

Reserve Selection in Boreal Forest

Focusing on Young Forest Biodiversity Potential

Johanna Lundström

Faculty of Natural Resources and Agricultural Sciences

Department of Ecology

Uppsala

Doctoral Thesis

Swedish University of Agricultural Sciences

Uppsala 2013

Acta Universitatis agriculturae Sueciae

2013:46

Cover: Forest landscape in the county of Dalarna
(photo: Samuel Bengtson)

ISSN 1652-6880

ISBN 978-91-576-7831-7

© 2013 Johanna Lundström, Uppsala

Print: SLU Service/Repro, Uppsala 2013

Reserve selection in boreal forest. Focusing on young forest biodiversity potential

Abstract

Most boreal forests in North Europe are intensively managed, and the forest landscape is far from its natural stage leading to hundreds of species being threatened in Sweden alone. Reserves are established to protect biodiversity, but since the resources available for conservation do not cover all species in need of protection, effective prioritization is essential.

In this thesis, a reserve selection model based on a goal programming approach was developed, finding the optimal age composition of reserves in boreal Sweden under different prerequisites. Forest data were derived from the Swedish National Forest Inventory (NFI) and the amount of structural indicators (proxy for biodiversity) registered in the NFI were maximized while simultaneously reassuring that all indicators were represented. I wanted to investigate how reserve selection could be made more effective by considering: (1) cost, (2) subjective preferences, and (3) future biodiversity potential, where the development over time was simulated using the forest analysis and planning tool Heureka PlanWise. To evaluate species response to retained structures in young managed forest, lichen species richness on retained aspen trees was surveyed. Results show that young forest is a cost-effective alternative. The proportion of young forest varied from 46% when subjective preferences were considered, to 76% when only the future values were considered. The cost-effective models were contrasted with area-effective models to show the pros and cons with such approaches. The area-constrained models often selected a more or less large proportion of old forest (77% when subjective preferences were considered, but 13% when only future values were considered), and were more expensive but covered less area to reach the same biodiversity value. In the aspen study higher lichen species richness was found on the retained trees that had been exposed for a longer time, including easily dispersed species and species often found in old forest. Scientists alone cannot find the optimal reserve network, since it depends on the goals that are set by society and how success is valued. Decision makers have to integrate societal, ecological and economic data and balance short term and long term constraints in terms of cost and available area in order to design cost-effective conservation strategies.

Keywords: AHP, conservation planning, cost-effective, early succession, goal programming, lichens, net present biodiversity value, retention

Author's address: Johanna Lundström, SLU, Department of Ecology,
P.O. Box 7044, 750 07 Uppsala, Sweden
E-mail: Johanna.Lundstrom@slu.se

Contents

List of Publications	7
Abbreviations	9
1 Background	11
1.1 Boreal forest	11
1.2 Biodiversity	12
1.2.1 How to measure biodiversity	13
1.3 Conservation	14
1.3.1 Forest conservation in Sweden	14
1.3.2 Retention actions	15
1.3.3 Systematic conservation planning	15
1.4 Methodological framework	17
1.4.1 Cost-effectiveness analysis	17
1.4.2 MCDA	18
1.4.3 Optimization	18
1.5 Young forests	19
1.6 Epiphytic lichens and aspen	19
1.6.1 Lichens in boreal forest	19
1.6.2 Aspen	20
2 Thesis aims	21
3 Methods	23
3.1 Study area	23
3.2 Data collection	25
3.2.1 National Forest Inventory	25
3.2.2 Interview with stakeholders	27
3.2.3 Retention trees	27
3.3 Data analysis	29
3.3.1 Opportunity cost and forest projections in Heureka	29
3.3.2 Reserve selection model	29
3.3.3 Weight determination with AHP	30
3.3.4 Statistical analyses	32
4 Results and discussion	33
4.1 Reserve selection in boreal forests	33

4.1.1	Cost-effective age composition in the selected forests	33
4.1.2	Effect on age composition when considering preferences	34
4.1.3	Effect on age composition when considering future potential	34
4.1.4	Comparing age composition from different reserve selection variants	36
4.1.5	Geographical distribution under different selection alternatives	37
4.1.6	Sensitivity analysis of the goal programming model	38
4.2	Lichen species richness on retained aspen	39
5	Conclusions	41
6	Acknowledgements	45
	References	47
	Svensk populärvetenskaplig sammanfattning	57
	Tack!	61

List of Publications

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

- I Lundström, J., Öhman, K., Perhans, K., Rönnqvist, M. & Gustafsson, L. (2011). Cost-effective age structure and geographical distribution of boreal forest reserves. *Journal of Applied Ecology* 48(1), 133-142.
- II Lundström, J., Öhman, K., Rönnqvist, M. & Gustafsson, L. How reserve selection is affected by stakeholder preferences in Swedish boreal forests (manuscript).
- III Lundström, J., Öhman, K., Rönnqvist, M. & Gustafsson, L. Considering future biodiversity potential in conservation planning (manuscript).
- IV Lundström, J., Jonsson, F., Perhans, K. & Gustafsson, L. (2013). Lichen species richness on retained aspens increases with time since clear-cutting. *Forest Ecology and Management* 293(1), 49-56.

Papers I and IV are reproduced with the permission of the publishers; John Wiley and Sons, and Elsevier.

The contribution of Johanna Lundström to the papers included in this thesis was as follows:

- I Main author and analysis. Idea and design with Lena Gustafsson, Mikael Rönnqvist, Karin Öhman and Karin Perhans.
- II Main author and analysis. Idea and design with Lena Gustafsson, Mikael Rönnqvist and Karin Öhman.
- III Main author and analysis. Idea and design with Lena Gustafsson, Mikael Rönnqvist and Karin Öhman.
- IV Main author and analysis. Idea and study design with Lena Gustafsson and Karin Perhans. Field work by Fredrik Jonsson.

Abbreviations

AHP	Analytic Hierarchy Process
CR	Consistency Ratio
GP	Goal Programming
IP	Integer Programming
LP	Linear Programming
MCDA	Multiple Criteria Decision Analysis
NFI	National Forest Inventory
NPBV	Net Present Biodiversity Value
NPV	Net Present Value

1 Background

1.1 Boreal forest

The boreal forest is the largest forest ecosystem on the planet, comprising over 30% of the global forest area (Hansen *et al.*, 2010). These forests can be found in a circular belt around the northern hemisphere. The boreal forest in Northern Europe (Sweden, Norway and Finland) has a homogenous structure due to the relatively low tree species diversity, dominated by the coniferous tree species Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). Among the deciduous tree species silver birch (*Betula pendula*), downy birch (*Betula pubescens*), aspen (*Populus tremula*), goat willow (*Salix caprea*) and rowan (*Sorbus aucuparia*) are characteristic of early successional stages, while alder (*Alnus glutinosa* and *A. incana*) is primarily found in wet areas. The fourth most common tree species (after pine, spruce and birch) is the exotic lodgepole pine (*Pinus contorta* var. *latifolia*), introduced from North America in the 1920s and cultivated on large scale since the 1970s. The forest floor in boreal forests of Northern Europe is often more dominated by lichens and mosses than by vascular plants, and compared to boreal forests elsewhere the shrub layer is less distinguished (Esseen *et al.*, 1997). Most Northern European forests are heavily managed and have been so for a long time, which has led to even aged forests with small amount of features that are common in a natural forest, e.g. dead wood and old trees (Östlund *et al.*, 1997; Löfman & Kouki, 2001). Before the introduction of large scale forestry practices the boreal forest was shaped by natural disturbances e.g. fires or storms, and the historic landscape was characterized by a mosaic of different forest ages (Zackrisson, 1977; Angelstam, 1998). The natural age distribution is difficult to reconstruct since the frequency, intensity and effect of the natural disturbances varied depending on climate, geology and species composition (Zackrisson, 1977; Bergeron, 1991; Ohlson *et al.*, 2011). The fire regime was probably different in

Northern Europe compared to North America. The intensity and frequency of fires in Northern Europe were most likely smaller, leading to a more diverse age composition without large homogenous even aged forests as might have been the case in North America (Kuuluvainen, 2009). A natural forest has a larger spatial variation than a managed forest, and to distinguish stands in a natural forest would be almost impossible, since disturbance and succession are occurring and progressing on different scales constantly. In the early 1900s fire was starting to be suppressed, and now forest fires have virtually disappeared (Östlund *et al.*, 1997). The largest natural disturbances at present are related to other climatic factors such as wind and snow, but also damages created by mammals, insects and fungi (Anon, 2007). Due to man's alteration of forest composition the forest landscape is far from its natural stage and as a consequence hundreds of species are threatened in Sweden alone (e.g. Berg *et al.*, 1994)

1.2 Biodiversity

The Rio Declaration established at the United Nations conference on environment and development in Rio de Janeiro 1992 states that “biological diversity means the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part: this includes diversity within species, between species and of ecosystems” (Anon, 1992a).

Biodiversity can also be divided into three types: compositional, structural and functional (Franklin, 1988; Noss, 1990; Ferris & Humphrey, 1999; Spanos & Feest, 2007). Composition captures what a system consists of, i.e. diversity of landscapes, species and genes, structure embraces how the components are organized e.g. spatial heterogeneity and microclimatic variation, and function is how the components are interacting, i.e. the processes that are performed by the system (Fig. 1).

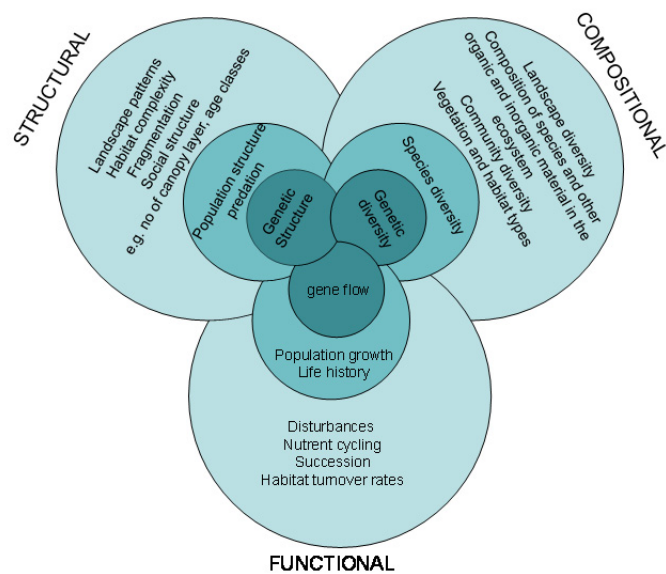


Figure 1. A modified version of Noss (1990) biodiversity model combining types and levels of biodiversity with expanded sphere characteristics (Ferris & Humphrey, 1999; Spanos & Feest, 2007).

1.2.1 How to measure biodiversity

A measure of biodiversity is needed when evaluating conservation value of an area and when prioritizing between areas to include in a reserve network. However, since the concept is so wide all included features cannot be summed up into one single parameter (Sarkar & Margules, 2002). Instead some kind of surrogate for the general diversity is needed. Traditionally species richness (compositional diversity) has been applied as a surrogate, although several studies have shown that environmental variables (structural diversity) also could serve as a surrogate for general biodiversity (Faith, 2003; Bonn & Gaston, 2005; Sarkar *et al.*, 2005). Functional diversity (processes e.g. nutrient cycling) is rarely estimated, based on the assumption that function would be indirectly captured in the estimation of structural or compositional diversity (Ferris & Humphrey, 1999). For example when using dead wood as an indicator, the idea is to capture its many functions, such as a habitat for many species groups, fuel for forest fires, part in the nutrient cycling and energy source for carbon cycling (Ferris & Humphrey, 1999).

1.3 Conservation

Destruction, fragmentation and homogenization of natural landscapes have dramatically decreased biodiversity worldwide and finding ways to mitigate diversity losses is an urgent task (Butchart *et al.*, 2010). Areas have been set aside to preserve natural values since ancient times, and in the last decades reserves have been established as a way of compensating human impact and to protect biodiversity (Anon, 1992b). The conservation value of an area does not depend only on its current ecological characteristics, but also on past conditions and also future states (Kouki *et al.*, 2004). Natural ecosystems have developed within a range of possible conditions, and different disturbance regimes are often the main drivers in creating the variety of conditions that exists in both time and space (Reynolds, 2002; Cyr *et al.*, 2009). Hence, biodiversity is affected by both large scale and long term natural dynamics. Since reserves comprise only a fraction of the total land area, land that is used by humans has to be incorporated into conservation strategies as well to secure a long term biodiversity protection (Bengtsson *et al.*, 2003). This realization has led to the integration of conservation actions into management practices within forestry (Franklin *et al.*, 1997).

1.3.1 Forest conservation in Sweden

According to FAO (2010) 12% of the world's forests are protected and the trend since 1990 is an increasing proportion. FAO figures also indicate that in Europe 4% of the forest land is protected for conservation purposes and in Sweden 10%. In Sweden the term forest is divided into productive forest land and unproductive forest land. A potential yield capacity of 1 m³ mean annual increment per ha (on average over 100 years) has to be reached in order to be classified as productive forest land (Anon, 2005). With this definition approximately 4% of the forest land in Sweden is protected from management actions in reserves, national parks or as nature management areas (Swedish Forest Agency, 2012), whereof a majority is located in the north-western parts of the country (Fridman, 2000).

The Swedish Forestry Act gives equal importance to timber production and biodiversity (Swedish Government, 1993), but it does not state how to evaluate if this is achieved. The strategy in Sweden is to have both formally protected areas and to practice general conservation measures in managed forests. Apart from legal obligations, certification standards also contribute to encourage biodiversity considerations in the managed forests. FSC (Forest Stewardship Council) and PEFC (Programme for the Endorsement of Forest Certification schemes) are the two largest certification agreements. One part of certification is voluntary set-asides, decided and applied by the forest owners.

Approximately half of the protected areas in Sweden consists of voluntarily set-asides (Swedish Forest Agency, 2012).

1.3.2 Retention actions

The few percent of formally protected boreal forest are not enough to maintain biodiversity, hence the production forests need to resemble natural forests to a greater extent to provide suitable habitats also in the matrix surrounding the reserves (Franklin *et al.*, 1997; Lindenmayer & Franklin, 2002). This is achieved by integrating conservation actions such as retention of living and dead trees into forestry operations (Gustafsson *et al.*, 2012).

The aim with tree retention is to: (1) function as lifeboats for species surviving from the previous old forest, (2) increase the structural diversity on the clear cut, (3) act as stepping stones and increase the possibility for species to disperse, (4) increase the amount of remnant structures in an early successional habitat, and (5) sustain ecosystem functions like mycorrhiza formation and nitrogen retention (Franklin *et al.*, 1997; Gustafsson *et al.*, 2010).

In Sweden today approximately 6 m³ of the volume of living trees is retained as conservation trees during clear-felling operations. Dead wood is also retained, on average 7 m³ ha⁻¹ (Swedish Forest Agency, 2012). Previous studies have shown positive effects of retention on biodiversity when comparing clear-cutting with and without retention (Rosenvald & Löhmus, 2008), but the level of retention is often too low to capture many species groups (Aubry *et al.*, 2009). Aspen is a suitable retention tree, since it is a pioneer species with regeneration promoted by disturbances, and it also hosts more unique epiphytic species than any other boreal tree species (Hedenås & Hedström, 2007). The reported effect on epiphytic lichens on aspen retained during clear-cutting or selective logging varies depending on the lichen species in question (Peck & McCune, 1997; Hazell & Gustafsson, 1999; Hedenås & Ericson, 2003). However, even if some lichen species are too sensitive to cope with the harsher environment on a clear cut, many lichens are still found on retained trees even after several years (Löhmus & Löhmus, 2010).

1.3.3 Systematic conservation planning

The role of reserves within systematic conservation planning is to represent the existing diversity of a region and to protect and separate that diversity from threatening processes. Due to an increasing human demand for natural resources and a strong competition for remaining habitats it is vital to have an effective and systematic approach when designing and finding new reserves (Margules & Pressey, 2000). In the last decades there has been a great

development of theories and techniques on how to make reserve selection more effective.

In this thesis I use the term effectiveness since the questions I address concern protecting as much biodiversity as possible for a specific amount of money or on a given area. Another possible measure would be efficiency where a specific amount of diversity should be protected on as small area or for as little money as possible (Fig. 2). Ideally the selection of reserves should be both efficient and effective, i.e. the reserve network should be as small or as cheap as possible (depending on what factor that is limiting), and at the same time come as close as possible to the conservation goal.

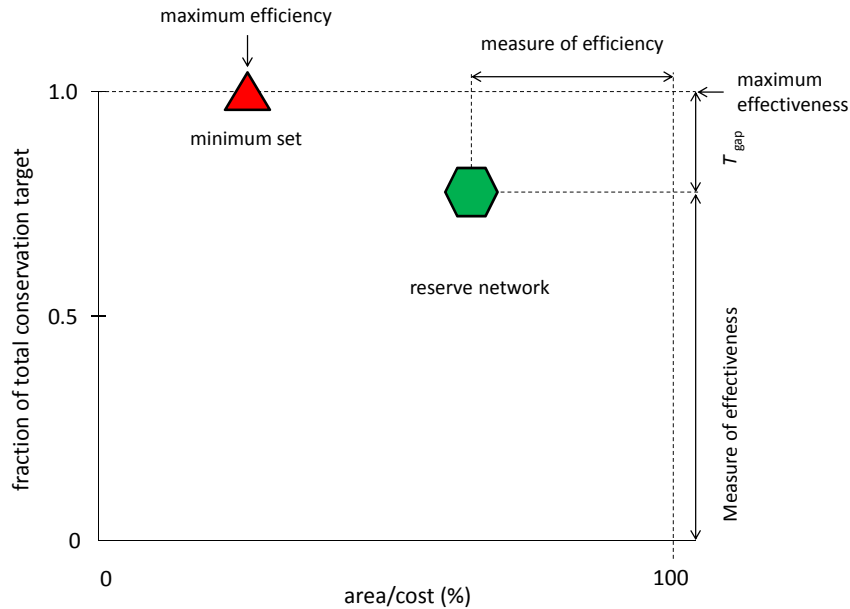


Figure 2. Illustration of the concepts of *efficiency* and *effectiveness*. Efficiency is larger when the area/cost of the sites in the reserve network is smaller. Maximum efficiency is obtained by the minimum set that attains the total representation target. Effectiveness is a measure of how close a reserve network is to attaining the representation target, T_{gap} (when T_{gap} is smaller, the effectiveness is larger) and maximum effectiveness is reached when $T_{\text{gap}} = 0$. Thus efficiency is measured based on the size or cost of the network (x-axis) while effectiveness is measured based on the performance of the network relative to the representation target (y axis). (Figure and caption adapted from Rodrigues et al. (1999))

Quantitative methods are a prerequisite for making effective and objective selections. The first quantitative applications for locating reserves were developed in the 1980's using iterative methods (e.g. Kirkpatrick, 1983) based on the concept of complementarity (Vane-Wright *et al.*, 1991). In those

methods scores are calculated for the selectable areas and the area with the highest score are selected first. In the second step the scores are adjusted to account for what was represented in the previous step, continuing iteratively until a goal is reached, i.e. a “greedy adding” rule. This was followed in the 1990’s by the recognition of the possibility to formulate reserve selection as an optimization problem, more precisely as an integer program (IP) (Possingham *et al.*, 1993). IP was considered as an improvement compared to the iterative methods since an exact mathematical optimum can be found (Williams *et al.*, 2004). A development from the first minimum reserve set problem, where the objective was to cover a given target in a minimum area, was the maximal covering problem, where the total area was fixed and the objective was to maximize the target in that area (Camm *et al.*, 1996; Church *et al.*, 1996). The development in the 2000’s has emphasized the complexity in the task of making effective conservation planning. Heuristic models i.e. models that generates a solution, but where we do not know if it is the optimal solution, or anything about the solution quality, have been suggested as an alternative for problem formulations that are too complex, e.g. due to stochastic parts of the problem or non-linearity in the objective function or in the constraints (Moilanen 2008). Maybe the most intriguing aspects that cannot be ignored in the planning process is that biodiversity is ever changing in both time and space, that threats from humans are increasing, and that climate change will fundamentally alter the conditions in the future (Pressey *et al.* 2007, Araujo *et al.* 2004). This implies that reserve selection models should be able to consider those aspects to be able to produce credible guidelines.

1.4 Methodological framework

1.4.1 Cost-effectiveness analysis

When evaluating conservation programs aiming to reduce biodiversity loss the focus historically has often been on ecological success, such as changes in the status of species (Salafsky & Margoluis, 1999). However, it is also fundamental to evaluate effectiveness and how much the programs cost, since there is a limit in both time and money available (Murdoch *et al.*, 2007). When budget is limiting, evaluation of how well the investments meet the conservation objective should always be made, and programs that give the greatest rate of return on investment should be prioritized (Wilson *et al.*, 2006; Murdoch *et al.*, 2007).

One way of evaluating resource allocation in public policy decision-making is cost-benefit analysis where an economic evaluation of an environmental quality is made. This way of putting a price tag on ecological values has been

criticized of being inflexible when assuming that the economic currency is the only way to measure value and ethical motivations, when in fact the task is much more complex (Gregory et al., 1993; O'Neill & Spash, 2000). One way of dealing with the problem of evaluating different types of values while keeping their original units is to use Multiple Criteria Decision Analysis (MCDA).

1.4.2 MCDA

MCDA was developed from the areas of operations research, decision theory and welfare economics (Hwang & Yoon, 1981). MCDA is an umbrella term describing a collection of formal approaches all explicitly accounting for different conflicting objectives in the decision process and also making the decisions easier to follow and understand (Belton & Stewart, 2002). The general idea is to help decision makers to organize and synthesize complex, conflicting, multidimensional and incommensurable decisions and in that way they can make better decisions (Belton & Stewart, 2002). These techniques make it possible to compare values that are measured on different scales. One of the most well-known MCDA techniques is the Analytic Hierarchy Process (AHP) (Ananda & Herath, 2009).

1.4.3 Optimization

Optimization is placed under applied mathematics and it comprises the use of mathematical models and methods to find the best solution to a problem with multiple possible alternatives. It is based on a goal, something that should be maximized or minimized, called the objective function. The objective function is limited by constraints. A criterion for being able to optimize a problem is that the objective function and the constraints can be described quantitatively using mathematical functions and relations (Lundgren *et al.*, 2010).

The variable that can be controlled, the decision variable, is in a reserve selection model the selected area. Linear Programming (LP) is an optimization technique where the decision variables that optimize a linear objective function subject to linear constraints are found. The decision variable can in this case be the fraction of an area that is selected, i.e. continuous values are possible. A branch of LP problems is Integer Programming (IP) problems where the decision variable(s) are restricted to being integers or binary, i.e. only discrete values are possible. The decision variable in a binary IP problem would be that an area is either selected or not (Haight & Snyder, 2009).

Goal programming (GP) is a multi-objective programming technique. The idea is that many complex decisions cannot be described with only one objective function, so the next best solution (or the only solution considering

all goals) is to try to reach several goals as closely as possible. GP is the most widely used multi-criteria decision making technique (Romero, 1991).

1.5 Young forests

Young forest is often neglected in present conservation strategies. Early successional forest systems developing after a disturbance are often species rich due to the combination of biological legacies consisting of remaining structures (living and dead trees) and surviving species (Franklin *et al.*, 2000), together with new colonizing species. These forests have a unique diversity considering all levels; compositional, structural and functional. A large proportion of dead wood and some remaining trees characterize a natural young forest; those legacies enable a wide range of suitable habitats for many species. Removing most of the tree layer makes previously limited resources available, such as light, moisture and nutrients, which enable species rich plant communities to develop (Swanson *et al.*, 2011).

1.6 Epiphytic lichens and aspen

1.6.1 Lichens in boreal forest

Lichens are a species rich group in boreal forests and constitute a substantial part of the total fungal diversity (Esseen *et al.*, 1997). They are important for many forest ecosystem functions, e.g. nutrient cycling and formation of structural complexity (Knops *et al.*, 1991; Gunnarsson *et al.*, 2004). The nitrogen fixation function provided by cyanolichens could be especially important in habitats with limited nitrogen access (Campbell *et al.*, 2010). The total number of lichens in Sweden is estimated to be 2400, of which 281 are red-listed (Gärdenfors, 2010). The number of red-listed lichens in boreal forests is 151 (Gärdenfors, 2010).

Lichens are symbiotic organisms consisting of a fungus (mycobiont) and one or several photosynthesizing components (photobiont). The photobiont can be either a species of green alga or a cyanobacterium. Most cyanolichens (lichens with cyanobacteria as photobiont) can utilize atmospheric nitrogen (Nash III, 2008), but need liquid water to activate positive net photosynthesis, whereas many green-algal lichens can activate photosynthesis by water vapor uptake alone (Lange, 1986). Based on the appearance of the lichen thallus three morphological groups are traditionally recognized; crustose (flat), fruticose (branched) and foliose (leafy) (Büdel & Scheidegger, 2008). Lichens can undergo vegetative reproduction via propagules that disperse both the mycobiont and the photobiont simultaneously. Most lichens can also reproduce

sexually, by fungal spores produced in fruiting bodies (mainly apothecia or perithecia) of the mycobiont. These spores have to merge with a photobiontic partner to produce a new lichen thallus, a process called lichenization (Büdel & Scheidegger, 2008).

1.6.2 Aspen

Deciduous trees in general are characteristic of intact boreal forest landscapes, especially in the early stages of the forest succession (Esseen *et al.*, 1997), and old deciduous trees are one of the most important habitat for red-listed species in boreal forests (Berg *et al.*, 1994). Aspen is a hotspot for boreal forest biodiversity, both as a direct habitat resource and because of the effect that the tree has on its immediate surroundings (Kouki, 2008). Over 130 red-listed invertebrates, fungi, lichens and mosses are for example found on dead aspens (Samuelsson & Ingelög, 1996), woodpeckers use aspen for nesting and foraging (Angelstam & Mikusinski, 1994), and ground-living species dwell in the favorable litter created by decomposing aspen leafs (Koivula *et al.*, 1999). Aspen has increased in recent years in Sweden (Hellberg, 2004), however it is decreasing in protected forests (Kouki *et al.*, 2004). Although aspen can exist in old forests where large scale disturbances have been absent for a long time, its long term persistence is threatened if regeneration is not secured (Kouki *et al.*, 2004; Latva-Karjanmaa *et al.*, 2007).

2 Thesis aims

The aim of this thesis was to investigate the optimal forest-age distribution when selecting reserves in boreal forests, and also to increase the knowledge on the biodiversity potential of young forest. The thesis covers several aspects of how to make the conservation planning process more effective, from considering the economic cost, stakeholder preferences and future biodiversity potential in the selected reserves to biodiversity survey and how to evaluate conservation efforts in managed forests. The specific aims in the four papers were to:

- I Analyze the cost-effectiveness and biodiversity potential of protecting forests in different age classes (paper I).
- II Identify how the optimal age distribution of selected reserves differs depending on whether the relative importance of the included biodiversity indicators is considered or not (paper II).
- III Investigate if reserve selection can be made more effective over time by considering age distribution and future biodiversity potential in the selected areas (paper III).
- IV Describe lichen species richness on retained aspen trees and how the lichen community changes with time since clear-cutting (paper IV).

3 Methods

3.1 Study area

All four studies were located in the boreal vegetation zone of Sweden (Ahti *et al.*, 1968) where approximately 54% of the area is defined as productive forest land (Swedish Forest Agency, 2012). These forests have been managed for a very long time, and intensively for over a century. The management has fundamentally shaped the forest landscape and now the managed forest is comprised by even-aged stands of which 76% are less than 100 years (Swedish Forest Agency, 2012).

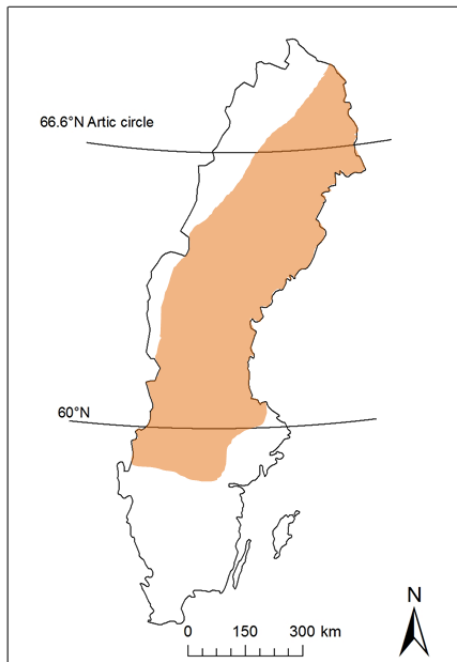


Figure 3. Study I-III covered an area that roughly coincides with the boreal zone of Sweden (study area marked in orange).

Almost half of the productive forest land is owned by private forest owners in northern Sweden, 29% is owned by forest companies and 28% is public forests (Swedish Forest Agency, 2012). In study I-III productive forest land outside reserves and below the mountain area in the boreal zone of Sweden was included (Fig. 3).

In study IV the focus was on a smaller section of the boreal zone, in mid-Sweden (Fig. 4). The most western part was avoided since that area has a distinct humid climate, and therefore host many oceanic lichens (Ahlner, 1948). The estimated mean precipitation in this area is 600-800 mm/year whereof 30-40% comes as snow, average temperature in January ranges from -10 °C to -8 °C and in July from 13 °C to 15 °C (Raab & Vedin, 1995).

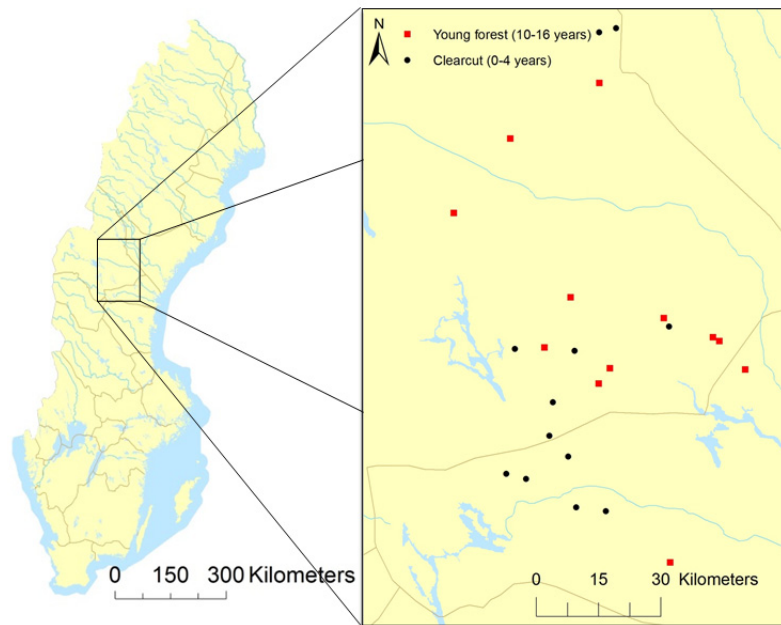


Figure 4. Location of the 24 sites in Jämtland and Västernorrland counties where the fieldwork for study IV was conducted.

3.2 Data collection

3.2.1 National Forest Inventory

Forest data for paper I-III were derived from the Swedish National Forest Inventory (NFI). NFI is a yearly inventory of all land in Sweden, starting in 1923 but with some alterations in design over the years. In 1953 a system with tracts were introduced and in 1983 permanent tracts were established. At present plots are selected using a systematic cluster design where squared tracts are systematically placed over the whole area of Sweden. Two thirds of the tracts are permanent and revisited every fifth year whereas the remaining tracts are temporary and only visited once. Each tract comprises circular plots (radius 7 or 10 m) placed alongside the borders of the tract, and with border length varying between 300 m and 1800 m. Plot and tract sizes differ depending on location in the country, and if the tract is permanent or temporary. Approximately 11 000 plots are surveyed each year (Anon, 2007). Plots on productive forest land outside existing reserves that were surveyed between 2003 and 2007 were used, in total 17 599 plots.

We identified 17 structural variables (Table 1), all registered in the NFI survey, to be used as biodiversity indicators in paper I, in paper II-III all indicators but “gap” were used. The selections of structural indicators were based on types of substrates considered important for many forest living species (Ferris & Humphrey 1999; Lindenmayer et al. 2000; Spanos & Feest 2007). The presence of those indicators was assumed to provide a habitat that possibly could hold a high species richness including many rare species. Each indicator’s registered value in the plot was translated into a point, and those points were later used in the reserve selection models.

For the analysis the plots were aggregated into 112 larger 50x50 km squares, and in paper I-II those squares were further grouped into 6 geographical regions based on administrative county borders. The study area covers eight administrative counties, and the four smallest counties were joined two and two to make the regions more equal in size.

The forest was also divided into five age classes: 0-14, 15-39, 40-69, 70-99, and ≥ 100 years. Unequal ranges were selected because tree retention practices, i.e. saving some trees for conservation purposes at clear-felling (Lindenmayer & Franklin, 2003), were introduced on a large scale about 15 years prior to the studied years. The retention practice has increased structural diversity in the youngest forests (Kruys *et al.*, 2013) and therefore one age class to cover that time was desirable. A normal rotation time in a managed boreal forest is about 100 years and thus 100 years was selected as a breaking point for the oldest age category.

Table 1. Biodiversity indicator data from the NFI plots: mean point, volume of dead wood, total area, and cost per hectare divided into the five age classes. Each NFI plot was assigned a point per indicator, and this point could be 0, 50 or 100, except the indicator volume of dead wood where a plot with $>20\text{m}^3/\text{ha}$ got 100 points, and plots with less dead wood got a normalized point from 0-100 according to the dead wood volume (here the actual volume per ha is shown).

	0-14	15-39	40-69	70-99	≥ 100
Indicator					
Uneven age ¹	8	30	45	63	74
Gaps ²	16	21	28	25	29
Stand character ³	0.04	0.12	0.14	0.62	3.67
Tree layer ⁴	25	43	44	48	45
Ground structure ⁵	35	37	31	29	35
Large pine ⁶	6	1	7	16	23
Large spruce ⁶	0.2	0.6	5.5	13.3	13.9
Large birch ⁶	0.4	0.2	1.6	1.9	0.9
Large aspen ⁶	0.3	0.1	0.6	0.7	0.6
Large (other) deciduous tree ⁶	0.1	0.2	0.4	0.3	0.3
Dead conifer tree lying ⁷	13	7	6	11	16
Dead deciduous tree lying ⁷	4	1	2	2	3
Dead conifer tree standing ⁷	5	1	3	8	12
Dead deciduous tree standing ⁷	0.9	0.2	0.8	2.4	2.4
Presence of rowan ⁸	35	32	29	22	15
Affected by water ⁹	1	1	2	2	2
Dead wood ($\text{m}^3 \text{ha}^{-1}$)	6.8	2.8	4.5	9.5	13.2
Total area (1000 ha)	2394	3479	3070	2029	3554
Cost (1000 SEK ha^{-1})	10	23	33	40	41

1. Could be totally even aged: $>95\%$ of the volume within an age interval of 5 years which gave 0 points, fairly even aged: $>80\%$ of the volume within an age interval of 20 years which gave 50 points, remaining plots got 100 points.

2. This indicator is only used in paper I, and the definition of a gap was: an area without main crop seedlings/main trees larger than a square with a length of 2.5 times the average distance between main crops/seedlings, but at least 5 m. A plot got 100 points if there were several gaps, 50 points if there were some gaps and 0 points when there were no gaps.

3. Could be pristine which gave 100 points and it meant that coarse dead wood were present and there were no trace of management actions during the last 25 years, otherwise the plot got 0 points.

4. Could be fully layered or have several layers which rendered 100 points, two layers gave 50 points, one or no layer gave 0 points. The definition of a tree layer was: a group of trees amongst which the height is approximately the same, but their mean height differs from other layers.

5. Classification based on height and frequency of irregularities (rocks, small hills and holes) on the ground, a very uneven or fairly uneven plot got 100 points, a fairly even got 50 points and an even plot got 0 points.

6. If there was a tree with diameter at breast height over 40 cm present, the plot got 100 points, if there was a tree present with over 30 cm dbh, the plot got 50 points, otherwise the plot got 0 points.

7. If there was a dead tree present with dbh over 20 cm, the plot got 100 points, otherwise the plot got 0 points.

8. If rowan was present in the plot it got 100 points, otherwise the plot got 0 points.

9. If the plot was affected by moving water, by spring flood or was temporarily flooded the plot got 100 points, otherwise the plot got 0 points.

3.2.2 Interview with stakeholders

In paper II the importance of considering stakeholder preferences when selecting reserves was evaluated. To establish how to weight the structural indicators individual interviews was made with one representative from each of the eight county administrative boards in boreal Sweden (Värmland, Örebro, Dalarna, Gävleborg, Jämtland, Västernorrland, Västerbotten and Norrbotten). The representatives (referred to as stakeholders from now on) were experts on how different indicators are valued since they all had been working practically with reserve establishment for at least four years; hence their weights mirror the applied weight in real selection scenarios. Each stakeholder was visited on the administrative county board in question and the interview was performed face to face.

3.2.3 Retention trees

In paper IV the change in lichen species richness with time since clear-cutting on retention trees, was studied. Aspen *Populus tremula* was selected since this tree species has a unique epiphytic flora. Aspen in two age classes of clear felled stands were inventoried (clearcut and young forest).



Figure 5. Two examples of a clearcut (0-4 years). Photos: J. Lundström



Figure 6. Two examples of a young forest (10-16 years). Photos: J. Lundström

The definition of a clearcut was that the clear felling had been carried out 0-4 years prior to the inventory. The inventoried clearcuts were open and comprised of both solitary and aggregated retention trees dispersed over the clear felled area (Fig. 5). The young forests had been clear felled 10-16 years prior to the inventory. They had a larger variation in tree vegetation height between the stands compared to the clearcuts; still the average tree height was considerably lower than that of an old forest (Fig. 6).

A total inventory of epiphytic lichens was made on stems of 720 randomly selected retained aspens (Fig. 7) distributed over 12 clearcuts and 12 young forests (30 trees per stand). The lichens were divided into different categories according to species traits. Aspen specialists were defined as lichens with aspen as a main substrate, or in some cases aspen and *Salix* spp. Dispersal mode, photobiont and if the lichen was sensitive to light or adapted to open environments was also recorded.



Figure 7. Inventory of an aspen by Fredrik Jonsson. Photo: K. Perhans (left); Three of the 195 epiphytic lichens found; *Caloplaca flavorubescens* (asporangelav). Photo F. Jonsson (top right); *Physcia aipolia* (rosettlav) and *Lecanora allophana* (veccakantlav). Photo F. Jonsson (bottom right).

3.3 Data analysis

3.3.1 Opportunity cost and forest projections in Heureka

Data from the NFI constituted the base for the forest projections used to calculate opportunity cost in paper I-III, and to estimate the indicators' future values in paper III. Opportunity cost of a plot was based on the net present value (NPV) of that plot. NPV is the sum of income and cost of activities from today and to infinity, where the future values were discounted back with a 3% interest rate. The projections in paper III were run in 5-year periods for 100 years using the application PlanWise, a part of the planning system Heureka that is developed for multiple-use forestry. Heureka uses projection of tree cover development as a base to predict the future state of the forest and estimates the outcome of different ecosystem services. The projection uses data on current conditions, applied management actions, and known ecosystem processes. There are numerous possible outputs that can be derived such as timber volume, forest age, species distribution, recreation index, and carbon storage (Wikström *et al.*, 2011).

Based on the projected values a net present biodiversity value (NPBV) was calculated for each indicator. NPBV gives us one single value capturing equity across time; four different NPBV variants were estimated, i.e. future values were discounted in four different ways: (1) put weight only on the value today, (2) put equal importance to all 100 years, (3) consider the risk of the indicator disappearing in the future due to storms, and also that this risk was increasing with time because of estimated increased effects from a changing climate in the future, and (4) focusing on the value in year 100.

3.3.2 Reserve selection model

The basic reserve selection model applied in paper I-III used a goal programming approach to find the best selection, defined as maximal sum of points from the indicators (the biodiversity indicator score) while jointly considering all indicators at the same time. This was done in two steps: first all indicators' potential maximal value was searched for, and second the formulation reassured that the difference between each indicator's maximal value and its value in the final solution was as small as possible. In all three papers two scenarios were compared, one where the model was limited by a budget and one where the model was limited by how much area could be selected. In paper I 100 different budgets and 100 different area restrictions were tested. In paper II and III one realistic budget and one equivalent area when it comes to the total biodiversity indicator score were used. The goal programming approach was evaluated in paper II by comparing it to a simple

LP model only maximizing the total biodiversity indicator score, and a model adding a normalization factor to the LP model to account for differences in how common the indicators were. In paper II the model was also expanded with the possibility to add different weights on the different indicators, and the possibility to add geographical or age restrictions. In paper III a time dimension was added to the model.

3.3.3 Weight determination with AHP

The pairwise comparisons procedure of the AHP (Saaty 1990) was used to decide the relative importance of each indicator in paper II. AHP is a mathematical method where complex decisions with multiple criteria are analyzed (Saaty, 1990) and it is often used within forest planning (Ananda & Herath, 2009). AHP aggregates different criteria into an integrated criterion. The process can be divided into four steps:

1. Arranging a hierarchy that objectively describes the relations between the criteria.
2. Constructing a matrix consisting of the relative values of a set of criteria. The relative values are systematically decided by the decision maker who makes pairwise comparisons of criteria on a nine point scale (Table 2).

Table 2. *The Saaty Rating Scale (adapted from Saaty 1977)*

Intensity of importance	Definition	Explanation
1	Equal importance	Two criteria contribute equally to the objective
3	Somewhat more important	Experience and judgment slightly favor one criteria over another
5	Much more important	Experience and judgment strongly favor one criteria over another
7	Very much more important	An criteria is strongly favored and its dominance is demonstrated in practice
9	Absolutely more important	The evidence favoring one criteria over another is of the highest possible order of affirmation
2,4,6,8	Intermediate values	When compromise is needed

Each criterion is compared to all other criteria belonging to the same branch on the same level. The pairwise comparison matrices are made up of $n \times n$ cells where $a_{i,j}$ is the ranking of criterion i over criterion j and this can be transformed to the ratio between w_i of criterion i and w_j of criterion j .

$$A = [a_{ij}] = \begin{bmatrix} 1 & w_1/w_2 & \dots & w_1/w_n \\ w_2/w_1 & 1 & \dots & w_2/w_n \\ \dots & \dots & 1 & \dots \\ w_n/w_1 & w_n/w_2 & \dots & 1 \end{bmatrix}$$

The comparison is only made in one direction since $a_{j,i}$ is assumed to be $1/a_{i,j}$ and comparing a criterion with itself gives the value 1.

3. Weights are calculated by finding the eigenvector that corresponds to the maximum eigenvalue, for each comparison matrix, i.e. the outcome on each level. The weights are then normalized to sum to 1. The consistencies of the judgments are checked, commonly done by using the consistency ratio (CR) (Saaty, 1990).
4. Producing an overall vector by using standard matrix calculations. Subsequent matrices with their own eigenvectors and CRs based on the hierarchy structure follow the first eigenvectors. Now an overall weight for each alternative can be established.

Problems with AHP include that it allows rank reversal and inconsistency. Rank reversal means that two alternatives may be reversed if a new alternative is considered (Dyer, 1990). This violates the independence of irrelevant alternatives axiom of decision theory (Arrow & Raynaud, 1986). The ability to detect inconsistent judgment is a strength of the method, but how to deal with inconsistency could be a problem. Inconsistency is easiest to describe with an example comparing three alternatives A, B and C. The decision maker can state that A is more important than B and B is more important than C but then that C is more important than A, which is logically invalid. Saaty (1990) suggests that if the consistency ratio is over 0.1, the set of judgments may be too inconsistent to be reliable. There are several alternatives to reduce inconsistency: the stakeholder could reconsider the judgments, the original judgments could be improved by the analyst and then presented to the stakeholders for approval, a numerical method for reducing inconsistency could be applied (Zeshui & Cuiping, 1999; Cao *et al.*, 2008) or a higher inconsistency ratio could be accepted. The weights were calculated in the Heureka application PlanEval together with the consistency ratio.

3.3.4 Statistical analyses

Lichen species richness was modeled based on stand and tree characteristics using a generalized linear mixed model (GLMM) in paper IV. To evaluate how well this model explained our data an information theoretic approach based on likelihood measures (AICc; Akaike, 1974) was used. Model averaging was used to handle the problem with model selection uncertainty (Burnham & Anderson, 2002) because several models had similar AICc values. When using model averaging you select an AICc interval and all candidate models with AICc values within this interval are weighted. This Akaike weight is the probability that the model is the best among the candidate models. Several explanatory variables were used, e.g. age class and tree diameter, and each of those variables that are included in at least one of the candidate models get an average parameter estimate, with a confidence interval and a relative importance. The relative variable importance is the probability that the variable will appear in the best model, and is proportional to the models' Akaike weights (Whittingham *et al.*, 2006).

In paper IV an analysis searching for species characteristic of one or the other of the two age classes was made by performing an indicator species analysis (Dufrene & Legendre, 1997). Further, estimators of total species richness were calculated (Magurran, 2004) and a sample based rarefaction curve (Gotelli & Colwell, 2001) was used to estimate how many trees that were needed to capture a certain proportion of the total lichen species pool.

4 Results and discussion

4.1 Reserve selection in boreal forests

Papers I-III in this thesis are all dealing with different variants of the reserve selection model. There are many aspects that have to be considered in the conservation planning process. In this thesis I touch upon several important factors for reserve selection like (1) subjective preferences, (paper II), (2) future biodiversity potential (paper III), and (3) uncertainties regarding the future, such as risks and effects of climate change (paper III). Using optimization models have several benefits apart from giving an optimal solution to a stated problem. The formulated problem is straight forward and transparent, meaning that everyone can see what has been asked for and changes are easy to make. It is also easy to replicate and use the same model on different data sets. This way of analyzing can also be flexible, by looking at near-optimal solutions, or by generating competing objectives, e.g. maximizing species richness vs. minimizing cost (Williams *et al.*, 2004). It is important to remember that when using optimization models the main purpose is to serve as a support for the decision maker, supplying information to be used in the planning process, not to deliver the final selection (Sarkar *et al.*, 2006)

4.1.1 Cost-effective age composition in the selected forests

In paper I we show that the optimal age composition was to a large extent comprised by young forests under a budget constraint by analyzing the results from our reserve selection model, at least at low budgets (Fig. 8). Under an area constraint on the other hand, old forests were dominating (Fig. 9). However, it was much more cost effective to use a budget-constrained model, which also has been shown several times before (e.g. Ando *et al.* 1998 and Polasky *et al.* 2001). In general the area-constrained model covered less area but costs were considerably much higher compared to the budget-constrained model to reach the same biodiversity indicator score. Hence, the selected

forests in the budget-constrained model had fewer points per area unit. A potential problem with the budget-constrained model is that the presence of the indicators might be too low per hectare for hosting associated species. This was tested in paper III where the additive point system was compared to a system based on threshold levels. Each indicator had to reach a minimum threshold to be assigned a point, and when using thresholds the budget-constrained model selected a smaller total area with a generally higher biodiversity quality. Hence, using thresholds could counteract a potential problem with “diluted” indicators. However, there was no difference in age composition between a model using additive score or threshold levels, thus the forests that were excluded since they did not meet the threshold levels were evenly distributed over the age classes.

4.1.2 Effect on age composition when considering preferences

After the interviews with the eight stakeholders in paper II subjective weights for the biodiversity indicators were established, i.e. we identified how important the stakeholders consider the indicators to be for boreal forest biodiversity. The proportion of the youngest age class represented in the selection varied between 32% and 60% in the budget scenarios when comparing models using the eight stakeholders’ individual indicator weight. When using the eight stakeholders average weight the proportion of the youngest age class was 46% (Fig. 8). The budget limit was 10 billion SEK in all variants of the budget scenario. A budget of 10 billion was considered to be realistic since it is only 4 billion higher than the budget allocated for reserve establishment in Sweden in 1998-2008 (Swedish Government, 2009). The middle aged forests were not favored in any of the selections, although they make up a substantial part of the total area.

It is important to reflect over how to use weights wisely; since the age composition of the selected forests differs depending on weight used. In real world situations preferences for estimating biodiversity values are often based on the knowledge and experience of one person or a group of persons. Hence, it is crucial that the members of those groups are reliable to ensure an effective decision base (Regan *et al.*, 2007).

4.1.3 Effect on age composition when considering future potential

The age composition of the selected forest varied depending on which discounting variant that was used (paper III). The first variant put weight only on the value today, leading to a solution in which 75% of the selected forests were less than 15 years, when a budget of 10 billion SEK was limiting the selection (Fig. 8). The second way was to put equal importance to all 100

years, and in this variant 64% of the selected forests were less than 15 years (Fig. 8). The third way was to consider the risk of the indicator disappearing in the future due to storms, and also that this risk was increasing with time due to climate change (Berg & Linder, 2010). When using this discounting variant 60% of the selected forests were less than 15 years (Fig. 8). Nicholson and Possingham (2007) concluded that it was important to incorporate uncertainty about the future when estimating persistence and viability of the species in focus of protecting, to make robust conservation decisions. Further, Araujo et al. (2004) found that some species' habitats might shift to non-protected areas if climate change was not recognized when selecting reserves. Finally, applying the fourth variant that only focused on the value in year 100, resulting in 76% of the selected forests being under 15 years (Fig. 8). Based on those results young forests were not more effective to protect when future biodiversity potential was taken into account. However, forest over 100 years was selected less when future potential was taken into account (11%, 3%, 6% and 0.3% for variant 1, 2, 3 and 4 respectively in the budget-constrained model and 57%, 19%, 23% and 13% for variant 1, 2, 3 and 4 respectively in the area-constrained model) (Fig. 8 and Fig. 9), indicating that we might overestimate the importance of protecting old forests.

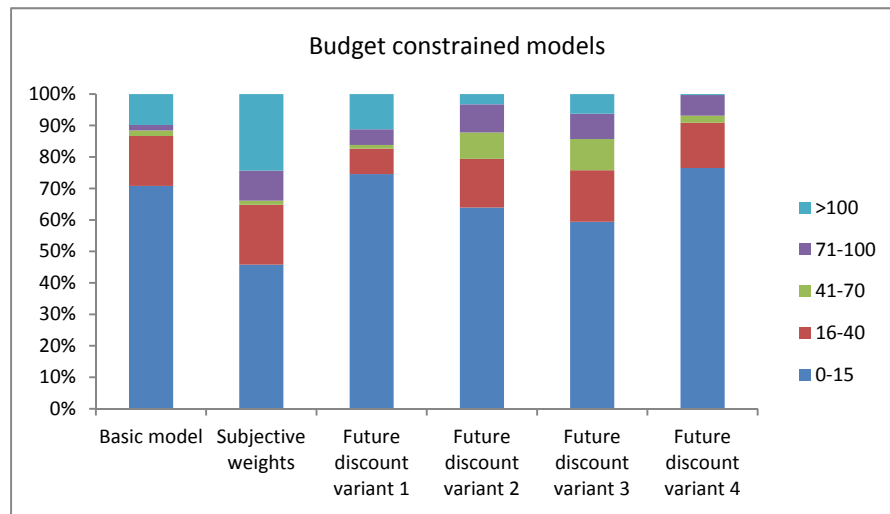


Figure 8. The optimal forest age composition from reserve selection models with a budget constraint of 10 billion SEK. The basic model is from paper I, the mean subjective weight from paper II, and the future discount variants from paper III.

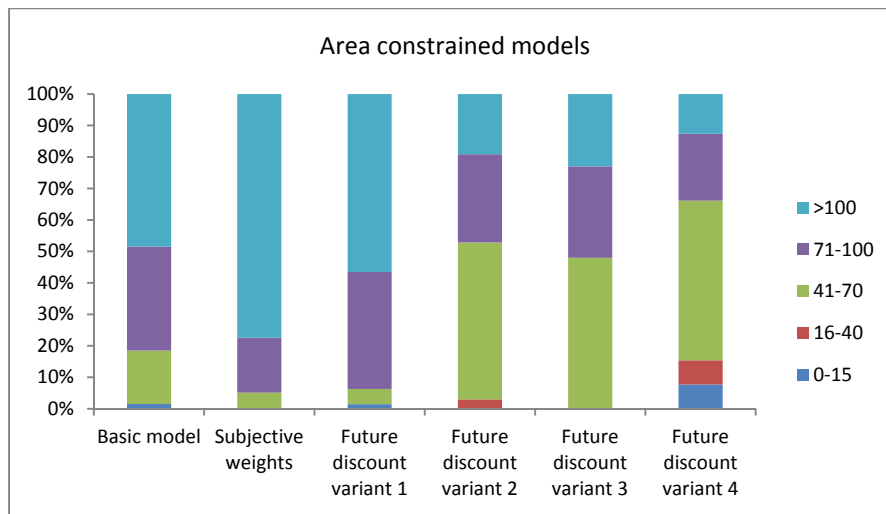


Figure 9. The optimal forest age composition from reserve selection models with an area constraint of 5% in paper I and III, and 4% in paper II. The basic model is from paper I, the mean subjective weights from paper II and the future discounting variants from paper III.

4.1.4 Comparing age composition from different reserve selection variants

We could see consistently in Paper I-III that it was most cost-effective to select a variety of forest ages, including a large proportion of young forests, when establishing new reserves. The actual proportion of young forest varied greatly though: when considering subjective weights the proportion was only 46%, compared to 76% when focusing the selection on the projected value in 100 years (Fig. 8). Hence, the selection differed substantially depending on which aspects were considered, indicating that it is important to reflect over how to formulate the objective and constraints so that they correspond to the actual conservation goals. What those goals are is a question that cannot be answered only scientifically, but should be addressed in collaboration with stakeholders and society.

The budget-constrained models were contrasted with area-constrained models to show the pros and cons with the different approaches. Since the area-constrained models have a strikingly different age composition (Fig. 8 vs. Fig. 9), and geographical distribution (Fig. 10 vs. Fig 11) compared to the budget-constrained models, a reserve network based on either of the two approaches differs fundamentally from the other. The area-constrained models are much more expensive, but the total area covered to reach the same biodiversity indicator score is smaller. Further, when future values were considered, the highest total score over 100 years was rendered with the NPBV variant that only considered current values, while it was the variant considering

only the values year 100 that rendered the highest total score for the budget-constrained model. Consequently, decision makers have to integrate ecological and economic data and balance short term and long term constraints in terms of cost and area in order to design cost-effective conservation strategies (Polasky *et al.*, 2001; Juutinen *et al.*, 2004; Messer, 2006; Naidoo *et al.*, 2006).

4.1.5 Geographical distribution under different selection alternatives

The geographical distribution differed much between a selection limited by a budget and a selection limited by area. When budget was limiting, areas in the northwestern parts of the study area were favored, and when area was limiting the selection was biased towards the southeastern parts (Lundström *et al.*, 2011). When subjective preferences were considered in paper II the geographical distribution was not as biased as it was in paper I. Geographical restrictions were also added to further avoid a geographical disequilibrium, and when this was done the age distribution and biodiversity indicator score were not affected more than marginally. This is interesting since if we would like to move away from the present situation where reserves are concentrated to the north western parts of boreal Sweden (Fridman, 2000) we would not lose much biodiversity values (as assessed by structural indicators) or money. The reason for wanting to force a different geographical pattern is that if species composition varies geographically, it would give us the possibility to protect habitats for species with a restricted geographical range.

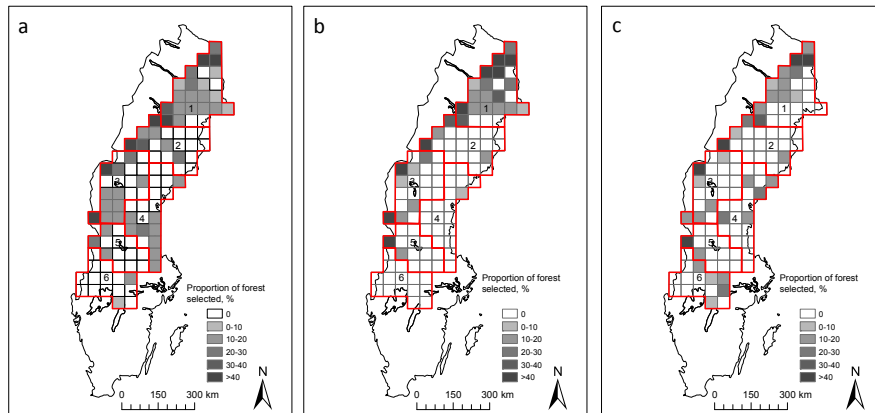


Figure 10. Geographical distribution for a model limited by a budget of 10 billion SEK, with the same weight on all indicators (a), the mean subjective weights added to the indicators (b), and the mean subjective weight and a geographical constraint stating that 12.5% of the total selected area should be situated in each geographical region (c). The regions are 1. Norrbotten, 2. Västerbotten, 3. Jämtland, 4. Västernorrland and Gävleborg, 5. Dalarna, 6. Värmland and Örebro.

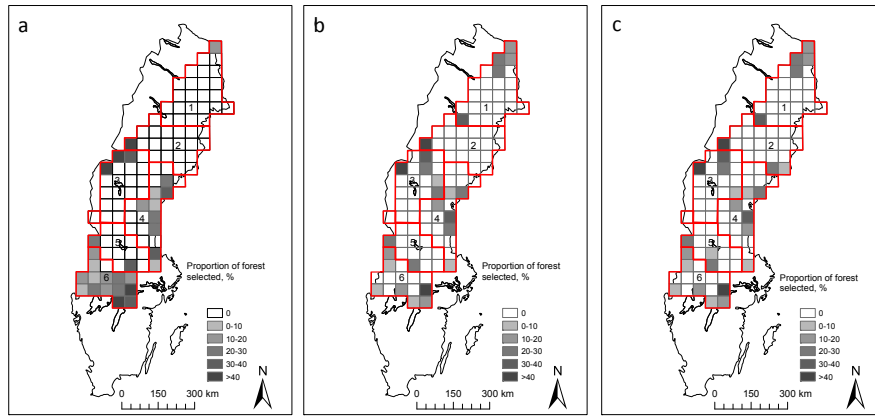


Figure 11. Geographical distribution for a model limited by area (in a the area limit was 5%, and in b and c the area limit was 4%) with the same weight on all indicators (a), the mean subjective weights added to the indicators (b), and the mean subjective weight and a geographical constraint stating that 12.5% of the total selected area should be situated in each geographical region (c). For names of the geographical regions see Fig. 10.

4.1.6 Sensitivity analysis of the goal programming model

A rare indicator will be disfavored in a model only maximizing the total score, and since the indicators are very unequal in how common they are (Table 2), two additional variants for solving the reserve selection problem were tested in paper II. When comparing those two models with the goal programming model, the most common indicator (volume of dead wood) dominated the selection in the simple LP variant, but when adding a normalization factor the dominance decreased and more uncommon variables increased instead (e.g. large aspen). The goal programming model and the LP model with a normalization factor gave fairly similar results, but the goal programming model was better in making the best selection considering all indicators. This is perhaps not surprising since that is what the goal programming model is designed to do. We have tested to add subjective weights to the indicators and also added discounting variants, and concluded that this is something that affects the selections and is important to consider. But it is also crucial to make sure that the indicators are treated correctly by accounting for the large difference in points that exists between them.

4.2 Lichen species richness on retained aspen

We show in paper IV that lichen species richness was higher on trees exposed for 10-16 years (age class: young forest) than on trees exposed for 0-4 years (age class: clearcut). This was also true when only including aspen specialist species. The total species richness in young forests was 182, of which 63 were aspen specialists, and the corresponding numbers for clearcuts were 131 and 47. This suggests that lichen species richness increases with time since clear-cutting on aspens retained at logging. When a tree is retained the stem is exposed to large microclimatic changes and becomes a more diverse habitat than before logging. The difference between the north and south side increases due to sun exposure, the tree could start to lean due to increased impact from wind or destabilization of the root system at clear cutting and scarification. A leaning tree is characterized by a larger structural heterogeneity, and the larger variation in bark pH between the upper and lower side could further increase the possibility for higher species richness. Thus we argue that easily dispersed species have the possibility to colonize a free standing, exposed tree with higher environmental heterogeneity after the clear-felling. This could explain our results of higher species richness on trees exposed for 10-16 years. Another possible explanation to the higher species richness could be that lichens situated higher up on the stem or in the crown have shifted their vertical position downwards when light and moist conditions changed after the clear felling.

Lichens sensitive to light were expected to disappear after the clear-cutting. Since extinction of epiphytic lichens is slow after clear-cutting (Rosensvald & Löhmus, 2008; Perhans *et al.*, 2009), aspen surveyed on clearcuts were assumed to reflect the species composition on aspen in the harvested forest. However, opposed to our expectations species sensitive to light were more common in the young forest. This could partly be explained by a delayed response, and some of the species found in the young forests might be doomed to extinction during the regeneration phase of the forest. However it might also be due to an overestimation of the sensitivity to logging, and field observations indicated that many lichens assumed to be light sensitive might survive on the north sides. One example of species often assumed sensitive to logging are cyanolichens, and their total number did not differ between clearcuts and young forests. This result suggests that cyanolichens can cope with logging disturbance quite well, at least for 10-16 years. Another explanation could be that the most sensitive cyanolichens had gone extinct already prior to the inventory.

5 Conclusions

I wanted to answer the question: How can reserve selection in boreal Sweden be made more effective, and what role does young forest have? And the answer is not a simple one. Based on the results in this thesis, young forest definitely has a large potential to preserve biodiversity within reserve networks in a cost-effective way, since structural diversity is high in relation to the land price. In my empirical study I also found a positive effect on lichen species associated with retained trees in young forests. Nevertheless, there are many aspects to consider. I would advise the stakeholders making decisions concerning reserve establishment to realize that there are several ways of making conservation planning more effective. First of all, considering the limited amount of money available is crucial, and it should be kept in mind that cost-effectiveness is not always equal to selecting the most valuable forests first. Second, there are conservation planning tools available to make the planning process easier, so far rarely used in Sweden today (however for a research application see Mikusiński *et al.*, 2007). Third, it is also important to reflect over future potential in the selected areas, especially since threats to biodiversity are increasing (Pressey *et al.*, 2007), and climate change will most likely have a fundamental impact on which forests are most valuable to protect (Araújo *et al.*, 2004). When in time to put emphasis on actions is an additional aspect that has to be considered. Young forests are especially interesting as reserve alternatives in areas where there are no pristine old growth forests left, and potential protected areas have to be searched for in the managed forest. To protect forests that have been harvested, but where large amounts of dead wood and living trees are retained might be a cost-effective way to protect forest biodiversity. Developing some kind of dynamic reserve network, where old protected forests would be systematically replaced by younger, could be a solution to the problem that there is a limit for how large areas that can be excluded from production without causing too much reduction in timber

volumes for the forest industry. Such a system might benefit both timber production and biodiversity protection. The dynamic reserve approach could also facilitate the adjustment to the likely change in habitats needed by a shifting species assembly due to climate change.

I will end with a summary of the main messages from the thesis, practical implications for conservation and also possible future studies.

➤ **Young forests are a cost-effective alternative when expanding the reserve network**

However, my results show that even if young forests were selected to a large extent, the most effective selection was always a combination of several age classes in both budget and area-constrained models (paper I-III). If future potential of the selected areas was considered the proportion of young forest selected was approximately the same or even smaller, also the proportion of old forest was smaller in the budget constrained models (paper III). This is challenging since it indicates that the present forest reserve strategy in Sweden, which almost exclusively focus on old forest, need to be reconsidered. This is especially evident if the purpose with reserves is to secure biodiversity for the future, since old forests were selected considerably less even in the area-constrained model when future values were considered.

➤ **Not considering cost when selecting reserves could lead to unnecessary waste of money**

We found that it would cost four times more to reach the same biodiversity indicator score when area was limiting compared to when budget was limiting. However, there is a risk that the conservation values are too sparsely distributed in the area selected in the budget-constrained scenario, since the total area selected is larger in such a model. A solution would be to use thresholds as was done in paper III or to have constraints requiring a minimum density.

➤ **Selection of reserves is not only depending on objective facts, but also on subjective preference from decision makers and stakeholders**

The forest selected varied depending on how the indicators were weighted, and the stakeholders interviewed in paper II preferred indicators more common in old forest. Consequently, the selection based on preferences favored the oldest and disfavored the youngest age class in both the budget and area constrained scenarios. Since subjective opinions have such impact

on the selection, it is important that reserve selection models have the possibility to consider and explicitly show different preferences. In order to create a sound basis for decision-making, reflections have to be made on how to estimate a representative biodiversity value, since it depends on both which criteria that is used and also its associated importance.

- **It is important to consider future potential in selected areas, however this can be done in different ways, and the best way cannot be decided by science alone but needs to evolve in collaboration with stakeholders and society**

Reserve selection was more effective if future potential was considered, in the sense that the total biodiversity indicator score over 100 years in the budget constrained model was higher when only the values in year 100 were considered. I evaluated the total score based on the projected values. To make a more true evaluation of the best selection, I would need larger knowledge on future conditions, for example regarding climate change.

A general shortcoming when using structural variables as indicators of biodiversity value is the complex relationship between structures and associated species: the presence of a structural indicator does not automatically mean that we will find the associated species. Species occurrences depend on a range of other factors, for example forest history and connectivity. Explicit measures of viability when considering the possible persistence of species, i.e. considering the spatial configuration of the selected area to maximize the probability of species protection, is important when planning reserve networks (Nicholson & Ovaskainen, 2009). My models are based on structural indicators, i.e. indirect measures of species diversity. Direct assessment of species diversity and associated geographical information would be a natural future development of my study. This could be done using the detailed species data available through the Swedish Species Information Centre.

Not only ecological processes need to be considered when estimating the potential biodiversity value of future forests. Also evolutionary and sociopolitical processes influence the value of reserves (Sarkar *et al.*, 2006). For example, the societal appreciation of what characterizes a valuable forest might be totally different in the future.

➤ **Lichen species richness increases with time since clear-cutting on retained aspen**

The species richness of all lichens, and also aspen specialists, was higher on aspen in young forest compared to aspen on clear cuts. One implication for conservation based on these results is that retention trees function as lifeboats for existing species for at least 10-16 years, while at the same time they provide early-successional habitat for colonizing species. However, we do not know the viability of the lichens and if they will be able to survive until the forest is old again, which is a prerequisite for the life-boating function. Furthermore, we do not know for certain if the higher species richness is due to colonizations, or if the forest that was clear-felled 10-16 years prior to the inventory was more species rich than the forest clear-felled 0-4 years prior to the inventory. Following the development of the lichen community on the retained aspens until the surrounding forest is old again would be very interesting and also doable since all trees are GPS marked. A future re-inventory would also make models analyzing colonization and extinction possible. Another development of this study would be to add a reference age class of old forest, to evaluate the assumption that trees on clearcuts (only exposed for 0-4 years) represent trees in the harvested forest. A secured regeneration of aspen is very important for the long term persistence of both aspen and its associated epiphytic species. I therefore recommend opening up of stands with aspen to facilitate regeneration, and also to leave a buffer zone without regenerating conifers around the retained aspens.

6 Acknowledgements

I would like to thank Lena Gustafsson, Karin Öhman, Mikael Rönnqvist, Karin Perhans, Victor Johansson and Anders Lundström for valuable comments on the thesis, and Martin Rölin and Ola Lundin for improving the Swedish summary. I would also like to thank Per Nilsson, Peder Wikström, and colleagues at SLU in Umeå for supplying data, helping with Heureka and answering questions. I am also grateful to Fredrik Jonsson for collecting lichen data. The studies in this thesis were funded by the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (Formas).

References

- Ahlner, S. (1948). Utbredningstyper bland nordiska barrträdslavar. *Acta Phytogeographica Suecica* 22. p. 257
- Ahti, T., Hämet-Ahti, L. & Jalas, J. (1968). Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici* 5, 169–211.
- Akaike, H. (1974). A new look at the statistical model identification. *Automatic Control, IEEE Transactions on Automatic control* 19(6), 716–723.
- Ananda, J. & Herath, G. (2009). A critical review of multi-criteria decision making methods with special reference to forest management and planning. *Ecological Economics* 68(10), 2535–2548.
- Ando, A., Camm, J., Polasky, S. & Solow, A. (1998). Species Distributions, Land Values, and Efficient Conservation. *Science* 279(5359), 2126–2128.
- Angelstam, P. (1998). Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. *Journal of Vegetation Science* 9(4), 593–602.
- Angelstam, P. & Mikusinski, G. (1994). Woodpecker assemblages in natural and managed boreal and hemiboreal forest- A review. *Annales Zoologici Fennici* 31, 157–172.
- Anon (1992a). Convention on Biological Diversity 1760 UNTS 79; 31 ILM 818. United Nations Environment Programme.
- Anon (1992b). *Global diversity strategy*. Washington DC: World Resources Institute, World Conservation Union and United Nations Development Program.
- Anon (2005). *RIS Riksinventeringen av skog Fältinstruktion 2005*. Umeå, Sweden (in Swedish; updated yearly): Institutionen för för skoglig resurshushållning och geomatik, SLU.
- Anon (2007). *Skogsdata 2007*. Umeå (in Swedish with English summary): Sveriges officiella statistik, Institutionen för skoglig resurshushållning, SLU.
- Araújo, M. B., Cabeza, M., Thuiller, W., Hannah, L. & Williams, P. H. (2004). Would climate change drive species out of reserves? An assessment of

- existing reserve-selection methods. *Global Change Biology* 10(9), 1618–1626.
- Arrow, K. J. & Raynaud, H. (1986). *Social Choice and Multicriterion Decision-Making*. Cambridge: The MIT Press.
- 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(4), 398–408.
- Belton, V. & Stewart, T. J. (2002). *Multiple Criteria Decision Analysis: An Integrated Approach*. Springer. ISBN 9780792375050.
- Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F. & Nystrom, M. (2003). Reserves, resilience and dynamic landscapes. *AMBIO: A Journal of the Human Environment* 32(6), 389–396.
- Berg, A., 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(3), 718–731.
- Berg, J. & Linder, S. (2010). Skogsbruket måste påbörja omställningen. In: *Formas Fokuserar "Sverige i ett nytt klimat-våtvärm utmaning"*. pp 185–202. Stockholm: Forskningsrådet Formas.
- Bergeron, Y. (1991). The Influence of Island and Mainland Lakeshore Landscapes on Boreal Forest Fire Regimes. *Ecology* 72(6), 1980–1992.
- Bonn, A. & Gaston, K. J. (2005). Capturing biodiversity: selecting priority areas for conservation using different criteria. *Biodiversity and Conservation* 14(5), 1083–1100.
- Burnham, K. P. & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. second edition. New York: Springer Verlag. ISBN 0387953647.
- Butchart, S. H. M., Walpole, M., Collen, B., Strien, A. van, Scharlemann, J. P. W., Almond, R. E. A., Baillie, J. E. M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K. E., Carr, G. M., Chanson, J., Chenery, A. M., Csirke, J., Davidson, N. C., Dentener, F., Foster, M., Galli, A., Galloway, J. N., Genovesi, P., Gregory, R. D., Hockings, M., Kapos, V., Lamarque, J.-F., Leverington, F., Loh, J., McGeoch, M. A., McRae, L., Minasyan, A., Morcillo, M. H., Oldfield, T. E. E., Pauly, D., Quader, S., Revenga, C., Sauer, J. R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S. N., Symes, A., Tierney, M., Tyrrell, T. D., Vié, J.-C. & Watson, R. (2010). Global Biodiversity: Indicators of Recent Declines. *Science* 328(5982), 1164–1168.
- Büdel, B. & Scheidegger, C. (2008). Thallus morphology and anatomy. In: Nash, T. H (ed) *Lichen biology*. Second edition. pp 40–68. Cambridge: Cambridge University Press.

- Camm, J. D., Polasky, S., Solow, A. & Csuti, B. (1996). A note on optimal algorithms for reserve site selection. *Biological Conservation* 78(3), 353–355.
- Campbell, J., Fredeen, A. L. & Prescott, C. E. (2010). Decomposition and nutrient release from four epiphytic lichen litters in sub-boreal spruce forests. *Canadian Journal of Forest Research* 40(7), 1473–1484.
- Cao, D., Leung, L. C. & Law, J. S. (2008). Modifying inconsistent comparison matrix in analytic hierarchy process: A heuristic approach. *Decision Support Systems* 44(4), 944–953.
- Church, R. L., Stoms, D. M. & Davis, F. W. (1996). Reserve selection as a maximal covering location problem. *Biological Conservation* 76(2), 105–112.
- Cyr, D., Gauthier, S., Bergeron, Y. & Carcaillet, C. (2009). Forest management is driving the eastern North American boreal forest outside its natural range of variability. *Frontiers in Ecology and the Environment* 7(10), 519–524.
- Dufrêne, M. & Legendre, P. (1997). Species Assemblages and Indicator Species: The Need for a Flexible Asymmetrical Approach. *Ecological Monographs* 67(3), 345–366.
- Dyer, J. S. (1990). Remarks on the Analytic Hierarchy Process. *Management Science* 36(3), 249–258.
- Esseen, P. A., Ehnström, B., Ericson, L. & Sjöberg, K. (1997). Boreal forests. *Ecological Bulletins* 46, 16–47.
- Faith, D. P. (2003). Environmental diversity (ED) as surrogate information for species-level biodiversity. *Ecography* 26(3), 374–379.
- FAO (2010). *Global Forest Resources Assessment 2010: Main Report*. Rome: Food and Agriculture Organization of the United Nations (FAO). (163).
- Ferris, R. & Humphrey, J. W. (1999). A review of potential biodiversity indicators for application in British forests. *Forestry* 72(4), 313–328.
- Franklin, J. F. (1988). Structural and functional diversity in temperate forests. In: Wilson O. E. (ed) *Biodiversity*. pp 166–175. Washington DC: National Academies Press.
- Franklin, J. F., Anderson, D. R., Thornburgh, D. A. & Tappeiner, J. C. (1997). Alternative silvicultural approaches to timber harvesting: variable retention harvest systems. In: Kohm K. A. and Franklin J. F. (eds) *Creating a forestry for the 21st century: The science of ecosystem management*. pp 111–139. Washington DC: Island Press.
- Franklin, J. F., Lindenmayer, D., MacMahon, J. A., McKee, A., Magnuson, J., Perry, D. A., Waide, R. & Foster, D. (2000). Threads of Continuity. *Conservation in Practice* 1(1), 8–17.
- Fridman, J. (2000). Conservation of Forest in Sweden: a strategic ecological analysis. *Biological Conservation* 96(1), 95–103.

- Gotelli, N. J. & Colwell, R. K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology letters* 4(4), 379–391.
- Gunnarsson, B., Hake, M. & Hultengren, S. (2004). A functional relationship between species richness of spiders and lichens in spruce. *Biodiversity and Conservation* 13(4), 685–693.
- Gregory, R., Lichtenstein, S. & Slovic, P. (1993). Valuing environmental resources: a constructive approach. *Journal of Risk and Uncertainty* 7(2), 177–197.
- Gustafsson, L., Baker, S. C., Bauhus, J., Beese, W. J., Brodie, A., Kouki, J., Lindenmayer, D. B., Löhmus, A., Martínez Pastur, G., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, J. A., Wayne, A. & Franklin, J. F. (2012). Retention Forestry to Maintain Multifunctional Forests: a World Perspective. *BioScience* 62, 633–645.
- 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(4), 295–308.
- Gärdenfors, U. (Ed.) (2010). *The 2010 Red List of Swedish Species*. Swedish University of Agricultural Sciences, Uppsala, Sweden: Swedish Species Information Centre.
- Haight, R. G. & Snyder, S. A. (2009). Integer programming methods for reserve selection and design. In: Moilanen, A. Wilson, K. A. and Possingham, H. P. (eds.) *Spatial conservation prioritization. Quantitative methods and computational tools*. pp 43–58. New York: Oxford University Press.
- Hansen, M. C., Stehman, S. V. & Potapov, P. V. (2010). Quantification of global gross forest cover loss. *Proceedings of the National Academy of Sciences* 107(19), 8650–8655.
- Hazell, P. & Gustafsson, L. (1999). Retention of trees at final harvest—evaluation of a conservation technique using epiphytic bryophyte and lichen transplants. *Biological Conservation* 90(2), 133–142.
- Hedenås, H. & Ericson, L. (2003). Response of epiphytic lichens on *Populus tremula* in a selective cutting experiment. *Ecological Applications* 13(4), 1124–1134.
- Hedenås, H. & Hedström, P. (2007). Conservation of epiphytic lichens: significance of remnant aspen (*Populus tremula*) trees in clear-cuts. *Biological Conservation* 135(3), 388–395.
- Hellberg, E. (2004). *Historical variability of deciduous trees and deciduous forests in Northern Sweden: effects of forest fires, land-use and climate*. Swedish University of Agricultural Sciences. ISBN 9157665427.

- Hwang, C. L. & Yoon, K. (1981). *Multiple attribute decision making: methods and applications: a state-of-the-art survey*. New York: Springer-Verlag.
- Juutinen, A., Mäntymaa, E., Mönkkönen, M. & Salmi, J. (2004). A Cost-Efficient Approach to Selecting Forest Stands for Conserving Species: A Case Study from Northern Fennoscandia. *Forest Science* 50(4), 527–539.
- Kirkpatrick, J. B. (1983). An iterative method for establishing priorities for the selection of nature reserves: An example from Tasmania. *Biological Conservation* 25(2), 127–134.
- Knops, J. M. H., Nash Iii, T. H., Boucher, V. L. & Schlesinger, W. H. (1991). Mineral Cycling and Epiphytic Lichens: Implications at the Ecosystem Level. *The Lichenologist* 23(03), 309–321.
- Koivula, M., Punttila, P., Haila, Y. & Niemela, J. (1999). Leaf Litter and the Small-Scale Distribution of Carabid Beetles (Coleoptera, Carabidae) in the Boreal Forest. *Ecography* 22(4), 424–435.
- Kouki, J. (2008). Aspen and forest biodiversity in North European boreal forests. *Proceedings of Aspen in Scotland: biodiversity and management*, Boat of Garten, 2008. Boat of Garten: Highland Aspen Group.
- Kouki, J., Arnold, K. & Martikainen, P. (2004). Long-term persistence of aspen—a key host for many threatened species—is endangered in old-growth conservation areas in Finland. *Journal for Nature Conservation* 12(1), 41–52.
- 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* In press.
- Kuuluvainen, T. (2009). Forest Management and Biodiversity Conservation Based on Natural Ecosystem Dynamics in Northern Europe: The Complexity Challenge. *AMBIO: A Journal of the Human Environment* 38(6), 309–315.
- Lange, O. L. (1986). Water vapor uptake and photosynthesis of lichens: performance differences in species with green and blue-green algae as phycobionts. *Oecologia* 71(1), 104–110.
- Latva-Karjanmaa, T., Penttilä, R. & Siitonen, J. (2007). The demographic structure of European aspen (*Populus tremula*) populations in managed and old-growth boreal forests in eastern Finland. *Canadian Journal of Forest Research* 37(6), 1070–1081.
- Lindenmayer, D. B. & Franklin, J. F. (2002). *Conserving forest biodiversity: a comprehensive multiscaled approach*. Washington DC: Island Press.
- Lindenmayer, D. B. & Franklin, J. F. (2003). *Towards forest sustainability*. Melbourne: CSIRO Publishing.

- Lindenmayer, D. B., Margules, C. R. & Botkin, D. B. (2000). Indicators of biodiversity for ecologically sustainable forest management. *Conservation Biology* 14(4), 941–950.
- Löhmus, A. & Löhmus, P. (2010). Epiphyte communities on the trunks of retention trees stabilise in 5 years after timber harvesting, but remain threatened due to tree loss. *Biological Conservation* 143(4), 891–898.
- Lundgren, J., Rönnqvist, M. & Värbrand, P. (2010). *Optimization*. Lund: Studentlitteratur.
- Lundström, J., Öhman, K., Perhans, K., Rönnqvist, M. & Gustafsson, L. (2011). Cost-effective age structure and geographical distribution of boreal forest reserves. *Journal of Applied Ecology* 48(1), 133–142.
- Löfman, S. & Kouki, J. (2001). Fifty Years of Landscape Transformation in Managed Forests of Southern Finland. *Scandinavian Journal of Forest Research* 16, 44–53.
- Magurran, A. E. (2004). *Measuring biological diversity*. Second edition. Oxford: Blackwell Publishing.
- Margules, C. R. & Pressey, R. L. (2000). Systematic conservation planning. *Nature* 405(6783), 243–253.
- Messer, K. D. (2006). The conservation benefits of cost-effective land acquisition: A case study in Maryland. *Journal of Environmental Management* 79(3), 305–315.
- Mikusiński, G., Pressey, R. L., Edenius, L., Kujala, H., Moilanen, A., Niemelä, J. & Ranius, T. (2007). Conservation Planning in Forest Landscapes of Fennoscandia and an Approach to the Challenge of Countdown 2010. *Conservation Biology* 21(6), 1445–1454.
- Moilanen, A. (2008). Two paths to a suboptimal solution – once more about optimality in reserve selection. *Biological Conservation* 141(7), 1919–1923.
- Murdoch, W., Polasky, S., Wilson, K. A., Possingham, H. P., Kareiva, P. & Shaw, R. (2007). Maximizing return on investment in conservation. *Biological Conservation* 139(3), 375–388.
- 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(12), 681–687.
- Nash III, T. H. (2008). Nitrogen, its metabolism and potential contribution to ecosystems. In: Nash, T. H (ed) *Lichen biology*. Second edition. pp 216–233. Cambridge: Cambridge University Press.
- Nicholson, E. & Ovaskainen, O. (2009). Conservation prioritization using metapopulation models. In: Moilanen, A. Wilson, K. A. and Possingham, H. P. (eds.) *Spatial conservation prioritization. Quantitative methods and computational tools*. New York: Oxford University Press.
- Nicholson, E. & Possingham, H. P. (2007). Making conservation decisions under uncertainty for the persistence of multiple species. *Ecological Applications* 17(1), 251–265.

- Noss, R. F. (1990). Indicators for monitoring biodiversity: a hierarchical approach. *Conservation biology* 4, 355–364.
- Ohlson, M., Brown, K. J., Birks, H. J. B., Grytnes, J.-A., Hörnberg, G., Niklasson, M., Seppä, H. & Bradshaw, R. H. W. (2011). Invasion of Norway spruce diversifies the fire regime in boreal European forests. *Journal of Ecology* 99(2), 395–403.
- O’Neill, J. & Spash, C. L. (2000). Conceptions of Value in Environmental Decision-Making. *Environmental Values* 9(4), 521–536.
- Peck, J. L. E. & McCune, B. (1997). Remnant trees and canopy lichen communities in western Oregon: a retrospective approach. *Ecological Applications* 7(4), 1181–1187.
- Perhans, K., Appelgren, L., Jonsson, F., Nordin, U., Söderström, B. & Gustafsson, L. (2009). Retention patches as potential refugia for bryophytes and lichens in managed forest landscapes. *Biological Conservation* 142(5), 1125–1133.
- Polasky, S., Camm, J. D. & Garber-Yonts, B. (2001). Selecting Biological Reserves Cost-Effectively: An Application to Terrestrial Vertebrate Conservation in Oregon. *Land Economics* 77(1), 68–78.
- Possingham, H., Day, J., Goldfinch, M. & Salzborn, F. (1993). The mathematics of designing a network of protected areas for conservation. In: Sutton D, Cousins E and Pierce C (Eds.) *Decision Sciences, tools for today. Proceedings of the 12th Australian Operations Research Conference*. pp 536–545. Adelaide: Australian Society for Operations Research.
- Pressey, R. L., Cabeza, M., Watts, M. E., Cowling, R. M. & Wilson, K. A. (2007). Conservation planning in a changing world. *Trends in Ecology & Evolution* 22(11), 583–592.
- Raab, B. & Vedin, H. (1995). *National atlas of Sweden: climate, lakes and rivers*. Stockholm: SNA Publisher. ISBN 9187760320.
- Regan, H. M., Davis, F. W., Andelman, S. J., Widyanata, A. & Freese, M. (2007). Comprehensive criteria for biodiversity evaluation in conservation planning. *Biodiversity and Conservation* 16(9), 2715–2728.
- Reynolds, C. (2002). Ecological pattern and ecosystem theory. *Ecological Modelling* 158(3), 181–200.
- Rodrigues, A. S. L., Tratt, R., Wheeler, B. D. & Gaston, K. J. (1999). The performance of existing networks of conservation areas in representing biodiversity. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 266(1427), 1453–1460.
- Romero, C. (1991). *Handbook of critical issues in goal programming*. Oxford: Pergamon Press.
- Rosenvald, R. & Löhmus, 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), 1–15.

- Saaty, T. L. (1977). A scaling method for priorities in hierarchical structures. *Journal of Mathematical Psychology* 15(3), 234–281.
- Saaty, T. L. (1990). *The Analytic Hierarchy Process: Planning, priority setting, resource allocation*. Second edition. Pittsburgh: R WS Publications.
- Salafsky, N. & Margoluis, R. (1999). Evaluación de Amenazas de Reducción: Una Estimación Práctica y Costo-Efectiva para Evaluar Proyectos de Conservación y Desarrollo. *Conservation Biology* 13(4), 830–841.
- Samuelsson, J. & Ingelög, T. (1996). *Den levande döda veden - bevarande och nyskapande i naturen*. Uppsala: Artdatabanken, Swedish University of Agricultural Sciences.
- Sarkar, S., Justus, J., Fuller, T., Kelley, C., Garson, J. & Mayfield, M. (2005). Effectiveness of Environmental Surrogates for the Selection of Conservation Area Networks. *Conservation Biology* 19(3), 815–825.
- Sarkar, S. & Margules, C. (2002). Operationalizing biodiversity for conservation planning. *Journal of Biosciences* 27(4), 299–308.
- Sarkar, S., Pressey, R. L., Faith, D. P., Margules, C. R., Fuller, T., Stoms, D. M., Moffett, A., Wilson, K. A., Williams, K. J. & Williams, P. H. (2006). Biodiversity conservation planning tools: present status and challenges for the future. *Annu. Rev. Environ. Resour.* 31, 123–159.
- Spanos, K. A. & Feest, A. (2007). A review of the assessment of biodiversity in forest ecosystems. *Management of Environmental Quality: An International Journal* 18(4), 475 – 486.
- Swanson, M. E., Franklin, J. F., Beschta, R. L., Crisafulli, C. M., DellaSala, D. A., Hutto, R. L., Lindenmayer, D. B. & Swanson, F. J. (2011). The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Frontiers in Ecology and the Environment* 9, 117–125.
- Swedish Forest Agency (2012). *Skogsstatistisk årsbok 2012*. Jönköping (in Swedish with English summary): Sveriges officiella statistik, Skogsstyrelsen.
- Swedish Government (1993). *En ny skogspolitik. Proposition 1992/93:226*. Stockholm (in Swedish): Swedish Government.
- Swedish Government (2009). *Hållbart skydd av naturområden. Proposition 2008/09:214*. Stockholm (in Swedish): Swedish Government.
- Vane-Wright, R. I., Humphries, C. J. & Williams, P. H. (1991). What to protect?-systematics and the agony of choice. *Biological conservation* 55(3), 235–254.
- Whittingham, M. J., Stephens, P. A., Bradbury, R. B. & Freckleton, R. P. (2006). Why Do We Still Use Stepwise Modelling in Ecology and Behaviour? *Journal of Animal Ecology* 75(5), 1182–1189.
- 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 & Natural-Resource Sciences (MCFNS)* 3(2), 87–94.

- Williams, J. C., ReVelle, C. S. & Levin, S. A. (2004). Using Mathematical Optimization Models to Design Nature Reserves. *Frontiers in Ecology and the Environment* 2(2), 98–105.
- Wilson, K. A., McBride, M. F., Bode, M. & Possingham, H. P. (2006). Prioritizing global conservation efforts. *Nature* 440(7082), 337–340.
- Zackrisson, O. (1977). Influence of forest fires on the North Swedish boreal forest. *Oikos* 29, 22–32.
- Zeshui, X. & Cuiping, W. (1999). A consistency improving method in the analytic hierarchy process. *European Journal of Operational Research* 116(2), 443–449.
- Östlund, L., Zackrisson, O. & Axelsson, A. L. (1997). The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Canadian Journal of Forest Research* 27(8), 1198–1206.

Svensk populärvetenskaplig sammanfattning

Vårt moderna skogsbruk har lett till att många växter och djur i den svenska skogen är hotade. För att motverka detta görs åtgärder på flera olika nivåer, allt från att lämna enskilda träd vid avverkning till avsättning av stora reservat. Alla dessa åtgärder kostar pengar, och eftersom det inte finns hur mycket pengar som helst öronmärkta till naturvård bör de pengar som spenderas göra så stor nytta som möjligt.

För närvarande består de flesta reservaten av gamla skogar, vilket är bra och nödvändigt för att bevara de få rester av orörd skog som finns kvar i Sverige. Men eftersom nästan all skogsmark är påverkad av skogsbruk kommer man att behöva inkludera även påverkade skogar när man väljer ut nya reservat. Unga skogar är billiga att köpa och i unga skogar som växer upp efter en naturlig störning, t.ex. brand eller storm, finns en stor del av mångfalden representerad. Där finns även arter som bara lever i den typen av miljöer. Därför kan man tänka sig att unga skogar skulle kunna vara ett kostnadseffektivt komplement till de reservat som finns dag.

I den här avhandlingen har jag tagit reda på hur åldersfördelningen ser ut när jag modellerat effektiva val av reservat i norra Sverige. För att bedöma hur bra de skogar som väljs ut är för mångfalden har jag använt olika strukturer som indikatorer. De olika strukturerna är sådana som är kända för att vara viktiga för många växter och djur, som till exempel död ved och grova träd. Vad som är det optimala urvalet är inte självklart, och jag har tittat på olika möjligheter att beskriva vad som kan påverka ett bra val. Det enklaste sättet är att bara maximera mängden av strukturer, och för att valet ska bli kostnadseffektivt satte jag begränsningar på hur mycket den utvalda skogen fick kosta. Detta sätt utvidgades senare, först genom att ta hänsyn till olika åsikter om hur viktiga de olika strukturerna är för mångfalden i skogen. Jag har intervjuat åtta personer som jobbar med att välja ut reservat på länsstyrelserna i

norra Sverige, och på så sätt har jag fått fram hur viktiga de anser att de olika strukturerna är. Sedan har jag också tittat på vad som händer om man tar hänsyn till hur strukturerna i de skogar man väljer utvecklas över tiden. Ett reservat är inte bara viktigt som det ser ut idag, det ska även fungera som en gynnsam miljö i framtiden. En nackdel med att använda strukturer är att det inte är säkert att de växter och djur som man vill skydda faktiskt finns på strukturerna i de skogar som valts. Därför har jag också gjort en studie där antalet lavararter på kvarlämnade aspar på hyggen inventerats. Tanken var att se om gamla träd i ung skog är en viktig miljö för lavar.

Den största delen av den här avhandlingen bygger på en reservatsselektionsmodell som jag har utvecklat, och information om skogens egenskaper har jag fått från riksskogstaxeringen. Modellen baseras på en optimeringsmetod som kallas flermålsoptimering. Fördelen med den metoden är att jag kan försöka nå flera mål samtidigt. Ett bra urval av skogar innehåller mycket strukturer, men jag har haft som mål att varje enskild struktur ska vara representerad så mycket som möjligt, alltså ett mål för varje struktur. Det slutgiltiga urvalet blir ett där alla strukturers representation är så nära sitt målvärde som möjligt, med hänsyn tagen till alla övrigas mål. Det är viktigt att se till att det inte bara är en av strukturerna som finns i reservaten, utan de bästa skogarna för mångfalden är de som innehåller så många olika miljöer som möjligt. Ju mer olika typer av habitat, desto större möjligheter för fler arter att hitta ett lämpligt habitat. För att ta reda på hur skogarna kommer att se ut i framtiden har jag använt Heureka PlanVis, ett skogligt planeringsverktyg som kan simulera skogens utveckling baserat på data från riksskogstaxeringen.

Det viktigaste resultatet från den här avhandlingen var att unga skogar är ett kostnadseffektivt alternativ när man ska avsätta reservat. Detta gällde för alla versioner av modellen: när enbart indikatorerna maximerades, när hänsyn togs till olika åsikter angående hur viktiga de olika indikatorerna är och när framtida värden beräknades på olika sätt. Men den exakta andelen ung skog varierade mycket, så hur man definierar sitt mål påverkar vilka skogar som väljs.

Jag använde också en modell som försökte uppnå samma mål fast på så liten yta som möjligt. Dessa två sätt att se på reservatsproblematiken ger väldigt olika urval. En areabegränsad modell var i alla versioner dyrare, men uppnådde samma mångfaldsvärde på en mindre yta. Det kan vara positivt med tanke på att de flesta arterna inte vill ha för gles mellan strukturerna. Det räcker oftast inte att en struktur finns representerad, det måste finnas en viss mängd för att de flesta arterna ska trivas. Nackdelen är dock att mer pengar än nödvändigt kommer att spenderas för att uppnå en viss mängd strukturer.

I studien där aspar på hyggen inventerades hade jag delat in dem i två åldersklasser, hälften stod på hyggen som avverkats 0-4 år innan inventeringen

och hälften på hyggen som avverkats 10-16 år innan inventeringen. Fler arter av lavar fanns på aspar som stått friställda under en längre tid. Det är intressant för det innebär att många av lavarna som lever på aspen när den står inne i skogen (som jag antagit motsvaras av de arter som hittas efter 0-4 år) verkar finnas kvar, samtidigt som det kommer till fler arter, som på ett eller annat sätt hittat till trädet. Eftersom jag bara har information från två tidpunkter, och inte från samma träd, så kan jag inte säga säkert att det verkligen är så att nya arter koloniserat trädet, de träd på hyggen som avverkades för en längre tid sedan hade kanske hela tiden varit artrikare. Jag vet dessutom bara hur förhållandena är på hygget och inte hur många arter som finns på aspar inne i skogen. Men eftersom lavar kan vara kvar ganska länge innan de dör, så har jag antagit att de arter som fanns på träd som bara stått friställda i några få år fanns redan innan avverkningen, när trädet stod inne i skogen. Det kan då också vara så att vissa av de arter som hittades på träd som stått friställda längre inte hunnit försvinna, fast de är dömda att dö på sikt. Trots dessa osäkerheter visar mina resultat att det gynnar mångfalden av epifytiska lavar att lämna aspar vid avverkning. Det är viktigt att se till att asparna få stå relativt öppet, alltså bör man lämna en skyddande zon runt stammen och inte plantera där. Detta gör att lavar som vill ha det lite mer öppet och soligt trivs bättre, men det gynnar också föryngringen av asp, eftersom aspen ofta sprider sig genom att skjuta rotskott och då slipper konkurrera med planterade träd.

Min slutsats är att det inte finns ett enkelt svar på hur det optimala urvalet av reservat borde ser ut. Det beror på hur man värderar vad som är ett bra reservat, vilken kunskap som finns tillgänglig och vilket tidsspann man tittar på. När man planerar måste man tänka på ekologiska konsekvenser, men det är också viktigt att väga in ekonomiska faktorer och samhällets mål, för att på ett mer övergripande sätt utveckla kostnadseffektiva och representativa strategier för hur den biologiska mångfalden ska bevaras.

Tack!

Oj, vad många som jag har att tacka för att det blev en avhandling tillslut!
Vi börjar med handledarna...

Jag tror faktiskt att jag haft den bästa handledargruppen man kan ha, jag har aldrig tvivlat på att ni skulle hjälpa mig på allra bästa sätt. Jag har både känt mig trygg och samtidigt fri att tänka och bestämma själv. Ni har på ett nästan perfekt sätt kompletterat varandra, och även om mitt projekt ibland känts lite spretigt och omfattar så många olika områden, har era olika expertiser varit en stabil grund.

Lena, du har varit ett enormt stöd genom allt som hänt dessa år, både jobbmässigt och privat. Du har alltid varit snabb på att hjälpa till och visat entusiasm och intresse för det jag gjort. Din positiva attityd har verkligen motiverat mig att prestera så bra jag har kunnat. Du har lärt mig väldigt mycket, och jag är så tacksam att du gav mig möjligheten att genomföra det här projektet!

Karin Ö, tack för att du peppade mig att söka tjänsten till att börja med, och för att din dörr alltid varit öppen när jag titt som tätt kommit till Umeå för att bara hälsa på, men också när jag behövt hjälp med planeringsdelarna i projektet. Inga frågor har varit för dumma från en novis på området som jag ju är.

Mikael, utan din hjälp hade optimeringsdelarna aldrig funkat. Du har fått mig att förstå vilka möjligheter som öppnas med dessa verktyg, och inga frågor verkar omöjliga, eller faktiskt ens svåra att svara på 😊

Karin P, jag har från första stund imponerats av ditt engagemang och intelligens, dina kommentarer på texterna känns alltid genomarbetade och relevanta. Även om du ofta varit på vift har jag haft mycket hjälp av dig och du har fyllt en viktig funktion i gruppen.

Jag hoppas verkligen att vi kommer samarbeta mer i framtiden!

Alla arbetskamrater i ekologihuset, jag har verkligen älskat att jobba här! Och det är till stor del på grund av att det varit så trevligt på fikaraster, kurser och i korridorerna. Förutom att det är himla trevligt här, så är det också en stimulerande vetenskaplig miljö, och jag har lärt mig väldigt mycket på litteratordiskussioner, seminarier och diskussioner i allmänhet. Det är häftigt med så otroligt mycket kompetens samlad under samma tak!

Doktorandgänget, speciellt **Barbara, Maria, Dennis** och **Victor** som har hängt med sen starten och som tillsammans med sina familjer bidragit till många roliga icke jobbrelaterade aktiviteter. **Matt, Måns** och **Ola** som stöttat och stressat tillsammans med mig den sista tiden. **Sofia, Diana, Camilla, Samuel, Linnéa, Jonas, David, Marcus, Anna, Jörgen** och **Nicole** för trevligt sällskap på konferenser, möten, Friskis, luncher och på kontoret. Och alla andra, det har varit ett privilegium att få jobba tillsammans med er!

Onsdagslöparna med **Per** och **Mats** i spetsen, jag gillar ju att svettas emellanåt och det har varit skönt att komma ut från kontoret, även om det ibland går lite väl fort i uppförsbackarna ☺

Dessa fem år har på många sätt varit de bästa åren i mitt liv, men också tunga, och jag hade inte klarat varken jobb eller livet i övrigt utan människorna runt omkring mig, ni betyder så mycket. Jag är så glad att det är många som flyttat söderut och funnits nära. Hela **Berghemsgänget** som till största delen faktiskt bor bara en timme bort har förhöjt den icke jobbrelaterade tiden, midsomrar, julfester, valborgsaftnar, nyårsaftnar, paltfester och övriga ej namnsatta resor och tillställningar, och det har varit skönt att hänga med några som håller på med helt andra saker. **Elin** vi har i princip vuxit upp tillsammans och nu har vi stadgat oss med varsin berghemskille, hur det kan bli ☺ tillsammans med **Elin O** och **Rebecca** har vi ett gäng som jag är väldigt glad över, även om vi inte träffas så ofta är ni viktiga för mig.

Gamla Umeåbiologgänget som följde med ner till Uppsala, om än bara för ett tag, **Stina** och **Karin**, och **Ola** som faktiskt handgripligen varit med och hjälpt till i fältjobbet till aspstudien. Och **Emma**, för att du varit min allierade och kunnat prata avhandlingsskrivande och artikelproblem nästan hur mycket och länge som helst.

Pappa och **Patrik** (med **Jenny** och lilla **Alma**) den speciella känslan för naturen och speciellt skogen har jag vuxit upp med, och även om vi ofta har olika åsikter så är det alltid kul att komma hem och diskutera skogsbruk, naturvård, eller bara strosa runt västtå och förhöras på växter som jag tyvärr alltid glömt ☺

Mamma, det gör så ont att du inte får vara med, jag saknar dig varje dag. Jag vet att du skulle varit så stolt, men också att du skulle varit lika stolt även om jag inte tagit mig hela vägen, så har du alltid varit och det betydde allt.

Martin, när jag skriver att jag inte skulle fixat detta utan dig så är det faktiskt sant. Alla timmar du hjälpt mig med pluggandet till optimeringskurserna, agerat databassupport, läst manus, hjälpt mig att formatera figurer, och nu på slutet dragit det absolut största lasset hemma med dagishämtning, matlagning och vabbande. Jag är oändligt tacksam. Du är min trygghet och min stora kärlek!

Mina älskade barn, ni är mitt allt! **Adam**, min stora kille jag förundras varje dag över din energi och nyfikenhet, jag jobbar hårt för att kunna svara på i alla fall några av alla dina frågor ☺. **Moa**, jag älskar att du är så viljestark och glad, det spelar ingen roll, du kan alltid få mig att le. Jag lovar, inga mer sena kvällar på kontoret (på ett tag), nu ska vi bara ha kul!