timber production. Doctoral dissertation. Umeå University, Umeå, Sweden.
- Larsen, C. P. S., 1997. Spatial and temporal variations in boreal forest fire frequency in northern Alberta. Journal of Biogeography, 24: 663-673.
- LeDoux, C. & Whitman, A., 2006. Estimating the capital recovery costs of alternative patch retention treatments in eastern hardwoods. International Journal of Forest Engineering, 17: 21-30.
- Leikola, M., 1969. On the termination of diameter growth of Scots pine in old age in northernmost Finnish Lapland. Silva Fennica, 3: 50-61.
- Lindenmayer, D. B. & Franklin, J. F., 2002. Conserving Forest Biodiversity: A Comprehensive Multiscaled Approach. Island Press, Covelo, California, 353 p.
- Lindenmayer, D. B. & Franklin, J., F., 2003. Towards Forest Sustainability. CSIRO Publishing, Collingwood, Australia, 231 p.
- Linder, P. & Östlund, L., 1998. Structural changes in three mid-boreal Swedish forest landscapes, 1885–1996. Biological Conservation, 85: 9-19.
- 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.
- Linder, S., 1987. Responses to water and nutrients in coniferous ecosystems. Ecological Studies, 61:180-202.
- Lindhe, A., Lindelöw, Å. & Åsenblad, N., 2005. Saproxylic beetles in standing dead wood density in relation to substrate sun-exposure and diameter. Biodiversity and Conservation, 14: 3033-3053.
- Lloyd, F. T. & Harms, W. R., 1986. An individual stand growth model for mean plant size based on the rule of self-thinning. Annals of Botany, 57: 681-688.
- Lonsdale, D., Pautasso, M. & Holdenrieder, O., 2008. Wood-decaying fungi in the forest: conservation needs and management options. European Journal of Forest Research, 127: 1-22.
- Lowenthal, D., 1956. Western Europe. In: A World Geography of Forest Resources. American Geographical Society Publisher, No. 33, Ronald Press Company, New York.
- Lõhmus, P. & Lõhmus, A., 2001. Snags, and their lichen flora in old Estonian peatland forests. In Annales Botanici Fennici, 38: 265-280.
- Lõhmus, A., & Lõhmus, P., 2011. Old-forest species: the importance of specific substrata vs. stand continuity in the case of calicioid fungi. Silva Fennica, 45: 1015-1039.
- Lõhmus, A., Kraut, A. & Rosenvald, R., 2013. Dead wood in clearcuts of semi-natural forests in Estonia: site-type variation, degradation, and the influences of tree retention and slash harvest. European Journal of Forest Research, 132: 335-349.
- Lundberg, J. & Moberg, F., 2003. Mobile link organisms and ecosystem functioning: implications for ecosystem resilience and management. Ecosystems, 6: 87-98.

- Lundmark, H., Josefsson, T. & Östlund, L., 2013. The history of clear-cutting in northern Sweden–driving forces and myths in boreal silviculture. Forest Ecology and Management, 307: 112-122.
- Lundmark, T., Bergh, J., Hofer, P., Lundström, A., Nordin, A., Poudel, B. C., Sathre, R., Taverna, R. & Werner, F., 2014. Potential roles of Swedish forestry in the context of climate change mitigation. Forests, 5: 557-578.
- Magurran, E. A. & McGill, J. B., 2013. Biological Diversity. Frontiers in Measurement and Assessment. Oxford University Press, Oxford, United Kingdom, pp. 56–57.
- Marklund, L. G., 1988. Biomass functions for pine, spruce and birch in Sweden. Rapport 45. Sveriges Lantbruksuniversitet, Institutionen för Skogstaxering, Umeå.
- Marland, G. & Schlamadinger, B., 1997. Forests for carbon sequestration or fossil fuel substitution? A sensitivity analysis. Biomass and Bioenergy, 13: 389-397.
- McCune, B., 2000. Lichen communities as indicators of forest health. The Bryologist, 103: 353-356.
- Mönkkönen, M., Juutinen, A., Mazziotta, A., Miettinen, K., Podkopaev, D., Reunanen, P., Salminen, H. & Tikkanen, O. P., 2014. Spatially dynamic forest management to sustain biodiversity and economic returns. Journal of Environmental Management, 134: 80-89.
- Nabuurs, G. J., Masera, O., Andrasko, K., Benitez-Ponce, P., Boer, R., Dutschke, M., Elsiddig, E., Ford-Robertson, J., Frumhoff, P., Karjalainen, T., Krankina, O., Kurz, W. A., Matsumoto, M., Oyhantcabal, W., Ravindranath, N. H., Sanz Sanchez, M. J. & Zhang, X., 2007. Forestry. In Climate Change 2007: Mitigation. Contribution of Working Group III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Metz, B., Davidson, O. R., Bosch, P. R., Dave, R., Meyer, L. A., (eds)], Cambridge University Press, Cambridge, United Kingdom, 584 P.
- Naidoo, R., Balmford, A., Ferraro, P. J., Polasky, S., Ricketts, T. H. & Rouget, M., 2006. Integrating economic costs into conservation planning. Trends in Ecology & Evolution, 21: 681-687.
- Nascimbene, J., Marini, L., Motta, R. & Nimis, P. L., 2008. Lichen diversity of coarse woody habitats in a Pinus-Larix stand in the Italian Alps. The Lichenologist, 40: 153-163.
- Newman, D. H., 2002. Forestry's golden rule and the development of the optimal forest rotation literature. Journal of Forest Economics, 8: 5-27.
- Nghiem, N. & Tran, H., 2016. The Biodiversity Benefits and Opportunity Costs of Plantation Forest Management: A Modelling Case Study of Pinus radiata in New Zealand. Forests, 7: 297.
- Niemelä, T., Wallenius, T. & Kotiranta, H., 2002. The kelo tree, a vanishing substrate of specified wood-inhabiting fungi. Polish Botanical Journal, 47: 91-101.
- Niklasson, M. & Granström, A., 2000. Number and size of fires: Long-term spatially explicit fire history in a Swedish boreal landscape. Ecology, 81: 1484-1499.
- Nilsson, S. G. & Baranowski, R., 1997. Habitat predictability and the occurrence of wood beetles in old-growth beech forests. Ecography, 20: 491-498.

- Nilsson, U. & Allen, H. L., 2003. Short-and long-term effects of site preparation, fertilization and vegetation control on growth and stand development of planted loblolly pine. Forest Ecology and Management, 175: 367-377.
- Nilsson, U., Agestam, E., Ekö, P.-M., Elfving, B., Fahlvik, N., Johansson, U., Karlsson, K., Lundmark, T. & Wallentin, C., 2010. Thinning of Scots pine and Norway spruce monocultures in Sweden: effects of different thinning programmes on stand level gross and net stem volume production. Studia Forestalia Suecica, 219: 1-46.
- Nimis, P. L., Scheidegger, C. & Wolseley, P. A., 2002. Monitoring with lichens—monitoring lichens. In: Monitoring with Lichens—Monitoring Lichens. Springer, Netherlands, pp. 1-4.
- Nunery, J. S. & Keeton, W. S., 2010. Forest carbon storage in the northeastern United States: net effects of harvesting frequency, post-harvest retention, and wood products. Forest Ecology and Management, 259: 1363-1375.
- Nurminen, T., Korpunen, H. & Uusitalo, J., 2006. Time consumption analysis of the mechanized cut-to-length harvesting system. Silva Fennica, 40: 335-363.
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M. H. H. & Oksanen, M. J, 2007. The vegan package. Community ecology package, 10.
- Oliver, C. D. & Larson., B. C., 1990. Forest stand dynamics. McGraw-Hill, New York, 567 p.
- Ortiz, C. A., Hammar, T., Ahlgren, S., Hansson, P. A. & Stendahl, J., 2016. Time-dependent global warming impact of tree stump bioenergy in Sweden. Forest Ecology and Management, 371: 5-14.
- Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A., Lewis, S. L., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S., McGuire, A. D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D. & Watson, C., 2011. A large and persistent carbon sink in the World's forests. Science, 333: 988-993.
- Pasanen, H., Junninen, K. & Kouki, J., 2014. Restoring dead wood in forests diversifies wooddecaying fungal assemblages but does not quickly benefit red-listed species. Forest Ecology and Management, 312: 92-100.
- Perhans, K., Gustafsson, L., Jonsson, F., Nordin, U. & Weibull, H., 2007. Bryophytes and lichens in different types of forest set-asides in boreal Sweden. Forest Ecology and Management, 242: 374-390.
- Pettersson, F. & Högbom, L., 2004. Long-term growth effects following forest nitrogen fertilization in Pinus sylvestris and Picea abies stands in Sweden. Scandinavian Journal of Forest Research, 19: 339-347.
- Petersson, H. & Ståhl, G., 2006. Functions for below-ground biomass of Pinus sylvestris, Picea abies, Betula pendula and Betula pubescens in Sweden. Scandinavian Journal of Forest Research, 21: 84-93.
- Phalan, B., Onial, M., Balmford, A. & Green, R. E., 2011. Reconciling food production and biodiversity conservation: land sharing and land sparing compared. Science, 333: 1289-1291.
- Pingoud, K., Perälä, A. L. & Pussinen, A., 2001. Carbon dynamics in wood products. Mitigation and Adaptation Strategies for Global Change, 6: 91-111.

- Ranius, T. & Roberge, J. M., 2011. Effects of intensified forestry on the landscape-scale extinction risk of dead wood dependent species. Biodiversity and Conservation, 20: 2867-2882.
- Ranius, T., Ekvall, H., Jonsson, M. & Bostedt, G., 2005. Cost-efficiency of measures to increase the amount of coarse woody debris in managed Norway spruce forests. Forest Ecology and Management, 206: 119-133.
- Ranius, T., Johansson, V., Schroeder, M. & Caruso, A., 2015. Relative importance of habitat characteristics at multiple spatial scales for wood-dependent beetles in boreal forest. Landscape Ecology, 30: 1931-1942.
- Ryan, M. G., Binkley, D., Fownes, J. H., Giardina, C. P. & Senock, R. S., 2004. An experimental test of the causes of forest growth decline with stand age. Ecological Monographs, 74: 393-414.
- Ringdahl, O., 2011. Automation in forestry: development of unmanned forwarders. Doctoral dissertation. Umeå University, Umeå, Sweden.
- Rolff, C. & Ågren, G. I., 1999. Predicting effects of different harvesting intensities with a model of nitrogen limited forest growth. Ecological Modelling, 118: 193-211.
- Rosenvald, R. & Lõhmus, A., 2008. For what, when, and where is green-tree retention better than clear-cutting? A review of the biodiversity aspects. Forest Ecology and Management, 255: 1-15.
- Rudolphi, J. & Gustafsson, L., 2011. Forests regenerating after clear-cutting function as habitat for bryophyte and lichen species of conservation concern. PLoS One, 6: e18639.
- Samset, I. 1990. Some observations on time and performance studies in forestry. Communications of the Norwegian Forest Research Institute. Ås. 43: 80.
- Schlamadinger, B. & Marland, G., 1996. Carbon implications of forest management strategies. In Forest Ecosystems, Forest Management and the Global Carbon Cycle. Springer, Berlin, Heidelberg, pp. 217-229.
- Schulze, E. D., Wirth, C. & Heimann, M., 2000. Managing forests after Kyoto. Science, 289: 2058-2059.
- Shannon, C. E., 1949. The Mathematical Theory of Communication. University of Illinois Press, Urbana, pp. 29-125.
- Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins, 49:11-42.
- Siitonen, J. & Saaristo, L., 2000. Habitat requirements and conservation of Pytho kolwensis, a beetle species of old-growth boreal forest. Biological Conservation, 94: 211-220.
- Similä, M., Kouki, J. & Martikainen, P., 2003. Saproxylic beetles in managed and seminatural Scots pine forests: quality of dead wood matters. Forest Ecology and Management, 174: 365-381.
- Simonsson, P., Gustafsson, L. & Östlund, L., 2015. Retention forestry in Sweden: driving forces, debate and implementation 1968–2003. Scandinavian Journal of Forest Research, 30: 154-173.
- Sirén, G., 1961. Skogsgränstallen som indikator för klimatfluktuationerna i norra Fennoskandien under historisk tid. Communicationes Instituti Forestalis Fenniae, 54: 1-66.

Skogsdata, 2017. SLU, Institutionen för skoglig resurshushållning, Umeå, Sweden.

- Spribille, T., Thor, G., Bunnell, F. L., Goward, T. & Björk, C. R., 2008. Lichens on dead wood: species-substrate relationships in the epiphytic lichen floras of the Pacific Northwest and Fennoscandia. Ecography, 31: 741-750.
- Stenger, A., Harou, P., & Navrud, S., 2009. Valuing environmental goods and services derived from the forests. Journal of Forest Economics, 15: 1-14.
- Stokland, J., Siitonen, J. & Jonsson, B. G., 2012. Biodiversity in dead wood. Cambridge University Press, Cambridge, United Kingdom, 524 p.
- Sundseth, K., 2006. Natura 2000 in the Boreal region. European Commission Environment-Directorate General, Belgium.
- Svedlund, L. & Löfgren, R., 2003. Protecting the forests of Sweden: legal protection in the form of national parks, nature reserves, habitat protection areas and nature conservation agreements. Skogsstyrelsen, Jönköping, Sweden.
- Svensson, M., Dahlberg, A., Ranius, T. & Thor, G., 2013. Occurrence patterns of lichens on stumps in young managed forests. PloS One, 8: e62825.
- Svensson, M., Johansson, V., Dahlberg, A., Frisch, A., Thor, G. & Ranius, T., 2016. The relative importance of stand and dead wood types for wood-dependent lichens in managed boreal forests. Fungal Ecology, 20: 166-174.
- Sverdrup-Thygeson, A. & Lindenmayer, D. B., 2003. Ecological continuity and assumed indicator fungi in boreal forest: the importance of the landscape matrix. Forest Ecology and Management, 174: 353-363.
- Sverdrup-Thygeson, A., Gustafsson, L. & Kouki, J., 2014. Spatial and temporal scales relevant for conservation of dead-wood associated species: current status and perspectives. Biodiversity and Conservation, 23: 513-535.
- Swedish Forest Agency, 2014. Swedish statistical yearbook of forestry. Skogsstyrelsen, Jönköping.
- SFS, 1974. Svensk författningssamling, 1974:1026.
- SFS, 1979. Svensk författningssamling, 1979:429.
- SFS, 1993. Svensk författningssamling, 1993:553.
- Swedish Species Information Centre, 2015. Rödlistade arter i Sverige. SLU, Uppsala (In Swedish).
- Tarasov, M. E. & Birdsey, R. A., 2001. Decay rate and potential storage of coarse woody debris in the Leningrad region. Ecological Bulletins, 49: 137-147.
- The Royal Swedish Academy of Agriculture and Forestry, 2015. Forest and forestry in Sweden. KSLA, Stockholm.
- Thor, G., 1997. Red-listed lichens in Sweden: habitats, threats, protection, and indicator value in boreal coniferous forests. Biodiversity and Conservation, 7: 59-72.

- Tikkanen, O. P., Martikainen, P., Hyvärinen, E., Junninen, K. & Kouki, J., 2006. Red-listed boreal forest species of Finland: associations with forest structure, tree species, and decaying wood. Annales Zoologici Fennici, 43: 373-383.
- Toivanen, T. & Kotiaho, J. S., 2010. The preferences of saproxylic beetle species for different dead wood types created in forest restoration treatments. Canadian Journal of Forest Research, 40: 445-464.
- Tönnes, S., Karjalainen, E., Löfström, I. & Neuvonen, M., 2004. Scenic impacts of retention trees in clear-cutting areas. Scandinavian Journal of Forest Research, 19: 348-357.
- Triviño, M., Juutinen, A., Mazziotta, A., Miettinen, K., Podkopaev, D., Reunanen, P., & Mönkkönen, M., 2015. Managing a boreal forest landscape for providing timber, storing and sequestering carbon. Ecosystem Services, 14: 179-189.
- Vesala, T., Suni, T, Rannik, Ü., Keronen, P., Markkanen, T., Sevanto, S., Grönholm, T., Smolander, S., Kulmala, M., Ilvesniemi, H., Ojansuu, R., Uotila, A., Levula, J., Mäkelä, A., Pumpanen, J., Kolari, P., Kulmala, L., Altimir, N., Berninger, F., Nikinmaa, E. & Hari, P., 2005. Effect of thinning on surface fluxes in a boreal forest. Global Biogeochemical Cycles, 19:1-11.
- Wagner, C., Schram, L. J., McMullin, R. T., Hunt, S. L. & Anand, M., 2014. Lichen communities in two old-growth pine (Pinus) forests. Lichenologist, 46: 697-709.
- Weslien, J. & Westerfelt, P. 2017. Drivning och markberedning slog hårt mot den döda veden 80 procent av lågorna skadades i Effaråsen. In Björheden, R. & Thor, M. (eds) Skonsam och produktiv skogsteknik. Rapport från ett treårigt program 2014–2016. Skogforsk, Uppsala, Sweden, 63 p.
- Wikström P., Edenius L., Elfving B., Eriksson L.O., Lämås T., Sonesson J. & Öhman K., Wallerman J., Waller C. & Klintebäck, F., 2011. The Heureka forestry decision support system: an overview. Mathematical and Computational Forestry and Natural-Resource Sciences, 3: 87-94.
- Williams, A.S, 1908. Logging by steam. For Quarterly. 6:1-33.
- Work, T. T., Shorthouse, D. P., Spence, J. R., Volney, W. J. A. & Langor, D., 2004. Stand composition and structure of the boreal mixedwood and epigaeic arthropods of the Ecosystem Management Emulating Natural Disturbance (EMEND) landbase in northwestern Alberta. Canadian Journal of Forest Research, 34: 417-430.
- Yoda, K., Kira, T., Ogawa, H. & Hozumi, K., 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. Journal of Biology of Osaka City University, 14: 107-129.
- Zackrisson, O., 1977. Influence of forest fires on the North Swedish boreal forest. Oikos, 29: 22-32.
- Zackrisson, O., 1980. Forest fire history: ecological significance and dating problems in the north Swedish boreal forest. In: Proceedings of the Fire History Workshop, USDA Forest Service. General Technical Report RM-81. Rocky Mountain Forest and Range Experiment Station, Ft. Collins, Colorado, pp. 120-125.

- Zanchi, G., Belyazid, S., Akselsson, C. & Yu, L., 2014. Modelling the effects of management intensification on multiple forest services: a Swedish case study. Ecological Modelling, 284: 48-59.
- Zenner, E. K., Acker, S. A. & Emmingham, W. H., 1998. Growth reduction in harvest-age, coniferous forests with residual trees in the western central Cascade Range of Oregon. Forest Ecology and Management, 102: 75-88.
- Zhang, D. & Pearse, P. H., 2011. Forest Economics. UBC Press, Vancouver, Canada, 412 p.
- Zobel, B. & Talbert, J., 1984. Applied forest tree improvement. John Wiley & Sons, New York, 505 p.
- Ågren, G. I., Bosatta, E. & Balesdent, J., 1996. Isotope discrimination during decomposition of organic matter: a theoretical analysis. Soil Science Society of America Journal, 60: 1121-1126.

Popular science summary

Forests provide a multitude of benefits such as firewood, building materials, and habitats for many species, as well as regulating carbon, nutrients and water cycles. Forest management tends to focus on only a few of these benefits, primarily wood production. Attention is however increasingly being paid to other services, such as biodiversity conservation and carbon storage, which is related to climate regulation. Trees store carbon during photosynthesis, a process that converts sunlight, CO₂ and water into carbohydrates (nutrients for the plants), while releasing oxygen. Carbon storing capacity varies with tree age. Young trees fix more carbon than older trees. Forests also release carbon, during decomposition of dead wood and soil respiration, performed by organisms that decompose organic matter. Dead wood is a fundamental substrate in forest, a habitat for many species (such as beetles, fungi, lichens and mosses) but its occurrence, in terms of volume and diversity, is threatened by forest management that tends to reduce the accumulation of non-merchantable materials.

Since the main objective of the forest industry is to maximize production while minimizing costs, the provision of multiple services is not always easy to achieve. For example, biodiversity conservation and carbon storage incur an economic cost but rarely produce immediate benefits for individual forest owners.

Today, in what is called sustainable forest management, the balance between ecological, economic and socio-cultural aspects is highly promoted, with the aim of ensuring the same benefits that forests provide now are also available to the future generations.

In this thesis, I have investigated the impacts of tree and dead wood retention practice on wood production, biodiversity (in relation to dead wood) and carbon stock, in Swedish Scots pine forest.

The experiments were conducted in 15 forest stands with varying tree retention levels, in which four categories of trees were retained at similar proportions: green living trees, damaged trees, standing cut trees and cut trees left on the ground. Three additional stands were left intact to monitor their natural development over time.

This thesis consists of three studies. In the first, I investigated how tree retention affects both the amount and diversity of dead wood and the economic outcomes for the landowner. In the second, I simulated outputs of commercial wood production, dead wood and carbon stock over a 100-year period at the scale of both the stand and the wider landscape. At the landscape scale, landscape size and volume of wood produced were kept constant, while forest management type and amount of unharvested land set-aside for conservation were varied. In the third study, I investigated how different dead wood types and their specific characteristics influence the occurrence of dead wood dependent lichens. The results showed that increased retention level leads to diminished income from wood production, decreased level of dead wood destruction, and a higher volume and diversity of dead wood. Furthermore, increased retention level promotes carbon storage at the stand scale. The stand-scale simulations showed that different retention levels have a large influence on the longterm delivery of the investigated variables. However, if merchantable wood production was maintained at a constant level among landscape-scale simulations, differences in the other outcomes were generally small. The lichen species composition differed significantly among the investigated wood types. Many species were highly associated with old and hard wood, a rare wood type in managed forest. The findings of this thesis can be used to guide future forest management plans.
Acknowledgements

This research has been financially supported by the EU through the Marie Curie Initial Training Networks (ITN) action CASTLE, grant agreement no. 316020, and by Skogforsk. The work has been carried out at Skogforsk and at the Swedish University of Agricultural Science, Ecology Department.

I would like to thank all the people that contribute to this international research platform.

I would like to thank my main supervisor, Thomas Ranius and my supervisors Jan-Olov Weslien, Line B. Djupström, Jörgen Rudolphi and Johan Sonesson, for their availability and for their determination to find the right solution to the problems. I would like to thank Sima Mohtashami, Hagos Lundström and Lars Eliasson for the wonderful daily support. I would like to thank also Lena Gustafsson for the valuable comments on the thesis, Gerard Malsher for the language improvement, and Pernilla Borgström for the contribution to the translation of the abstract.

I would like to thank Edo for having been always at my side, accepting a very special style of life. This thesis is also yours! I would like to thank our families for the distance-support, with special regards to the beloved Silente and Spank. I would like to thank my friends without borders, with special regard to "Donne del Nord", for the love and for the stories shared drinking tea and dreaming of a more compassionate world. I would like to thank them for the time spent knowing each other, our feelings, our languages, and our dreams. Thank you for having increased my knowledge of the world and consequently of myself. This four years were an excellent school of life, mostly because of you.

In this thesis, I enhanced the importance of forest structural diversity. In here I wish to enhance the importance of humans' structural diversity. For some strange reasons, it seems like the differences among individuals have never been welcome. By reducing the diversity, we reduce our common knowledge which is probably the most valuable treasure of all time. I'm glad to have had the chance to learn from diversity and I will do my best to keep it alive. So, thank you diversity.

Finally, I would like to thank Nature for being so marvellous. I hope to be lucky enough to reach the day when we will all realize the terrible mistakes committed without asking You the permission. We belong to You, we don't own You. What we own is just our soul, the rest is borrowed.



Figure 14. A friend. Photo: Io.