Cost-efficient Conservation Strategies for Boreal Forest Biodiversity

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Cover: Retention patch on a harvested area in Hälsingland, Sweden.
(Photo: Fredrik Jonsson)

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Abstract

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Long and intensive forest management has made conservation measures in the forest landscape necessary to maintain forest biodiversity. The most common measure is to set aside land for conservation purposes. This, however, requires large financial resources and available budgets are generally insufficient. In this thesis, a set of key factors affecting the cost-efficiency when selecting conservation areas were investigated.

I studied (1) the conservation quality and economic land value of three common types of conservation areas: nature reserves, woodland key habitats, and retention patches on harvested areas; (2) the capacity of retention patches to harbour bryophytes and lichens over time; and (3) factors determining what information should be used when selecting conservation areas, including the conservation goal, correlation and variability of different types of data, and the costs for collecting information. Two large field studies formed the basis for the studies, where data on bryophytes, lichens and structural characteristics were collected, and economic land values were calculated. Site-selection analyses were used in combination with other analytical tools to investigate and compare efficiency of different conservation strategies.

The results showed that woodland key habitats had a very high conservation quality, and were generally also the most cost-efficient type of conservation area for the measures of biodiversity used in the studies. Different types of retention patches complemented each other in terms of species composition and the variation in conservation quality and economic value was large among patches. Many bryophytes decreased in retention patches following harvesting, while some lichens decreased and others increased. The costs for obtaining information on conservation quality of areas were generally low compared to the economic land values.

The studies indicate that a conservation strategy based on many types of conservation areas is most likely efficient for long-term conservation of forest biodiversity. To increase cost-efficiency, systematic selection of areas within each conservation area type should be carried out, where both conservation quality and economic values of areas are taken into account.

Keywords: Bryophytes, conservation planning, economic land value, green-tree retention, information, lichens, nature reserve, reserve selection, retention patch, woodland key habitat

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Papers I-V

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

I Perhans, K., Gustafsson, L., Jonsson, F., Nordin, U. & Weibull, H. 2007. Bryophytes and lichens in different types of forest set-asides in boreal Sweden. *Forest Ecology and Management 242*, 374-390.

II Wikberg, S., Perhans, K., Kindstrand, C., Djupström, L.B., Boman, M., Mattsson, L., Schroeder, L.M., Weslien, J. & Gustafsson, L. Cost-effectiveness of implemented conservation strategies in boreal forests: selection of set-asides. *Submitted manuscript.*

III Perhans, K., Kindstrand, C., Boman, M., Djupström, L.B., Gustafsson, L., Mattsson, L., Schroeder, L.M., Weslien, J. & Wikberg, S. Conservation goals and the relative importance of costs and benefits in reserve selection. *Conservation Biology, in press*.

IV Perhans, K., Appelgren, L., Jonsson, F., Nordin, U., Söderström, B. & Gustafsson, L. Six-year responses of bryophytes and lichens in forest retention patches following harvesting. *Submitted manuscript.*

V Perhans, K., Glöde, D., Gilbertsson, J., Persson, A. & Gustafsson, L. Small-scale conservation planning for cost-efficient management of forest biodiversity outside of reserves. *Manuscript.*

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My contributions to the papers

In paper I and III-V, I designed and performed most (paper I, III, and V) or all (paper IV) of the data analyses and wrote most (paper I and III) or all (paper IV and V) of the text. In paper II, I performed the GIS-analyses and contributed to discussions and improvement of the text. Original ideas to paper I, II, IV, and V came from the authors of each paper jointly, while the ideas for paper III were my own.

Background

Boreal forest management and biodiversity

The boreal forest forms a belt across large parts of the northern hemisphere. In the Fennoscandian parts (Sweden, Norway and Finland), the forests are dominated by Norway spruce (*Picea abies*) on mesic to moist sites and Scots pine (*Pinus sylvestris*) on drier sites. Deciduous trees constitute a smaller part and the most common are birch (*Betula* spp.), aspen (*Populus tremula*), goat willow (*Salix caprea*), and rowan (*Sorbus aucuparia*). The forest floor vegetation is normally made up of more bryophytes and lichens than vascular plants (Esseen *et al*., 1997). The most important natural large-scale disturbance regime is fire (Angelstam, 1998), especially in pine-dominated areas, although today fires are very scarce (Niklasson & Granström, 2000). In spruce forests, small-scale gap-phase dynamics, mediated by wind, fungi and insects, is the most important type of disturbance (Fig. 1; McCarthy, 2001; Kuuluvainen, 2002). In natural forest systems, these disturbance regimes create multi-layered forests with different age classes of trees and with large amounts of dead wood.

Figure 1. Norway spruce (*Picea abies*) forest with natural regeneration of spruce saplings.

Compared to many other forest biomes in the world, the boreal forests in Fennoscandia have been extensively transformed by forest management (Löfman & Kouki, 2001). Starting in the beginning of the 20th century, clear-felling, planting and repeated thinning have been applied almost all over the forest landscape

(Östlund, Zackrisson & Axelsson, 1997; Axelsson, Angelstam & Svensson, 2007) and only a small proportion of natural or semi-natural forests remain. Human-induced disturbances have thereby to a large extent replaced natural disturbance regimes. There are large differences between natural and human-induced disturbances; in a forest fire for example, only 10 % of the biomass normally disappears, while in clear-felling, as much as 95 % is normally extracted (Lindenmayer & Franklin, 2002). Further, the remaining old forests in Sweden are becoming severely fragmented, with substantial negative effects on flora and fauna (Saunders *et al*., 1991; Fahrig, 2003).

The intensive use of the forests have greatly contributed to the fact that today, about 2000 forest-living species are on the Swedish red list (Gärdenfors, 2005) because they are now so rare, have declining populations and in many cases run the risk of going nationally extinct. Cryptogams (lichens, bryophytes and fungi) and invertebrates are species groups with many threatened species. Many are dependent on substrates such as dead wood, old trees and large deciduous trees, which are structures that are rare in well-managed (from a forester's perspective) forest landscapes with altered disturbance regimes (Berg *et al*., 1994; Tikkanen *et al*., 2006). Others need the climatologically stabile conditions of interior forests and are negatively affected by edge-effects (Chen, Franklin & Spies, 1995; Gignac & Dale, 2005).

Conservation policy and strategies

Forest conservation policy

Acknowledging the need for a more conservation-oriented forest management, the Swedish government revised the Swedish Forestry Act in 1993 to give equal importance to timber production and biodiversity (Lämås & Fries, 1995; Swedish Government, 2002). Although it is difficult to translate this balance into concrete figures and targets, it nonetheless implied a larger awareness and focus on ecological and environmental aspects of forests. Sweden has also an explicit biodiversity objective, stating that all naturally occurring species should be maintained in viable populations (Swedish Government, 2001). The Swedish model for conservation measures in the forest landscape has an emphasis on conservation in the managed forests (the "matrix"; Lindenmayer & Franklin, 2002), a strong focus on voluntary measures, and a moderate proportion of formally protected forest. In total, about 3 % of the productive forest land is currently protected by law (1 % below the mountain areas) (Swedish Forest Agency, 2007a). However, according to a political goal, the area set aside from forestry in 2020 should be almost three times that of 1998, which means an increase from 900 000 hectares to 2 600 000 hectares (Swedish Forest Agency, 2007b).

Types of conservation areas

Several different strategies for setting aside forest land are used in Sweden in parallel. Except for the very few and in most cases very large national parks in Sweden, the most common way to formally protect forest areas larger than ca 20 hectares is as nature reserves. Nature reserves are in general completely designated for conservation purposes and sometimes also for recreation. The mean size of forested or partly forested nature reserves is 130 ha, but the size varies from a few hectares up to several thousands of hectares (Svedlund & Löfgren, 2003). Nature reserves consist mainly of areas with high conservation quality but can also, in order to achieve a coherent area, contain areas with lower quality (max 30 % of the area according to current instructions). Nature reserves are established by the County Administrative Boards (Länsstyrelserna) and the identification of areas is based on information from the Swedish Forest Agency, forest companies, private persons and conservation organizations, followed by a brief inventory of forest structures. Nature reserves are either bought by the state or the land owners are compensated economically in other ways.

Smaller forest areas of high conservation quality are generally protected as habitat protection areas (Svedlund & Löfgren, 2003), or, in cases where management is required to maintain or develop the conservation quality of an area, a nature conservation agreement between the forest owner and the Swedish Forest Agency can be signed, normally for 50 years. Since 2005, a comprehensive national plan exists to guide decisions of when each conservation area type should be used and how to prioritize land for establishment of set-asides (Swedish Environmental Protection Agency & Swedish Forest Agency, 2005). In addition to the formal types of set-aside areas, forest owners committed to certification agreements (FSC; Forest Stewardship Council, and PEFC; Programme for the Endorsement of Forest Certification schemes) also set aside 5 % of their forest holdings for conservation purposes. These voluntary forest set-asides comprise about half of the total set-aside forest area below the mountain region (Swedish Forest Agency, 2007a).

Woodland key habitats (hereafter called "key habitats") have also come to play an important role in forest conservation in Sweden, as well as in other countries in Scandinavia and the Baltic states. The Swedish Forest Agency initiated a long-term survey in 1993 on all forest land in order to find the remaining forest patches with a high conservation quality (Nitare & Norén, 1992). According to the definition, a key habitat is a forest area of great importance to sensitive flora and fauna because of its structural, historical and physical characteristics and should contain or be expected to contain red-listed species (Norén *et al.*, 2002). The inventory is based mainly on structural characteristics and on a set of indicator species of bryophytes, lichens and fungi, supposed to indicate forests with high conservation value. Key habitats are generally small with a mean size of 3.1 ha (Swedish Forest Agency, 2007a). Until 2007, slightly more than 1 % of the productive forest land had been classified as key habitat. The classification of forest as key habitats has no legal meaning, except that forest owners must consult with the Swedish Forest Agency before logging. However, they are normally prioritized to be set aside within the 5 % voluntary set-asides made according to the forest certification commitments.

Retention patches on harvested areas

During the last decade in Sweden, as well as in many other countries, focus within forest conservation has shifted from a strong emphasis on protected areas towards conservation measures in the matrix (Ricketts, 2001; Lindenmayer & Franklin, 2002; Debinski, 2006). In countries such as Sweden, with a comparably low proportion of formally protected forest, conservation in the matrix is regarded as even more important. Along with measures such as leaving dead wood at final harvest and promoting a diverse tree species composition in thinning operations, the retention of living trees on harvested areas is a very important and widely applied conservation practice throughout the boreal forest landscape (Simberloff, 2001; Lindenmayer & Franklin, 2002; Heithecker & Halpern, 2007; Rosenvald & Lõhmus, 2008). Two main approaches of retention harvesting are normally used in parallel: single trees are dispersed over the harvested area, or trees are left in more or less undisturbed forest patches of 0.1-1 ha (Nelson & Halpern, 2005a; Lõhmus, Rosenvald & Lõhmus, 2006). In North America, aggregated retention (patches of 0.2-1 hectares) is practiced within the entire range of the northern spotted owl (*Strix occidentalis caurina*; Nelson & Halpern, 2005a; Heithecker & Halpern, 2007) and similar recommendations apply in e.g. Finland and Estonia (Vanha-Majamaa & Jalonen, 2001; Lõhmus, Rosenvald & Lõhmus, 2006). Retention patches in Sweden are small compared to other countries such as the US (Franklin *et al*., 1997), generally smaller than 0.5 hectares. However, the average size of harvested areas in Sweden is only 4.2 hectares (Swedish Forest Agency, 2007a).

Retention patches are thought to benefit forest biodiversity in three main ways (Franklin *et al*., 1997): (1) as "life-boats" for sensitive flora and fauna over the stand regeneration phase, (2) by increasing the structural variation in the new developing stand, both in a short-term (disturbance-phase species) and a long-term (old-forest species) perspective, and (3) by increasing the spatial and temporal connectivity in the forest landscape. According to the Swedish forestry act, retention patches or dispersed trees should always be left when there is a need for conservation measures to benefit the flora and fauna in the forest stand (SKSFS, 1993). Also, forest companies and most small private forest owners in Sweden today leave around 10 large trees per hectare at final harvest as a part of their certification commitments, normally aggregated in small patches (Holmen Skog, 2007; SCA, 2007). In practice, this means that retention measures are applied on most harvested areas. However, forest owners are not expected to leave more than about 5 % of the total timber value without compensation. Across the whole forest landscape in Sweden, on average 2.6 % of the original forest stand area was left as retention patches between 1996 and 2000 (Swedish Forest Agency, 2007a). The identification and delimitation of retention areas is based almost exclusively on structures and is done either by the forest owner him/herself or by an entrepreneur hired for planning and logging.

Introduction to research themes

Setting aside land for conservation purposes requires large financial resources (Johannesen, 2007; Marris, 2007) and available budgets are generally insufficient (Murdoch *et al*., 2007). The Swedish state spent 1 billion SEK for establishing nature reserves in 2006 (1 SEK = 0.17 USD, April 2008), of which 90 % were used for buying land and the remaining for planning, inventory, decision-making and delimitation of areas (Swedish Agency for Public Management, 2007). The costs for habitat protection areas and nature conservation agreements were 120 million SEK and 32 million SEK, respectively. In addition to this, conservation measures in the matrix also imply substantial costs for individual landowners. It is therefore important to evaluate the cost-efficiency of different implemented conservation strategies as well as, on a more general level, to study key factors that determine cost-efficiency in conservation (Simberloff, 2001; Saterson *et al*., 2004; Wätzold & Schwerdtner, 2005; Naidoo *et al*., 2006).

Factors affecting the cost-efficiency of conservation strategies

Conservation quality in relation to land cost of areas

When selecting conservation areas, cost-efficiency can be increased either by selecting areas with a higher conservation quality for a given level of investment, or by selecting areas with a given level of conservation quality but for a lower level of investment (Naidoo *et al*., 2006; Murdoch *et al*., 2007). Thus, the conservation quality and the land costs (i.e. costs for setting aside an area for conservation) of areas together determine the cost-efficiency. The conservation quality of areas can be measured in many ways (Noss, 1990; Magurran, 2004) and in this thesis both species (bryophytes, lichens and wood-living beetles) and structural characteristics of areas have been used to assess conservation quality. Because large-scale species inventories are expensive, conservation areas are generally identified on the basis of stand characteristics or indicator species assumed to indicate forests of high conservation quality (Nitare, 2000). Thus, to a large extent the actual species richness and diversity in conservation areas is normally unknown.

In paper I, nature reserves, key habitats and retention patches are compared in terms of species richness and structural characteristics. The conservation quality of different types of retention patches is studied in paper V. The costs for setting aside nature reserves, key habitats and retention areas are compared in paper II, and an analysis of the cost-efficiency per area of these conservation strategies is carried out. Likewise, in paper V, the land costs of different types of retention patches are compared, as well as the cost-efficiency of the different types.

Size of conservation areas

The size of conservation areas has large implications both for their short-term and for their long-term cost-efficiency. In the short term, there are factors that make conservation quality appear higher in smaller areas. Firstly, in fragmented forest landscapes, where the areas of old and high-quality forest are small and scattered, studies indicate that small conservation areas can capture with greater precision the remaining areas with a high conservation quality (Götmark & Thorell, 2003; Groeneveld, 2005; Ranius & Kindvall, 2006). Secondly, according to the species-area relationship (Rosenzweig, 1995), smaller areas generally have a proportionally larger number of species than larger areas, because species number increases with a diminishing rate with area. Thirdly, many small areas are often more scattered in the landscape than are fewer large areas and thus their beta diversity (between-area diversity; Whittaker 1972) will be high, causing species composition to be complementary among areas.

On the other hand, the theory of island biogeography predicts that larger areas can hold a larger number of species at equilibrium through lower rates of extinction (Diamond, 1975; Simberloff & Abele, 1976), given that conservation areas in the matrix can be regarded as true islands. Additionally, smaller areas that recently have been separated from a larger area of undisturbed forest might be subject to an extinction debt (Tilman *et al*., 1994), an assumption that was later on assessed by e.g. Hanski (2000), Hanski & Ovaskainen (2002) and Berglund & Jonsson (2005). Small areas are also highly affected by edge effects (Chen, Franklin & Spies, 1995). This is especially true for retention patches on harvested areas, because of their small size and their exposed location. Yet, one important objective of retention patches is to "life-boat" species that otherwise might not survive over the regeneration phase (Franklin *et al*., 1997).

The (current) conservation quality per area of conservation areas of different sizes, as well as their cost-efficiency, is studied in paper I and II. The capacity of small retention patches to harbour bryophytes and lichens of conservation concern over time is the topic of paper IV.

Considering information on conservation quality, land costs, or both

Recently, researchers have emphasized the need to include information about both land costs and conservation quality when selecting conservation areas (reviewed by Naidoo *et al*., 2006). Studies of the potential gains in conservation cost-efficiency from accounting for land costs of areas along with conservation qualities in reserve selection (e.g., Ando *et al*., 1998; Balmford *et al*., 2000; Polasky *et al*., 2001; Juutinen *et al*., 2004; Messer, 2006; Strange *et al*., 2006) show that these can be substantial. It has even been suggested that incorporating information about costs could be more important than incorporating information about conservation quality of areas (Naidoo *et al*. 2006). In spite of this, both internationally (Brooks *et al*., 2006) and in Sweden (Ingemarsson, Hedman & Dahlin, 2004; Swedish Environmental Protection Agency & Swedish Forest Agency, 2005), conservation areas are selected almost exclusively based on their conservation qualities. However, there are indications that private forest owners include economic aspects at least to some extent when selecting areas to set aside as part of their certification commitments (Glöde *et al*., 2003).

The effect on conservation cost-efficiency of using information about conservation quality only, costs only, or about both factors integrated when selecting reserves is the topic of paper III. In this paper, factors that determine the relative importance of different types of information are also studied and discussed. The gains in cost-efficiency by including information on costs along with information on conservation quality when selecting retention patches is studied in paper V.

Correlation and variability in data

Because relevant information for reserve selection is often expensive and difficult to acquire, it is valuable to know when integration of economic and biological information is crucial and under what conditions one type of information is likely more important than the other. Babcock *et al*. (1997) and Ferraro (2003) point out two main factors that can guide planners: the relative variability in costs and conservation quality, and how the two are correlated. If the costs associated with each site are more variable than the conservation quality, it follows that the costs will play a larger role in determining conservation cost-efficiency, and vice versa. Selecting sites on the basis of the less variable of costs or conservation quality leads to losses in cost-efficiency, the size of which depends on how much their variability differs. However, a negative correlation between costs and conservation quality acts to reduce this loss because the least costly sites selected under an optimal cost-selection scheme would generally also have high conservation quality. Conversely, a positive correlation makes it even more important to base the selection on the most variable type of information. The variability in, and correlation between, land costs and conservation quality of spruce forest areas is studied in paper III, and for retention patches in paper V.

The conservation goal for a set of reserves can be formulated in several ways (Metrick & Weitzman, 1998; Sarkar *et al*., 2006). Two broad types of conservation goals (or ways of quantifying conservation targets) have been applied in the research on cost-efficient reserve selection. In the first type, the conservation value of a site is seen as constant, regardless of which other sites are also selected for inclusion in the reserve network. In this type of conservation goal, conservation quality is often expressed in terms of conservation value scores given to sites on the basis of habitat characteristics (Messer, 2006) or their number of rare species (Margules & Usher, 1981). By contrast, in the second type of conservation goal, the conservation value of a site must be assessed in relation to all other selected sites. The most commonly used goal of this type is to maximize the total number of species in a reserve network (e.g., Ando *et al*., 1998; Polasky *et al*., 2001; Moore *et al*., 2004). This type of conservation goal is commonly referred to as being complementarity-based (Vane-Wright *et al*., 1991) because selection favors sites that are complementary in their species composition.

How the conservation goal affects the relative variability in conservation costs and conservation quality of sites, and thereby their relative importance to include in cost-efficient reserve selection is studied in paper III.

Information costs

Even though using more detailed information leads to better conservation decisions, e.g. regarding where to locate new conservation areas (Freitag & Van

Jaarsveld, 1998; Gladstone & Davis, 2003; Grand *et al*., 2007), collecting information is also resource-demanding and time-consuming (Cleary, 2006). In the process of selecting conservation areas, the cost of obtaining information on candidate areas is the most relevant transaction cost for the selection process. As a consequence, conservation decisions are constantly made with insufficient information, in most cases about both land costs and conservation quality of areas. How much data should ideally be collected for conservation to be cost-efficient is rarely studied (Possingham, Grantham & Rondinini, 2007). In paper II, the costs associated with conservation quality inventories of varying degree of detail are analyzed in terms of how they affect the over-all cost-efficiency of different types of conservation strategies.

Aims of thesis

The aim of the thesis was to investigate the cost-efficiency of different conservation strategies for boreal forest biodiversity. The focus was on a set of factors that affect the cost-efficiency when selecting conservation areas. A combination of descriptive and theoretical approaches was used to study the conservation quality and conservation costs of different types of conservation areas, as well as the importance of different types of information when selecting areas. The specific objectives of each of the five papers in the thesis were to:

- Compare the species richness and composition of bryophytes and lichens in three types of forest conservation areas: nature reserves, key habitats, and retention patches on harvested areas (paper I).

- Compare the cost-efficiency of three implemented conservation area strategies in Swedish forests, focusing on the selection process of areas and the information costs associated with selection (paper II).

- Study the effect of different conservation goals on the relative importance of information about land costs and conservation qualities of areas in reserve selection, and the variability in and correlation between land costs and conservation quality (paper III).

- Assess the direction and magnitude of changes in richness and abundance of red-listed and indicator species of bryophytes and lichens in retention patches over six years (paper IV).

- Investigate the potential for small-scale forest owners to increase cost-efficiency when establishing retention patches, by including information about both land costs and conservation quality and by acknowledging the complementarity of different types of patches (paper V).

Study areas and data sets

Two field studies were conducted in central Sweden (Fig. 2; central position 61°45'N, 16°15'E and 62°30'N, 17°15'E, respectively) within the middle boreal vegetation zone (Ahti *et al*., 1968). The forests in this part of Sweden, like in boreal Sweden in general, cover a majority of the land area, have been used for commercial harvesting for more than a century and consist of even-aged stands in different rotation phases (Esseen *et al*., 1997). About 45 % of the productive forest land is privately owned, 46 % is owned by forest companies and 9 % by the state (Swedish Forest Agency, 2007a). The dominating tree species are Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) with varying components of mainly birch (*Betula* spp.) and aspen (*Populus tremula*). Mean yearly precipitation is 700 mm (Raab & Vedin, 1995) and the terrain is hilly, with elevations ranging from 0 to 500 m above sea level. The prevailing wind direction is westerly, although with large local variations (Raab & Vedin, 1995).

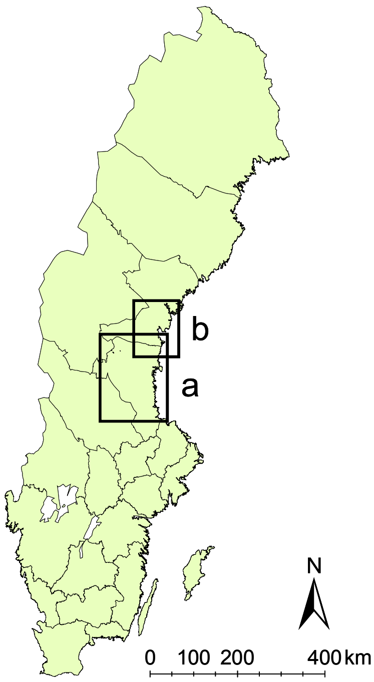

Figure 2. Location of the two study areas.

Key habitats, nature reserves and retention patches (data set A)

Selection of sites

We made a stratified random selection of a total of 80 sites in the county of Gävleborg, 20 in each of four forest categories: nature reserves, key habitats, retention patches and old managed forests (Fig. 3). The selection of sites was made by using the satellite map "wRESEx" (Angelstam *et al*., 2003), in which all forest land is divided into 33 classes according to dominant tree species and stand age, and GIS-layers with nature reserves and key habitats from the County Administrative Board and the Swedish Forest Agency. Selected forest sites should have (i) >70 % Norway spruce, (ii) a tree age of >110 years and (iii) mesic to moist soil. A retention patch was here defined as an island of forest, larger than 25x25 m (0.06 hectares) but not larger than 0.5 hectares, completely surrounded by clear-cut area. Retention patches were selected with wRESEx and through interviews with personnel at the Swedish Forest Agency and at the forest company Stora Enso. The time since establishment of the retention groups varied between 2 and 12 years.

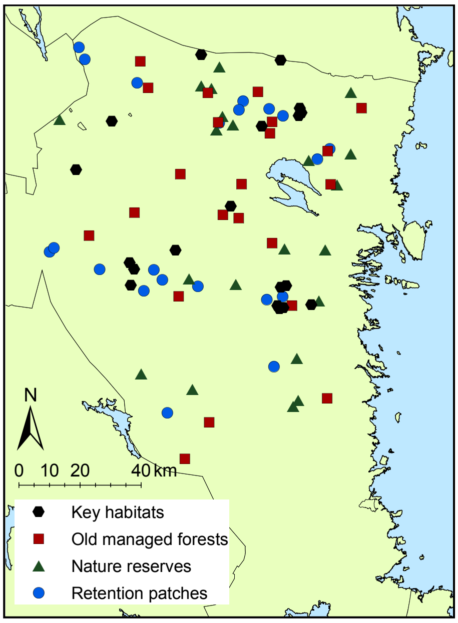

Figure 3. Location of the 80 study sites in the county of Gävleborg (data set A).

Data collection

Presence of bryophytes, lichens and wood-living beetles were recorded in a circular study plot with 10 m radius in each of the 80 sites and in a larger 50x50 m study plot in key habitats, nature reserves and old managed forests. Bryophytes were recorded on all substrates and lichens on living and dead spruce trees (see paper I), while wood-living beetles were sampled by sieving bark from each of five dead lying or standing spruce trees (Djupström *et al.*, 2008). We recorded a total of 649 species, of which 302 were bryophytes, 206 were lichens, and 141 were beetles. Of the species, 13 bryophytes, 14 lichens, and 15 beetles were red-listed (Gärdenfors, 2005) and considered threatened or nearly threatened in the forest landscape. There is currently a bias in terms of organism groups in focus in conservation studies; most concern vertebrates and vascular plants (Fazey, Fischer & Lindenmayer, 2005). With respect to species groups, beetles, bryophytes and lichens make up almost 50 % of the red-listed forest species in the study area (Gärdenfors, 2005), and are in general important species groups in boreal forests. In each site we also estimated the volumes of tree structures known to be lacking in managed forests (Berg *et al*., 1994): dead wood, deciduous trees and large-diameter trees, as well as the presence of brooks, springs, and cliffs.

Land costs (opportunity costs) were measured as the net present value of lost forestry revenues, taking both the land expectation value and the value of standing timber into account. The standing volume per hectare for each plot was estimated from growth functions on the basis of vegetation type (Hägglund & Lundmark, 1977), site-quality index (Hägglund, 1981), stem number, basal area, stand age, latitude, elevation, and thinning history. We calculated the net present value of each site in Plan 33 (Ekvall, 2005), in which simulations of stand management were made to maximize the net present value over an infinite number of rotations with a real interest rate of 3 %. Prices for timber and pulpwood and costs for silvicultural measures were obtained from Mellanskog, a Swedish forest owner's association (Ekvall, 2005; Ranius *et al*., 2005).

We also estimated the information costs associated with the different types of conservation areas, i.e. the costs for identifying and delimiting the areas. For retention patches, we asked the forest companies Holmen, Korsnäs and Sveaskog and the Swedish Forest Agency to estimate the information cost. For key habitats we used the sum spent by the Swedish Forest Agency for identification of key habitats in Gävleborg county, and divided this with the area identified as key habitat. For nature reserves, the County Administrative Board in Gävleborg estimated the cost.

Different types of retention patches (data set B)

Selection of sites

In year 2000, 74 retention patches on land owned by small-scale private forest owners were randomly selected. The patches were distributed over 37 harvested areas within a region of approximately 80x70 km in the provinces of Medelpad and Ångermanland (Fig 4). The patches were of six main types (sample size within parenthesis) with regard to their forest composition, site characteristics and location on the harvested area: buffer zones to open mire (22), buffer zones to stream or lake (14), rocky outcrop patches (11), free-standing tree groups dominated by coniferous trees (10), free-standing tree groups dominated by deciduous trees (9), and moist-wet paludified forest patches (8). The average patch size differed between the types, from 0.06 hectare (paludified areas) to 0.16 hectares (buffer zones to water).

Data collection

In each retention patch, red-listed and indicator species of bryophytes and lichens were recorded in two identical inventories in 2000/2001 and 2006/2007 (the first shortly after harvest). Many bryophytes and lichens are strongly affected by altered forest microclimate (Busby, Bliss & Hamilton, 1978; Sillet, 1994; Esseen & Renhorn, 1998) and are suitable study organisms for evaluating the capacity of retention patches to "life-boat" species over the forest regeneration phase. Species were recorded on all substrates up to a height of 2 m in 5 m wide belt transects covering the whole patches. In total, the dataset included 60 species, of which 19 were bryophytes and 41 lichens.

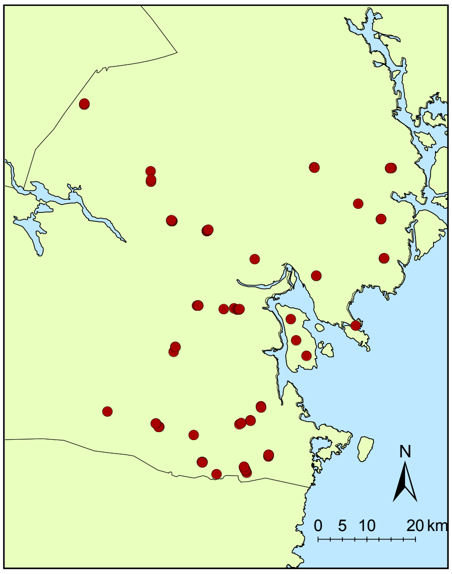

Figure 4. Location of the 74 retention patches in the provinces of Medelpad and Ångermanland (data set B).

We also made a more coarse-scale assessment of the biodiversity potential in each retention patch, according to an established method developed by Drakenberg & Lindhe (1999). The assessment is simple and based on structural characteristics, site factors, and important forest processes (e.g. large-diameter trees, seasonal flooding, degree of sun-exposure, and diversity of tree ages; in total 50 factors were evaluated for each patch). The method has been used extensively by Swedish forest companies and forest owner's associations to assess the conservation quality of forest stands and can be applied on stands of very different sizes.

The cost for setting aside each retention patch from forestry was calculated as the net present value of lost forestry revenues, taking both the land expectation value and the value of standing timber into account. To calculate the volume of standing timber, all trees >8 cm in diameter at breast height were measured in the field. Site productivity and costs for optimal forest management schemes were included in the calculation of the net present value and prices for timber as well as costs for management measures were derived from current price lists for the region at the time of the study. The retention patches were assumed to be set aside from forestry for all future and we used a real rate of discount of 2.5 % (Ekvall, 2005).

Data analysis

Statistical analyses

Sample-based rarefaction curves (Gotelli & Colwell, 2001) were used in paper I and IV to study differences in species richness. Similarity in species composition among sites of different types (proportion of shared species among pair-wise study plots) was measured by Sørensen index (Sørensen, 1948). Multi-response permutation procedure tests (MRPP; McCune & Grace, 2002) were used in paper V to test whether species composition differed significantly between types of retention patches. ANOVA, Kruskal-Wallis, Mann-Whitney U-test and Wilcoxon matched pairs test (Quinn & Keough, 2002) were used in all studies where appropriate, to investigate differences in e.g. species density, land costs, biodiversity potential scores, and amount of dead wood.

In paper II, species-investment curves (Murdoch *et al*., 2007) were constructed to compare the average number of species in each type of conservation area for different levels of land cost. Sample-based species accumulation curves were first used to calculate the average number of species for each number of sampled sites of the different types of conservation areas. The number of sites was then multiplied with the average opportunity cost for sites of each type.

Multiple linear regression (Quinn & Keough, 2002) was used in paper IV to analyze the potential influence of different site characteristics on species responses. Because I wanted to test the relative explanatory effect of the five variables rather than find an optimal model from which to make predictions, I only fitted a global model for each response variable, i.e. a model with all explanatory variables, without simplifying it further (Mac Nally, 2000; Whittingham *et al*., 2006).

Site-selection analyses

I used site-selection analyses (Margules & Pressey, 2000; Cabeza & Moilanen, 2001) to study different aspects of cost-efficiency of conservation areas and cost-efficiency of strategies to select them. In paper I, I used site-selection analyses to investigate how efficiently the set-aside types could represent all species at least once. I also performed the analyses for three representations of each species, because it has been shown to greatly increase the probability of species long-term persistence in a reserve network (Rodrigues *et al*., 2000). In paper V, site-selection analyses were used to investigate the cost-efficiency of different types of retention patches. To do this, I studied the proportions of sites of different types in an optimal (i.e. cost-efficient) selection of patches compared to their original proportions in the data set. In paper III and V, I used site selection analyses to investigate potential gains by including information about land costs of sites along with information about conservation quality, and in paper III to investigate how the relative importance of different types of information (here land costs and conservation quality) was affected by the conservation goal. The site-selection problems were formulated as optimization problems in an integer linear programming framework (Possingham, Ball & Andelman, 2000), or as rankings of sites where linear programming was not needed.

Re-scaling of area in site-selection

Because the average sizes of retention patches of the different types differed substantially in our data set, an optimal selection scheme with a target of maximizing the number of species would inevitably favor the smaller patches. This is because smaller patches have comparably more species than larger patches, i.e., species number does not increase in a linear way with area (Rosenzweig, 1995). I corrected for this size bias by re-scaling the area of each patch upwards according to the species-area relationship in the data set. An artificially linear relationship between species number and area was thus created that allowed for comparisons of cost-efficiency of patch types with different average sizes. To re-scale land costs of patches accordingly, I multiplied the re-scaled area of each patch with the economic value per hectare.

Variability measure

Standard measures of variability, such as the coefficient of variation or the Gini coefficient (Sen, 1973), can only be used to investigate variability in data that can be measured on a per-site basis. For the conservation goal of maximizing total species richness in a reserve network, the conservation value of each site is dependent on which other sites are also selected. To measure the variability in conservation quality ("benefits") over sites, I constructed a new variability index that was based on the difference in outcome between a best possible selection of sites and a worst possible. The index can be used to measure variability in all kinds of information, also in situations where there is interdependence between sites.

Main results and discussion

Conservation quality of different types of conservation areas and old managed forest (paper I, V)

Key habitats, nature reserves and retention patches (data set A)

Key habitats had (on average per study plot) a higher number of bryophytes than nature reserves, retention patches, and old managed forest (paper I). Further, key habitats and nature reserves had a higher number of red-listed bryophytes and indicator species of bryophytes than retention patches and old managed forest. For lichens, the only difference was between key habitats and retention groups for red-listed species. According to rarefaction curves, the total number of bryophyte species was significantly higher in key habitats than in all the other three forest categories, while there were no differences for lichens. The most important structural differences were a larger amount of dead wood and deciduous trees in nature reserves than in old managed forest and a more frequent occurrence of brooks or springs in key habitats than in the other forest categories.

Nature reserves had the most similar species composition among sites (66 % shared species among pair-wise study plots), and key habitats the least (53 % shared species). The largest number of unique species, i.e. species that were not found in any other category, was found in key habitats; 76 such species (61 bryophytes and 15 lichens) occurred in key habitats compared to 9 and 23 species in nature reserves and retention groups, respectively. In the site-selection analyses to investigate how efficiently the set-aside types could represent all species at least once, key habitats constituted the largest part of selected plots in the optimal solutions, except for red-listed lichens. However, when three representations of each species were required, the nature reserves and key habitats were equally efficient at representing the different subsets of bryophyte species.

The most important explanation for the high species richness and complementarity between plots in key habitats is likely that key habitats are small hotspots that do not contain buffers, as opposed to nature reserves which usually are considerably larger and contain a mixture of high and low quality parts. Presence of brooks or springs was also comparatively more common in the key habitats than in the other categories. Consequently, more bryophytes connected to moist and wet conditions were found in the key habitats, contributing to their high species richness. In general, areas that contain a wide variety of different habitats and unusual substrates would harbour the greatest species diversity (Gignac & Dale, 2005). Further, all retention patches in this study were free-standing patches of forest on the harvested area. If also other types of spruce-dominated retention patches would have been included, such as buffer zones to mires or lakes (see paper V), their conservation quality might have been higher.

The old managed forests were in many aspects similar to the key habitats and the nature reserves. Earlier studies (e.g. Gustafsson *et al.*, 2004) have shown that in this part of boreal Sweden, there are large areas of biodiversity-rich old managed forests with a high number of red-listed bryophytes and lichens. Detailed studies on the forest history in the region are sparse, but it is likely that the old managed forests here, as in many other parts of boreal Sweden, never have been clear-cut (Östlund *et al*., 1997) and thus are first-generation managed forests with high conservation quality.

Forest set-asides cannot be regarded as islands in an inhospitable sea, as the surrounding matrix functions both as habitat and dispersal area for many species. Consequently, the theory of island biogeography (Diamond, 1975; Simberloff & Abele, 1976), is not readily applicable to explain differences in species number between set-aside types of different size (Ricketts, 2001). However, the size difference will have a large impact on how the set-asides can be predicted to change over time. It has been proposed by Berglund & Jonsson (2005) that an extinction debt (Tilman *et al*., 1994) might be present in key habitats and that they over time will lose some of their species. The proportion of the total area that could be affected by edge effects from adjacent land clearing is much lower in nature reserves, but even higher in retention patches (see paper IV). As many bryophytes and lichens are dependent on habitat with interior characteristics (Hilmo & Holien, 2002; Hylander, 2004), a larger proportion of species consequently run the risk of local extinction in the retention groups and key habitats than in the nature reserves.

Retention patches of different types (data set B)

The moist-wet paludified areas contained the largest proportion of unique species, followed by the buffer zones to mire, while the rocky outcrop patches contained the lowest proportion of unique species (paper V). The species composition differed between the retention patch types according to the MRPP (multi-response permutation procedure) test. Rocky outcrop patches was the type that differed most from the others, and significantly to deciduous groups, paludified areas and buffers to water. Deciduous groups and buffers to mire also differed significantly from each other.

From a conservation management perspective, the dense spatial occurrence of retention patches in the forest landscape and the temporal continuity with which they are established can make them an important complement to traditional protected areas. If the patches can retain their species long enough, the likelihood of maintaining dispersal of species to all parts of the matrix within the time span between successive forestry rotations will be high (but see paper IV). This points to the importance that the selection of patches to be retained is made in a representative way of the forest landscape as a whole, as the selection in a long-term perspective might have a high influence on which species are found in the matrix. Acknowledging the fact that different types of retention patches are complementary in their species composition when there are different potential patches to retain on an area to be harvested will lead to a more diverse species representation on the harvested area. Fenton *et al*. (2003) argue that similar habitats to those being cut should be selected as retention patches to ensure maintenance of all populations in need of conservation measures.

Life-boating of bryophytes and lichens in retention patches (paper IV)

In total, we noted 455 species records of bryophytes in the first inventory and 308 records in the second inventory. For lichens, the number of records was almost the same; 1061 records at the first inventory and 1047 six years later. Four species of bryophytes increased in total number of records, 14 species decreased and two species were found in equal number of records both years. All four red-listed bryophyte species (liverworts) decreased. For lichens, 17 species increased while 22 species decreased and five species were found in equal numbers. Based on pair-wise tests of species number in retention patches over the two inventories, bryophyte species number had decreased while species number of lichens had not changed significantly. Rarefaction curves indicated no significant differences in total species richness of all patches together between the years for either bryophytes or lichens.

Liverworts decreased slightly more than mosses, but more clearly so if measured as relative change (-66 % and -28 %, respectively). Responses of green-algae lichens did not differ from lichens with cyanobacteria as photobiont and neither group decreased or increased significantly. Responses of bryophytes differed between the six different types of retention patches, with smallest decreases in tree groups dominated by deciduous trees and largest decreases in buffer zones to water. For lichens, there was no difference between the six types of retention patches. The multiple regression analysis showed that bryophytes and lichens decreased less in larger forest patches and that bryophytes decreased more in irregularly shaped patches.

Bryophytes have been reported to be more sensitive to altered moisture and light conditions than lichens (Moen & Jonsson, 2003; Lõhmus, Rosenvald & Lõhmus, 2006). This difference might be due to a set of physiological characteristics among lichens, which could make them less prone to desiccation. These characteristics include: (1) their ability to photosynthezise using only air humidity (excluding cyanolichens), while bryophytes to a larger extent depend on liquid water (During, 1992; Green & Lange, 1995), (2) their general preference for higher light levels (Longton, 1988; Hallingbäck, 1996; T. Hallingbäck, unpublished data), (3) a substantially lower optimum thallus water content than most bryophytes (Green & Lange, 1995), and (4) their capacity to adjust to high light intensities by increasing thallus thickness (Hilmo, 2002) or the concentration of protective pigments (Gauslaa & Solhaug, 2001). In closed forests, lichens seldom photosynthezise at maximum rates due to low light intensity (Green *et al*., 1995). All liverwort species decreased over the six years in our study, which is in line with the general conception that liverworts are more sensitive to forestry operations than mosses through higher demands on substrate quality, shading and air humidity (Söderström, 1988; Marschall & Proctor, 2004; Frisvoll & Prestø, 1997; Fenton, Frego & Sims, 2003; Nelson & Halpern, 2005b).

A key question is whether species actually can be "life-boated" over the regeneration phase in forest remnants. A second question is whether retention patches can function as sources of dispersal for those species into the new regenerating stand. The conditions in a previously harvested area may remain inhospitable to sensitive bryophytes and lichens for at least as long as 30-50 years (Dynesius & Hylander, 2007) and largely lack critical substrates such as de-composing logs and large deciduous trees. The decreases that we observed for many species, especially liverworts, might be far too drastic for them to survive long enough for successful dispersal to be possible, although the exact rate of the decreases could not be measured by only two inventories. However, for some of the species that increased in our study, and for other species such as wood-living beetles (Kaila, Martikainen & Punttila, 1997), the new conservation practice potentially provides a critical habitat type that is lacking in the managed forest landscape: sun-exposed forest with old-growth characteristics such as large amounts of dead wood.

Cost-efficiency of different types of conservation areas (paper II, V)

Key habitats, nature reserves and retention patches (data set A)

Key habitats and retention patches were the most cost-efficient types of con-servation areas for bryophytes, lichens as well as for wood-living beetles, measured by the species-investment curves (paper II). This means that for any given level of investment, more species were represented per area by a conservation strategy based on key habitats and retention patches than by a strategy based on nature reserves. However, the differences were not significant for lichens. Retention patches were less cost-efficient for large-diameter trees (>30 cm in diameter at breast height) than key habitats and nature reserves. For dead wood and deciduous trees, there was no difference in cost-efficiency between the three conservation area types.

The land cost for retention patches was much lower than for the other types; 29 000 SEK per hectare compared to 50 300 SEK for key habitats and 51 300 SEK for nature reserves. This made them very cost-efficient even though their con-servation quality was generally moderate (see Paper I). The concern of the forest owner when selecting retention patches is likely somewhat different from that of the Swedish Forest Agency and the County Administrative Board when selecting key habitats and nature reserves. While key habitats and nature reserves are selected with the intention of maximizing conservation quality, retention patches may often be selected in order to minimize costs while still complying with legal and certification requirements. Accordingly, easily identified structures with low economic value (dead wood and deciduous trees) were cost-effectively included in retention patches. On the other hand, biodiversity parameters requiring more information (red-listed species), or with high economic value (large diameter trees), were less effectively included.

The intention of the County Administrative Boards when selecting nature reserves is, just as for key habitats, to select areas with high conservation value. However, an additional requirement is that areas should be large (>20 ha). As the old growth forest in Sweden is very fragmented it can be difficult to combine the two objectives of the reserve strategy (high conservation value and large size), and therefore so-called developmental areas with lower conservation value are often included in reserves. This leads to a selection with lower cost-effectiveness (Ranius & Kindvall, 2006). Accordingly, smaller conservation areas such as key habitats can be located with greater precision in the landscape to efficiently capture the true "hot-spots" for forest biodiversity (Groeneveld, 2005).

Comparisons of different implemented conservation actions and especially analyses of their efficiency are still very scarce (Sutherland *et al*., 2004; Fazey, Fischer & Lindenmayer, 2005; Ferraro & Pattanayak, 2006). An important reason for this is likely that it is inherently difficult to disentangle all factors that contribute to the over-all cost-efficiency of a conservation measure or strategy. In paper II, we limited the study to the cost-efficiency with which each conservation area can represent biodiversity per area today. Thus, in the comparison we did not consider the effect of size-differences on the long-term persistence of biodiversity, which most likely would act to increase the cost-efficiency of the larger nature reserves.

Retention patches of different types (data set B)

The average land cost per hectare varied between 43 200 SEK (deciduous groups) and 21 600 SEK (paludified areas) but the variation within the six types was very large and the differences between types were not significant (paper V). In site-selection analyses among all 74 retention patches to represent as many species as possible for an increasing total budget, the moist-wet paludified areas and the deciduous tree groups constituted the largest proportions of selected sites in relation to their original proportions. Buffer zones to mire and rocky outcrop patches were selected least in relation to their original proportions in the data set and were thus interpreted as the least cost-efficient types. When patches were ranked according to a quotient between biodiversity potential scores and land cost, the paludified areas were still the most cost-efficient (ranked higher than their average rank) and the buffer zones to water the least cost-efficient.

When I corrected for the size bias among patch types by re-scaling the area and the cost of each patch according to the species-area relationship in the data set, buffer zones to mire were selected to a much larger extent and were the most cost-efficient patch type. The deciduous groups were still cost-efficient and the rocky outcrop patches were still not.

The choice of regarding the sizes of patches as fixed or flexible thus affected their relative cost-efficiency. In practice, it might in fact be so that the two smallest types of areas in this study, the paludified areas and the deciduous tree groups, generally occur as very small patches within a forest stand. In that case, the analyses based on the scenario with the true costs should be regarded as the most relevant. For both measures of biodiversity (species richness and biodiversity potential scores), and for true costs as well as for re-scaled costs, the most cost-efficient set of patches was almost always comprised of patches of all six types. This was likely an effect of the large variation in both land cost and conservation quality of patches within each type together with the fact that the different types of patches were complementary in their species composition.

Gains in cost-efficiency by using information about costs (paper III, V)

In our data set of spruce forest sites in Gävleborg (data set A), the increase in cost-efficiency by considering land costs along with conservation quality when selecting sites was on average 6.5 % but differed depending on how biodiversity was measured (paper III). For a conservation goal of maximizing the total species richness in all selected sites, the gains were only 1.1 %. However, when the goal was to maximize the number of species per site (species records), the increase was 10.3 % and when sites were selected according to a conservation value score assigned to each site (based mainly on structural characteristics of sites), the gains in cost-efficiency were 8.1 %. For data set B, the gains from using information about both costs and conservation quality of sites when selecting patches optimally within each harvesting area to maximize species richness were 3.4 % (paper V). When the re-scaled costs were used (see above), the gains were on average 9.2 %. Finally, for biodiversity potential scores the gains in cost-efficiency by ranking patches according to a quotient between scores and costs rather than according to scores alone were 10.5 %.

The relative variability of costs and conservation quality of sites determines their relative importance for the outcome of site-selection (Babcock *et al*., 1997; Ferraro, 2003; paper III). In the two most influential previous studies on the gains in cost-efficiency from including information about costs in reserve selection (Ando *et al*., 1998; Polasky *et al*., 2001), costs varied by a factor of almost 2000, whereas in both our studies (paper III and paper V) the corresponding factor was only about 10. This in turn made the differences we found in cost-efficiency between site-selection models rather small in absolute terms. If the sites we included had been more heterogeneous (e.g., sampled from different forest types), the variability in costs would have been larger. In practice, however, the relevant reserve selection problem is often rather to make an optimal selection of sites within each broad land type than between types, so as to secure a high complementary of land types within a reserve network. Further, the correlation between costs and benefits affects the magnitude of efficiency loss from use of a suboptimal selection strategy (Babcock *et al*., 1997) and this is further discussed under “Correlation and variability in conservation quality and costs” below.

In practice, the use of a selection model that integrates information on both costs and benefits means that the absolute “hotspots” for biodiversity might never be selected or may receive low priority and be selected late in the selection process. Conservation benefits will also be less aggregated than after a selection on the basis of biological criteria alone because cheaper but more sites with slightly lower conservation quality will be selected (Balmford *et al*., 2000; Messer, 2006). However, given that no conservation goal can encompass all important aspects of biodiversity, there is a potential advantage in this fact too. Less-aggregated conservation benefits over larger areas can be seen as a low-risk conservation alternative in the face of uncertainty over time, such as possible range shifts of species caused by climate change (Parmesan, 2006), but is also advantageous both for recreation and for securing ecosystem services.

Conservation goals and importance of conservation quality and costs (paper III)

The conservation goal for a reserve network strongly affected the relative importance of including information about conservation quality (benefits) and land costs. For a conservation goal of maximizing the number of species per site (species records), information about costs were more important to include than information about benefits to make a cost-efficient selection of sites. Conversely, for a conservation goal of maximizing total species richness in the entire set of selected sites, information about benefits were more important to include than information about costs. For a conservation goal of maximizing conservation value scores of each site (calculated from amounts of important forest structures, site characteristics, and number of species of conservation concern), costs and benefits were about equally important to include.

Babcock *et al*. (1997) and Ferraro (2003) showed that the variability in data determines how important they are to include for reserve selection to be efficient. According to the variability index I constructed, benefit variability was highest in the conservation goal to maximize the total number of species, lowest in the conservation goal to maximize species records per site, and intermediate in the conservation goal to maximize conservation value scores. Because variability in costs was the same regardless of conservation goal, the variability in benefits for different conservation goals had a major influence on the relative importance of including information about benefits and costs for selection to be cost-efficient.

Thus, although derived from the same species data set, the goal with interdependence between sites implied higher benefit variability. One can imagine conservation goals in which the interdependence between sites would play an even bigger role and benefit variability consequently would be even greater. That would, for instance, be the case if the conservation value of each species were regarded as dependent on which other species were also included (e.g., a species might have a higher value as long as it lacked close phylogenetic relatives in the reserve network; Forest et. al., 2007). Furthermore, one can also imagine a relationship between species and sites. This could be the case if the benefit value of including a species were dependent on how much of a particular site type (e.g., important foraging habitat) was also included or if the probable survival of a species in the reserve network were secured only if a threshold amount of suitable habitat was included. In these kinds of scenarios, the difference between the best possible selection of sites and the worst possible selection (from a benefit perspective) would be even greater than in the goal we included here of just maximizing the total number of species, and the relative importance of information about these relationships would be very high.

Correlation and variability in conservation quality and costs (paper III, V)

Correlation

The number of bryophyte species was negatively correlated with land costs in the data set of spruce-forest sites in Gävleborg (data set A; paper III). There was no correlation between land costs and species number of lichens or wood-living beetles, respectively, nor between land costs and conservation value scores. Also when analyzing red-listed species separately, no correlation were found for any of the species groups. For the 74 retention patches in data set B, however, there was a positive correlation between the biodiversity potential scores and the land costs per hectare, as well as between number of species records per hectare and land costs per hectare (paper V).

The correlation between costs and conservation benefits affects the importance of using the most relevant (i.e. most variable) information when selecting conservation areas (Babcock *et al.*, 1997; Naidoo *et al.*, 2006). The negative correlation between species records in sites and land costs in paper III therefore made the selection based only on conservation quality slightly more cost-efficient for the species records goal than would have been the case with a positive correlation. With a positive correlation, land costs would have been even more important to include, because they represented the most variable type of data. Similarly, the positive correlation between conservation quality and land costs in paper V made gains from including costs larger than would have been the case with a negative correlation.

A well-managed (e.g. repeatedly thinned) forest stand may be expected to have lower conservation qualities and a high economic value of the standing timber, and in that respect negative correlations should not be surprising. On the other hand, large-diameter old trees are important for many forest species (Berg *et al.*, 1994), which could imply a positive correlation between species and costs. To date, there are very few studies on the correlation between conservation quality and land costs, and most of them for very large spatial scales (e.g. Moore *et al.*, 2004). More studies are needed to assess whether the correlation between conservation quality and land costs is generally negative or positive at spatial scales relevant to conservation planning in boreal forests (see Naidoo *et al.*, 2006).

Variability

According to the variability index I constructed (see Conservation goals and the importance of costs and benefits above), benefit variability was 0.31 for the conservation goal to maximize the total number of species, 0.21 for the conservation goal to maximize conservation value scores and 0.10 for the conservation goal to maximize species records per site. The variability in land costs among sites was 0.24 when measured with the same index.

The variability we found in opportunity costs among the 60 forest sites was moderate compared with the variability found in studies conducted on larger geographical scales (e.g., Ando *et al.*, 1998; Polasky *et al.*, 2001; Moore *et al.*, 2004). Contrary to the empirical studies cited by Naidoo *et al*. (2006), our results show that conservation benefits can be relatively more variable than conservation costs. It is thus important to note that costs do not always vary more than benefits, but for conservation planning in a boreal Swedish context, costs nonetheless vary enough to be a critical factor to systematically include when selecting conservation areas.

Information costs and benefits (paper II)

The information cost for identifying and selecting each type of conservation area was estimated to an average of 300 SEK per hectare for retention patches, 1200 SEK per hectare for key habitats, and 500 SEK for nature reserves, although the figure for nature reserves is probably the least accurate due to the complex identification process of nature reserves. The corresponding land costs per hectare for these three types of conservation areas were on average 29 000 SEK, 50 300 SEK, and 51 300, respectively. Thus, the information costs were low in comparison to the opportunity costs (i.e. between 1 % and 2.5 %). When comparing the cost-efficiency with which the different types of conservation areas could represent species and structures, including the information costs or not in the evaluation had a minor influence on the result.

Given the large difference in the magnitude of these two types of costs, and the large variation in land costs between individual areas (paper II and V), it seems reasonable that more resources generally should be spent on more thorough conservation value assessments when prioritizing among areas to set aside for conservation purposes. Estimations of the economic value of areas are likely even cheaper to make and can be valuable to aid identification of the most cost-efficient areas to set aside (see also Drechsler & Wätzold, 2001; Naidoo & Adamowicz, 2006; Naidoo *et al*., 2006; Murdoch *et al*., 2007). The optimal degree of collection of different types of information is an important area for future studies.

Synthesis and perspectives

A landscape perspective on conservation strategies

The critical role of conservation in the matrix

The probability of maintaining a species in a region over time depends on the configuration of the entire pattern of protected and non-protected forest areas (Costello & Polasky, 2004). A local population of a species may become extinct from a forest area due to stochastic environmental or demographic events, but the species may still persist in the region as a metapopulation (Hanski, 1999; Hanski & Ovaskainen, 2000). This requires, however, that the matrix allows for sufficient mobility of species among sites.

In this perspective, "stepping stones" such as retention patches may fulfill a critical role by enhancing the connectivity in the landscape (Franklin *et al*., 1997). It is important to acknowledge that connectivity is species-specific and that the critical distance between patches varies both between and within organism groups (Lindenmayer & Franklin, 2002). For species groups that disperse randomly, such as cryptogams and most vascular plants, a high general quality of the matrix is more important than specifically designed dispersal corridors. There are indications that many bryophytes and lichens can establish and persist even in younger, managed forest if dispersal sources are present close enough (Hilmo & Såstad, 2001). A key question is thus the threshold density of source patches in the landscape but to assess this, better knowledge of species' spatial- and temporal dispersal abilities will be needed.

Diversity of conservation strategies

Species groups, as well as separate species within groups (see paper IV), respond differently to conservation measures (e.g. Chambers *et al*., 1999; Lindenmayer & Franklin, 2002; Sullivan *et al*., 2008) both in terms of preferred habitat types and substrates and in terms of required size of undisturbed forest. Therefore, traditional protected areas should not be put in opposition to conservation measures in the matrix; the key question should instead be to strike the right balance between the two approaches. Similarly, the different types of conservation areas studied in this thesis (nature reserves, key habitats and retention patches) partly fulfill different functions and should therefore be used in parallel. Within each conservation area type, however, e.g. when selecting which key habitats to formally protect as habitat conservation areas, the scope for prioritization may be much larger. Different types of retention patches also fulfill different roles, and the most important selection situation is likely the one between candidate patches of the same broad type, e.g. coniferous-dominated patches.

Applying a complementary set of conservation measures at spatial scales from the retention of single trees to large tracts of undisturbed forest is also a way to spread risks associated with imperfect ecological knowledge and uncertainties over time. Forests are slow systems that once harvested take many decades to re-establish. Thus, to secure regional possibilities for adaptation to altered land use patterns or species range shifts due to e.g. climate change (Parmesan, 2006), focusing on a broad range of strategies across the landscape may be a less risky approach. Likewise, to further strengthen a risk-spreading approach, postponement of harvesting of old stands with high conservation values (Eid *et al*., 2002) as well as application of alternative silvicultural systems such as continuous cover forestry (Axelsson *et al*., 2007) could be considered.

Spatial scales for conserving biodiversity

The Swedish environmental objective to conserve all naturally occurring species in viable populations (Swedish Government, 2001) poses an obvious question with huge practical implications for conservation planning: At what spatial scale should each species be conserved in the landscape? Within scientific studies of reserve selection, as well as in real-world conservation planning, the choice of planning region within which to maximize biodiversity is far from easy to make (Simberloff, 2001).

In paper V, a planning region as small as a single harvested area was used to study cost-efficiency of different approaches to select which patches to retain, and the implicit assumption was thus that each forest owner should maximize species richness and complementarity of habitats within each harvested area. Conversely, in the Swedish national plan for how to select areas to protect formally (Swedish Environmental Protection Agency & Swedish Forest Agency, 2005), there is a strong focus on concentrating conservation efforts to regions with high conservation potential for different aspects of biodiversity. In practice this means a quantitative aggregation of conservation effort in the landscape, but a qualitative division in terms of what species and habitat types are in focus. Gjerde *et al*. (2007) present a promising approach to find small areas with high conservation values, a "complementary hotspot inventory" based on habitat types and environmental gradients, but even using this type of approach the question remains whether all important types (with their respective species communities) should be prioritized evenly all over the forest landscape or concentrated into core areas for different aspects of biodiversity.

Systematic conservation planning in practice

What information to collect and consider

When selecting areas to set aside for conservation purposes, a set of factors determines the importance of using a systematic approach for selection and how resources should be divided between collecting different types of information. In this thesis, three such key factors have been assessed and discussed: the variability in data, the correlation between different types of data, and the costs for collecting data (Fig. 5). When the variability in a certain type of data, e.g. conservation quality or land costs of sites, is high it is important to collect information on that type of data because the conservation outcome will vary dramatically depending on which sites are selected.

Further, costs for collecting information on different types of data affect the necessary trade-offs in allocating inventory resources. Thus, data with low information costs (i.e., data that are cheap to collect) and with high variability (1a and 1b in Fig. 5) would generally be the most strategic to collect from a cost-efficiency point of view. Conversely, data with a low variability and high information costs (2a and 2b in Fig. 5) would be less strategic to collect. The correlation between different types of data also affects which data type to focus most inventory resources on, but works in two ways. When two types of data both represent conservation benefits, e.g. ecological and recreational values of sites, a strong positive correlation means in principle that only one factor needs to be considered because sites selected to maximize one type of benefit will also have high values in terms of the other type of benefit. Conversely, when two types of data instead represent conservation benefits and conservation costs, such as in paper III and paper V, a negative correlation would have the same effect, i.e. that only one factor needs to be considered. There are very few studies on correlations between conservation quality and conservation costs on different spatial scales in boreal forests (to my knowledge none except from the studies presented here), and thus it is not possible yet to say how large impact correlations generally have on information needs. Finally, the conservation goal for the conservation project affects all of these three factors as it influences the way of regarding and quantifying conservation benefits of sites (see paper III).

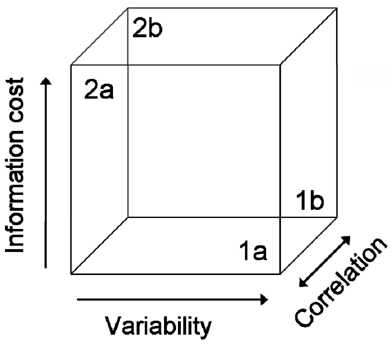

Figure 5. Three factors that affect cost-efficient allocation of resources for data collection in systematic reserve selection. Data with a high variability and low information costs (1a and 1b) are generally the most strategic to collect from a cost-efficiency point of view. Conversely, data with low variability and high information costs (2a and 2b) are less strategic. The correlation between different types of data also plays a central role, but the direction depends on whether two types of data both represent conservation benefits, or one type represents benefits and the other costs.

In future studies on cost-efficient allocation of resources to data collection, an important aspect to consider is the temporal dynamics of the planning system (Costello & Polasky, 2004; Meir *et al*., 2004; Pressey *et al*., 2007). Uncertainties and threats over time, such as rates of harvesting or change of land use, influence the necessity of investing in comprehensive information. In cases where the rate of land conversion is high, the focus should shift from spending time and money to collect comprehensive information on candidate areas to simply secure that as many or large areas as possible are preserved. The current situation in Sweden, with a very small amount of old forest left and a high rate of yearly harvesting, is likely approaching the latter scenario, although it differs among regions and forest types.

A systematic approach to conservation

For a long time, systematic methods developed to guide conservation planning have had a minimal impact on applied conservation practice (Stokland, 1997; Prendergast, 1999; Margules & Pressey, 2000). Today, comprehensive and straightforward guidelines to aid the entire planning process are available (Noss, 2003) and examples of successful applications of a systematic approach to reserve selection increases. The re-zoning of the Great Barrier Reef is perhaps the most well-known of these (Fernandes *et al*., 2005). During a six-year long process of iterative refinement of the conservation plan, data on habitat types, interests of the tourism sector as well as costs to the fishing industry were integrated to create a cost-efficient re-zoning of the entire marine region. Also in the Cape Floristic Region in South Africa, systematic procedures have been used to find complementary sets of new conservation areas (Cowling *et al*., 2003; Rouget *et al*., 2003). New prioritization software (e.g. C-Plan, Marxan, SITES, Zonation, Worldmap), developed to aid cost-efficient spatial conservation planning, was an important tool for these and similar projects.

In Sweden, the possibilities for using systematic conservation planning methods are somewhat different compared to countries where forestry or other land management has been less intense. Most likely, when it comes to preserving the remaining large tracts of old-growth forests as national parks or nature reserves, the majority of relevant areas are already well-known and on the “waiting-list” to be protected as soon as resources allow for it. For smaller areas, at the spatial scale of forest stands (e.g. 1-10 hectares), the flexibility may be much larger regarding which areas to prioritize for conservation. A more systematic approach for selecting which key habitats to formally protect as habitat protection areas, or a more coordinated approach to selecting areas for forest owner’s voluntary set-asides, could be advantageous. Also for selecting retention patches within a forest stand to be harvested, when alternatives exist and the Forest Act allows for it, an approach that favors complementarity and that takes both conservation quality and land costs in to account will increase over-all cost-efficiency.

Implementation and motivation

Although not studied in this thesis, an individual forest owner’s motivation and interest to take part in conservation is important, both for successful implementation of state-initiated conservation strategies and for functional conservation measures in the matrix (Fischer & Bliss, 2008). Studies indicate that Swedish forest owners generally value a high conservation quality in the forest landscape (Boman *et al*., 2008; Kindstrand *et al*., in press) and the possibilities to reinforce this concern for biodiversity should be embraced and further developed.

One factor that may have a large impact on a forest owner's motivation to participate actively in conservation is the degree to which the forest owner feels that the measures applied really contribute to over-all conservation goals. More information from the part of e.g. state agencies on improvements of the conservation status of species or habitat types in the landscape would be central in this regard. A second factor that would likely affect motivation is the extent to which forest owners can influence location and type of conservation areas (Pouta *et al*., 2002). Finally, greater flexibility in the legislation and administrative routines to give room for alternative silvicultural methods, or for possibilities to offer landowners replacement land instead of monetary payments when formal protected areas are established, may be promising ways forwards.

Conclusions

In this thesis, I have investigated both methodological aspects of conservation planning and more applied aspects of forest conservation strategies in boreal Sweden. I list below the main findings and conclusions from my thesis. For clarity, I separate them into methodological developments for research on conservation planning, main results, implications for conservation, and future studies.

Methodological developments

- A variability index that can be used to measure variability in all types of data that cannot be measured on a per-site basis.
- An approach to re-scale the area of selection units to compensate for size biases when reserve selection is intended for comparative purposes of different types of areas.

Main results

- For the different ways of measuring biodiversity used in this thesis, key habitats generally had a higher conservation quality than nature reserves, retention patches on harvested areas, and old managed forest. Also in terms of cost-efficiency for representing biodiversity, key habitats were in most cases the most efficient type of conservation area.
- Most bryophytes in retention patches on harvested areas decreased over time, especially liverworts, while some lichens increased and others decreased.
- Different types of retention patches had a complementary species composition, and there was a large variation in economic value among patches.
- The cost for collecting information on conservation quality of nature reserves, key habitats and retention patches was low compared to the economic value of the forest land.
- The conservation goal for a set of conservation areas greatly affects the relative importance of including different types of information into conservation planning.

Implications for conservation

- The studies indicate, when all central factors are taken into account, that the present Swedish strategy with a combination of different types of conservation areas most likely is efficient for forest biodiversity conservation. To further increase cost-efficiency, prioritizations of which areas to set aside should therefore mainly be made within each type of area.
- When there is room for choosing which patches to retain in a stand subject to harvest, a complementary set of patches should preferably be selected, both regarding structural characteristics, size, and location on the harvested area.

- Cost-efficiency in forest conservation could be increased by collecting information on both the economic values and the conservation quality of candidate areas to set aside, and using both types of information together to guide selection of areas. Because the economic value of areas often varies at least as much as the conservation quality, it plays an important role for cost-efficiency.

Future studies

- More studies are needed on how different factors affect the long-term cost-efficiency of conservation strategies, including temporal uncertainties and threats, species' ability to persist in - and disperse among - conservation areas, and the development of new silvicultural management methods.
- The most cost-efficient allocation of resources for collecting different types of data, as well as the optimal degree of intensity of data collection, are important future research areas. Likewise, implementation issues and motivation of landowners to actively participate in conservation measures have so far received little attention.
- To generalize the results from this thesis regarding the conservation quality and cost-efficiency of different types of conservation areas, future studies should also comprise other geographical regions, other forest types, and organism groups.

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Svensk populärvetenskaplig sammanfattning

Kostnadseffektiv naturvård för biologisk mångfald i skogen

Sverige har en lång tradition av skogsbruk. Från och med mitten av 1900-talet har de allra flesta skogarna brukats med moderna metoder såsom kalavverkning, plantering med barrträd, röjning och gallring. En stor del av skogen är ung och de flesta gamla skogar som finns kvar är små och utspridda i landskapet. Många skogslevande djur och växter är beroende av lövträd, gamla träd och döda träd och har svårt att klara sig i dagens skogar. Omkring 2000 arter anses i dagsläget vara hotade eller missgynnade och en stor del av dessa är mossor, lavar och insekter.

För att förbättra naturvården i skogen har Sverige, liksom de flesta andra länder, under den senaste tiden börjat anpassa skogsbruket för att gynna den biologiska mångfalden. En ny skogspolitik infördes 1993, där skogsproduktion och naturvård är två jämställda mål. Den svenska modellen för naturvård i skogen innebär att en viss mängd, i dagsläget ungefär 3 % av skogsmarken, skyddas av staten medan resten av skogen brukas med ett visst mått av hänsyn till natur- och kulturvärden. Ungefär 4 % av skogsmarken sätts dessutom också av på frivillig väg av markägare.

Ett viktigt inslag i naturhänsynen i den brukade skogen är att lämna kvar trädgrupper på hyggen vid avverkning. Trädgrupperna är tänkta som ”livbåtar” för arter som annars inte skulle överleva ute på hygget. Ett problem med trädgrupperna är dock att de är så små att vind och sol gör miljön i dem torrare och ljusare än i vanliga, slutna skogsbestånd. Arter som kräver en fuktig och stabil miljö löper därmed risk att torka ut. Olika typer av trädgrupper lämnas och de vanligaste är skyddszoner mot myrar och vattendrag, lövdungar, barrdungar, små sumpskogsfläckar och områden runt hällmarker.

Svenska staten betalar nästan en miljard kronor per år i ersättning till markägare för att skydda skog i form av reservat, biotopskyddsområden eller för att teckna naturvårdsavtal med markägare. Därtill kommer de kostnader som enskilda skogsägare har för naturhänsynen på sina marker, till exempel för att lämna trädgrupper på hyggen. Trots dessa satsningar finns det mycket som tyder på att ännu mer naturhänsyn och fler skyddade områden skulle behövas för att långsiktigt säkerställa den biologiska mångfalden. Det är därför väldigt viktigt att naturvården utförs på ett så kostnadseffektivt sätt som möjligt. Man bör alltså se till att få så mycket naturvårdsnytta som möjligt för de medel som finns att tillgå.

Den här avhandlingen handlar om hur naturvården i skogen kan bli mer kostnadseffektiv. Tillsammans med kollegor har jag undersökt några nyckelfaktorer som påverkar kostnadseffektiviteten och utgångspunkten för undersökningen har varit data som vi samlat in i två stora fältstudier i Hälsingland, Medelpad och Ångermanland. Som mått på biologisk mångfald har vi använt artrikedom av mossor och lavar, men även mängden döda träd, gamla lövträd och annat som har stor betydelse för många djur och växter.

I den ena studien, i Hälsingland, jämförde vi den biologiska mångfalden i granskog i tre vanliga typer av skogliga avsättningar: naturreservat, trädgrupper på hyggen och nyckelbiotoper. Naturreservat är oftast stora områden som skyddas formellt av staten, medan nyckelbiotoper normalt sett är mindre och kan skyddas antingen av staten eller av enskilda markägare på frivillig väg. Vi undersökte även den biologiska mångfalden i vanlig, äldre brukad skog som jämförelse. För var och en av de fyra typerna räknade vi också ut det ekonomiska värdet på skogsmarken.

I den andra studien, i Medelpad och Ångermanland, undersökte vi om känsliga mossor och lavar kan överleva i trädgrupper på hyggen. Mossorna och lavarna inventerades första gången strax efter det att avverkningen skett och sedan en gång till sex år senare. Även för dessa ytor mätte vi det ekonomiska värdet. Vi uppskattade också trädgruppernas kvalitet för den biologiska mångfalden med hjälp av en översiktlig naturvärdesbedömning, som baseras bland annat på mängden gamla träd, döda träd och trädens åldersfördelning.

Studien i Hälsingland visade att nyckelbiotoperna generellt sett hade flest arter av mossor per provyta. Ser man bara till hotade och missgynnade arter hade nyckelbiotoperna och reservaten fler mossor än trädgrupperna och de vanliga brukade skogarna. Nyckelbiotoperna hade också fler lavar än trädgrupperna, men för lavar var skillnaderna i övrigt små. Att nyckelbiotoperna hade så höga naturvärden kan bero på att de är små och utgör de (ekologiskt sett) allra finaste områdena i skogen, medan naturreservaten är mycket större och därför innehåller områden av både något högre och något lägre kvalitet. De vanliga brukade skogarna hade också förhållandevis höga naturvärden. Till stor del kan det bero på att de ännu inte har hunnit bli kalavverkade med moderna skogsbruksmetoder, och de skiljer sig därför sannolikt från framtida brukade skogar.

Det ekonomiska värdet på skogsmarken var ungefär lika högt i naturreservat, nyckelbiotoper och i vanlig brukad skog, men lägre i trädgrupperna på hyggen. Detta gör att när man utvärderar hur kostnadseffektivt mossor och lavar kan skyddas i dessa fyra kategorier av skog, är nyckelbiotoperna och trädgrupperna de som sammantaget är mest kostnadseffektiva. Man måste då komma ihåg att detta ger en ögonblicksbild av situationen, och att mycket kan hända med den biologiska mångfalden i framtiden.

Långtidsstudien av trädgrupperna i Medelpad och Ångermanland visade att lavarna klarade sig bättre än mossorna gjorde. Särskilt dåligt gick det för levermossorna, som ofta är känsligare för uttorkning än bladmossor. Det är därför tveksamt om trädgrupper fungerar som ”livbåtar” för känsliga mossor fram till dess att den nya skogen runtomkring vuxit upp. Å andra sidan verkar det som om vissa lavar trivs ännu bättre i den ljusare miljön i trädgrupperna än inne i sluten skog och andra studier har visat att även många insekter gynnas i trädgrupperna.

När vi undersökte hur kostnadseffektiva de olika typerna av trädgrupper var, visade det sig att lövdungarna och de små sumpskogsfläckarna var de mest kostnadseffektiva, men variationen i både naturvärde och ekonomiskt värde var stor inom alla typer. I alla sex typer av trädgrupper fanns dessutom arter som inte hittades i någon av de andra. Det verkar därför vara viktigt att se till att flera olika typer av ytor lämnas i skogslandskapet för att gynna så många arter som möjligt.

Med hjälp av datamaterialet från de två fältstudierna kunde vi också undersöka vilken typ av kriterier som bör användas när man väljer vilka områden som ska lämnas kvar på ett hygge eller skyddas som t ex biotopskyddsområden. Resultaten visade att man ofta kan få mer biologisk mångfald till samma kostnad om man tar hänsyn till både naturvärdet och det ekonomiska värdet på skogen, och inte bara till naturvärdet som man oftast gör idag. Hur mycket mer kostnadseffektivt det kan bli beror bland annat på hur mycket naturvärdet och det ekonomiska värdet varierar på de ytor man har att välja mellan, och vad målet med avsättningarna är.

Ett viktigt resultat var också att kostnaden för att göra en översiktlig inventering av naturvärdet eller det ekonomiska värdet i ett område ofta är mycket låg, åtminstone om man jämför med hur mycket det kostar att skydda skogsmark och hur mycket denna kostnad kan variera mellan områden. Genom att göra något noggrannare inventeringar än man gör idag, och använda den informationen när man väljer områden att skydda, är det troligt att man kan öka kostnads-effektiviteten.

Olika artgrupper har olika krav på sin livsmiljö och det är därför naturligt att alla arter inte gynnas av samma naturvårdsinsatser. Genom att fortsätta arbeta med en mångfald av åtgärder inom naturvården, men där var och en utformas på ett så effektivt sätt som möjligt, skapas förutsättningar för både skogsproduktion och biologisk mångfald. Mer studier behövs dock för att utvärdera hur mycket skyddad och avsatt skog som krävs totalt sett och hur den bör fördelas i landskapet.

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