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Oak as Retention Tree in Commercial Spruce Forests

Effects on Species Diversity of Saproxylic Beetles and Wood Production

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Cover: Oak retained in a spruce plantation (photo: Andreas Larsson)

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Abstract

Retaining trees valuable for biodiversity is a common conservation measure. There are indications that such trees have important benefits for the diversity of many species groups. However, retaining trees may also have negative effects on timber production. The aim of this thesis was to study the benefits of retaining oaks (*Quercus robur*) in spruce forests (*Picea abies*) for the diversity of oak associated saproxylic (wood-living) beetle species and to assess the negative effects on wood production of spruce.

The first three papers, as presented in this thesis, relates to the biodiversity aspect: the effect of openness on species richness (Paper I); the benefit of retaining oaks in spruce plantations, in relation to pasture oaks (Paper II); and the short-term effects of clearing on species richness and composition (Paper III). In Paper IV, the negative effects of gap formation around oaks on wood production of spruce was assessed.

The results showed a significant decrease in species richness of oak beetles with decreasing openness. Moreover, spruce trees on the southern side of the oaks appeared to have a larger impact than trees of than those on the northern side (Paper I). According to the results in Paper II, low shaded oaks in spruce plantations harbored slightly more oak associated species than did pasture oaks, and the species composition differed somewhat, although it seemed to be partially overlapping. The amount of dead wood in the oak crown appeared to one of the major explanatory factor for differences in species richness and composition between forest and pasture. Thus, oaks in plantations can harbor a comparatively high number of species. Regarding the short-term effects of clearing (Paper III), there was a significant positive effect on species richness of saproxylic oak beetles of larger clearings (under and outside the crown) already the first three years after clearing, compared to non-cleared oaks. Smaller clearings (solely under the oak crown) did not yield the same increase in species richness as the larger clearings. However, both small and large clearings differed in species composition when compared to the non-cleared oaks.

Retaining oaks has a negative effect on the growth of spruce (Paper IV). The basal area in the area around retained oaks was on average about 83% of the basal area in satellite plots without retained oaks. Since there was no difference in production level between large and small gaps, this study indicates that with the thinning treatments imposed on the studied stands, the reduction in production will be about the same irrespective of gap size for gaps at least up to about 350 m^2.

In summary, increased openness has apparent positive effects on species richness of saproxylic oak beetles and the response to clearing has immediate positive effects on both species richness and composition of oak associated beetles. Retained oaks in spruce forests may, if cleared of encroaching spruce trees, harbor a species richness comparable to, or even higher, than that of pasture oaks. A certain loss in timber volume from the gaps is expected, however, trees lining the edge of gaps can partly compensate for the loss with the gap. The increase in timber loss is smaller for smaller gap sizes, as compared to large. Retaining several oaks in small gaps should thus be more cost-efficient compared to few oaks in large gaps. However, oaks in large gaps may attract additional species that favor high levels of insolation. One single large gap may thus capture more species than several small gaps together, even if the total gap area is equal. These aspects should be considered when planning for clearing around retained oaks in a spruce forest or plantation.

Keywords: retention, *Quercus robur*, saproxylic, coleoptera, clearing, light, production, spruce, economy

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Dedication

Till Mormor och Morfar
Till Farmor och Farfar

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 Maria Koch Widerberg, Thomas Ranius, Igor Drobyshev, Urban Nilsson, and Matts Lindbladh (2012). Increased openness around retained oaks increases species richness of saproxylic beetles. *Biodiversity and Conservation* 21(12), 3035-3059.

II Maria Koch Widerberg, Thomas Ranius, Urban Nilsson, and Matts Lindbladh (2013). Oaks retained in commercial spruce forests function as a complementary habitat to oaks in wood pastures for saproxylic beetles. *Biological Conservation* (under review).

III Maria Koch Widerberg, Urban Nilsson, and Matts Lindbladh. Short-term effects on beetle diversity of clearing around retained oaks in a spruce plantation. Submitted manuscript.

IV Maria Koch Widerberg, Urban Nilsson, and Matts Lindbladh. Growth compensation of Norway spruce in gaps around retained oaks. Manuscript.

Paper I is reproduced with the permission of the publishers.

The idea of the scope for this thesis was developed by Matts Lindbladh, Urban Nilsson, Leif Mattsson, and Mattias Boman. The contribution of Maria Koch Widerberg to the papers included in this thesis was as follows:

I MKW, Matts Lindbladh, and Urban Nilsson developed the idea and designed the experiment. MKW did 80 % of the field work. MKW did 90 % of the data analysis; data management, modelling, and statistics. MKW did as a first author 80 % of the writing. Total input 70 %.

II MKW and Matts Lindbladh developed the idea and designed the experiment. MKW did 60 % of the field work. MKW did 80 % of the data analysis; data management, modelling, and statistics. MKW did as a first author 70% of the writing. Total input 70 %.

III Matts Lindbladh and Urban Nilsson developed the idea and designed the experiment together with MKW. MKW did 60 % of the field work. MKW did 90 % of the data analysis; data management, modelling, and statistics. MKW did as a first author 80% of the writing. Total input 80 %.

IV MKW and Urban Nilsson developed the idea and designed the experiment. MKW did 60 % of the field work. MKW did 30 % of the data analysis; data management, modelling, and statistics. MKW did 60% of the writing. Total input 60 %.

Abbreviations

BA – Basal Area
DBH – Diameter at Breast Height
GTR – Green Tree Retention
SI – Shade Index

Terminology

Species richness – number of species
Species abundance – number of individuals
Species composition – the different species, and the relative abundance of each species, that that make up a community

1 Introduction

1.1 Cost-effectiveness of conservation strategies

To implement nature conservation within forestry is often costly. Due to this, it is important to find cost-efficient strategies for maximizing both wood production and biodiversity. During the last two decades, there has been more focus on these issues within ecological research (Wikberg et al. 2009). My thesis is a contribution to the knowledge on retention trees, with emphasis on how to manage such trees for biodiversity with respect to effects on timber production.

1.2 Green tree retention in forest management

The major part of Swedish productive forest land is used for production of timber, however, there should also be implications of general nature conservation, such as dead wood or green tree retention (GTR). Retaining trees valuable for biodiversity to grow old and die from natural causes is one of the most common general conservation measures. It is mandatory in the Forestry Act, and mandatory under the FSC and PEFC certification standards. According to both of these standards, at least ten coarse, old trees per hectare should be set aside at final harvesting.

There are strong indications that GTR have important benefits for the diversity of many groups of organisms (Vanha-Majamaa and Jalonen 2001). Until today, most studies on the benefits of GTR for biodiversity has mainly focused on mammals (Moses and Boutin 2001, Sullivan and Sullivan 2001), birds (Merrill et al. 1998, Rodewald and Yahner 2000, Schieck and Hobson 2000, Tittler et al. 2001), and vascular plants (Halpern et al. 2005, Nelson and Halpern 2005). A number studies have also found benefits for invertebrate species, mainly saproxylic beetles (Hyvärinen et al. 2006, Rosenvald and Lõhmus 2008). Saproxylic beetles are important as they constitute a considerable part of the species diversity in both temperate and boreal forests (Grove 2002, Gärdenfors 2010). However, knowledge on how to manage a plantation stand with retained trees in order to maximize both the conservation values and wood production is still lacking.

1.3 Objectives

The primary aim of the thesis was to study the effects of shade and clearing around oaks (*Quercus robur*) in spruce (*Picea abies*) plantations on biodiversity and wood production. The biodiversity benefit, i.e. species richness of saproxylic oaks beetles, was related to the cost for the forest owner in terms of reduced stem wood production. The effect of shade on biodiversity on oaks (*Quercus robur*) was studied in already established gaps, both natural and man-made in forests of spruce (*Picea abies*) (Paper I). The importance of retaining oaks for biodiversity was also assessed by comparing the species richness and composition of saproxylic oak beetles of oaks in spruce forests to that of pasture oaks (free standing oaks in a cultural landscape) (Paper II), which are regarded as highly valuable for the diversity of saproxylic insects. In this way, the potential of retained mature oaks in spruce stands to act as favorable habitat for saproxylic oak beetles species was analyzed, and the contribution of retained oaks to beetle diversity on the landscape level could be evaluated. Further, the effect of different levels of clearing was studied through a controlled experiment with three levels of clearing (Paper III). Here, the short-term effects on species richness and composition of oak beetles could be determined. In the fourth study (Paper IV), the effect on timber production in the surrounding stand was assessed, using the same stands as in Paper I and Paper II. In this study, the size of the gaps around the oaks and the growth of the spruce trees lining the gaps were used in order to estimate the loss in timber production. Finally, I have estimated and valued the benefit of retention trees in terms of increased species richness with regard to the corresponding loss in timber production. This final synthesis is presented in the last chapter of the thesis.

1.3.1 Hypotheses

The hypotheses are presented paper by paper below:

Paper I: Increased canopy openness around retained oaks in spruce plantation has a positive effect on oak-associated saproxylic beetles, in terms of both species richness and abundance. Other factors related to the oaks, such as increasing amounts of dead wood, increasing age, girth, and crown dimension should positively influence species richness and abundance of oak-associated saproxylic beetles on the retained oaks.

Paper II: Retained oaks in spruce forests were expected to host a beetle fauna of oak associated beetles with fewer species and a different composition, as compared with pasture oaks in the near surroundings. It was also expected that increasing age, trunk diameter, and amount of dead wood on the oaks have positive effects on species richness. Further, the distance to forest edge was assumed to have a negative effect on species richness for oaks isolated within the spruce forests.

Paper III: Oaks in clearings sustain a higher species richness compared to *Control* oaks, in particular the more extensive clearing. Clearing should also affect species composition and hence the composition should differ between treatments.

Paper IV: Production loss around retention trees, due to the combined effect of competition from the retained trees and the loss of area from gaps, is higher than would be expected from the area loss alone.

2 Background

2.1.1 Biodiversity in Swedish forests

Today, the rate at which the number of species decline in this part of the world, and in the world as a whole, is increasing. Hence, the interest in conservation biology has long attracted attention of biologists (Griggs 1940, Preston 1948), however, especially during recent years (Berg et al. 1994, Lindenmayer and Franklin 2002).

Changes in biodiversity over the last thousand years have mainly been due to human activities. Hence, changes of forest- and land use, and the ever growing human population have had a tremendous impact on the landscape. It has been estimated that when the original forest covers less than 20 percent of its original distribution, it can cause local extinctions of forest species (Niklasson and Nilsson 2005). This is due to the fact that many species have a limited dispersal ability, e.g. lichens (Dettki et al. 2000) and invertebrate species such as beetles (Ranius and Hedin 2001). Today, natural habitats have declined regarding quantity and quality, and this has caused a decrease in the diversity of many species groups.

In southern Sweden planting of conifers has caused a fragmentation of natural forest habitats, and has limited dispersal further by inducing a physical barrier to many species associated with deciduous habitat (Brunet and Isacsson 2009).

2.1.2 The importance of oak for biodiversity

In the nemoral and boreo-nemoral zones of northern Europe, oak (*Quercus spp.*) is regarded as an important tree genus for biodiversity; oak is associated with the highest number of red-listed inverterbrate species in Sweden (Jonsell et al. 1998) and it also associated with a comparatively high number of saproxylic insect species for Europe. The conservation potential of retaining oak is therefore high compared to many other tree species. Moreover, due to their longevity, retained oaks can maintain their conservation value very long, compared to most tree species.

During long periods of the Holocene, southern Scandinavia has been covered with mixed deciduous forests (Southwood 1961, Iversen 1973, Berglund and Digerfeldt 1976, Vera 2000, Sverdrup-Thygeson and Birkemoe 2009), and oak was formerly a common tree in these forests. However, over the centuries the forests dramatically changed. Comparatively large expansion of monocultures of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) (Bakke 1968) gradually replaced the deciduous forest during the 19th and 20th centuries (Emanuelsson 2009, Lindbladh and Foster 2010, Aspenberg and Jansson 2011). Today, coniferous tree species, Norway spruce and Scots pine, dominate whereas birch (*Betula pendula* and *Betula pubescens*), European aspen, (*Populus tremula*), oaks (*Quercus robur* and *Q. petraea*), and European beech (*Fagus sylvatica*), represent the less common deciduous species (Nilsson 1996).

For many centuries, oak was used for ship construction and other purposes, and hence a large part of the mature oaks were cut (Eliasson and Nilsson 2002). Therefore, oak, in particular old oaks (Diekmann 1996), are rare today (Hannah et al. 1995, Nilsson 1997) and this has naturally affected several associated species groups. Old trees provide a wide range of microhabitats and structures, such as cavities, dead wood, and coarse bark, structures that are important for many species of invertebrates, birds, bats, fungi, and lichens. The lack of high quality habitat has caused a decline, and even extinction, of many species, e.g. saproxylic beetle species (Berg et al. 1994, Jonsell et al. 1998, Brändle and Brandl 2001).

2.1.3 Tree retention and the effect on stand increment

To benefit biodiversity it is important to create favorable conditions for the organisms connected to oak. Oak is a relatively light demanding tree species, hence many species associated with old oaks are dependent on a relatively high level of sun exposure, e.g. several red-listed species (Berg et al. 1994). Several studies have shown positive effects of increased sun exposure on oak associated species, e.g. on oaks in beech forests (Müller and Gossner 2007) and in larch plantations (Ohsawa 2007). Ranius and Jansson (2000) and Franc and Götmark (2008) both found that oaks surrounded by a high density of surrounding tree vegetation had lower beetle species richness. Thus, species connected to oak should benefit from increased sun exposure in dense coniferous stands, e.g. by clearing gaps around the oaks.

The possible cost of clearing for the forest owner is determined by the size of the gap, as this area is not available for production. However, the loss could be larger due to competition from the retained trees, or smaller because of growth compensation of plantations trees close to the gaps. The effects of green tree retention on stand increment has not been studied much, however, some studies have observed reductions in volume increment in stands with retained overstorey compared to stands with no overstorey (Acker et al. 1998, Bassett and White 2001). Acker et al. (1998) and Basset and White (2001) suggested that the regeneration increment is reduced by 13-55% when some part of the initial stand is retained as overstorey. Studies of the effects of other forms of overstorey retention, e.g. shelterwood systems, have shown that the regeneration increment is lower with than without retained overstorey (Hagner 1962, Jäghagen 1997, Dignan et al. 1998, Nilsson et al. 2006). For example, the height increment of spruce seedlings, located two meters from an overstorey of spruce trees, was 60% lower compared to seedlings at eight meters distance (Hagner 1962). Jacobsson and Elfving (2004) estimated that retaining ten trees of Scots pine per hectare, a common recommendation in Swedish forestry, would result in 2.5% loss of volume over one rotation.

2.1.4 The potential effects of clearing on oak vitality

Management operations should be performed in a way that enables the retained tree to survive, and grow large and old, in order to develop the characteristics associated with old trees that are important for diversity. Regarding oak, which is the study species in this present thesis, light is a key factor. A cornered oak loses its vitality and becomes stress sensitive (Templeton and Putz 2003), and may die far before its full potential of wood structures, branch dimensions and microenvironments have time to develop. Thus, clearing at some point in time is recommended. However, rapid transformations of the surrounding stand might be harmful to the oak itself; clearing may e.g. lead to increased water content of the soil, and in turn lead to waterlogged conditions, which can cause hypoxia and death of the roots, and eventually death of the whole tree. The soil texture affects the water retaining capacity of the ground, with smaller grain size leading to higher capillary action. Hence, the risk of hypoxia should be considered, especially when clearing around trees growing on soils with high clay content. Albeit, so far, no study has actually shown that a mature oak may die because of light stress due to one single clearing event.

3 Materials and methods

3.1 Study areas

All fieldwork was conducted in southern Sweden – in the boreo-nemoral zone (Ahti et al. 1968) or on the border between the nemoral and the boreo-nemoral zone. For papers I, II, and IV, the fieldwork was performed on nine locations, selected to cover a range of sites from the counties of Blekinge in the south to Östergötland in the north, and from Halland in the west to the easternmost parts of Småland in the east. For paper III, the fieldwork was performed in Asa Experimental Forest.

3.1.1 Papers I, II, and IV

The locations used for papers I, II, and IV (Table 1) were former wood pastures that contained at least 90% Norway spruce and several retained mature Pedunculate oaks (*Quercus robur*). All stands were managed according to common Swedish silvicultural practice, which includes both pre-commercial and commercial thinning. The mean annual temperature in this region ranges typically between 5°C and 8°C, the mean temperature in January ranges between -4°C and 0°C, and the mean temperature in July between 15°C and 16°C. There is a large variation in precipitation between the western (up to 1200 mm/year) and the eastern (500 mm/year) part of the region.

3.1.2 Paper III

Data for Paper III was sampled in a forest stand of 5.5 hectares, located at the Asa Experimental Forest (Lat. $57^{o}08'$N, Long. $14^{o}45'$E). The stand consisted mainly of Norway spruce, but contained also various deciduous trees, such as Pedunculate oak, European aspen, and Norway maple (*Acer platanoides*). Many of these trees originated from a wood pasture that was planted with spruce in 1975. The mean annual temperature, as measured between 1988 and

2010, was 6.4°, and the mean annual precipitation for the same period was 681 mm.

Table 1. Data on the stands used in Papers I, II and IV. Kosta was not used in Paper II.

	Stand data		P. oak		N. spruce
Location	Coordinates	Size (ha)	Age[a]	Age Std[b]	Age
Johannishus	N 56° 14.372', E 15° 31.270'	1.6	149/95	40/2	43-45
Strömsrum	N 56° 55.560', E 16° 27.817'	4.3	194/234	19/12	varying
Hornsö	N 57° 0.959', E 16° 14.016'	0.8	110/120	5/21	70
Kosta	N 56° 48.924', E 15° 28.861'	2.5	296/99	70/16	38
Boxholm	N 58° 11.382', E 15° 7.850'	1.4	150/127	12/33	53
Sandvik	N 58° 7.197', E 15° 10.110'	1.6	123/83	13/40	48
Malexander	N 58° 4.132', E 15° 21.423'	0.7	141/100	31/21	50
Adelsnäs	N 58° 8.599', E 15° 57.128'	0.4	146/76	13/47	47
Tönnersjö	N 56° 42.249', E 13° 8.383'	0.4	168/165	56/20	varying

[a] Age of forest/pasture oaks

[b] Standard deviation

3.2 Window trap sampling (Papers I, II, and III)

In order to collect data on beetles, two slightly different types of window traps were used; for Papers I and II, the traps consisted of a plexiglass window (40×60 cm) tied to a funnel with a bottle. The traps were mounted on branches and stabilized with nylon wires (ø 10 mm). The wires enabled an easy emptying of the traps through a hiss construction (Figure 1). For Paper III, the traps consisted of a somewhat smaller plexiglass (30×50 cm) attached to a tray (Figure 2). These traps were mounted directly on the stem, using a consol. Both types of trap were positioned on the southern side, as the activity of light-demanding oak beetles was assumed to be higher on this side compared with the northern side. The traps were positioned at a height of approximately 5 m (the height of the upper edge of the tray/funnel). At this height, the majority of dead branches were usually found. The bottles/trays were filled with propylene glycol (60%) and a few drops of detergent. They were emptied once a month and the beetles were collected and stored in ethanol (60%).

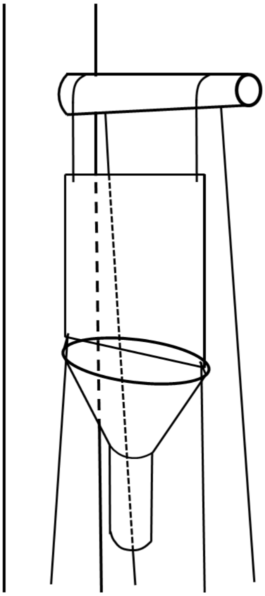

Figure 1. The lift construction used for mounting window traps used in Paper I and Paper II.

Figure 2. Position of a window trap for beetle sampling in Paper III.

3.3 Saproxylic beetles and tree host association

All saproxylic beetles were species determined by taxonomist Rickard Andersson (Andersson (formerly Baranowski)), Höör. The beetle data was divided into different groups according to species' association to oak and/or spruce (Dahlberg and Stokland 2004). This division was due to the fact that the habitat surrounding the retained oaks consisted mainly of spruce. It is thus reasonable to believe that both oak and spruce should have a major effect on the composition of beetle fauna sampled in the studies.

In Paper I, the saproxylic beetles were divided into five different functional groups and subgroups: Group 1a) all species associated with oak; Group 1b) species associated with oak and not with spruce; Group 1c) species with preference for oak; Group 2a) all species associated with spruce; and Group 2b) species associated with spruce and not with oak. Thus, Group 1b and Group 1c were subgroups to Group 1a, and Group 2b was a subgroup to Group 2a.

In Paper II, independent, non-nested beetle groups were used, instead of overlapping, nested groups (groups and subgroups) as in Paper I. This was in order to more specifically display which functional group contribute to the difference in species richness and composition between the oak categories, compared to Paper I. Thus, the revised functional groups were: Group I) species associated to both oak and spruce; Group II) species associated to oak and not to spruce (same as Group 1b in Paper I); and Group III) beetles not associated to oak.

In Paper III, the functional groups were based on the same division as in Paper II. However, Group III (beetles not associated to oak) was excluded in order to focus on oak beetles and to reduce the number of compared groups.

3.4 Experimental design, statistical analyses, and modelling

3.4.1 Paper I

Experiment

The study was performed in nine different stands of Norway spruce. Each stand harbored several scattered Pedunculate oaks in a variety of gap sizes, both natural and man-made. The aim was to study the influence of openness on species richness of saproxylic beetles. For this purpose, six oaks per stand were selected in a range of gap size, from very small gaps (spruce trees growing under the oak crown) to large gaps (>3m outside the oak crown perimeter). For the selected oaks, several parameters were measured; age (estimated through coring), diameter at breast height (DBH), height, crown radius, and amount of dead wood. As estimates of dead wood, several different factors related to branches were measured, such as the maximum diameter of dead branches and the percentage of dead crown.

Beetles were collected on each oak with window traps from mid May to early September during 2008 and 2009.

Estimates of shade

The relative degree of shade around oaks was estimated with an index. This index, SI, was based on the competition from the surrounding stand, calculated as

$$\mathrm{SI} = \sum_{i=1}^{n} \left((DBH^2 / d) * h \right)_i$$

where DBH_i is the diameter of neighboring tree i, d_i is the distance between oak and neighboring tree i, and h_i is the height of neighboring tree i within a set radius. Including the sun exposure angle in the equation, derived the following function

$$\mathrm{SI}_\alpha = \sum_{i=1}^{n} \left((DBH^2 / d) * h * \mathrm{I}_\alpha \right)_i$$

where I_α is an angular index ranging from 0 to 1, with trees to the north (0°/360°) equaling 0 and trees to the south (180°) equaling 1. The compass angle (α) was measured from the center of the oak trunk to the center of the spruce stem (Figure 3).

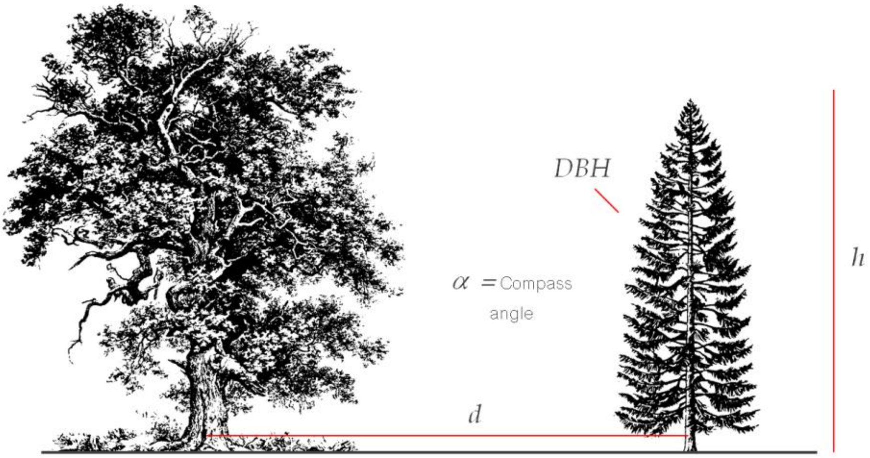

Figure 3. Measurements taken for the shade index calculation.

Analyses

Species richness of the host-association groups (1a, 1b, 3b, 2a, and 2b) were tested against both indexes SI and SI_{α} respectively with univariate linear regression analysis. The response variables showed Shapiro-Wilks non-normal distribution and were thus ln-transformed to obtain normal distribution. The index among SI and SI_{α} which exhibited the highest significance for the response variables in the univariate regression analysis was selected for further statistical modeling with general linear models (PROC GLM). In this model, also location identity (as class variable), age and DBH of the oaks, and the diameter of the thickest dead branch were included. All statistics were performed using the SAS program version 9.2 (SAS Institute Inc., Cary, NC, USA).

3.4.2 Paper II

Experiment

Six mature oaks of about the same DBH were selected in eight locations; four oaks inside the spruce plantations and two oaks in the near surrounding cultural landscape (category *Pasture*). The four oaks inside the stands were chosen among those six oaks used in Paper I; the two oaks with the highest shade index (category *Dark*), as calculated in Paper I, (in all cases with spruces encroaching the oak crown) and the two oaks with the lowest shade index (≥3 m outside the crown perimeter on the southern side) (category *Light*). The majority of the *Pasture* oaks were in open conditions in pastures without neighboring trees, whereas a few were in a sparse tree layer of other broadleaved trees. The stand in Kosta was not used in this study. This was due to major differences in age between the oaks categories, and because of difficulties to make reliable age determinations of several of the oaks due to cavities in the trunk.

Beetles were collected from the 48 oaks from mid May to early September 2008 using window traps (Figure 3).

Analyses

Analyses on species richness were performed with generalized linear mixed models (PROC GLIMMIX in SAS 9.2). According to scores of AIC (Aikaike's information criterion) (Akaike 1974), *Oak category, Dead crown*, and *Location* (as CLASS) were included in the final model, the latter as a covariate. Further, the effect of distance to forest edge was also analyzed, however for this model shade index was used as a continuous predictor variable, and *Dead crown* and *Location* as covariates.

The relationship between species composition and the oak variables was analyzed with Canonical Correspondence Analysis (CCA). For comparison of species composition between the oak categories we also used a MRPP (Multiple Response Permutation Procedure). MRPP is a non-parametric test of the difference between two or more groups or categories (Mielke and Berry 2001).

3.4.3 Paper III

Experiment

For this study, a scheme was designed in order to study the effect of clearing around Pedunculate oak on beetle diversity in a stand of Norway spruce. This scheme included two different degrees of clearing and a control with no clearing (*Control*). The first degree included clearing solely under the oak crown (*Small* clearing), while the second degree was under the oak crown and extending two meters outside the crown range (*Large* clearing) (Figure 4). Trees were selected in eleven blocks distributed over the entire stand, each block containing each of the three treatments. Thus, for the experiment a total of 33 oaks were used. In each each block, the three treatments was assigned to the oaks randomly.

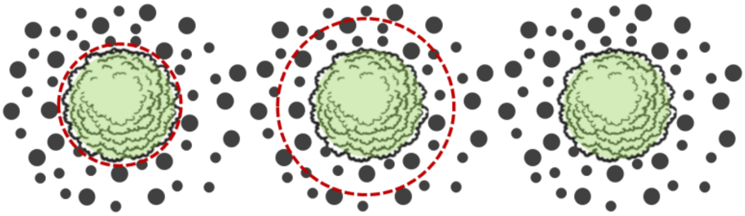

Figure 4. Clearing experiment. The left image shows the *Small* clearing treatment, the middle image shows the *Large* clearing, and the right image shows the non-cleared *Control*.

All stems to be cut around the 22 treatment oaks were marked and measured (DBH and distance to the oak). The marked trees were later removed with a harvester, and simultaneously the entire stand was thinned according to common Swedish silvicultural practice.

Beetles were sampled on all 33 oaks during three seasons. In order to exclude variations due to other causes than the clearing treatment, a Before-After-Control Increment design (BACI) (Underwood 1994) we used for the experimental setup. The season prior to clearing (2007), beetles were sampled from early May to the end of August 2007and the oaks were then re-sampled during two seasons after the clearing; directly after clearing from early June to the end of August in 2008, and from early May to the end of August in 2010.

Analyses

The effect of treatment was analyzed for both beetle groups (I and II separately, as well as I+II) with mixed models (PROC MIXED in SAS 9.2). In the model, *Treatment* and SR_B (species richness of each respective group before treatment) were used as fixed variables, and *Block* and as a random variable (covariate).

To analyze the response of species composition to different clearing treatments, multi response permutation procedure (MRPP) was used. In this analysis, all oak beetles were used (I + II). A qualitative comparison of species diversity and evenness was also made between treatments for the same group of beetles, and for this rank–abundance diagrams (Whittaker plots) were applied (Whittaker 1965).

3.4.4 Paper IV

This study, was performed on the same stand oaks as used in Paper I (and partly in Paper II). The radius around the oaks, within which the measurements of the surrounding spruces were conducted, was determined for each oak by measuring the crown radius and adding at least 3 meters. In order to measure a sufficient number of trees around each oak, this radius should include at least two rows of spruce tree in each cardinal direction of the oak. If not, the radius was expanded further until it included two tree rows. The distance and angle to, as well as the diameter at breast height (1.3 m; DBH) of each spruce, were then measured within the set radius. In addition, total height of every fourth spruce was measured. As a reference to the spruces around the gaps, diameter at breast height and height was measured for spruces on 24 “satellite” plots, four plots for each oak (Figure 5). Each plot had a radius of five meters and was centered at a distance of 15 meters from the oak along each cardinal direction. If overlapping with the area used for gap measurements, the plots were placed another five meters away from the oak.

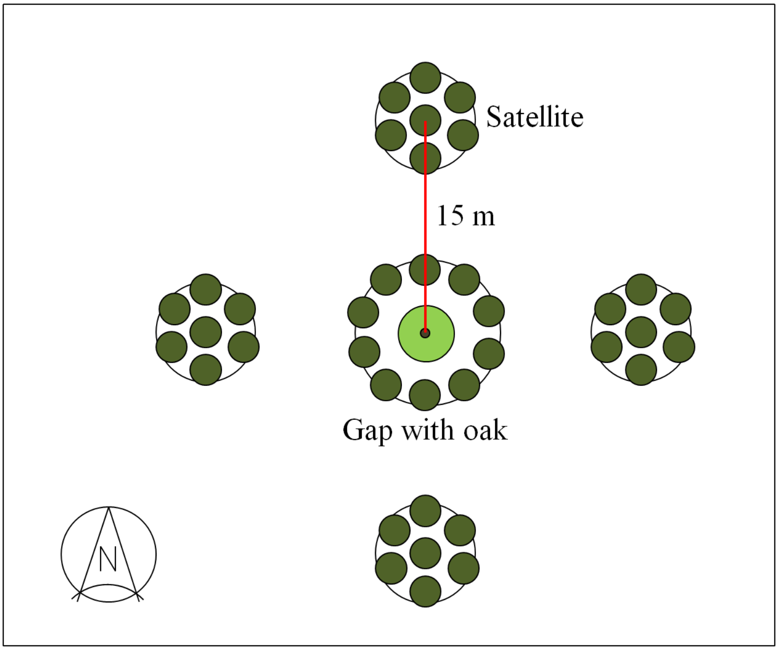

Figure 5. Design of plots around individual retention trees.

Gap area calculation

The area of the gap around each oak was calculated as the sum of circular sections where each section had the radius of the average distance from two neighboring edge-trees to the center oak (Figure 6). One half spacing was subtracted from the average distance to account for the edge-trees share of the gap. Since the spacing of edge-trees was unknown, average spacing for all satellite plots in the stand was used. The proportion of the total circle for each circle-section was determined from the coordinates of the two neighboring edge-trees. In the analysis, two different areas were used for determination of basal area per hectare. First, the net area for the neighboring trees was determined as the total measured area subtracted by the gap area was used for analysis of exploration of the gap of edge-trees. Secondly, the area of the total measured area including the gap was used for the effect of the gaps on total stand-level production. The basal area and number of trees per hectare that were calculated for the area around the gaps were compared to the same measurements in reference plots.

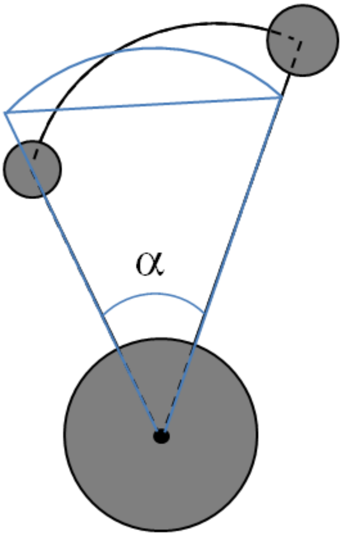

Figure 6. Area calculation of a section between two edge trees around the oak. The blue radii denote the average radius of two neighboring trees and the blue section is thus an approximation of the actual section (black) between the two trees.

Analyses

Analyses were performed on differences in diameter, stem-density and basal area in the area surrounding gaps, in the area around retained oaks including the gaps and in reference satellite plots. The effect of gap-size on diameter, stem-density and relative basal area (the ratio between basal area in the area around oaks including gaps and basal area in reference satellite plots) were analyzed with mixed effects models in R (Crawley 2013) with variations in intercept and between locations.

4 Results

4.1 Paper I: Increased openness around retained oaks increases species richness of saproxylic beetles

The first paper, as presented in this thesis, treats the positive effect of openness on species richness of saproxylic oak beetles. For this study, a total of 2117 saproxylic oak beetles were sampled, belonging to 138 species. The general linear model (GLM) revealed a significant increase in species richness of oak beetles with increasing openness (measured as shade index, SI). Including compass direction α in the index (SI_{α}) (spruce trees to the south was assigned a higher index than those to the north) resulted in an even better fit of the model ($p=0.0018$). This result indicates that competition had most effect from trees in the southern direction. There was also a significant positive effect of increasing dimension of dead oak branches ($p=0.0142$), as well as location ($p<0.0001$). Species richness of oak beetles not associated with spruce (group 1b) also responded positively to increasing SI_{α} ($p=0.0091$), as well as to increasing dimension of dead oak branches ($p=0.0076$) and location ($p<0.0001$).

There were few red-listed species sampled on the oaks, and there were no significant relationship between shade index and species richness of this particular group.

4.2 Paper II: Oaks retained in commercial spruce forests function as a complementary habitat to oaks in wood pastures for saproxylic beetles

For this study, a total of 1173 saproxylic beetles of 168 species were sampled. Of these were 97 species (891 individuals) associated to oak, whereof 38 species (381 individuals) were associated to both oak and spruce (Group I), 59 species (510 individuals) to oak and not to spruce (Group II), and 71 species (282 individuals) not associated to oak (Group III).)

The generalized linear mixed models (PROC GLIMMIX) showed that stand oaks in low shade (*Light*) harbored significantly more species of Group I than did *Pasture* oaks (p=0.025), but they also had significantly more species of this group compared to oaks in high shade (*Dark*) (p=0.003). Group II and III did not differ between any of the oak categories. The model also showed that dead oak crown had a near significant positive effect on species richness for Group I (p=0.052).

The results of the MRPP revealed a significant difference in species composition between pasture oaks and stand oaks (both *Light* and *Dark*) for Group II. There was however, no difference in composition of Group I between the oak categories. The CCA showed that the species composition was relatively well separated between the different categories, and shade and dead oak crown were the major explanatory factors. For more details regarding species assembly, I refer to the appendix in Paper II.

4.3 Paper III: Immediate responses of beetle diversity to clearing around retained oaks in a spruce plantation

During three summer seasons, 1184 saproxylic oak beetles of 96 species on 33 oaks were sampled. The mixed models revealed a significant positive effect of treatment on species richness of all oak beetles (Group I+II) regarding *Large* clearings compared to non-cleared *Control* oaks (p=0.024) over the two years beetles were sampled after treatment. The two beetle groups I and II differed in response; Group I (beetles associated with both oak and spruce) showed a significant positive response to *Large* clearings, when compared to C*ontrol* treatments (p=0.048), whereas there was no significant response for Group II (beetles associated with both oak and not with spruce) (p=.0.112). The positive response to *Small* clearings was near significant for Group I (p=0.057), however, it was not significant for Group II. The difference between *Large* and *Small* clearings was not significant.

The results of the MRPP showed a significant difference in species composition of oak beetles (Group I+II) (p=0.008) after clearing between oaks in *Large* clearings and *Control*, as well as between oaks in *Small* clearings and *Control* oaks (p=0.021). Both Group I and II differed significantly between the two treatments and *Control* (Group I: *Large* vs. *Control* p=0.005 and *Small* vs. *Control* p=0.011; Group II: *Large* vs. *Control* p=0.019 and *Small* vs. *Control* p=0.043). There was no significant difference between *Large* and *Small* clearings.

Rank–abundance curves of oak beetles (Group I+II) showed that the evenness of species composition differed between the two clearing treatments, *Large* and *Small*, and the *Control*. For all three treatments, a few species dominated the catch whereas many species were represented by only one or two individuals. The *Control* oaks were, however, dominated by fewer species than oaks in *Large* and *Small* clearings, and there was a tendency towards higher evenness for the two clearing treatments, compared to the *Controls*.

4.4 Paper IV: Growth compensation of Norway spruce in gaps around retained oaks

Oak plots had higher mean quadratic diameter compared to reference plots. There were also a higher number of stems in the tree zone around gaps compared to reference plots. However, when comparing number of stems per total gap size, there was no statistically significant difference between oak-plots and reference plots. When calculating basal area per m^2, calculated per total gap size, we found that it was lower in oak plots compared to reference plots. However, there was no difference in basal area when comparing diameter growth, calculated for the tree zone around gaps, between oak plots and reference plots.

The number of trees per hectare in the areas surrounding gaps was significantly negatively correlated to the size of the gaps. Mean quadratic diameter of the same trees was positively correlated to gap-size. Because the number of trees was negatively correlated to gap-area and diameter was positively correlated, basal area in the area surrounding gaps was not significantly correlated to gap-size.

The relative basal area (the ratio between the basal area of the area around oaks including the gaps and basal area in neighboring satellite plots) was not significantly correlated to gap-size. Since the slope of the regression was not significant, a regression without slope (which corresponds to the mean value) indicated an overall relative basal area of 0.83 indicating that basal area in the area around retention oaks was on average about 83% of the basal area in satellite plots.

5 Discussion of major results

5.1 The importance of openness and shade for beetle diversity on oak in spruce forests

The study on the effect of canopy openness (Paper I), revealed that increased openness from the surrounding spruce trees has a clear positive effect on species richness of oak associated beetles. This is in concordance with other studies on sun exposure and oak associated species (Ranius and Jansson 2000). In addition, spruce trees in the southern direction of the oaks appeared to have a more negative effect on species richness than trees in the northern direction. However, no traps were positioned on the northern side of the trunk, and thus it is not possible to definitely exclude that spruce trees in the northern direction may a negative effect on species richness. Yet, with the exception of one single oak, there were no spruce trees growing close to the oak trunk and interfering with the trap. Hence, it can be assumed that either 1) the abundance of beetles circulating close to the trunk (and the trap) is equal in all cardinal directions (north, south, east, or west) or 2) beetle abundance is higher on the southern side, as most oak associated species thrive in rather high levels of insolation (section 2.1.3). Thus, it is reasonable that positioning traps also on the northern side of the oak should have a minor influence on sampling efficiency.

The final conclusion is that oaks in gaps positioned more to the south of the trunk should attract a higher number of oak-associated species, compared with oaks where the gap was positioned more to the north. This could be expected, as it is likely the sun exposure in the gap rather than the openness *per se*, that is determinant of species richness of shade-intolerant beetles in spruce forests. Thus, two different gaps of the same size, positioned differently in relation to the oak with regard to sun exposure angle, will yield different amounts of direct sunlight on the oak stem during the day (Figure 7). Hence, when clearing of spruce trees around retained oaks, it should be more cost-effective, regarding both timber production and biodiversity, to remove trees mainly in the southern direction and to retain spruce trees on the northern side.

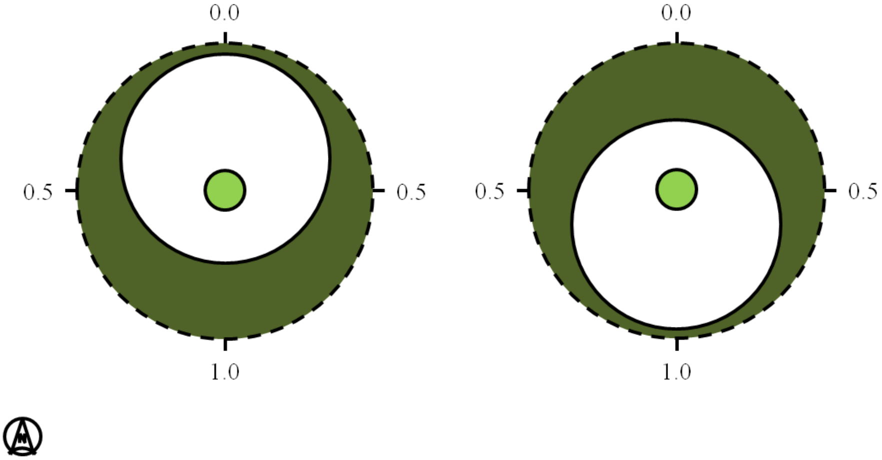

Figure 7. The importance of gap position in relation to sun exposure angle. The image shows two different oaks (light green circles) in the same gap size (white area). The gap around the oak to the right is more open towards the southern direction from the stem and will thus yield a higher amount of sunlight during the day, compared to the oak to the left.

5.2 Retained oaks for biodiversity at the landscape level

One of the major incentives for GTR is that they may increase the quality, quantity and diversity of habitat for many species. In order to provide this, though, retained trees must provide a habitat which is comparable also to that of oaks in the open landscape. In Paper II, species richness of oak beetles was compared between oaks in closed stands and oaks in pastures. As a previous study (Paper I in this thesis) confirmed that shade has a detrimental on species richness of oak associated beetles, pasture oaks were compared to stand oaks in two different shade levels.

The highest number of species was not found on the pasture oaks, as expected, but on stand oaks in low shade (*Light*). Hence, it is reasonable to believe that some species are favored by the specific conditions prevailing on and around sunlit oaks in spruce forests. Several of the sampled species use both oak and spruce during part of its lifecycle (Group I), however, the majority use solely oak and not spruce (Group II). Species using both oak and spruce were relatively few on highly shaded oaks (*Dark*), compared to low shaded oaks, in closed stands. Thus, it appears that most of these species prefer light. However, there were minor differences in species composition between stand oaks in low shade and oaks in pastures, why it is reasonable to believe that species that thrive on oaks in pastures may also use oaks in gaps in spruce forests. Regarding oak beetles not using spruce, though, there was no difference in species richness between the categories. However, species composition differed between both categories of forest oaks (*Light* and *Dark*) and pasture oaks. Hence, there might be a rather limited exchange of species from this particular group between oaks in forests and oaks in pastures. This indicates that oaks in spruce forests may constitute a rather different and unique habitat that favors some species that do not particularly thrive on oaks in pastures.

Differences in species composition between forest and pasture were analyzed with regard to different environmental variables (canonical correspondence analysis). The composition was mainly determined by shade index and amount of dead wood in the crown. As shade and dead wood differed between the plantations and the open pastures, it is expected that species richness and composition are forced by differences in microclimate and/or amount of dead wood on the oaks.

Thus, oaks in plantations can harbor a comparatively high number of species, even though the composition differs somewhat from that of freestanding oaks. One possible explanation is that Pedunculate oak, is a mid-successional forest tree, and hence many of the species using oak as habitat may prefer the intermediate microclimate around oaks in low shade rather than that of open pastures. Hence, it is obvious that other factors, besides light, force the differences in species richness between forest and pasture. One such factor, as mentioned above, could be differences in the amount of dead wood on the oaks in forests compared to pastures. Another explanation could be that oaks in plantations to a higher degree attract species connected to both oak and spruce, compared to pasture oaks.

The question whether retained oaks may benefit the overall species diversity on a landscape scale remains to be answered. May such oaks provide suitable substrates for species considered as dependent on pasture oaks? The differences found regarding species composition, indicate that some species may benefit, while others might not. This shows that a more stable environment in terms of e.g. temperature, wind, and/or humidity can be beneficial for species associated with mature oaks.

In conclusion, oaks retained in spruce plantations can sustain a diversity of species comparable to, or even larger than that of more and less freestanding oaks in pastures, provided the shade from the surrounding plantation is kept to a relatively low level. However, retention trees in closed stands appear to favor several additional beetle species, and hence should have a beetle fauna complementary to that of pasture oaks. Thus, managing retained oaks in spruce plantations for biodiversity should increase the total species richness of oak associated beetles in northern Europe.

5.3 Openness and dead wood

Previous studies have shown that cavities on old oaks are important for the diversity of saproxylic beetles (Ranius et al. 2009a, Ranius et al. 2009b). However, several results in this thesis point to the fact that the saproxylic oak beetle fauna is favored also by dead branches on the trees. Comparing oaks on stand scale, showed that dead branches of large dimensions have a significant positive effect on species richness (Paper I). Further, when comparing stand oaks with pasture oaks, species richness increased significantly with increasing percentage of dead oak crown (Paper II). Thus, this clearly states that factors related to branches are important for many oak associated beetles. The oaks used in Paper I and Paper II were overall relatively young; the mean age was <200 years in seven out of nine stands in our study, whereas cavities are formed in oaks when they are between 200 and 400 years old (Ranius et al. 2009a). Very few trees in our study had exposed dead wood on the trunk or hollows within the trunk, structures that are frequent in older trees. It is possible that differences in species richness between oaks in different degree of shade, or between forest and pasture, decreases with tree age and increasing amount of dead or decaying wood.

Oaks in small gaps had a significantly higher percentage of dead wood in the crown, and this implies that competition from the surrounding spruce stand could have an impact on the formation of dead wood. However, oaks in larger gaps had fewer, but coarser dead branches, compared to oaks in small gaps. This could be due to a higher radial growth rate of oaks in gaps. However, it could also be that vital oaks with large crowns (in Paper I and II) are more likely to be well managed for, and thus more extensively cleared around. In any sense, oaks in spruce stands can develop a useful substrate for saproxylic species faster than do freestanding oaks. This is manifested in higher species diversity, but only as long as the oaks are not too heavily shaded. It should thus be important to consider maintaining dead wood in the crown of retained mature oaks, in order to attract more oak associated beetle species.

5.4 Short-term responses in beetle diversity to clearing

Paper III shows that there are short-term benefits of clearing around oaks for saproxylic oak beetles. There were significant differences in both species richness and composition of oak associated beetles between treatments; the large clearings had a higher impact on species richness and composition than the small ones. Moreover, the composition was more even for the two clearing treatments, compared to the control. The study further shows that the effect is visible as early as the first three years after clearing.

The response in species richness to clearing seemed to depend on whether the oak beetles were associated to spruce or not; only species associated with both oak and spruce (Group I) showed a significant increase in species richness (to large clearings compared to the control). This result was not expected, as it appears more likely that oak beetles that do not use spruce (Group II) are more dependent on high levels of insolation, compared to beetles that can use both oak and spruce. Moreover, in Paper I, species richness of Group II (named Group 1b) displayed a significant positive relationship to increased openness. Hence, these somewhat contradicting results remain unexplained.

5.5 Effects on timber production

When assessing the effects of retained oaks on timber production, there were no negative effects of gaps on the growth of the surrounding Norway spruce trees. On the contrary, there was a higher growth in the oak plots, compared to reference plots, which partly compensated for the loss with the gap. The diameter growth of single spruce trees lining gaps increased with increasing gap size. However, with increasing gap size, stem density of trees in the area close to gaps decreased, which could be due to lower thinning intensity alongside small gaps compared to large. Thus, the increased basal area along larger gaps was probably due to both higher stem density and more efficient exploration of resources in the gap. The effect of gap size on basal area per m^2 in the fringe of the gaps was almost significant, and it is likely that without the effect of different thinning intensity, there would have been a more clear effect of gap size on basal area.

The overall basal area in gaps and neighboring trees around retained old oaks were about 83% lower than for the satellite plots in the stand unaffected by oaks. Since there was no difference in production level between large and small gaps, this study indicates that with the thinning treatments imposed on the studied stands, the reduction in production will be about the same irrespective of gap size for gaps at least up to about 350 m^2.

5.6 The cost of increasing species richness on retention trees in commercial plantations

The final aim of this thesis was to estimate the benefit of increasing species richness with the corresponding cost in terms of lost timber volume. So far, the incentives for clearing around oaks are evident; this thesis shows there is a clear effect on species diversity of oak associated wood-living beetles, and other studies show that there are apparent benefits for the vitality of the oak tree itself. Regarding oak associated species, several of which are favored by light (Berg et al. 1994), it seems to be most beneficial to clear a gap in the southern direction of the oak. This was revealed by the increased fit of the model (species richness as a function of tree competition) when the surrounding trees were ranked from zero to one according to compass direction (in relation to the oak; 0 corresponding to North and 1 to South) (Paper I). This way of ranking reduced the effective radius by half, which resulted in an area (A_{gap}) reduction by four ($A_{insolation}$), the effective gap area, (Figure 4), as shown by

$$\frac{A_{insolation}}{A_{gap}} = \frac{\pi\left[3\frac{r_{gap}}{4}\right]^2}{\pi {r_{gap}}^2} \rightarrow A_{insolation} = 3\frac{A_{gap}}{8}$$

where r_{gap} is the radius of a gap with area A_{gap} (the radius of A_{gap} is approximately $r_{gap} \times 3/4$).

Considering the vitality of oak itself, it could be necessary to extend the clearing somewhat outside the crown perimeter, possible one or two meters. Trees growing under the oak crown are often highly suppressed, or dead, a fact that was evident during my field inventories. In any case, such trees should be removed, as they might interfere with the oak crown. The extended gap area, here referred to as A_{oak}, will thus have a radius equal to; $r_{gap} \times 3/4$ extended with the crown radius, r_{crown}, plus the additional one or two meters, d_{clear}, divided by two ($(r_{crown}+d_{clear})/2$). The area loss, calculated as

$$\frac{A_{oak}}{A_{gap}} = \frac{\pi\left[3\frac{r_{gap}}{4} + \frac{(r_{crown} + d_{clear})}{2}\right]^2}{\pi {r_{gap}}^2}$$

gives thus an indication of how much area will be lost in relation to the initial area, A_{gap}. For further calculations on cost-benefits, only the first equation was used, as the primary aim was to establish a model applicable for biodiversity and timber production, and not for oak vitality

The second equation is dependent on the radius of the oak crown, and as such it is difficult to apply, unless you have a specific case with a defined radius.

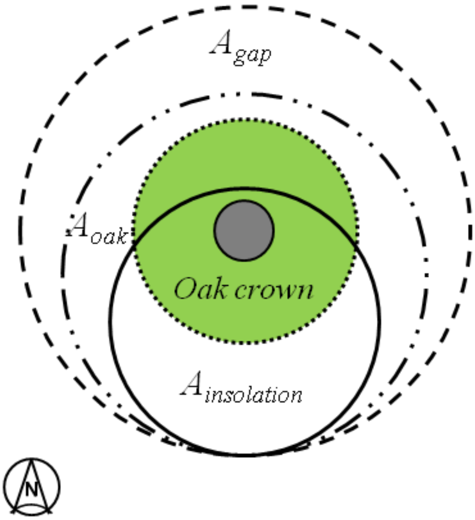

Figure 6. Suggestion to clearing according to shade index. The effective gap ($A_{insolation}$), where the insolation angel is considered, is denoted by the inner circle. The middle circle refers to the extended gap around the crown of the oak (A_{oak}), and the outer circle refers to a gap where the insolation angle is not considered (A_{gap}).

Estimating species richness accordingly was rather complex, as there were substantial variations in beetle diversity between localities. To get around this problem, species richness was calculated as an average function of shade index. This calculation was based on the regression curves obtained for each of the nine locations (in Paper I)

$$y = \mathrm{a}x + \mathrm{b}$$

where y is the number of species, in this case the total number of oak associated beetle species, referred to as Group 1a (Paper I) or Group I (Paper III), whereas x is the corresponding shade index. To obtain the new function, I used the mean of the inclination a, and the mean of the y-intercept b (Figure 7).

$$y = -0.0087\mathrm{x} + 19.3$$

It is important to mention, though, that there were variations between site locations regarding how the shade index was estimated. As the gap range differed, the radius used for the measurements varied somewhat. However, as the impact of the surrounding trees decreases linearly with distance, *d*, according to 1/*d*, this should have a minor influence on the final result.

The next step was to calculate the amount of timber volume lost with a certain shade index (Table 2). For this purpose, a fictive example was used; a Norway spruce plantation with 1000 stems/ha, with an average DBH of 18 cm, and an average height of 17 m. Since the gaps were calculated as the actual area lost, i.e. the radius minus one half spacing, and since the spacing was on average about 3 meters, a gap-size of 350 m^2 will amount to a circular gap with a radius of about 11.5 m. Hence, in this example, we used a maximum radius of 12 m. Included in the calculations was also the growth compensation of 20 % from the threes neighboring the gap (included in production loss).

5.6.1 Calculation of costs and benefits

This section relates to Table 2, and the numbers 1-13 refer to the different steps in the calculation of costs and benefits.

In this final synthesis, the aim was to calculate the number of species and the timber loss for a certain gap radius (steps 1-8). Previously, the number of species was estimated as a function of shade index, as described in section 5.6 (and papers I and II), and in order to obtain the gap radius, shade index had to be transformed into gap radius. For this calculation, the fictive stand, as previously described in section 5.6, was used. The shade index was then calculated for gaps ("Gap SI") between 1 and 12 meters (12 meters is the maximum gap size used in the studies). In order to do so, the 12 m radius was divided into circular sections of one meter intervals (Figure 8) and the shade index was calculated for each section (SI per section; 4). This was done by first calculating the shade index per tree (SI per tree; 1) (the equation is presented in section 5.6) for all trees at the average distance from the oak for each circular section. Area per section and thereafter stems per section was calculated (2-3). The "SI per section" (4) was obtained as the product of "SI per tree" and the number of "Stems per section". Because all trees were assumed to be of the same size and regularly spaced, the SI per section was the same for all section. The total shade index (SI total; 5) was then calculated for each radius as the sum of "SI per section" up to that radius, which in the case of 12 m gave a total shade index of 4153. This number corresponds to no gap, i.e. regularly spaced, even sized trees in a circular area with 12 m radius. The relative shade index for gaps with a certain radius (Gap SI; 6) was then calculated by subtracting the SI lost with a gap from the maximum “SI total” (4153). Hence, the “Gap SI” for gaps of 12 meters was zero (4153-4153=0), for 10 m 692 (4153-3461), and so on. This gave a relative value of gaps up to 12 meters, with 12 meter representing the maximum gap size, thus having a shade index of zero. The “Effective gap SI” used for calculating species richness included compass angle and corresponds to about 3/8 of the total SI in a gap, as described above in section 5.6 and Figure 6. Hence, this index was used for the final calculation of the “Number of species” (8) (described in section 5.6.). Thus, species richness for different gap radii was now obtained (Table 2).

The next step was to calculate loss in timber production for a certain gap radius between 1-12 meters (steps 9-13). In this example, a one hectare plot with production=1 was used. Gaps of different sizes were assumed to be placed in the center of the one-hectare plot and production due to the gap was reduced according to the calculation described below. The area used for the estimation of production loss (Area for prod. reduction; 9) was calculated as a circular plot with radius equaling the gap radius plus two tree rows (6 meters). Thus, for a gap with 4 m radius, production-loss was considered in a circular plot with a radius of 10 m. Two tree rows were included in the production loss plot in order to include both the actual loss from the gap and the growth compensation of the two tree rows lining the gap. According to the results in Paper IV, production in gaps and an area corresponding to about two tree rows outside the gaps was 80% of that in the stand irrespective of gap size. Thus, the relative production loss due to the gap (“Prod. loss due to gap”; 10) was 0.2x”Area for prod. loss” (where the area for production loss included two tree rows outside the gap as described above). Since the stand was assumed to be one hectare in size and relative production on this hectare was one, the relative production of the whole stand including gap (“Rel. prod.”; 11) was calculated as 1-“Prod. loss from gap”. The production loss (“Prod. loss”; 12) was the “Rel. prod.” (11) as a percentage of a stand without gaps with production equaling one. The production in the effective gap (Prod. loss eff. gap; 13) was 3/8 of “Prod. loss” and corresponds to a gap placed in order to optimize shade index by including the effect of angular direction to each tree (see above for definition).

Below, species richness (green) (8) and timber loss, both in total gap (blue) (13) and in effective gap (red) (14), are plotted against gap radius for gaps up to 12 meters (Figure 8).

Table 1. Results of the calculations used for the final synthesis on costs and benefits of retention trees.

	Gap radius (m)	1	2	3	4	5	6	7	8	9	10	11	12
Species richness	1. SI per tree	1102	367	220	157	122	100	85	73	65	58	52	48
	2. Area per section (m2)	3.1	9.4	15.7	22.0	28.3	34.6	40.8	47.1	53.4	59.7	66.0	72.3
	3. Stems per section	0.3	0.9	1.6	2.2	2.8	3.5	4.1	4.7	5.3	6.0	6.6	7.2
	4. SI per section	346	346	346	346	346	346	346	346	346	346	346	346
	5. SI total	346	692	1038	1384	1730	2076	2423	2769	3115	3461	3807	4153
	6. Gap SI*	3807	3461	3115	2769	2423	2076	1730	1384	1038	692	346	0
	7. Effective gap SI	1428	1298	1168	1038	908	779	649	519	389	260	130	0
	8. No. of beetle species	6.9	8.0	9.2	10.3	11.4	12.6	13.7	14.8	15.9	17.1	18.2	19.3
Timber production	9. Area for prod. loss	0.015	0.020	0.025	0.031	0.038	0.045	0.053	0.062	0.071	0.080	0.091	0.102
	10. Prod. loss due to gap	0.003	0.004	0.005	0.006	0.008	0.009	0.011	0.012	0.014	0.016	0.018	0.020
	11. Rel. prod.	0.997	0.996	0.995	0.994	0.992	0.991	0.989	0.988	0.986	0.984	0.982	0.980
	12. Prod. loss (%)	0.31	0.40	0.51	0.63	0.76	0.90	1.06	1.23	1.41	1.61	1.82	2.04
	13. Prod. loss eff. gap (%)	0.12	0.15	0.19	0.24	0.29	0.34	0.40	0.46	0.53	0.60	0.68	0.76

*SI=Shade index
**BA=Basal area

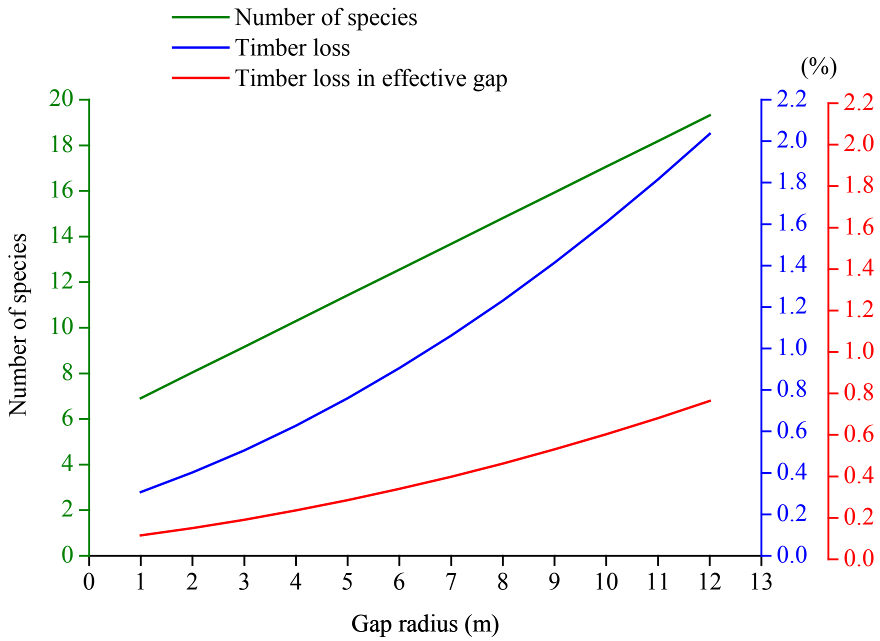

Figure 8. Synthesis of biodiversity benefits and production loss for a specific gap size.

The number of species increased as a linear function with increasing gap radius, whereas timber loss was fitted to a polynomial function, in this case increasing with increasing radius. From this graph (Figure 8), it is obvious that there is no threshold (in gap radius) at which the timber loss is higher than the gain in species richness, and therefore it is not possible to suggest what gap size is most optimal in terms of costs and benefits. However, it is clear that the increase in timber loss is smaller for smaller gap sizes, as compared to large. Despite this, this final graph can be very useful as it enables an easy estimation of how much timber (%) is lost with a certain gain in species richness.

Based on Figure 8, it could be argued that retaining several oaks in small gaps is more cost-efficient compared to few oaks in large gaps. However, as single large gaps resulted in higher species richness, compared to single small gaps, large gaps probably capture several species that favor high levels of insolation. Thus, it is likely that such species would not be attracted to oaks in smaller gaps, even though such oaks might be present in high numbers in a single stand. The reduction in timber production is however not very large even for rather large gaps, especially if the insolation is optimized by positioning the gap on the southern side of the oak (“effective gap”), but the gain in species richness with large gaps is substantial. The question is then how many gaps are possible in a one ha stand? Theoretically, retaining ten gaps of a 12 meter radius with two tree rows outlining the gap is possible (about 0.1 ha per gap). This would result in a production loss of 20%. If the number of gaps is 10, then the production loss is 10%, and with the “effective gap” the loss is only 4%, which seems highly acceptable. Hence, I here recommend at least five oaks in ”effective gaps” (“effective radius” = 9 meters) per ha to obtain a sufficient effect in biodiversity and an acceptable loss in timber production.

6 Conclusions

Green tree retention at final felling in production forests have only been carried out at larger scale a couple of decades (Vanha-Majamaa and Jalonen 2001, Halpern et al. 2005, Nelson and Halpern 2005, Gustafsson et al. 2010, Gustafsson et al. 2012) and the stands used in our study – mid-age production stands with mature retained trees – hence are rather rare in today's Scandinavian landscapes. This thesis is among the first attempts to evaluate this system, and is also a glimpse into the future when this situation will be more common.

In summary, the studies in this thesis show that mature standing oaks, if managed with regard to the demands of oak associated species, are important elements for conservation in plantation forests. As expected, increased openness had a positive effect on species richness of saproxylic oak beetles and the response to clearing was immediate effects on both species richness and composition.

Unexpectedly though, retained oaks in plantations may, if cleared of encroaching spruce trees, harbor species richness comparable, and even higher, compared to that of freestanding pasture oaks. A certain loss in timber production from the gaps was expected. However, trees lining the edge of gaps can partly compensate for the loss with the gap. Retaining oaks in large gaps have a substantial benefit for species richness of saproxylic oak beetles and it appears to be more cost-effective with a few oaks in large gaps, compared to several oaks in small gaps.

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Retaining trees valuable for biodiversity in commercial forests is a common conservation measure. There are indications that such trees have important benefits for the diversity of many species groups. However, retaining trees may also have negative effects on timber production. This thesis contributes to the knowledge of how mature oaks in spruce forests benefit species diversity of wood-living beetles. It also explores how to manage retained oaks in order to maximize the biodiversity benefit at a low cost for the forest owner.

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