Conservation of Saproxylic Species

An Evaluation of Set-asides and Substrates in Boreal Forests

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Cover: Emergence hole of *Peltis grossa*
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Abstract

Forest management has altered the prerequisite of many species in forest landscapes. The new, more conservation-oriented forest management includes a range of different strategies that aim to prevent losses of biodiversity. Evaluating these strategies is essential in order to identify where they might fall short of their aims and to identify where to make any necessary improvements.

In this thesis the importance of different conservation strategies is evaluated in terms of what they might contribute to the conservation of beetles dependent on deadwood. Furthermore, patterns of biodiversity and mechanisms that affect biodiversity are explored. In one study, species richness, composition and substrate characteristics were compared in three conservation strategies: nature reserves, woodland key-habitats and retention patches; and old managed forests that had not been set-aside. In a second study, high-cut stumps and other retained dead wood in clear-cuts were evaluated for their importance in the recruitment of the red-listed beetle *Peltis grossa* at the landscape level. A third study explored species richness co-variation, surrogate capacity and β-diversity among bryophytes, lichens, saproxylic beetles and dead wood. A fourth study examined the priority effects among beetles and fungi colonizing high stumps in clear-cuts over a period of 15 years.

Overall, woodland key-habitats were found to have a high conservation value in terms of species richness, richness of red-listed species, and diversity of dead wood. Reserves had the highest dead wood diversity; old managed forests had a relatively high number of red-listed species; and retention patches deviated in species composition. Leaving sun-exposed, coarse wood, which eventually develops into brown-rotten wood due to the fungi *Fomitopsis pinicola*, in a late stage of decay appeared to be a particularly efficient conservation strategy for *P. grossa.* The third study showed that the richness of red-listed lichens and bryophytes can be used to indicate each other's presence, and dead wood diversity appeared to be an efficient surrogate for beetles and bryophytes. A study of priority effects revealed that two early-colonizing species, *Hylurgops palliatus* and *F. pinicola,* positively affected the later colonizing species, *P. grossa*, whereas *Monochamus sutor* had a negative effect.

Keywords: β-diversity, Swedish boreal forests, dead wood, community assemblage, conservation, saproxylic beetles, species diversity, surrogate capacity, priority effects

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Dedication

Till minnet av Jack.
Tack för ditt sällskap och för din ovillkorliga kärlek… till död ved och vatten!

Contents

List of Publications

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

I Djupström B.L, Weslien, J. & Schroeder L.M. (2008). Dead wood and saproxylic beetles in set-aside and non set-aside forests in a boreal region. *Forest Ecology and Management* 255:3340-3350.

II Djupström B.L, Perhans K., Weslien, J., Schroeder, L.M., Gustafsson L. & Wikberg, S. (2010). Co-variation of lichens, bryophytes, saproxylic beetles and dead wood in Swedish boreal forests. *Systematics and Biodiversity* 8(2):247-256.

III Weslien J., Djupström B.L., Schroeder, L.M. & Widenfalk O. Long term priority effects among insects and fungi colonizing decaying wood. (*Under review*).

IV Djupström B.L, Weslien, J., Schroeder L.M. & ten Hoopen, J. Recruitment of the red-listed saproxylic beetle *Peltis grossa* -importance of retained dead wood on clear-cuts. (Manuscript).

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The contributions made by Line B. Djupström to the papers included in this thesis were as follows:

Ideas: Together with supervisors for all papers.

Field and lab work: Main responsibility in Papers I, II and IV and 40 % of field and lab work.

Analyses: Main analyser in Papers I, II and IV, co-analyser in Paper III.

Writing: Main author in Papers I, II and IV, co-author in Paper III.

1 Introduction

The ways in which forests have been managed has changed over time such that today clear-cutting, plantations, and repeated thinnings have been applied in almost all forest landscapes (Axelsson, Anglestam & Svensson, 2007). Since the 1970s there has been growing concern about the ecological effects of forestry on flora and fauna. It is now recognized that forest management has altered the availability of habitat for many species in forest landscapes by changing the forest age structure, and through increased fragmentation and the reduction of both habitat area and quality. One of the key changes in the boreal forests of Sweden is the decrease in diversity and availability of dead wood (Linder & Östlund, 1992; Siitonen *et al.*, 2000; Dahlberg & Stokland, 2004). Populations of many wood dependent species have declined due to these changes and some species face extinction if conservation and restoration measures are not implemented (Essen *et al.,* 1997).

In natural forest ecosystems, dead wood is created by disturbances operating at small- and large-scales: e.g. fire, wind, snow breakage, competition, insects, and various pathogens (Kuuluvainen, 1994; Engelmark & Hytteborn, 1999; Jonsson *et al.*, 2005). The complexity of dead wood substrates in forests are naturally built up over a long time period such that old forests generally provide the highest diversity of dead wood (Siitonen *et al.,* 2000, Siitonen, 2001; Fridman & Walheim, 2000; Stenbacka, 2009). Old forests are therefore important for the survival of many species adapted to forest ecosystems. Today, old forests (i.e. those > 150 years old) constitute only a small proportion (≈ 2 %) of the landscape (Axelsson & Östlund, 2001) and in the future, most of these forests will probably be harvested, except for those that have been set aside. According to the latest Swedish Red List, a considerable number of red-listed species are either directly or indirectly associated with forest land (Gärdenfors *et al.*, 2010). As a consequence of the situation in which many forest-dependent species exist, the Swedish government revised the Swedish Forestry Act in 1994 to give production goals and conservation goals equal importance. The new, more conservation-oriented forestry now strives towards sustainable land–use, which includes the adoption of measures to enhance species' survival in their changing forest habitat. In Sweden, the strategy is both to formally set aside small and large forest areas, and to apply general conservation measures in the managed forests, e.g. the voluntary set-asides made by forest owners. Because set-asides only constitute a small proportion of the total forest land, the ways in which non set–aside forests are managed are important for the conservation of biodiversity (Lindenmayer & Franklin, 2002). A new environmental goal for 2020 was proposed in 2008, based on a report made by the Swedish Forest Agency. By 2020 the goal is to have established an approximately three-fold increase in the area set–aside from forestry from the current area of 900 000 ha to 2 600 000 ha (Swedish Forest Agency, 2007). Large amounts of money will be invested in the future to achieve that goal. From both economic and conservation perspectives it is important that the conservation measures applied are evaluated in terms of the degree to which they contribute to the conservation of biodiversity (i.e. their conservation value) in the Swedish boreal forests. Furthermore, in order to identify where measures might fall short of their goals and to improve their conservation value it is important to identify patterns of biodiversity and improve our understanding of the mechanisms that affect biodiversity.

2 Background

2.1 Conservation strategies in boreal forests

Estimates of the amount of protected forest land in Sweden vary depending on what is included. However, the generally recognized amount of productive forest land protected by law is about 3.2 %, i.e. 900 000 ha including the mountain forest area (Swedish Forest Agency, 2009). The most common way to preserve areas of forest greater than 20 ha has been to set aside land as national parks or nature reserves. Nature reserves are, in general, completely designated for conservation purposes, but sometimes also for recreation. The mean size of forested or partly forested nature reserves is 130 ha, but the actual size ranges from a few ha to several thousand ha (Svedlund & Löfgren, 2003). The selection of areas to be designated as nature reserves has often been based on structural elements that are assumed to be associated with high species diversity or vulnerable species most in need of preservation. The forests in reserves are generally older and have greater quantities of dead wood than managed stands (Fridman, 2000), but in order to create larger continuous forest areas, younger forest stands with lower conservation values may also be included.

Another type of set-aside, which was introduced in the 1990s, is the woodland key-habitats. These areas have either been identified in a large national inventory on privately owned forest ground carried out by the Swedish Forest Agency, or by forest companies themselves. Strictly speaking, they are not protected in law; however, forest owners must formally confer with the Swedish Forest Agency if any forestry operations are to be carried out in them. Key-habitats are usually smaller than reserves, having a mean size of about 5 ha (Timonen *et al.,* 2010). A key-habitat is defined as a forest area, which, because of its stand structure, historical and physical characteristics, is of great importance to sensitive flora and fauna; it should contain or be expected to contain red-listed species (Nitare & Norén, 1992; Norén *et al.*, 2002). The main criteria for selecting woodland key-habitat are the abundance of relevant structural elements and the presence of certain indicator species among various vascular plants, bryophytes, lichens and macrofungi, many of which are red-listed (Norén *et al.*, 2002). Key-habitats generally have larger volumes of dead wood than the managed forest landscape (Jonsson *et al.*, 2005).

During the last decade the focus within forest conservation has changed from setting aside large and small areas to one in which conservation measures are applied in managed forests. One such conservation measure commonly used in Sweden is tree retention patches. This involves retaining patches with living trees, usually 0.01 ha - 0.5 ha, at final cuttings in order to reduce any negative impact of clear-cutting on biodiversity (e.g. Hazell & Gustafsson, 1999). Generally, little or no information is available on inhabiting/resident species. The duration of patches after their establishment is uncertain since there is no legislation to hinder forest owners from cutting them later on. Indeed, many of them seem to be cut, thinned or cleared of dead trees (Persson & Gustafsson, 2002, Larsson & Elander, 2004). Due to their relatively high exposure to wind, tree mortality within a retention patch is considerably higher than in an equivalent/corresponding area of forest (Esseen, 1994; Jönsson *et al.,* 2007).

Retaining single living or dead trees at final cuttings, and creating high stumps from living trees, has received increasing attention in Sweden over the last ten years. In the certification standard stipulated by the Forest Stewardship Council (FSC) and the Program for the Endorsement of Forest Certification schemes (PEFC) in Sweden, the requirements are that some (often interpreted as three per ha) high stumps or girdled trees have to be created at final harvest or during thinning operations (www.fsc.sweden.org; www.pefc.se), the purpose of which is to increase the amount and diversity of dead wood in clear-cuts.

2.2 Measuring biodiversity

The conservation value of different strategies can be evaluated by measuring biodiversity with a range of methods. The easiest way is to sample species in a spatially defined unit, e.g. a forest stand to give α-diversity, which can be used in comparative investigations where all species are given the same weighting. If the spatial unit of interest is very large, e.g. a forest landscape or region, the sample may represent the total species pool (γ-diversity). Since species richness represents just one level of biodiversity, other dimensions should also be considered, such as species composition, which can be used to describe and compare species assemblages between habitats or to analyze species heterogeneity within and between taxonomic groups and sites, i.e. β-diversity. β-diversity has received increasing attention in biodiversity conservation as it can reflect biotic changes or species replacements in two or more spatial units (Magurran, 2004). Species replacement or "species turnover" is usually measured along an ecological gradient (e.g. dry-moist, poor-rich) but can also be used to examine changes in diversity over time. Such changes in species assemblages over time i.e. species succession, is another important issue in the conservation of biodiversity. It is important to understand the patterns and mechanisms that underlie diversity if we want to improve the quality of a conservation measure and identify where it might fall short of its intended goals. Which patterns and mechanisms are essential in the formation of a community or assemblage of species, and so explain β-diversity, has been debated in ecology since the early 20th century. One of the early notions was that the prior arrival of certain species might have important impacts on the future community composition (Tansley, 1935). Thus, the early arriving species can modify the habitat or resources to such an extent that it influences the establishment of later arriving species and the structure of communities (Diamond, 1975; Connell & Slatyer, 1977). Three driving mechanisms have been proposed by Connell & Slatyer (1977): facilitation, inhibition and tolerance. That is, early species can either promote (facilitation model), or have no effect (tolerance model), or reduce (inhibition model) the establishment of later species. These models have become widely accepted and now provide the conceptual framework for understanding the mechanisms that underlie the succession of species in communities. The term "priority effect" is defined as: the impact that a particular species can have on the development of an ecological community due to its prior arrival at a site (Young *et al.,* 2001; Lulow 2004; Fukami *et al.,* 2005). These effects have important implications for understanding changes in natural and managed environments as well as ecological restoration efforts (Fukami *et al.* 2005; Young *et al.*, 2005).

Species composition can also be used to describe the complementarity between sites. Biological features that can be used to represent biodiversity in conservation planning are termed surrogates (Humphries *et al.*, 1995). The surrogate capacity can be defined as: the efficiency with which a specific taxonomic group, or some other biological feature, is able to represent other taxonomic groups in a reserve network; a definition that focuses on the concept of complementarity among sites (Van-Wright *et al.*, 1991). However, when conserving biodiversity in practice, it is not possible to measure total richness of even a small area. The selection of forest areas for preservation would be easier and more effective if some structural characteristics, such as dead wood, could be used to guide prioritization, and if habitats that are species-rich for one taxon were also species-rich for other taxa, especially if they support rare and threatened species (Prendergast *et al.*, 1993). A better understanding of surrogacy patterns in forest ecosystems would therefore provide opportunities for more effective selection of conservation areas.

2.3 Beetles, bryophytes, lichens, fungi and dead wood

The main focus in this thesis is the richness and diversity of saproxylic (i.e. species dependent on dead wood) beetles (Coleoptera) as well as on dead wood *per se*. However, some attention has also been given to bryophytes, lichens and polypore fungi. The reasons for studying these organism groups are that they contribute significantly to total biological diversity and are important components of the ecological processes in forest ecosystems (Longton, 1992; Siitonen, 2001). Many species of beetles, bryophytes and lichens are highly sensitive to environmental changes and have specific habitat requirements, which make them suitable candidates for monitoring biodiversity. They are also relatively well-known taxonomic groups and their substrates and habitat requirements have long been subjects of study in Fennoscandia (e.g. Saalas, 1917; Palm, 1951, 1959; Darbishire, 1914; Räsänen, 1927; Söderström, 1983 (and references cited therein)). The decreasing amount and diversity of dead wood in the forest landscape has been identified as one of the biggest threats to beetles, lichens and bryophytes (Berg *et al.,* 1994; Gärdenfors, 2010). Polypore fungus species have important roles in wood decay and there are many known associations between fruiting bodies or mycelia and saproxylic beetles (Boddy & Jones, 2008). Many saproxylic species do not feed on wood directly but on the fungi colonizing the wood.

Beetles are among the most species-rich saproxylic taxonomic groups in Fennoscandia with more than 1250 species in Sweden (Siitonen, 2001; Dahlberg & Stokland, 2004). About 40 % of these saproxylic beetles are red-listed (Gärdenfors, 2010). In Sweden there are about 1000 bryophyte and 2000 lichen species; of these about 300 bryophytes are associated with forest, and 900 lichens are associated with dead wood and bark (Hallingbäck, 2007;

Spribille *et al.,* 2008). Almost 70 species of bryophytes and 190 species of lichens associated with forest are red-listed (Gärdenfors, 2010).

The technique of measuring the amount and type of dead wood as an indicator has much appeal, as it is usually less costly to execute than the compilation of species inventories. By calculating the number of different types of dead wood and including data on the stage of decay, tree species, and whether the material is from logs or trunks etc., a common unit of measure can be generated which summarizes the different aspects of resource availability, and which can be interpreted intuitively (Hottola *et al.*, 2009).

3 Aims of the thesis

This thesis aims to develop a more efficient conservation of forest-dwelling species in the Swedish boreal forests. Different types of conservation strategies are evaluated and compared with non set-aside forest areas. Distribution patterns of species richness and the relationships among different taxonomic groups and stand structures are also explored at both small- and large-scales. All studies consist of large-scale field inventories in which species and stand structures are included.

3.1 The specific objectives of each of the four papers

I To compare the species richness and species composition of assemblages of saproxylic beetles, as well as the amount and diversity of dead wood, in three different types of set-aside and a non set-aside forest: nature reserves, woodland key-habitats, retention patches, and old managed spruce forests.

II To analyze the co-variation in species richness between lichens, bryophytes, saproxylic beetles and dead wood diversity. To explore the effectiveness (i.e. surrogate capacity) with which one taxonomic group or dead wood diversity is able to represent the species composition of other taxa in a reserve network. To explore β-diversity among forest sites for lichens, bryophytes and saproxylic beetles.

III To study priority effects among beetles and fungi colonizing high stumps created in clear-cuts. More specifically, to test the long-term priority effects hypothesis that the identity and abundance of early-colonizing species affects the colonization success of later arriving species. To identify the mechanisms, e.g. facilitation or inhibition, that account for observed priority effects.

IV To evaluate the effect of created and retained dead wood in clear-cuts on the population of the red-listed beetle, *Peltis grossa* at the landscape level. To study the population growth of *P. grossa* over a period of 16 years on high-cut stumps of Norway spruce, and to explore what characterize a suitable host-tree and future prospects of *P. grossa*.

4 Study area and species sampling

The results presented in this thesis are based on data from two field studies located within the middle boreal vegetation zone in central Sweden. Data set A (Fig. 1 and 2) used in **Papers I** and **II** was collected in the Swedish province of Hälsingland (central point, 61°N, 16°E) and the studied landscape covers 1 534 000 ha. Data set B (Fig. 1 and 3) used in **Papers III** and **IV** was collected in forest landscape of about 10 000 ha situated in the province of Dalarna in the southern boreal zone close to the village of Grangärde (60°16'00"N; 014°59'00"E). Forest dominates the land area at both locations; the dominant tree species are Norway spruce (*Picea abies* L. Karst.) and Scots pine (*Pinus sylvestris* L.) with varying components of mainly birch (*Betula pendula* and *B. pubescens*) and aspen (*Populus tremula* L.).

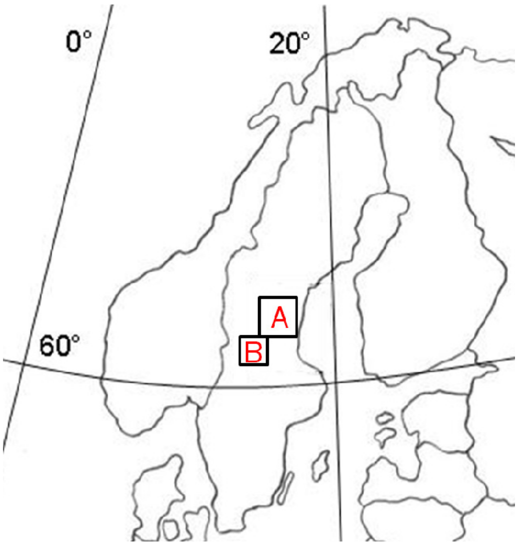


Figure 1. Location of the two study areas, A) Hälsingland, B) Dalarna.

4.1 Dataset A - Hälsingland (*Papers I and II)*

In total 80 sites, equally distributed between nature reserves, woodland key-habitats, retention patches, and old managed forests were included in the studies (Fig. 2). Reserves, key-habitats, and most of the retention patches were randomly selected using GIS layers from the County Administrative Board and the Swedish Forest Agency, and the "wRESEx" satellite map (Angelstam *et al.*, 2003). Complementary data from local forestry boards and the forest company Bergvik Skog AB were used to identify the rest of the retention patches. The old managed forest sites, which were not within the boundaries of either a reserve or a key-habitat, were randomly selected from those characterized by being old forest stands (>110 years) dominated by Norway spruce (> 70 % of the volume of living trees) with a *Vaccinium myrtillus* type of ground vegetation, on mesic or moist soil (Hägglund & Lundmark, 1981), > 5 km from the Baltic sea coast, and at an altitude of < 500 m. a. s. l.

Abundance data on beetles and incidence data on bryophytes and lichens were collected in a circular plots (0.0314 ha) randomly placed in each forest site. Beetles were sampled by sieving bark from standing or lying dead spruce wood. If possible, trees with a diameter > 20 cm in decay classes 2 and 3 were chosen. Beetles were extracted by placing the finer fractions obtained from sieving, under a lamp in Tullgren funnels (Southwood & Henderson, 2000) and only adult beetles were included in the analyses. In contrast to sampling using flight traps, this direct sampling method ensures that the collected beetles had colonized the inspected substrate. In total 129 beetle species were recorded of which 12 were red-listed.

Bryophytes were recorded on all substrates and lichens on living and dead spruce trees. Only data on bryophytes and lichens were included in **Paper II**. In total 252 bryophyte species, of which 10 were red-listed, and 176 lichen species, of which 10 were red-listed, were found in the 80 study plots.

Dead wood was measured in different numbers of sample plots depending on the size of the forest site (see **Paper I**). The amount both in terms of volume, bark area and number of different dead wood types were recorded. Dead wood types were defined based on five variables: (1) tree species (Norway spruce (*P. abies*), Scots pine (*P. sylvestris*), birch (*B. pendula* and *B. pubescens*), grey alder (*Alnus incana*), aspen (*Populus tremula*), rowan (*Sorbus aucuparia*), and goat willow (*Salix caprea*)); (2) diameter (> 20 cm or ≤

20 cm); (3) bark cover (with or without bark); (4) decay stage (six stages according to Siitonen & Saaristo (2000)); and (5) position (standing or lying). These five variables yield 336 possible dead wood types of which 180 different dead wood types were found in this study. Hereafter, richness or diversity of dead wood refers to the number and composition of dead wood types as defined above.

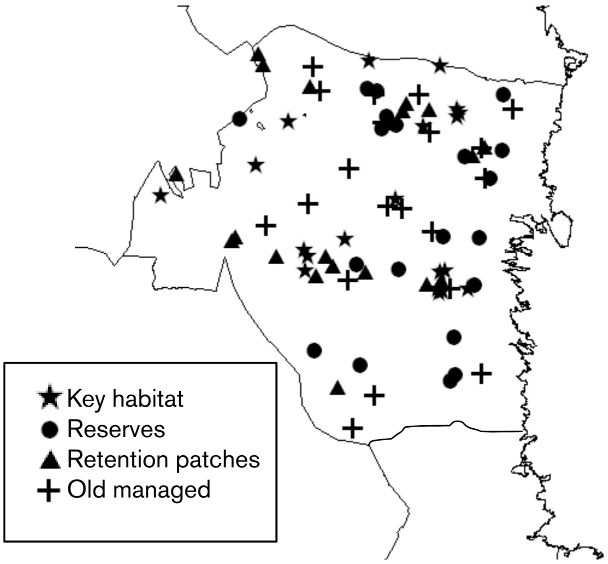


Figure 2. Location of the 80 study sites in the province of Hälsingland.

4.2 Dataset B - Grangärde (*Papers III and IV)*

The long-term dataset in **Paper III** originates from inventories made during 15 years on six experimental clear-cuts situated throughout the study landscape of Grangärde (Fig. 3). At each clear-cut 45-100 high-cut stumps were created at the time of felling in 1994 and 1995. The sequential arrival of the wood-inhabiting beetles and fungi were recorded for 363 of the 425 stumps between 1994 and 2009. The data recorded were: the number of emergence holes of *P. grossa* and *M. sutor;* the area colonized by *H. palliatus, I. typographus* and *P. chalcographus*; the number of fruiting bodies of the polypore species *Fomotopsis pinicola*; the degree of occurrence of *T. abietinum*; the percentage bark coverage, and the decay stage of the stump. The diameter and height of each stump were also recorded. See box 1. for species description.

Data in **paper IV** constitute of different parts: (1) yearly inspections of the six experimental clear-cuts as described for **paper III**; (2) an inventory in 2005 of all clear-cuts harvested from 1990 to 2000 in a landscape of about 10 000 ha; (3) an inventory in 2005 of 42 randomly selected forest transects in the landscape; and (4) an inventory in 2006 of the forest adjacent to the experimental clear-cuts (Fig. 3).

In total 53 clear-cuts (508.9 ha) of different age categories were inventoried (Fig. 3), including the six experimental clear-cuts. The total number of studied high stumps was 425. The randomly selected forest transects were 500 m long and 20 m wide, i.e. constituted 42 ha. The forests adjacent to the experimental clear-cuts were surveyed in 50 m wide strips following the clear-cut edge 25-75 meters into the forests, and constituted about 8 ha. In total the forest inventories constituted ≈ 1 % (50.2 ha) of about 5550 ha forest land in this study landscape.

All standing dead trees with a diameter at breast height >10 cm (>15 cm for the forest adjacent to experimental clear-cuts) and number of emergence holes of *P. grossa* were recorded in all clear-cuts and forest areas. Six other variables were recorded for each dead wood object: number of fruiting bodies of *F. pinicola*, tree species, diameter at breast height, decay stage i.e. six stages according to Siitonen and Saaristo (2000), and substrate type i.e. whole tree or high-cut stump. Stand age for all forest areas was determined by coring living trees.

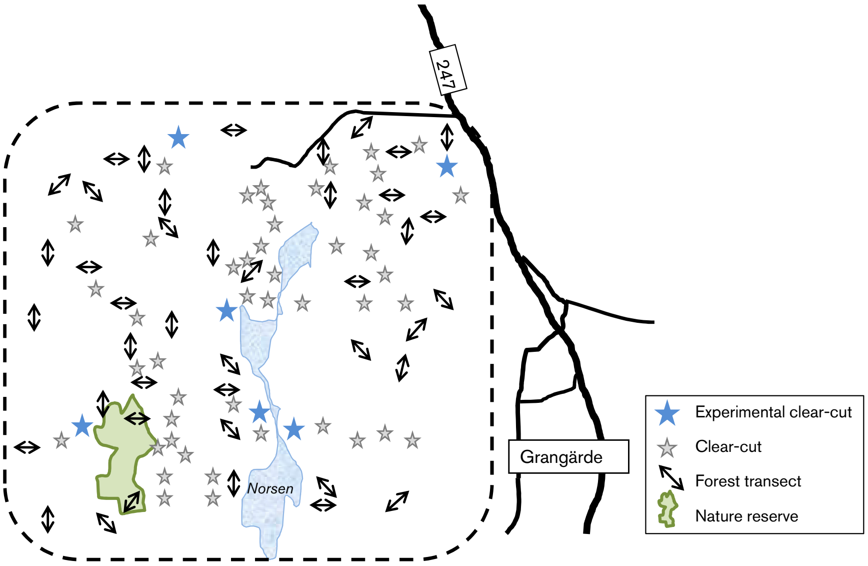


Figure 3. The study landscape (≈ 10 x 10 km) of Grangärde and the location of experimental clear-cuts, inventoried clear-cuts in 2005; and forest transects.

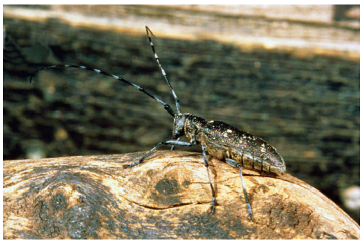
Box 1. Description of species included in **Papers III** and **IV**

Peltis grossa (L.) (Coleoptera, Trogossitidae) breeds in standing, brown-rotted wood of both deciduous and coniferous tree species (Ehnström, 2001; Ehnström & Axelsson, 2002). The developmental time is 2-3 years (Ehnström & Axelsson, 2002). The emergence hole of the adult beetle has a characteristic oval shape, about 5 mm x 12 mm in size. The adults are active during the night and feed on the fruiting bodies of wood-decaying fungi. Due to decreasing amounts of breeding substrates in today's managed forests the species' populations are at high risk of extinction and is according to the IUCN (the International Union for Conservation of Nature) criterion, classified as "vulnerable" on the Swedish Red List (Gärdenfors, 2010).

Hylurgops palliatus (Gyll.) is a common bark beetle species on newly dead conifers. In Fennoscandia the main hosts are Norway spruce and Scots pine. The species is considered as beneficial since it hosts many predatory and parasitic invertebrates common to tree-killing bark beetle species (Nuorteva, 1956). It is a monogamous species with galleries that are usually recognized by being stained very dark, almost black, by associated fungi (*Leptographium* spp. and *Graphium* spp.).

Ips typographus (L.) is a bark beetle species found in Europe and in northern Asia where it is considered as a major pest species. The main host tree is Norway spruce. Like most aggressive bark beetle species it has an efficient aggregation pheromone and carries a tree-killing fungus (in Scandinavia *Ophiostoma polonicum*). Storm fellings trigger outbreaks, and *I. typographus* is the main reason for the regulations in the Swedish Forestry Act regarding the maximum amounts of fresh coarse wood of spruce in the forest. The male initiates the gallery and is typically followed by 2-3 females that make long egg galleries parallel to wood fibers.

Pityogenes chalcographus (L.) is a small polygamous bark beetle species of the Palearctic region with Norway spruce as main host tree. The species is less aggressive than *I. typographus*, but can cause considerable damage in young forests during dry summers. The male, which initiates the gallery, has a deep depression in the head where associated fungi are carried. The male is followed by 4-6 females, which form a star-shaped gallery with egg galleries directed mainly across wood fibers.



Monochamus sutor (L.) is a large cerambycid beetle. It is more common in northern than southern Sweden. The species reproduces in sun-exposed, newly-dead wood of both Scots pine and Norway spruce, such as burnt trees or tree tops left on clear-cuts and, as shown in **Paper III**, on coarse high stumps of spruce. The generation time is 1-3 years depending on climate and its larval galleries go deep into the sapwood and degrade the quality of timber. *M. sutor* has in recent years gained considerable interest in research since it is a potential vector of the invasive pinewood nematode *Bursaphelenchus xylophilus*. The occurrence of *M. sutor* is recognized by very coarse frass of wood fibers, an oval larval entrance hole into the wood, and a circular emergence hole of the adult.

Fomitopsis pinicola (Sw.) P. Karst) is a common polypore species throughout the temperate and boreal northern hemisphere. The fungus causes brown rot in the wood of several species by selectively removing cellulose and hemicelluloses. It is not regarded as a pathogen of economic importance. The fruiting bodies are perennial and spores are dispersed by wind or carried by arthropods. The fungus has some practical applications (http://www.cabi.org/compendia/fc/), for example it can be used as a biological control agent against root rot pathogens such as *Heterbasidion* spp. and *Armillaria* spp. The fungus has a positive impact on biodiversity and is often referred to as an important precursor of rare, vulnerable and threatened wood dependent species (e.g. Nimeleä *et al.*, 1995).

Trichaptum abietinum (Dicks.:Fr.) Ryv, is a polypore fungus with annual fruit bodies that sporulate late during the growing season. Spores may be dispersed by wind or arthropods. The species degrades both cellulose and lignin, so causing white rot in the wood of mostly coniferous tree species. *T. abietinum* and *F. pinicola* are regarded as antagonists but they often colonize the same trunk, although when they do they are spatially separated (Renvall, 1995).

Photo by: J. Weslien (*P. grossa*), R. Axelsson (*H. palliates, I. Typographus* and *P. chalcographus*), N. Jerling (*M. sutor)* L.B. Djupström (*F. pinicola* and *T. abietinum*).

5 Data analysis

5.1 α-diversity and rarified species richness

Species richness, i.e. α-diversity of saproxylic beetles and dead wood was used to compare different types of set-asides with non set-aside old managed forests. The species-area relationship states that larger areas tend to contain larger numbers of species than small areas. This also means that when more individuals are sampled, more species are found. Hence, since sampling effort has a considerable impact on apparent species richness, it is important to use a sampling unit that allows meaningful comparisons to be made. In dataset A for **Papers I** and **III** the beetles were sampled by a standardized method, while the number of dead wood types was sampled in different numbers of plots depending on the size of the forest site (see chapter 4.1 for a detailed description). This was done to sample a comparable proportional of forest area from the different forests. As expected, an uneven number of "individuals" of dead wood types was obtained. However, statistical methods are available that can take into account large differences in the numbers of individuals between samples. Rarefaction is a common method used to compare the specie richness in different areas. In **Paper I** a sample-based rarefaction method was used with a rescaled x-axis to accommodate the number of dead wood types for each set-aside and non set-aside forest type.

5.2 β-diversity in space and time

In **Paper I** the species composition of beetles was compared between reserves, key-habitats, retention patches, and old managed forests by using a non Metric Multidimensional Scaling (nMDS) ordination method.

Graphical ordination techniques are often used to explore the differences between species communities; they can also be complemented with parametric statistical tests to achieve a stronger statistical power of discrimination. The nMDS used in **Paper I** was combined with Multi-response Permutation Procedures, MRPP (McCune & Grace, 2002) in order to explore differences in species composition between the different set-asides and non set-aside forests.

In **Paper II**, the heterogeneity of species composition within and between bryophytes, lichens and saproxylic beetles was analyzed using β-diversity indices. Three β -diversity indices were used: Sørensen's measure of similarity (Sørensen, 1948), β_{sim}, and β_{-2}. The first two focus more precisely on differences in composition and reduce the impact of any imbalance in species richness (Lennon *et al.*, 2001; Magurran, 2004) while the latter controls for uneven sampling effort (Harrison *et al.*, 1992; Cardosa *et al.*, 2009).

In **Paper II** the relationship in species richness between lichens, bryophytes, saproxylic beetles and dead wood was explored in two ways. First, co-variations of species richness between different groups of sub-species (total species richness, richness of red-listed species, and richness of coniferous-associated species) were compiled in correlation matrices. Second, surrogate capacity of each of the taxon as well as dead wood, was analyzed using a reserve selection method. Sites were optimally selected to maximize the total species richness for one taxonomic group (called the target taxon) at a time. The number of species represented in the two taxonomic groups was noted. One representation of each species in selected sites was required. Sites were selected until all species in the target taxon were represented. The numbers of species represented in the two non-target taxa then were compared with the numbers in a random selection of sites.

In **Paper III** the abundance and arrival time of beetles and fungi on high stumps of spruce were studied over a period of 15 years. A model of causal relationships between species was tested, with the arrival time of species as the strongest organizing factor in this model. First, variables were analyzed using generalized mixed models with a Proc GLIMMIX statement in SAS 9.1. The variables recorded at stump level, which were found to be statistically important in explaining the number of emergence holes of *P. grossa,* were included in the path analysis. Path analysis allows one to test hypothesized causal links between variables. By comparing the standardized correlation coefficients from a multiple regression with the coefficient from a simple regression (also standardized) one can estimate the indirect and direct effects of the variables. Thus it is possible to unravel direct and indirect effects where one predictor affects a second predictor, which in turn affects a response variable; and there may be two or more response variables that can affect each other (Quinn & Keough, 2004).

5.3 Importance of dead wood at the landscape-scale for a red-listed beetle species

The population growth of *P. grossa* was analyzed from the long-term dataset on experimental clear-cuts. The importance of different substrates types was analyzed by comparing the extent to which the different substrate types had been utilized, with the availability of those substrates in the landscape. This was illustrated by plotting, for each substrate type, its proportional contribution to the total number of utilized substrates, against its proportional contribution to the total available dead wood. The effect of three substrate characteristics on number of emergence holes of *P. grossa* was analyzed using generalized linear mixed models, with the Proc GLIMMIX statement in SAS 9.2. The tested variables were: (1) diameter at breast height in cm; (2) decay stage (6 categories); and (3) number of fruiting bodies of *F. pinicola*. The response variable was the number of emergence holes of *P. grossa*. Future prospects of *P. grossa* were assessed based on the long-term dataset from the experimental clear-cuts and the amount and availability of dead wood in the landscape.

6 Main results & discussion

6.1 Contribution of different conservation strategies

6.1.1 Woodland key-habitats and nature reserves compared with non set-aside forest (*Paper I*)

Overall there were small but noteworthy differences between key-habitats, reserves, and old managed forests regarding species richness and diversity of saproxylic beetles. Key-habitats had significantly more beetle species per site than the old managed forests, whereas the reserves did not differ from old managed forests in this respect. The most important structural difference was that reserves had a significantly higher volume of deciduous trees and a higher mean number of dead wood types than the old managed forests.

Comparatively low numbers of red-listed species were found in reserves: 0.3 species per plot compared to 0.75 species per plot in key-habitats, and 0.6 in the old managed forests. The most important explanation for the low number in the reserves is probably that they are mostly large areas and consequently contain a mixture of high and low quality habitats. In contrast the key-habitats are small biodiversity hotspots identified by the presence of red-listed species and indicator species. The relatively high number of red-listed species found in the old managed forests indicates that in this part of boreal Sweden there are still biodiversity-rich areas that have yet to be found and preserved.

A problem associated with the Red List species data in the present study was that the numbers of species recorded were relatively low. This means that the basis for the statistical evaluation of differences between the conservation measures is weak, which implies that there may be substantial uncertainties when using red-listed species for evaluating the conservation values of forest stands. Norwegian studies on the co-occurrence of red-listed species indicate a lack of spatial clustering and a weak hierarchical structure in the communities (Sætersdal *et al.,* 2005; Gjerde *et al.,* 2004). The authors suggest that habitat variables (e.g. amounts of dead wood) across productivity and humidity gradients should be used as criteria to set aside forest stands as habitats for red-listed species (Gjerde *et al.,* 2007).

Similar findings to those reported in **Paper I** were observed in a related paper conducted in the same sample plots, but on bryophytes and lichens (Perhans *et al.,* 2007). In that study the number of species of red-listed bryophytes was significantly higher in key-habitats compared to old managed forests but with no difference between reserves and old managed forests. Several other studies have also evaluated key-habitats, with varying results. In a study conducted in Norway, the number of red-listed saproxylic beetles did not differ between key-habitats and forests that had not been set aside (Sverdrup-Thygeson, 2002). In two Finnish studies, key-habitats were evaluated as being of less importance in conserving threatened wood-decaying fungi since low numbers or only small differences in red-listed species were observed between key-habitats and other control forests (Junninen & Kouki, 2006; Hottola & Siitonen, 2008). Studies on lichens have found that key-habitats are important for the preservation of rare species (Johansson & Gustafsson, 2001; Gustafsson, 2002).

Obviously, key-habitats are highly valuable areas for some species and less important for others. In a recent study conducted in Finland, the value and role of key-habitats as part of a whole reserve network was evaluated with a graph-theoretical connectivity approach. Key-habitats were found to enhance habitat connectivity, especially for those species with intermediate levels of dispersal ability (Laita *et al.,* 2010).

To summarize: the differences regarding the richness of saproxylic beetles and the diversity of dead wood documented between reserves, key-habitats and the old managed forests that had not been set-aside, indicate that both key-habitats and reserves provide valuable habitats for saproxylic beetles and other wood-dependent species.

6.1.2 Tree retention patches (*Paper I*)

In Paper I, retention patches had the highest variation in species composition and differed most from reserves and old managed forests. They also had a significantly lower total number of beetle species than key-habitats, and significantly fewer red-listed species than key-habitats and old-managed forests. Furthermore, retention patches had a significantly lower rarified-number of dead wood types than the key-habitats and reserves, and a significantly lower volume of deciduous trees than reserves. The average diameter of the dead wood objects in these patches was significantly smaller than that in the key-habitats.

The overall lower figures relating to species and dead wood found at retention patches indicate that conservation quality is not always the highest priority when these areas are selected. For example, in the legislation and certification regulations related to tree retention, no information is required on existing resident species. Furthermore, the retention patches in this study were not representative of the harvested stand as the patches were generally younger, often situated where logging machines could not gain easy access, and often consisted of trees with low economic value (Wikberg *et al.*, 2009).

The differences between species composition among the retention patches may be explained by the various times since the surrounding forest between the patches had been felled. Disturbance-induced local extinctions and invasions probably also differed between the patches, so causing a high level of heterogeneity in species composition among the patches. Dead wood is also more exposed to the sun in retention patches, which might explain why species composition differed from that in key-habitats, reserves and the old managed forests.

To summarize, even though retention patches have fewer species than the other types of set-aside, and differ in their species composition, they still have an important function in preserving saproxylic beetle species. They promote those species with high dispersal power and preferences for sun-exposed wood, some of which are uncommon. A Finnish study has also shown that high levels of tree retention in clear-cuts are associated with a high species richness of saproxylic beetles (Hyvärinen *et al.*, 2006). Unfortunately the persistence of retention patches is uncertain. Many of these patches seem to be cut, thinned or cleaned of dead wood, and no legislation hinders forest owners from doing so (Persson & Gustafsson, 2002; Larsson & Elander, 2004).

6.1.3 High stumps and other retained wood in clear-cuts (*Paper IV*)

All emergence holes of *P. grossa* in this landscape were found on clear-cuts; none were found in the forests. The long–term dataset from the six experimental clear-cuts indicated that it takes approximately 10 years before high-cut stumps of Norway spruce start to produce individuals of *P. grossa,* and that the stumps can be utilized for more than seven years. During the inventory period the number of colonized high stumps increased from 18 in 2003 to 171 in 2010, with no indication of emergence leveling off, despite the fact that the stumps were all of a similar age. Considering that the high stumps only formed 7 % of the total number of dead wood objects in the experimental clear-cuts, they contributed a significantly large proportion (56 %) of the total number of emergence holes found in 2005 (Fig. 6). Data from all clear-cuts in the landscape (only those ≥ 10 years old) showed that high-cut stumps of Norway spruce and retained dead grey alder were utilized to a higher extent and producing more beetles per m^3 than any other dead wood type. A suitable breeding substrate of *P. grossa* was characterized by dead wood in the later stages of decay, large diameter wood, and wood colonized by *F. pinicola*.

The expert opinion that *P. grossa* prefers semi-open to open habitats (Palm, 1951; Dahlberg & Stokland, 2004) is in agreement with the result that not a single emergence hole were found in any of the inventoried forests. The dead wood in forests was to a less degree colonized by *F. pinicola,* which was found to have a positive effect on the occurrence of *P. grossa*. Another interesting finding was that in clear-cuts we found that grey alder constituted 2.1 % of the total number of dead wood objects and colonized to a high degree; the corresponding number in forests was 8.6 %, but none of them was utilized in forests.

Nevertheless, there is a risk that colonized objects might have been missed in the forest due to a lower sampling effort there: approximately 1 % (50.2 ha) of the total forest area compared to 100 % (508.9 ha) of the clear-cut area. In order to evaluate whether dead wood in forests produces *P. grossa* beetles to the same extent as dead wood in clear-cuts, the number of substrates producing *P. grossa* in forests was estimated by basing calculations on some data and assumptions relating to clear-cuts. Any dead wood in forests was assumed to produce beetles to the same extent as dead wood in clear-cuts. Furthermore, all dead wood types were assumed to be equally good breeding substrates for *P. grossa*. Data from all clear-cuts showed that about 2 % of all standing dead wood produced beetles. Moreover, the forest transects were shown to contain 16.6 ± 4.3 standing dead wood objects ha^{-1}. The total area of the forest landscape was 5551 ha. Based on these assumptions and figures we estimate that there would have been 17 ± 4.3 standing dead wood objects producing *P. grossa* in the 50.2 ha of inventoried forests, from which we conclude that forests in this landscape do not produce beetles to the same extent as clear-cuts.

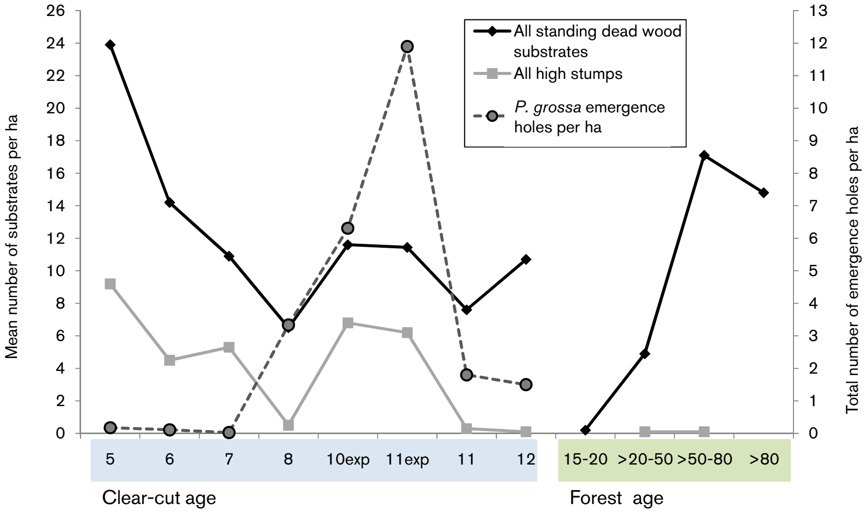


Figure 6. Mean density of all standing dead wood substrates and all high-cut stumps (i.e. high stumps of Norway spruce, Scots pine, birch and rowen) on clear-cuts and in forest stands of different age (left vertical axis) and mean density of emergence holes of *P. grossa* (right vertical axis). Experimental clear-cuts are indicated with "exp" at their age category.

To summarize: creating high stumps of Norway spruce and retaining other standing dead wood i.e. grey alder, had a significant positive effect on the population of *P. grossa* in this landscape. This is interesting since empirical studies on the recruitment of red-listed species and the possible effects of active conservation measures at landscape scale are rare. The amounts of high stumps and other standing dead wood objects on clear-cuts have increased strongly in recent years. The density of high stumps in the five years old clear-cuts is of approximately the same magnitude as on the experimental clear-cuts. These high stumps, now ten years later, are probably starting to produce *P. grossa* and will contribute even more in future to the beetle population than could be observed at the time of this study (Fig. 6). To create and retain dead wood on clear-cuts is most likely beneficial also for other wood dependent species since there are many saproxylic species that prefer sun-exposed dead wood (e.g. Jonsell *et al.*, 1998; Martikainen, 2000; Sverdrup-Thygeson & Ims, 2002; Lindhe *et al.*, 2005) and sun-exposed wood is scarce in the closed managed forests (Dahlberg & Stokland, 2004).

6.2 Patterns of biodiversity

6.2.1 Co-variation in α-diversity of lichens, bryophytes, saproxylic beetles and dead wood (*Paper II*)

The strongest correlation was found between red-listed lichens and red-listed bryophytes, and between red-listed bryophytes and total richness of bryophytes. Beetles were only correlated (weakly) with total richness of bryophytes. Dead wood diversity was also tested against species richness revealing significant, but weak, correlations with red-listed lichens, red-listed bryophytes, and saproxylic coniferous species of bryophytes.

Correlations between species richness among different taxonomic groups were difficult to demonstrate, an observation also made by others (see the meta-analysis made by Wolters *et al.* (2006)). Low levels of association between lichens and beetles have been observed in other studies (e.g. Jonsson & Jonsell, 1999) but in a study by Nilsson *et al.* (1995) conducted on hollow trees, red-listed lichens and some red-listed beetle species were correlated. The common factor driving the correlation was their preference for same habitat. Common habitat dependency is a factor that could explain the co-variations found between lichens and bryophytes in **Paper II**. Both taxa include many species that are dependent on forests that remain undisturbed for long periods of time (Berg *et al.*, 1994; Hallingbäck, 1995, 1996). High diversity of dead wood usually signifies low intensity of forest management and long continuity and may thus be associated with ecological characteristics and conditions of sites that are important not only for species directly dependent on dead wood. Hence, this can explain the positive relationship found between bryophytes and dead wood diversity.

To summarize, that high species richness among different taxa coincide or that red-listed species should occur in the most species rich spots is not obvious. The positive relationship documented between lichens and bryophytes was explained as a result of common habitat dependency. Nevertheless, better understanding of mechanisms underlying richness correlations is needed.

6.2.2 Cross-taxon and dead wood surrogate capacity (*Paper II*)

The main result from the analysis of surrogate capacity was that dead wood was significantly more able to represent saproxylic beetles and bryophytes than was the random solution. Furthermore, when the optimal selection of forest sites was based on dead wood composition, fewer forest sites were needed than in those cases when selection was based on species composition

(Table 1). Also, when dead wood was used as a surrogate, a higher proportion of the total species richness were obtained for beetles, lichens and bryophytes, respectively, than if any of the species taxa were used as surrogate (Table 1, red box). The analysis indicates that none of the tested species taxa was suitable as a surrogate for other taxa.

Explanations of the positive relationship between bryophytes and dead wood diversity must be indirect since the studied bryophytes were mainly confined to other substrates. The most likely explanation is that a high diversity of dead wood indicates low intensity forest management and long continuity, which are factors known to be important to this species group (Fritz *et al.*, 2008).

Surrogate capacity studies on terrestrial ecosystems, including dead wood, are scarce, most having been conducted in marine systems. One earlier Finnish study, which used a similar method to that used in the present study to measure and analyze dead wood diversity, found that the surrogate capacity of dead wood can be a valuable tool for indicating richness of saproxylic species (Similä *et al.*, 2006).

To summarize, our results indicate that dead wood diversity may be an efficient tool for identifying forest sites with high species complementarity among saproxylic beetles and bryophytes.

Table 1. *Surrogate capacity of different target taxa or dead wood. Proportion (%) of species represented for each of the tested taxon when different taxa or dead wood were target taxa in the reserve selection. Number of forest sites needed to obtain 100% of species richness for each target taxon.*

Target taxa	# of sites	Beetles	Lichens	Bryophytes
Dead wood	28	84	90	83
Beetles	35	-	88	79
Lichens	30	78	-	79
Bryophytes	30	74	88	-

6.2.3 β-diversity among lichens, bryophytes and saproxylic beetles (*Paper II*)

All three β-diversity indices tested showed that beetles' species composition was most dissimilar between forest sites, with bryophytes intermediate and lichens lowest. All taxa differed significantly from each other in this respect.

The reason for these findings may be that saproxylic species are constrained to a resource that has a limited duration; they must therefore constantly seek and find new patches to colonize. The duration of the resource is also highly variable and because its duration may also depend on the structure of the community that inhabits the wood, the habitat is unpredictable. Beetles are therefore often referred to as dispersal-prone species that can respond relatively quickly to changes in the quality of their dead wood habitat, and so drive a change in species composition. Nevertheless, dispersal ability is highly variable among beetle species and studies have shown that both low and high dispersal abilities exist (Ranius & Hedin, 2001; Forsse & Solbreck, 1985). Species composition of lichens and bryophytes build up over a long time period in these old forests and there will be a time lag between changes in habitat quality and extinction (Ovaskainen & Hanski, 2002). This may cause an apparently more homogenous species composition than might be expected for the saproxylic beetles.

To summarize: overall, species compositions of beetles differed greatly among forest sites and exhibited little association with the other taxa. These results imply that beetles ought to be treated separately in the planning and evaluation of conservation measures.

6.2.4 Priority effects among beetles and fungi colonizing high stumps in clear-cuts (*Paper III*)

Almost 40 % of the variation in the numbers of *P. grossa* emergence holes was explained by factors relating to four species: the number of *F. pinicola* fruiting bodies; the number of *M. sutor* emergence holes; the degree of *T. abietinum* occurrence; the area of bark colonized by *H. palliatus*; and the two stump variables - diameter and height. *M. sutor* and *T. abietinum* had a negative effect whereas the other variables had positive effects (Fig. 6).

Twenty five percent of the variation in the numbers of *F. pinicola* fruiting bodies was explained by factors relating to the three other species, diameter, and height. The three species *T. abietinum, M. sutor* and *H. palliatus* had mainly direct effects on *F. pinicola*. Bark area covered by *H. palliatus,* diameter, and height explained 8 % of the number of *M. sutor* emergence holes. Diameter and height explained 7 % of the variation in *T. abietinum* frequency. *H. palliatus* had a positive effect (r = 0.34, p < 0.001) on bark coverage.

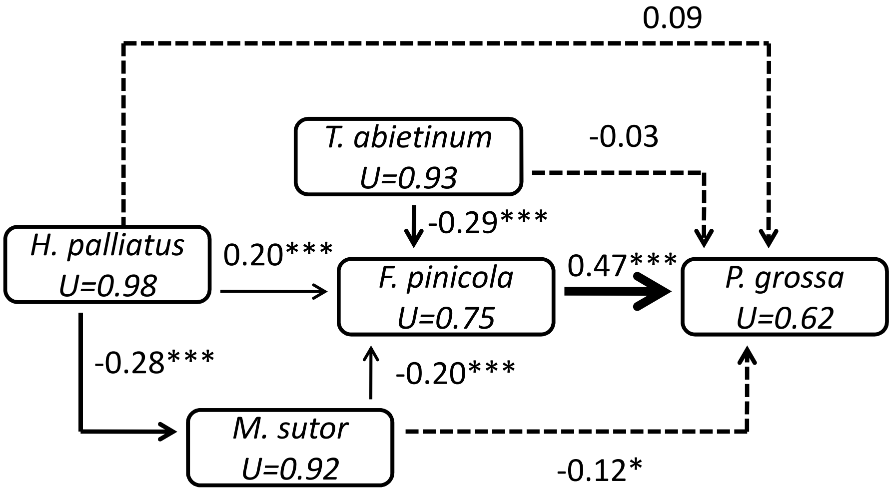


Figure 6. Figures on arrows indicate the size of a direct effect, negative or positive effect that was found in the path analysis. U = unexplained variance (1-R^2). * $P < 0.05$, *** $P < 0.001$. Figures in boxes are unexplained variance. *F. pinicola* had only direct effects; *M. sutor* acted both directly and indirectly via *F. pinicola;* whereas *T. abietinum* and *H. palliatus* acted mainly indirectly via *F. pinicola.*

The analyses are based on correlations and it is important that the tested relationships are biologically rational:

- *F. pinicola* creates a suitable habitat (brown-rotted wood) for the larvae of *P. grossa.*
- *H. palliatus* adults colonizing newly-dead wood may carry spores and/or mycelia of *F. pinicola* and facilitate colonization by creating holes in the bark.
- There is an antagonism between *T. abietinum* and *F. pinicola.* High frequency of occurrence of *T. abietinum* may reduce the potential area for *F. pinicola.*
- *M. sutor* had a negative effect on bark coverage whereas bark coverage had a positive effect on *F. pinicola*. Larvae of *M. sutor* borrow deeply into the sapwood and reduce habitat quality there for *P. grossa*. Hence, *M. sutor* is lowers habitat quality for both *F. pinicola* and *P. grossa.*

In accordance with the theories of Connel and Slayter (1977) this path analysis indicates that priority effects are important in species assemblages and that both facilitation (*H.palliatus* → *P. grossa*) and inhibition (*M. sutor* → *P. grossa*) exist.

To summarize: the practical implications of this study are not straightforward. Priority effects have so far been overlooked as an issue in forest biodiversity conservation. Much attention has been given to the distribution and abundance of specific habitats; less attention to how such habitats emerge. The large variation in coarse wood structure and how a dead wood object eventually develops into a preferred habitat for a given species has so far largely been assigned to random effects. In this study we have been able to explain a lot of this apparently random effect as being dependent on which insect species colonize first. Further studies on priority effects may help to improve cost-efficiency of species-directed conservation programs.

7 Reflections and future prospects

This thesis has mainly focused on conservation measures implemented in the Swedish boreal forests and their effects, especially on saproxylic beetles. The first study (**Paper I**) showed how different aspects of biodiversity might be used to evaluate different forest conservation set-asides. By using species richness and species composition of red-listed species and dead wood (**Paper I**) the conservation strategies of using reserves, key-habitats, or retention patches were compared. The key-habitats in particular were found to be especially valuable for the conservation of saproxylic species, but all the other strategies were also of value.

When evaluating the conservation value of different conservation measures, population viability should also be considered. The life-histories of species should then be considered, as should extinction debt, which is the idea that although species may initially survive habitat change, they later become extinct without any further habitat modification (Kuussaari *et al.* 2009). The risk of drawing wrong conclusions about the effects or benefits arising from a conservation measure might be high if an extinction debt is overlooked. Moreover, the occurrence and survival of species are greatly affected by species life-history traits, as well as by the amount and availability of habitats in the landscape. Dispersal ability is a life history trait that often determines how species might benefit from different conservation efforts. In this thesis, a long-term dataset on population growth of the red-listed beetle species *P. grossa*, in relation to the landscape composition of dead wood, was used to evaluate the conservation measures of high-cut stumps and the retention of dead wood in clear-cuts (**Paper IV**). Similar approaches have the greatest potential to provide quantitative targets applicable in forest management and conservation. But a still better understanding of how to distribute *P. grossa* habitats optimally in space and time across the landscape requires more life-history data of this species, e.g. its longevity, fecundity and dispersal ability.

Even though the focus in conservation assessment has changed from red-listed species to habitat structures and history (Norén *et al.* 2002), areas with red-listed species are often highly ranked when it is necessary to prioritize between areas to set aside. This might be due to the fact that: 1) red-listed species are considered to be most in need of conservation actions; or 2) there is a confidence that the presence of a red-listed species indicates an overall high conservation value for other species and species groups. As an example, the identification of key-habitats is based on, besides habitat structures, the occurrence and/or richness of red-listed or indicator species - particularly bryophytes, lichens and polypore fungi. As shown in **Paper II**, co-variations in richness among bryophytes, lichens and saproxylic beetles are not obvious. Hence, it might be insufficient to rely simply on the richness of some taxonomic groups or red-listed species to indicate richness of other taxa. Furthermore, the lack of detailed knowledge concerning population size and the range of saproxylic species limits the application of the IUCN Red List criteria on saproxylic species (Komonen *et al.* 2008). More long-term studies are needed which aim to better estimate population trends and thereby estimate extinction risks.

As mentioned above, the probability of population growth (or risk of extinction) is much affected by the amount and availability of habitats in the landscape. Much of the research in this context points at dead wood as a key factor for population viability of many species in boreal forests. Nevertheless, knowledge of the mechanisms that create variation in dead wood and other habitats is still lacking. **Paper III** shows one example of how priority effects can affect habitat quality for late colonizing species. In this case much of the unexplained variation in species composition between habitat patches, normally assigned to "random effects", could be explained by colonization history. More studies on what it is that drives variation in species composition and diversity are needed if we want to understand how to conserve or restore biodiversity. One challenge for the future may be the creation of a set of guidelines for conservation, based on such an emerging body of knowledge.

References

Angelstam, P., Eriksson, J.A., Jaxgård. P., Kellner, O., Koffman, A., Mikusinski, G., Ranneby, B., Roberge, J.M., Rystedt, S. & Seibert, J. (2003). *Gap analysis and planning of habitat networks for the maintenance of boreal forest biodiversity – a technical report from the wRESEx case study in Sweden*. Department of Natural Sciences, Örebro University, p. 119.

Axelsson, R., Angelstam, P. & Svensson, J. (2007). Natural forest and cultural woodland with continuous tree cover in Sweden: how much remains and how is it managed? *Scandinavian Journal of Forest Research* 22:545-558.

Axelsson, A-L. & Östlund, L. (2001). Retrospective gap analysis in a Swedish boreal forest landscape using historical data. *Forest Ecology and Management* 147:109-122.

Berg, Å., Ehnström, B., Gustavsson, L., Hallingbäck, T., Jonsell, M. & Weslien, J. (1994). Threatened plant, animal, and fungus species in Swedish forests: Distribution and habitat associations. *Conservation Biology* 8:718-731.

Boddy, L. & Jones, T.H. (2008). Interactions between Basidiomycota and Invertebrates. In: (eds) Boddy L., Frankland J.C. & vanWest P. *Ecology of Saprotrophic Basidiomycetes* The British Mycological Society. Elsevier Ltd, United Kingdom. p. 155-179.

Cardosa, P., Borges, P.A.V. & Veech, J.A. (2009). Testing the performance of beta diversity measures based on incidence data: the robustness to undersampling. *Diversity and Distributions* 15:1081-1090.

Connell, J. H. & Slatyer, R.O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist* 111:1119-1144.

Dahlberg, A., Stokland, J.N. (2004). *Vedlevande arters krav på substrat- en sammanställning och analys av 3600 arter*. Rapport 7.- Skogsstyrelsen, Jönköping. (in Swedish).

Darbishire, O. V. (1914). Some remarks on the ecology of lichens. *Journal of Ecology* 2: 71-82.

Diamond, J.M. (1975). Assembly of species communities. In: Cody M.L. & Diamond, J. M. (eds), *Ecology and Evolution of Communities*, Belknap Press, Cambridge, MA. p. 342-444

Ehnström, B. (2001). Leaving Dead Wood for Insects in Boreal Forests - Suggestions for the Future. *Scandinavian Journal of Forest Research* 16:91-98.

Ehnström, B., & Axelsson, R., (2002). *Insekts gnag i bark och ved*. ArtDatabanken, SLU, Uppsala.

Engelmark, O. & Hytteborn, H. (1999). Coniferous forests. *Acta phytogeographica suecica* 84:55-74.

Esseen, P.A. (1994). Tree mortality patterns after experimental fragmentation of an old-growth conifer forest. *Biological Conservation* 68:19-28.

Esseen, P-A., Ehnström, B., Ericson, L. & Sjöberg, K. (1997). Boreal forests. *Ecological Bulletins* 46:16-47.

Fukami, T., Bezemer, T.M. Mortimer, S.R. & van der Putten W.H. (2005). Species divergence and trait convergence in experimental plant community assembly. *Ecology Letters* 8:1283-1290.

Forsse, E. & Solbeck, C. (1985). Migration in bark beetle Ips typographus L.: duration timing and height of flight. *Zeitschrift für angewandte Entomologie* 44:1787-1795.

Fridman, J. (2000). Conservation of forest in Sweden: a strategic ecological analysis. *Biological Conservation* 96:95-103.

Fridman, J. & Walheim, M. (2000). Amount, structure, and dynamics of dead wood on managed forestland in Sweden. *Forest Ecology and Management* 131: 23-36.

Fritz, Ö., Gustafsson, L. & Larsson, K. (2008). Does forest continuity matter in conservation? – A study of epiphytic lichens and bryophytes in beech forests of southern Sweden. *Biological conservation* 141:655-668.

Gustafsson, L. (2002). Presence and abundance of red-listed plant species in Swedish forests. *Conservation Biology* 16:377-388.

Gärdenfors, U. (ed.) (2010) *The 2010 redlist of Swedish species*. ISBN 978-91-88506-35-1.

Gjerde, I., Sœtersdal, M., & Blom, H.H. (2007). Complementary Hotspots Inventory – A method for identification of important areas for biodiversity at the forest stand level. *Biological Conservation* 137:549-557.

Gjerde, I., Sœtersdal, M., Rolstad, J., Blom, H.H., & Storaunet, K.O. (2004). Fine-scale diversity and rarity hotspots in Northern forests. *Conservation Biology* 18:1032-1042.

Hallingbäck, T. (1996). *The bryophytes of Sweden and their ecology*. ArtDatabanken, SLU, Uppsala.

Hallingbäck, T. (1995). *The lichens of Sweden and their ecology*. ArtDatabanken, Uppsala.

Hallingbäck, T. (2007). Working with Swedish cryptogam conservation. *Biological Conservation* 135:334-340.

Harrison, S., Ross, S.J. & Lawton, J.H. (1992). Beta diversity on geographic gradients in Britain. *Journal of Animal Ecology* 61:151-158.

Hazell, P., & Gustafsson, L., (1999). Retention of trees at final harvest-evaluation of a conservation technique using epiphytic bryophyte and lichen transplants. *Biological Conservation* 90:133-142.

Hottola, J., Ovaskainen, O., & Hanksi, I. (2009). A unified measure of the number, volume and diversity of dead trees and the response of fungal communities. *Journal of Ecology* 97:1320-1328.

Hottola, J. & Siitonen, J. (2008). Significance of woodland key habitats fpr polypore diversity and red-listed species in boreal forests. *Biodiversity and Conservation* 17:2559-2577.

Humphries, C.J., Williams, P.H., & Vane-Wright, R.I. (1995). Measuring biodiversity value for conservation. *Annual Review of Ecology and Systematics* 26:93-111.

Hyvärinen, E., Kuoki, J. & Martikainen, P. (2006). Fire and green-tree retention in conservation of red-listed and rare deadwood-dependent beetrles in Finnish boreal forests. *Conservation Biology* 20(6):1711-1719.

Hägglund, B. & Lundmark, J-E. (1981). *Hanledning i Bonitering med Skogshögskolans Boniteringssystem* Del 1.2.3. Swedish Forest Agency, Jönköping, (in Swedish)

Johansson, P. & Gustafsson, L. (2001). Red-listed and indicator lichens in woodland key habitats and production forests in Sweden. *Canadian Journal of Forest Research* 31:1617-1628.

Jonsell, M., Weslien, J., & Ehnström, B., (1998). Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biological Conservation* 7:749-764.

Jonsson, B.G. & Jonsell, M. (1999). Exploring potential biodiversity indicators in boreal forests. *Biodiversity and Conservation* 8:1417-1433.

Jonsson, B.G., Kruys, N. & Ranius, T. (2005). Ecology of species living on dead wood – Lessons for dead wood management. *Silva Fennica* 39(2): 289–309.

Junninen, K. & Kouki, J. (2006). Are woodland key-habitats in Finland hotspots for polypores (Basidiomycota)? *Scandinavian Journal of Forest Research* 21:32-40.

Jönsson, M.T., Fraver, S., Jonsson, B.G. Dynesius, M., Rydgard, M. & Esseen, P.A. (2007). Eighteen years of tree mortality and structural change in an experimentally fragmented Norway spruce forest. *Forest Ecology and Management* 242:306-313.

Kuulivainen, T. (1994). Gap disturbance, ground microtopography, and the regeneration dynamics of boreal coniferous forests in Finland: a review. *Annales Zoologici Fennici* 31:35-51.

Kuussaari, M., Bommarco, R., Heikkinen, R.K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel M., Pino J. Rodá F., Stefanescu C., Teder T., Zobel, M. & Steffan-Dewenter I. (2009). Extinction dept: a challenge for biodiversity conservation. *Trends in Ecology and Evolution* 24(10):564-571.

Laita, A., Mönkkönen, M. & Kotiaho, J.S. (2010). Woodland key habitats evaluated as part of a functional reserve network. *Biological Conservation* 143:1212-1227.

Larsson, K., & Elander, J. (2004). Management of retention trees and dead wood after final felling in the county of Östergötland, Sweden. Thesis, Dept of Physics, Chemistry and Biology, University of Linköping, Sweden.

Lennon, J.J., Koleff, P., Greenwood, J.J.D. & Gaston, K.J. (2001). The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology* 70:966-979.

Lindemayer, D.B. & Franklin, F.J. (2002). *Conserving Forest Biodiversity: a comprehensive multiscaled approach.* Washington D. C. Island Press.

Linder, P., Östlund, L., (1992). Changes in the boreal forests of Sweden 1870-1991. *Svensk Botanisk Tidskrift* 86:199-215. (in Swedish with English summary).

Lindhe, A., Lindelöw, Å., Åsenblad, N. (2005). Saproxylic beetles in standing dead wood – density in relation to substrate sun-exposure and diameter. *Biodiversity and Conservation* 14: 3033-3053.

Longton, R.E. (1992). The role of bryophytes and lichens in terrestrial vegetation. In: J.W. Bates & A.M. Farmer (eds). *Bryophytes and lichens in a changing environment.* Clarendon Press. Oxford. p.32-76.

Lulow, M.L. (2004). *Restoration in California's Inland Grasslands: the role of priority effects and management strategies in establishing native communities and the ability of native grasses to resist invasion by non-native grasses*. PhD Thesis. University of California, Davis, California, USA.

Magurran, A.E. (2004). *Measuring biological diversity*. Blackwell, Bodmin, Cornwall.

Martikainen, P. (2000). Conservation of threatened saproxylic beetles: significance of retained aspen *Populus tremula* on clearcut areas. *Ecological Bulletins* 49:205-218.

McCune, B. & Grace, J.B. (2002). *Analysis of Ecological C ommunities*. MjM Software Design, Oregon, USA.

Niemelä, T., Renvall, P. & Penttilä, R. (1995). Interactions of fungi at late stages of wood decomposition. *Annales Botanici Fennici* 32:141-152.

Nilsson, S.G., Arup, U., Baranowski, R. & Ekman, S. (1995). Tree-dependent lichens and beetles as indicators in conservation forests. *Conservation Biology* 9(5):1208-1215.

Nitare, J., & Norén, M. (1992). Key-habitats of rare and endangered species will be mapped in a new project of the national Board of Forestry. *Svensk Botanisk Tidskrift* 86:219-226. (in Swedish with English summary).

Norén, M., Nitare, J., Larsson, L., Hultgren, S., & Bergengren, I., (2002). *Handbok för inventering av nyckelbiotoper*. Skogsstyrelsen, Jönköping (in Swedish).

Nuorteva, M. (1956). Conserning the spruce trunk bark beetle, *Hylurgops palliates* Gyll., and its insect enemies. *Acta Entomologica Fennica* 13:1-118.

Ovaskainen, O. & Hanski, I. (2002). Transient dynamics in metapopulation response to perturbation. *Theoretical Population Biology* 61:285-295.

Palm, T. (1951). Die Holz- und Rindenkäfer der nordschwedischen Laubbäume. *Meddelanden från Statens Skogsforskningsinstitut* 40(2):1-172.

Palm, T. (1959). Die Holz- und Rindenkäfer der süd. Und mittelschwedischen Laubbäume. *Opuscula Entomologica Supplement* XVI:1-374.

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

Persson, A., & Gustafsson, L. (2002). *Conservation on final felling in family enterprise forestry*. Resultat16/2002, Skogforsk. (in Swedish with English abstract).

Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C. & Gibbons, D.W. (1993). Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* 365:335-337.

Quinn, G.P. & Keouugh M.J. (2004). *Experimental design and data analysis for biologists*. Cambrige University press. p.145.

Ranius, T. & Hedin, J. (2001). The dispersal rate of a beetle, Osmoderma eremite, living in tree hollows. *Oecologia* 126:363-370.

Räsänen, V. (1927). Über Flechtenstandorte und Flechtenvegetation im westlichen Nordfinnland. *Annals Society Zoology Botany Fennica Vanamo* 7:1-202.

Renvall, P. (1995). Community structure and dynamics of wood-rotting Basidiomycetes on decomposing conifer trunks in northern Finland. *Karstenia* 35:1-51.

Saalas, U. (1917). Die Fichtenkäfer Finnlands I. *Annales Academiae Scientarium Fennicae Ser. A*. 8:1-547.

SAS, Institute Inc. (2003). *SAS for Windows ver. 9.1.3*. SAS Institute Inc., Cary, NC.

SAS, Institute Inc. (2008). *SAS/Stat 9.2 User's Guide,* Cary, N. C., SAS Institute Inc.

Sœtersdal, M., Gjerde, I., Blom, H. H. (2005). Indicator species and the problem of spatial inconsistency in nestedness patterns. *Biological Conservation* 122:305-316.

Siitonen, J. (2001). Forest management, coarse woody debrise and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins* 49:11-41.

Siitonen, J., Martikainen, P., Punttila, P. & Rauh, J. (2000). Coarse woody debrise and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. *Forest ecology and Management* 128:211-225.

Siitonen, J., & Saaristo, L. (2000). Habitat requirements and conservation of *Pytho kolwensis*, a beetle species of old-growth boreal forest. *Biological Conservation* 94:211-220.

Similä, M., Kouki, J., Mönkkönen, M., Sippola, A-L.& Huhta, E. (2006). Co-variation and indicators of species diversity: Can richness of forest-dwelling species be predicted in northern boreal forests? *Ecological Indicators* 6:686-700.

Söderström, L. (1983). Hotade och sällsynta mossarter I norrlänska granskogar. *Svensk Botanisk Tidskrift* 77:4-12.

Sørensen, T. (1948). A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analyses of the vegetation on Danish commons. *Biologiske Skrifter Kongelige Danske Videnskabernes Selskab NS* 5:1-34.

Southwood, T.R.E., & Henderson, P.A. (2000). *Ecological Methods.* 3rd edition. Blackwell Science, Oxford.

Spribille, T., Thor, G., Bunnell, F.L., Goward T. & Björk, C.R. (2008). Lichens on dead wood: species-substrate relationships in the epiphytic lichen floras of the Pacific Northwest and Fennoscandia. *Ecography* 3:741-750.

Stenbacka, F. (2009). *Response of Saproxylic Insect Communities to Forestry: Implications of Conservation.* Doctoral Thesis No. 2009:69. Swedish University of Agricultural Sciences, Umeå, Sweden.

Swedish Forest Agency (2007). *Fördjupad utvärdering av levande skogar.* Meddelande 4. Skogsstyrelsen, Jönköping, Sweden (in Swedish).

Swedish Forest Agency (2009). *Swedish statistical yearbook of forestry.* Jönköping, Sweden.

Svedlund, L. & Löfgren, R. (2003). *Protecting the forests of Sweden: legal protection in the form of national parks, nature reserves, habitat protection areas and nature conservation agreements.* Swedich Forest Agency, Jönköping, Swedish Environmental Protection Agency, Stockholm, Sweden.

Sverdrup-Thygeson A. (2002). Key-habitats in the Norwegian production forest: A case study. *Scandinavian Journal of Forest Research* 17:166-178.

Sverdrup-Thygeson, A. & Ims, R.A. (2002). The effect of forest clearcutting in Norway on the community of saproxylic beetles on aspen. *Biological Conservation* 108:377-378.

Tansley, A. (1935). The use and abuse of vegetational concepts and terms. *Ecology* 16:284-307.

Timonen, J., Siitonen, J., Gustafsson, L., Kotiaho, J.S., Stokland, J.N., Sverdrup-Thygeson, A. & Mönkkönen, M. (2010). Woodland key-habitats in northern Europe: concept, inventory and protection. *Scandinavian Journal of Forest Research* 25:309-324.

Vane-Wright, R.I., Humphries, C.J. & Williams, P.H. (1991). What to protect? – Systematics and the agony of choice. *Biological Conservation* 55:235-254.

Wikberg, S., Perhans, K., Kindstrand, C., Djupström, B.L., Boman, M., Mattsson, L., Schroeder, L.M., Weslien, J, & Gustafsson, L. (2009). Cost-effectiveness of conservation strategies implemented in boreal forests: The area selection process. *Biological Conservation* 142:614-624.

Wolters, V., Bengtsson, J. & Zaitsev, A.S. (2006). Relationship among the species richness of different taxa. *Ecology* 87(8):1886-1895.

Young, T. P., Chase, J. & Huddleston, R. (2001). Community succession and assembly: comparing, contrasting and combining paradigms in the context of ecological restoration. *Ecological Restoration* 19:5-18.

Young, T. P., Petersen, D. A. & Clary, J.J. (2005). The ecology of restoration: historical links, emerging issues and unexplored realms. *Ecology Letters* 8:662-673.

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