Insect Diversity on Clearcuts in Boreal Forest Landscapes

Diana Rubene

Faculty of Forest Sciences
Department of Ecology
Uppsala

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Cover: Boreal forest with clearcuts and retention trees in Dalarna
    (photo: D. Rubene)

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Abstract

Intensive management and loss of natural disturbance dynamics in boreal forests leads to habitat loss and degradation for forest dwelling species. As a consequence, many species have become threatened, especially those dependent on dead wood. Integration of conservation in forest management is therefore essential for protecting boreal forest species diversity. To optimise conservation efforts, we need to understand species habitat requirements and diversity patterns in managed forests. This thesis aims to increase our understanding of insect species diversity patterns on clearcuts in boreal forest landscapes. I have surveyed beetles, bees and wasps on clearcuts in two boreal forest regions in Sweden and assessed the importance of clearcut properties and composition of surrounding landscape for species occurrence and diversity. Locally, amount of dead wood was positively associated with high species richness and individual species occurrence of certain wood-dependent beetles. Bee and wasp species richness increased with high local flower richness and clearcut size. Landscape composition was at least as important as local habitat characteristics for shaping diversity patterns. Burned forest land in surrounding landscape increased wood-dependent beetle species richness, while burning of clearcuts had only a weak effect on beetles, bees and wasps. This is probably because burned forest land on landscape scale includes higher habitat diversity with larger dead wood amounts, compared to burned clearcuts. Bee and wasp species richness increased with amount of early-successional habitats in the landscape, indicating that most species are associated with open habitats. The bee and wasp fauna differed considerably between landscapes. Therefore, conservation efforts need to be dispersed throughout the region to preserve the entire fauna. To promote insect species diversity on clearcuts in managed boreal forests, larger amount and diversity of dead wood needs to be created. Species dependent on sun-exposed dead wood or flowering plant richness can be favoured by prolonged open-habitat stage on parts of clearcuts. Concentrating certain conservation efforts to some clearcuts in the landscape is probably necessary in order to create high-quality habitats.

Author's address: Diana Rubene, SLU, Department of Ecology,
P.O. Box 7044, 75007 Uppsala, Sweden
E-mail: Diana.Rubene@ slu.se

Insekters mångfald på hyggen i boreala skogslandskap

Sammanfattning

Intensivt skogsbruk och brist på naturlig störningsdynamik i boreala skogar leder till en minskning och försämring av habitat för skogslevande arter. Det leder till att många arter minskar och riskerar att försvinna, framförallt arter som är beroende av död ved. Därför är det nödvändigt att integrera naturvårdsåtgärder i skogsbruket för att bevara mångfalden av arter i den boreala skogen. För att kunna optimera naturvårdåtgärder behöver vi förstå arters habitatkrav och diversitetsmönster i brukade skogslandskap. Målet med denna avhandling är att öka förståelsen för insekters diversitetsmönster på hyggen i brukad boreal skog. Jag har inventerat vedskalbaggar och gaddsteklar i Hälsingland och Dalarna och undersökt betydelsen av lokala habitatfaktorer och det omkringliggande landskapets sammansättning för arters förekomst och diversitetsmönster. Mängden död ved på hyggen var viktig för hög artrikedom och förekomst av enskilda vedskalbaggsarter. Artrikedomen av gaddsteklar ökade med hög rikedom av blommande växter och hyggesstorlek. Landskapets sammansättning var minst lika viktig som lokala faktorer för de observerade diversitetsmönstren. Mängden bränd skogsmark i omgivande landskap var positiv för artrikedomen av skalbaggar, medan lokal hyggesbränning hade liten påverkan på skalbaggar och gaddsteklar. Detta beror troligtvis på att bränd skogsmark på landskapsskala innefattar högre habitatdiversitet med större mängder död ved jämfört med brända hyggen. Gaddsteklarnas artrikedom ökade med mängden tidiga successionshabitat i landskapet, vilket tyder på att de flesta arter är knutna till öppna habitat. Olika landskap hade även olika arter av gaddsteklar. Därför behöver naturvårdsåtgärder spridas ut i regionen för att bevara hela faunan. För att öka artrikedom av insekter på hyggen behöver större mängder och variation av död ved skapas. Arter beroende av solexponerad död ved eller hög blomrikedom skulle gynnas om delar av hyggen hålls öppna längre. För att skapa habitat av tillräckligt hög kvalitet i landskapet behöver naturhänsynen troligtvis koncentreras så att nivån av hänsyn blir högre på vissa hyggen i varje landskap.

Nyckelord: död ved, vedskalbaggar, gaddsteklar, hyggesbränning, skogsbruk, tidiga successionshabitat

Dedication

To forests, in all their shapes – may you ever persist…

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   Rubene, D., Wikars, L-O. & Ranius, T. (2014). Importance of high quality early-successional habitats in managed forests to rare beetle species. *Biodiversity and Conservation* 23, 449-466.

II Rubene, D., Schroeder, M. & Ranius, T. Diversity patterns of wild bees and wasps in managed boreal forest: effects of local habitat and surrounding landscape. (manuscript).

III Rubene, D., Schroeder, M. & Ranius, T. Landscape composition, local dead wood amount and fire shape saproxylic beetle richness patterns on clearcuts in boreal forest. (manuscript).

IV Rubene, D., Schroeder, M. & Ranius, T. Estimating bee and wasp (Hymenoptera: Aculeata) diversity in forest landscapes – an evaluation of sampling methods. (submitted manuscript).

Paper I is reproduced with the permission of the publisher.

The contribution of Diana Rubene to the papers included in this thesis was as follows:

I   Main author and field work. Research questions and study design together with Lars-Ove Wikars and Thomas Ranius. Analysis together with Thomas Ranius.

II   Main author, field work and analysis. Research questions and study design together with Martin Schroeder and Thomas Ranius.

III Main author, field work and analysis. Research questions and study design together with Martin Schroeder and Thomas Ranius.

IV   Main author, field work and analysis. Research questions and study design together with Martin Schroeder and Thomas Ranius.

1 Introduction

1.1 Boreal forests

1.1.1 Disturbances and successions

Boreal forest dynamics are driven by a continuous cycle of disturbances and successions. Disturbances – fire, windstorms and insect outbreaks, together with small-scale gap dynamics – used to be the dominant forces that shaped the boreal forest landscapes of Fennoscandia and created a structural and functional mosaic that hosted formidable species diversity (Esseen et al. 1997; Kuuluvainen 2009). Fire of varying severity was a common feature in boreal forests (Zackrisson 1977). Nevertheless, unlike the severe fires in continental North America, the fires in Fennoscandia were seldom stand-replacing, allowing development of heterogeneous stand structure with more complex successional dynamics (Kuuluvainen 2009). Old-growth Fennoscandian forests are characterised by high abundance of standing dead wood, large diameter trees and a considerable component of deciduous trees (Östlund et al. 1997; Linder and Östlund 1998). Forest-living species have presumably evolved under selection pressure from various disturbances, and are adapted to the habitat dynamics created by these (Moretti and Legg 2009).

1.1.2 Dead wood dynamics

Dead wood is created when trees die due to senescence, competition, disease or disturbance. Characteristics of dead wood change throughout its cycle of decomposition, e.g. moisture content, level of carbon dioxide and nutrient content (Stokland and Siitonen 2012). The complete decomposition process may take from a few years up to several hundreds of years (Stokland and Siitonen 2012). Throughout this time, the dead wood can house a variety of living communities, from fungi and bacteria, bryophytes, insects and their larvae, to cavity-living mammals and birds. Dead wood is a key resource for

forest biodiversity and in Fennoscandia, dead wood dependent (saproxylic) species constitute about 25% of all forest species (Siitonen 2001).

The abundance of dead wood varies throughout forest succession. In forests with natural dynamics, the amount of dead wood is high in early succession (after stand-replacing disturbances), then declines being the lowest in mid-succession and then increases again due to mortality of old trees (Jonsson and Siitonen 2012a). Early-successional stages are dominated by large amounts of fresh and sun-exposed dead wood, while the dead wood in later successions is more likely to be decayed and shaded.

Dead wood with different properties attracts different species. Many saproxylic species are specialised to certain types of wood, like snags or logs, sun-exposed or shaded, fresh or decayed wood, or wood with different fungal flora (Jonsell et al. 1998, Wikars 2002, Boulanger and Sirois 2007, Johansson et al. 2007). Therefore, wood with different qualities is necessary for high species diversity.

1.1.3 Management and its consequences

In Eurasia and North America, large areas of boreal forests are managed for wood production. Most of Fennoscandia has a particularly long history of intensive management, which has created a very different forest structure from that of natural forests (Östlund et al. 1997; Linder and Östlund 1998).

The main consequences of intensive management are changes in tree age, tree species composition, stand density, dead wood amount and loss of natural disturbance dynamics. Managed forests are dominated by even-aged stands of usually a single species, which are harvested by clear-cutting, and are thereby very unlike forests with complex size and age structures created by natural dynamics (Kuuluvainen 2009). The trees in managed Swedish forests reach significantly lower age compared to old-growth forests; the volume of very large trees and snags has been reduced by 90% and only 1% of the original old-growth area remains (Linder and Östlund 1998). As planted conifers are prioritised, the proportion of deciduous trees has decreased (Fransson 2011). The amount of dead wood has decreased substantially, resulting in loss of structural diversity (Siitonen 2001, Paillet et al. 2010). Salvage logging is widely practiced after large-scale disturbances, which has negative effects on species diversity and ecosystem processes (Lindenmayer 2004, DelaSalla 2006, Cobb 2011).

Clear-cutting is a common harvesting practice used in boreal forests worldwide. It is a cost-efficient and simple method of harvesting trees and facilitating establishment and rapid growth of a new stand (Keenan and Kimmins 1993). Initially, clearcutting was claimed to mimic effects of natural

stand-replacing disturbances like storms and forest fires (Kuuluvainen 2009). However, as the negative effects of clearcutting on the forest ecosystems and biodiversity became better studied, concerns arose about the long-term impacts and sustainability of such management.

The management-induced changes in boreal forests result in extensive degradation and loss of habitat for species dependent on old living trees, logs, snags, and other elements typical for old-growth forests (Berg et al. 1994). Reduced amount and diversity of dead wood is one of the main reasons why reduction of biodiversity in managed forest is occurring in Fennoscandia (Berg et al. 1994; Linder and Östlund 1998; Fridman and Walheim 2000). Many saproxylic forest species are today red-listed (Gärdenfors 2010, Stokland et al. 2012), and the species diversity that managed forests can sustain is limited by the low amount and diversity of dead wood (Similä et al. 2003, Siitonen 2001).

1.2   Early-successional habitats

Early-successional forest habitats are created when trees are killed by disturbances. The transformation from mature to early-successional forest is a dramatic event, accompanied by changes in habitat characteristics and creation of new features. Many of the new characteristics are uncommon in mature forests – abundant sunlight, large amounts and diversity of dead wood, flowering herbs and exposed mineral soil (Swanson et al. 2010) – and they create conditions for new types of species diversity. Natural early-successional forest habitats are characterised by high biodiversity, because they are a combination of legacies from the previously existing forest and the new characteristics created by the disturbance (Lindenmayer and Franklin 2002, Swanson et al. 2010). Many species utilise these habitats, especially those that are dependent on dead wood, and species communities differ between early-successional habitats and mature forest (Similä et al. 2002, Boucher et al. 2012).

1.2.1 Habitat dynamics

Species that depend on early-successional habitats, in particular fire-associated species are faced with a challenge, as their habitat is highly dynamic in space and time. As succession proceeds, existing habitat patches lose their suitability to many species, while new habitats are created in other parts of the landscape. This means that the species need to be able to track changes in habitat availability on landscape level and long-term persistence of populations is only possible on landscape scale (Jonsson 2012). If the amount of suitable habitat in the landscape is low, species may face threat of extinction, because new

colonisations cannot compensate for local extinctions in old patches. For early-successional species, landscape composition and connectivity between suitable open habitat patches is important (Schroeder et al. 2006). Fire suppression together with degraded quality of forest habitats due to forest management are likely explanations for why fire-associated species have become threatened or extinct in many regions (Saint-Germain et al. 2012).

1.2.2 Insects in early-successional habitats

Early-successional forest habitats can host high insect diversity (Swanson et al. 2010). Warm and sunlit environments, particularly post-fire habitats with blackened wood and ground surfaces, promote insect activity, as their body temperature depends on the temperature of the surroundings (Taylor 1963, Arroyo et al. 1985). High abundance and diversity of dead wood attracts saproxylic species. Finally, high flowering plant diversity make early-successional forest habitats attractive places to a large variety of flower visiting insects, such as bees, wasps and butterflies (Taki et al. 2013, Miller and Hammond 2009).

Saproxylic beetles require dead wood for reproduction; larvae of most species develop inside wood where they feed on wood, fungi or predate other arthropods and their larvae (Ehnström and Axelsson 2002). Some species are generalists and some are highly specialised to specific types of dead wood, e.g., single tree species or decomposition stages. Adults of saproxylic beetles have varying habitat requirements. Some species are predators in- or outside the dead wood substrate, others are herbivores or fungivores, while adults of some species do not feed at all. Some species visit flowers and feed on pollen and nectar (Alexander 1998, Ehnström and Axelsson 2002) and certain species are associated with habitats created by fire (Boucher et al. 2012, Kouki et al. 2012). Saproxylic beetles are among the largest dead wood dependent groups and are widely studied. However, limited knowledge exists on landscape scale diversity patterns and colonization-extinction dynamics, which could be used to improve conservation efforts.

Bees and wasps (Hymenoptera: Aculeata) are generally associated with open habitat types (New 2012). Most species depend to some degree on flowering plants, and especially bees (families within Apoidea) are important pollinators. Species in other families are predominantly predators (e.g., Crabronidae) or cleptoparasites (e.g., Chrysididae). Many species use dead wood for nesting – some excavate their own tunnels, while others use existing cavities made by e.g., saproxylic beetles (Morato and Martins 2006). A majority of solitary bee species nest in the ground and benefit from moderate soil disturbances (Linkowski et al. 2004, New 2012). While diversity patterns

and habitat associations of bees and wasps are widely studied in agricultural landscapes, they have rarely been studied in forest landscapes, despite important functional roles of bees and wasps as pollinators of flowering plants (among them berry-producing dwarf shrubs) and predators/parasites of pest insects.

1.3   Biodiversity conservation

Conservation in boreal forest is applied on several spatial scales. On the largest scale, forest biodiversity is protected by setting aside, e.g., nature reserves and national parks, which are exempt from exploitation. However, set-asides typically cover only a fraction of forest area and cannot protect all species (Franklin and Lindenmayer 2009). The main goal of nature reserves in Fennoscandian forests has been to protect remaining old-growth forests and disturbances are rarely introduced in these areas. Thus, in order to prevent loss of biodiversity, conservation actions in managed forests are of high importance (Franklin 1993, Kouki 2001, Bengtsson 2003).

Conservation has been integrated into forest management during last 10 – 20 years in attempt to minimize the negative impacts on biodiversity and improve the long-term biological sustainability of forest ecosystems (Gustafsson et al. 2012). In order to support biodiversity hotspots in managed forests and increase connectivity of protected areas, a network of woodland key habitats (WKH), has been established in Fennoscandia. These are small forest patches (in Sweden on average 4.6 ha, Timonen et al. 2010) with documented conservation values (occurrence of red-listed species or structures likely to support red-listed species). On a scale of a single stand, retention of living trees, in particular deciduous trees, and creation of dead wood on clearcuts is practiced in order to restore some of the structural and functional elements (Franklin et al. 1997, Gustafsson et al. 2012). Dead wood present before clearcutting is usually maintained and fresh dead wood is created by cutting of high-stumps and leaving some of the cut tree tops and branches. Also, prescribed burning of forest and clearcuts is being used in order to mimic natural fire-disturbance and favour fire-associated species (Toivanen and Kotiaho 2007, Vanha-Majamaa et al. 2007).

Even though the retention levels for dead wood in Fennoscandia are too low to fully mimic natural post-disturbance habitats (Gustafsson 2010), retained and created snags and logs provides sun-exposed substrate similar to that created by natural disturbances, improving the habitat for saproxylic species (Vanha-Majamaa and Jalonen 2001, Hyvärinen et al. 2009, Gustafsson et al. 2010). Retention thus improves structural diversity on stand level, and also

mitigates to some degree loss of forest species from clearcut stands (Rosenvald and Lõhmus 2008). On landscape level, however, planning conservation and ecosystem management is a challenge. How landscape context may affect diversity benefits of green tree and dead wood retention is largely unknown, as well as the importance of dead wood availability on different spatial scales (Sverdrup-Thygeson et al. 2014).

1.3.1 Clearcuts as early-successional habitats

In managed forest landscapes, clearcuts make up the predominant proportion of all early-successional habitats. Clearcuts differ from natural post-disturbance habitats in several substantial ways, and it is in the early-successional stage that the difference between natural and managed forests is the largest (Kouki et al. 2001). The amount and diversity of dead wood resources is relatively low on clearcuts, because there is little dead wood to retain from mature managed stands and limited amount is created at clearcutting. Fire-created habitats are rare and wildfire events are usually followed by salvage logging. Soil preparation and planting speeds up reforestation and shortens the time span when clearcuts can be used by early-successional species (Swanson et al. 2010), as dead wood becomes shaded when planted conifer stands reach about 10-20 years (Jonsson et al. 2006).

As natural early-successional habitats have become rare in managed forest landscapes, species specialised on these habitats occur mainly on clearcuts (Kaila 1997, Jonsson and Siitonen 2012b). Therefore, it is particularly important that conservation actions are directed at improving the quality of clearcuts for early-successional species. Especially, saproxylic species will benefit from actions oriented at increasing the amount and diversity of dead wood (Stokland et al. 2012). Considering that clearcutting is applied worldwide in boreal forests and has in Fennoscandia almost completely replaced natural forest disturbances, it is important to study characteristics of clearcut habitats and the species that live in these habitats.

2 Thesis aims

This thesis aims to increase our understanding of species diversity patterns and dynamics on clearcuts in boreal forest landscapes. For successful conservation of boreal forest species diversity, appropriate conservation-oriented management needs to be applied. In order to develop such management, we need to know which local and landscape characteristics are important for species diversity.

The specific questions addressed in each paper were:

I What are the habitat requirements of threatened, dead wood dependent beetle species on clearcuts, and how are their occupancy and colonisation-extinction patterns in the landscape influenced by habitat properties?

II Which local and landscape factors shape species diversity patterns of bees and wasps on clearcuts? Do species groups with different nesting or foraging preferences respond differently to habitat properties? Is the total regional diversity mainly due to high local diversity or high species turnover between sites or landscapes?

III Do clearcut characteristics and surrounding landscape affect species richness of saproxylic beetles with different habitat specialisation? Do the local and landscape effects interact, i.e., does the effect of local conditions differ depending on the landscape context?

IV How do sampling methods influence the obtained diversity estimates of bees and wasps and do different methods collect different species?

3 Methods

3.1 Study landscapes

All studies have been conducted on clearcuts in southern boreal forests in Sweden. The study area in paper I is located in the province of Hälsingland in central Sweden (Figure 1). It is about 300 km^2 forested landscape, dominated by managed stands of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), in mixture or monoculture, with some interspersed birch (*Betula pendula*, *B. pubescens*) and aspen (*Populus tremula*). Historically, forest fires have been common in the area and the forests have had a considerable component of deciduous trees; also, two wildfires have occurred during the last decade.

In papers II, III and IV, we used eight landscapes (approximately 100 km^2 each) dispersed throughout provinces of Dalarna and Gävleborg; the entire region covers about 30 000 km^2 (Figure 1). All landscapes were dominated by managed boreal forests, with the same tree species as in the study area in Hälsingland. The locations of landscapes and survey sites were chosen based on use of prescribed fire by the forest managers (Bergvik Skog AB and Sveaskog AB). We used 3-5 year old clearcuts, with or without prescribed fire. In each landscape, two burned and two unburned clearcuts were selected, separated by at least 500 metres. However, in some landscapes only one burned site was available, so an additional burned site was added in other landscape to create a more balanced design. The number of burned and unburned clearcuts surveyed was 15 and 17, respectively.
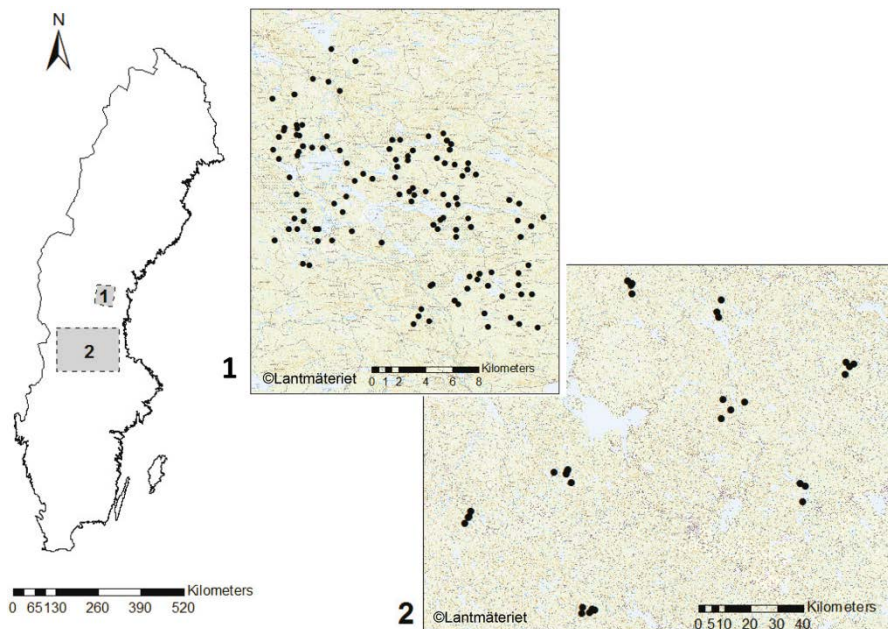
Figure 1. Location of study areas and study sites; 1= Hälsingland, paper I and 2= Dalarna and Gävleborg, papers II, III and IV.

3.2 Species surveys

For paper I, I surveyed occurrence of four saproxylic beetles (*Upis ceramboides, Platysoma minus, Rhagium mordax* and *Trichius fasciatus*) inhabiting dead birch wood (Figure 2). Within the study area, all 3-14 years old clearcut stands were located using forestry data register (Holmen Skog AB) and surveyed for beetle occurrence on two occasions, in 2004 (Wikars and Orrmalm 2005) and in 2010. During the repeated survey (2010), all clearcuts surveyed in 2004 were revisited, even if they had become older than 14 years. We surveyed 73 clearcuts in 2004 and 213 clearcuts in 2010.

Two of the species are considered habitat specialists on birch and are included in the Swedish red-list (*U. ceramboides* VU and *P. minus* NT), because their distributions are fragmented and currently shrinking (Gärdenfors 2010), and the remaining species are common and more generalistic. The collected data was presence/absence of each species in up to 20 logs per clearcut. The method used was peeling off approximately 0.25 m^2 of bark from birch logs and recording occurrence of larvae of *U. ceramboides, R. mordax* and *T. fasciatus*, and adults of *P. minus*.

Figure 2. A birch substrate (left) and study species in paper I – *Upis ceramboides* (top right) and *Platysoma minus* (bottom right). Photos: Diana Rubene and Thomas Ranius.

I used traps to survey bees and wasps (Hymenoptera: Aculeata) for papers II and IV, and saproxylic beetles for paper III. Three types of trap were used: pan traps, window traps and trap-nests (Figure 3). Window traps and pan traps collected bees, wasps and beetles, while trap-nests only collected bees and waps. The window traps were made of a Plexiglas plate (20 x 20 cm) with a rectangular plastic tray (3 l) attached beneath. The pan traps consisted of white plastic buckets (1.5 l) spray-painted with ultraviolet-bright white, yellow or blue paint (Spraycolor Leuchtfarbe, Germany). Trap-nests were made of 30 cm long bamboo sticks with a node in the middle, to allow colonization from both ends. The bamboo sticks were combined in bundles of 10, with similar proportions of three size classes: hole diameter 3-6 mm, 7-10 mm and 10-14 mm.

Three window traps and four trap-nests were set up on each clearcut, on the south-facing sides of snags at a height of 1.5 m. Six pan traps were set up in two groups of three (one of each colour). Each cluster was attached to a wooden pole at vegetation height, approximately 0.5 m above ground level. Pan and window traps were filled with a mix of propylene glycol and water.

Figure 3. A burned clearcut (top) sampled for papers II, III and IV, and the trap types used (from the left): a window trap, a trap-nest and a cluster of pan traps. Photos: Diana Rubene.

Insects were collected from the traps throughout summer 2011 and bees, wasps and beetles were extracted from the samples in the laboratory. Bees and wasps from trap-nests were reared indoors during winter. Species identification was done by taxonomy experts: Sven Hellqvist, Erik Sjödin (bees and wasps) and Olof Hedgren (beetles). Species were assigned to ecological groups based on available literature and expert knowledge. We studied the following groups of bees and wasps: ground nesters, dead wood nesters, pollinators, predators and parasites, and the following groups of saproxylic beetles: conifer wood specialists, deciduous wood specialists, fire-favoured species and flower visitors.

3.3 Habitat surveys

Habitat properties were measured on local and landscape level. For papers I – III, the amount of dead wood was estimated on local scale. In paper I only the amount of dead birch wood estimated, based on previous knowledge on habitat requirements of the studied species. The dead wood survey was done on entire clearcut areas. Properties of surveyed substrates were also recorded, such as size, decay stage, presence of fungi and contact with other objects. For papers II and III, total volume of standing and lying dead wood of all tree species was estimated, as species richness was studied. All dead wood objects were measured within an area surrounding traps with a 50 m buffer on each clearcut, average size (±S.D.) of 2.3 (±0.5) ha. We recorded if the surveyed clearcuts were burned or not in all surveys. Other local habitat properties measured were clearcut age (paper I), area (papers I – III) and flowering plant species richness (papers II and III).

   We measured several landscape components using ArcMap 10.1 (ArcGIS, ESRI, Redland, CA, USA). We were interested in estimating the amount of habitat for the studied species; therefore we included landscape components that we considered potentially important – e.g., open habitats for bees and wasps and habitats rich in dead wood for saproxylic beetles. In paper II, we assessed proportion of landscape area covered by i) early-successional habitats (clearcuts and burned forest combined) and ii) nature reserves, woodland key habitats (WKH) and forest with high volume of deciduous trees, which were combined to obtain a proxy for forest heterogeneity. Forest reserves, WKH and deciduous-rich forest were even used in paper III, as an estimate of dead wood rich habitats. We also estimated area of burned forest land (wildfires, prescribed and conservation fires combined) and average amount of dead wood on landscape level (SNFI data, 2012) in paper III.

   Landscape components were calculated in radii of 500m, 1000m and 2000 m (paper II), and 1000m, 2000m and 5000m (paper III). The studied scales for each species group were chosen based on which landscape scales have been found relevant for species response to habitat in other studies (e.g., Steffan-Dewenter et al. 2002, Götmark et al. 2011). We used data and GIS materials from forest managers (Bergvik Skog AB, Sveaskog AB), Swedish Civil Contingencies Agency, county boards (Dalarna and Gävleborg), Swedish Forest Agency and Swedish National Forest Inventory.

   We also used GIS to localise all clearcuts (Swedish Forest Agency data) within the study landscape and surrounding 2 km buffer area in paper I. The data on clearcut locations was then used to calculate connectivity of surveyed clearcuts.

3.4 Analyses

3.4.1 Mixed models

To investigate importance of habitat characteristics (predictor variables) on species richness and occurrence (response variables), we used generalised linear mixed models in R (R Core Team 2014). Mixed models allow controlling for dependence structure in the data through adding random structure to the models (Bunnefeld and Phillimore 2012). We controlled for non-independence of spatially grouped observations (within clearcuts or within landscapes). Depending on the characteristics of response variables, we used different methods. For species presence/absence (paper I) and proportion of collected species (paper IV), binomial error structure was used (R package *lme4* and *MASS*) (Bates et al. 2012) and for species richness we used Poisson or Gaussian errors (*lme4, nlme*) (Pinheiro et al. 2013). Model selection was based on Akaike´s Information Criterion (AIC, Akaike 1974) corrected for finite sample sizes (AICc) and models with lowest AICc were considered to provide best fit to the data.

3.4.2 NMDS

To analyse variation in species composition (papers II and IV), we used non-metric multidimensional scaling (NMDS) in the R package *vegan* (Oksanen et al. 2013). This is a non-linear method which only uses rank information, thus it can handle species response of any shape and find underlying environmental gradients. Association between community ordination and other variables (fire and landscape affinity in paper II and collection method in paper IV) were fitted to the ordination with *envfit* function, which estimates a test statistic (r^2) and uses random permutations of the data to assess its significance.

3.4.3 Diversity partitioning

In paper II, the total (gamma) diversity in the studied region was partitioned into its components alpha and beta using diversity partitioning in PARTITION 3.0 (Veech and Crist 2009). This method allows studying relative importance of local (alpha) diversity versus species turnover on different spatial scales (beta) (Lande 1996, Jost et al. 2010). We used additive richness method, which partitions number of species, with no sample weighing (equal weights given to rare and common species). A null distribution is produced by PARTITION, which represents diversity structure if all individuals were distributed randomly. The null distribution can be compared to observed diversity structure and significance of differences between observed and expected

distributions assesses by randomisation tests (Monte Carlo methods) (Crist et al. 2003, Partition 3.0 User's Manual, unpublished document).

3.4.4 Rarefaction and species richness estimates

To assess species richness (papers II and III) or density (paper IV), we used sample-based rarefaction in EstimateS 9.1.0 (Colwell 2013). In paper IV, increase in number of collected species with increasing sample size was studied in order to compare performance of different sampling methods. In papers II and III, rarefaction was used to evaluate sampling quality and estimate species richness. Since rarefaction showed that sampling was not sufficient to estimate species richness from observed data with extrapolation to recommended levels (Colwell et al. 2012), we calculated non-parametric richness estimators. EstimateS calculates several estimators: abundance-based (ACE, Chao2), incidence-based (ICE, Chao1), Jacknife, Bootstrap, and the choice of estimator can then be made based on e.g., its stability and variability (Hortal et al. 2006).

4   Results and Discussion

4.1   Dead wood and diversity

Characteristics of dead wood substrates were important for occurrence of two red-listed beetle species, *U. ceramboides* and *P. minus* (paper I), especially wood decay stage (Figure 4) and presence of white-rot wood decay fungi. Also, both species were more frequent in wood from intact dead birch trees, compared to cut stem fragments, branches or tops. Such wood may provide a more long-lived habitat to beetles, as different parts of the tree decay at different speed. Also, dead wood from intact trees was on average larger than other substrates (mean bark area 6.4 m^2 vs. 1.6 m^2), and large diameter trees are known to provide high-quality substrate to rare beetles (Similä et al. 2003). *Upis ceramboides* was more frequent in substrates which were aggregated within clearcuts, while *P. minus* was more frequent on clearcuts with high densities of aggregated wood. This indicates that spatially aggregated dead wood may be more beneficial to biodiversity than dispersed dead wood, which has also been suggested by Schiegg (2000). To provide suitable substrate for *U. ceramboides* and *P. minus*, groups of birches should be felled and left intact after clearcutting. Retention of live birch trees on clearcuts improves habitat availability for these species, as they supply substrate in the future.
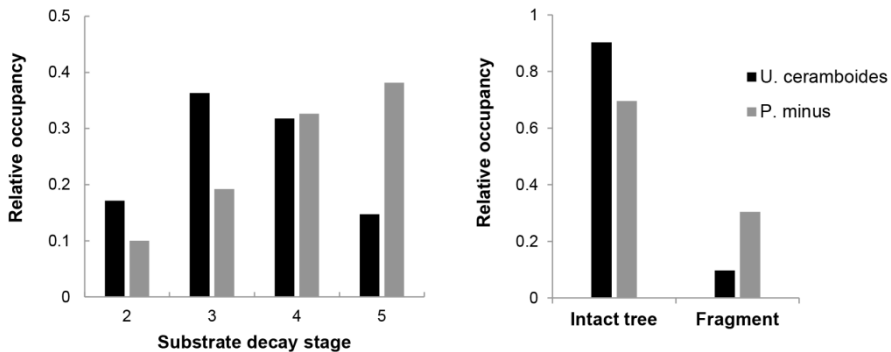
Figure 4. Occupancy of *Upis ceramboides* and *Platysoma minus* in substrates with different decay stage (left) and in intact dead trees vs. other substrates (right).

Amount of dead wood on local (clearcut) scale increased probability of individual species occurrence (paper I). Amount of dead wood represents amount of habitat for saproxylic species, and local species richness often responds positively to dead wood on clearcuts (McGeoch et al. 2007). Importance of habitat amount and quality for species persistence is well known, and it is usually more important than the spatial arrangement of habitat patches (Hodgson et al. 2011, Fahrig 2013). Accordingly, we also found that connectivity of clearcuts did not affect species occurrence or colonisation probability, while the amount of dead wood did (paper I, Figure 5). This is not surprising, as flying insects are mobile organisms, and studies of other saproxylic species have shown that they are good dispersers (Jonsson and Nordlander 2006). Species richness of bees and wasps was not affected by local amount of dead wood (paper II), while species richness of saproxylic beetles responded positively to dead wood amount (paper III). Higher species richness of all saproxylic beetles and fire-favoured species on dead wood rich clearcuts (paper III) indicates higher population persistence with higher habitat availability (Gaggiotti and Hanski 2004). Also, larger amount of dead wood likely includes higher diversity of dead wood characteristics and, consequently, habitat for more species.

Dead wood amount on landscape scale had a negative effect on saproxylic beetle richness (paper III). We had expected a positive effect, which would indicate more species on sites in high-quality landscapes, as has been observed for saproxylic beetles by Franc et al. (2007). Negative effects are more difficult to explain. It may be that in landscapes with high average dead wood amount, other habitats with more dead wood exist, which attract larger proportion of

dispersing individuals; therefore, clearcuts are colonised by fewer species. If, on the contrary, landscape quality is low, clearcuts may constitute relatively attractive habitats. The amount of dead wood rich habitats (reserves, WKH, deciduous-rich forest) in surrounding landscape had no effect on species richness of bees, wasps and most beetles. Two possible reasons for this are i) these habitats are rare in managed landscapes and constitute a too low proportion of the landscape to significantly affect species richness in the managed forest, and ii) these habitats mostly contain late-successional stages, while the majority of species found on clearcuts are associated with early-successional habitats.

4.2   Fire and diversity

In paper I, the studied beetle species were not more frequent in burned substrates or on burned clearcuts. This means that they do not require burned wood. The great majority of early-successional beetle species are dependent on high abundance and diversity of sun-exposed wood, but not on burned wood (Kaila et al. 1997, Johansson et al. 2007). Higher species richness of saproxylic beetles specialised on deciduous wood was found on burned sites, slightly lower richness of flower visitors, while no effect was found on other beetle groups (paper III). These results suggest that biodiversity benefits of prescribed fire on clearcuts are dependent on which species are studied and the effect of fire is overall weak. When burning clearcuts, compared to forest, less dead wood is created by fire and thus, the effect of fire on species diversity is probably smaller. Saproxylic beetles may benefit more if prescribed fire is used to create habitats that resemble more those created by natural fires, e.g. if forest patches or high retention level cuts are burned (Toivanen and Kotiaho 2007, Hyvärinen et al. 2009).

On landscape scale, proportion of burned forest land (both burned clearcuts and forest included) increased richness of all saproxylic beetles, conifer specialists and flower visitors, probably due to higher habitat diversity created by fire on landscape scale. Landscapes with large burned areas were often made up by mosaics of burned forest, burned clearcuts and unburned forest habitats. Our results indicate that such landscapes host high species diversity. Additionally, because of more dead wood in sun-exposed environments, population sizes of many species increase. Thus, higher number of individuals colonise clearcuts, which contributes to higher species richness.

Species richness of most groups of bees and wasps was not affected by fire, except a negative effect on predator species richness (paper II). Species composition of dead wood nesting bees and wasps differed significantly

between burned and unburned sites. Two species, a ground nesting predatory wasp (*Cerceris ruficornis,* Crabronidae) and a dead wood nesting bee (*Heriades truncorum,* Megachilidae) were found in rather high numbers (19 and 10 individuals, respectively) only in burned sites, which may indicate their association with burned habitats. Other studies have found that fire increases bee diversity (Campbell et al. 2007, Mateos et al. 2011), but the effects have often been confounded by other habitat properties, such as openness, more dead wood and higher flower richness of burned sites. Negative effects, probably due to direct mortality and nest site destruction, have also been reported (Winfree et al. 2009, Williams et al. 2010). Our results similarly suggest that some bee and wasp species may be positively and others negatively affected by fire. However, there does not seem to be any clear effect on diversity of this group; thus, fire as a conservation measure has probably limited value for promoting bee and wasp diversity on clearcuts.

4.3   Flowers and diversity

Species richness of most groups of bees, wasps and some beetles was positively affected by high flower richness on clearcuts (papers II and III). Flower resources were expected to be important for species that feed on nectar and pollen, as other studies have shown increase in bee richness on flower-rich sites (Potts et al. 2003). Some saproxylic beetles, in particular Cerambycidae, are also known to visit flowers (McDowell 2011). We found that flower richness was important factor for richness of other groups than pollinators (bees) and flower visitors (beetles), such as predatory wasps and deciduous specialist beetles. This could mean that flowering plants on clearcuts constitute an important resource for many Aculeates and saproxylic beetles, but it could also mean that flower richness is correlated with some unmeasured habitat properties which are important for species diversity, e.g. site productivity, moisture or high abundance of deciduous trees. It is probably difficult to promote flower species richness on clearcuts. However, clearcuts on sites that have historically been grasslands can have high flowering herb diversity, and have been shown to host grassland specialist butterfly species (Ibbe et al. 2011). Ensuring that such sites remain open longer, e.g. through delayed planting of conifers or allowing natural regeneration would likely benefit bees and wasps, and possibly even some beetle species.

4.4 Red-listed species

In this thesis, habitat requirements of three red-listed species were studied in detail. These were *U. ceramboides*, *P. minus* (paper I) and *Tragosoma depsarium* (paper III). *Upis ceramboides* and *P. minus* showed different patterns of habitat use, which indicates different levels of habitat specialisation: occurrence of *U. ceramboides* was limited to habitats of highest quality (clearcuts with largest dead wood amount), while *P. minus* appeared less demanding and occupied even clearcuts with relatively low dead wood amount (Figure 5). Because high quality habitats are very rare (Figure 5), these patterns may have implications for species persistence probability. *Upis ceramboides* faces a higher risk of extinction on landscape scale, unless amount of high quality habitats is increased. The observed changes in species occupancy over a six-year period (*U. ceramboides* decreased from 31 to 7 % occupied clearcuts, while *P. minus* increased from 32 to 60 %) are consistent with *U. ceramboides* being more specialised and thereby more threatened by habitat loss (Henle et al. 2004). Thus, these two red-listed species have variable capabilities to utilise dead wood on clearcuts and their conservation may require different approaches.
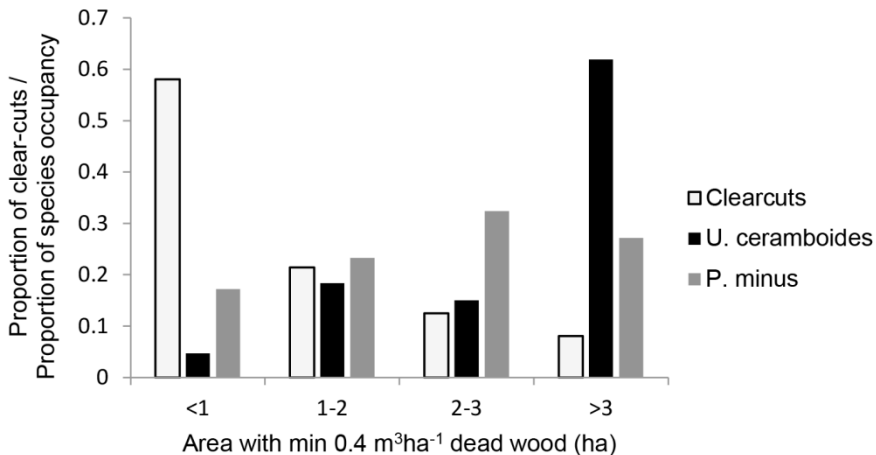

Figure 5. Amount of clearcuts with different dead wood amounts in the studied landscape (paper I) and relative occupancy of *U.ceramboides* and *P. minus*.

Tragosoma depsarium (Cerambycidae) is dependent on sun-exposed large pine logs, and is listed as vulnerable in the Swedish red-list (Gärdenfors 2010). Highest abundances of *T. depsarium* were found in landscapes with low proportion of burned area, despite that the species was more frequent on

burned than on unburned clearcuts (Figure 6). The species has limited occurrence area and probably small populations (Gärdenfors 2010, Anonymous 2014). In landscapes with much burned forest land, more high-quality habitats (burned forest patches) are available with large amounts of fresh dead wood. Thus, few individuals are spread out across large landscape areas, resulting in a dilution effect. This might last several years, until population sizes build up within the burned sites, as *T. depsarium* has a long generation time and can utilise the same substrate for several generations. The species was also favoured by a high dead wood amount on landscape scale and high flower richness. The latter is unexpected, as the species is not known to visit flowers for feeding (Ehnström and Holmer 2007). To improve conservation status of *T. depsarium*, improving landscape quality by using fire to create open habitats rich in dead wood is important.
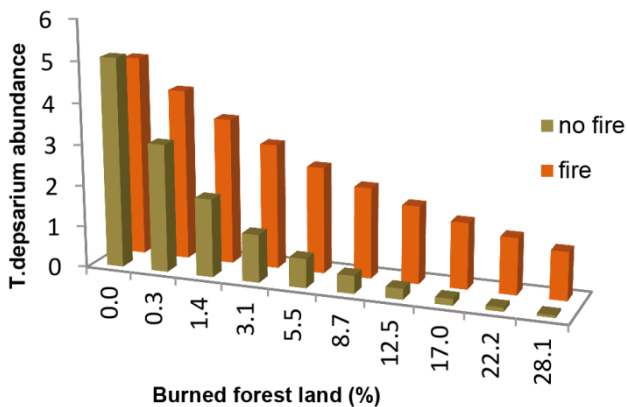

Figure 6. Interaction between abundance of T. depsarium (number of individuals per clearcut) on clearcuts with fire (n=15) or without fire (n=17) and burned forest land within 2 km radius. Data points were calculated from the final model, with variables not included in the interaction set to constant (mean) values. We used square-root transformed and centered values of burned forest land in the model. Values displayed on the x-axis have been recalculated back to landscape proportion in the raw data, to simplify interpretation.

In addition to the species studied in detail in papers I and III, we collected six red-listed saproxylic beetle species and two wasp species. The main threat to the red-listed beetle species is loss of habitat amount and quality, thus population decline is occurring or predicted to occur (Gärdenfors 2010). All species can be considered habitat specialists, as they depend on specific resources that are rare in managed forests. The beetle species require specific types of dead wood, e.g. large hollow trees (*Mycetochara obscura*), wood with high abundance of decay fungi (*Hallomenus axillaris*), sun-exposed large-size deciduous snags (*Necydalis major*) or dying spruce trees infested with bark-

beetles (*Corticeus suturalis*) (Anonymous 2014). The wasp species are also specialised to uncommon resources, the cleptoparasitic wasp, *Chrysis brevitarsis* (Chrysididae), is dependent on rare host species and the predatory wasp, *Dipogon vechti* (Pompilidae), inhabits sandy forest habitats (Anonymous 2014). It is important that suitable habitats (diverse dead wood characteristics) are created for red-listed species at clearcutting, and during other management stages, to improve their persistence probability in managed forests.

4.5 Landscape effects and regional diversity patterns

Composition of surrounding forest landscapes affected species richness of several studied species groups on clearcuts (papers II and III). For bees and wasps, a high proportion of early-successional habitats (clearcuts and burned forest land combined) in the landscape was positive, specifically for ground nesting species (paper II). Also, higher species richness was found in larger clearcut patches. This is in accordance with other studies which have found that most bees and wasps prefer open habitats (New 2012), however some species are associated with mature forest (Winfree et al. 2007). As discussed above, saproxylic beetle richness was affected by burned forest land and amount of dead wood in surrounding landscape (paper III). Thus, we observed somewhat different effects of surrounding landscape on beetles and hymenopterans, but for both, landscape composition turned out to be at least as important in shaping diversity patterns as local habitat properties.

Interactions between landscape and local factors were studied in paper III, but only one significant interaction was found, between local prescribed fire and burned landscape area (positive for abundance of *T. depsarium*). Importance of landscape context for effectiveness of local conservation management is documented in agricultural landscapes (Tscharntke et al. 2012), but rarely studied in forest landscapes. Indications that landscape history affects success of local restoration of habitats for fire-dependent species have been found by Kouki et al. (2012). Results from this thesis suggest that larger variation in landscape properties may be necessary in order to observe interactions. In managed forest landscapes, such effects may be too weak to observe, due to high habitat homogeneity on landscape scale. Thus, in such landscapes, it may not be necessary to consider landscape composition when planning conservation actions on local scale.

Patterns of bee and wasp species diversity in the region were mainly determined by high beta diversity (species turnover between clearcuts or landscapes), while alpha diversity (species per clearcut) made up a relatively

small proportion of regional gamma diversity (paper II, Figure 7). The largest proportion of diversity was species turnover between landscapes, and species composition confirmed that species communities are geographically structured in the region. Other studies have also found higher than expected beta diversity on large spatial scale (Murray et al. 2011, Clough et al. 2007). There may be different species pools between different landscapes, shaped by environmental gradients and historical management. Even though the current managed forest landscapes are apparently homogeneous, effects of their varying land use history may be retained in species communities. This means that conservation efforts need to be applied in several areas throughout the region, in order to protect the entire regional diversity.
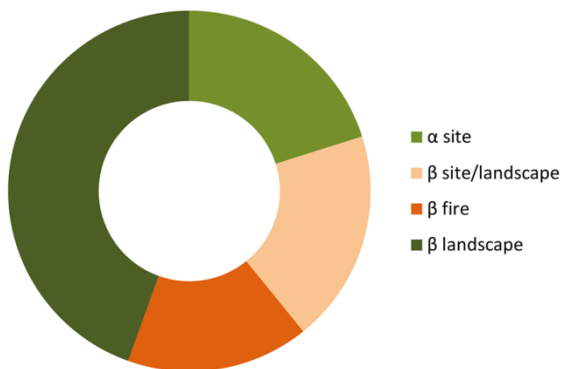

Figure 7. Proportion of the regional bee and wasp diversity contained in the local alpha diversity, and in the different levels of beta diversity: species turnover between sites within same landscape, between burned and unburned sites and between landscapes.

4.6 Sampling effects

We found that when collecting bees and wasps on clearcuts for estimating diversity, the trapping method is important (paper IV). Dead wood associated species (bees and wasps) were most efficiently collected with window traps attached to snags; while pollinators (i.e. bees) were mainly collected with coloured pan traps (Figure 8). Trap-nests collected fewest species and no unique species; nevertheless some species were strongly associated with trap-nests. Combinations of different trap types collected similar number of species as single type pan or window traps on regional scale, yet there were differences in species composition captured by each trap type. Thus, combining several trap types is probably better if the goal is to sample as many species as possible from the regional pool. Many species were collected throughout the sampling season (from 1st of June to 22nd of August) and we estimated that a sampling period of 5-6 weeks would sample approximately 70-80 % of the species from the full season. Evaluation of bee sampling methods has been done in agricultural habitats (Westphal et al. 2008) and Mediterranean shrub habitats

(Nielsen et al. 2011), with conclusion that pan traps were the most efficient and recommended method. We have showed that, in forest habitats, window traps are an at least as efficient method, which is especially suitable if dead wood associated species are of interest.
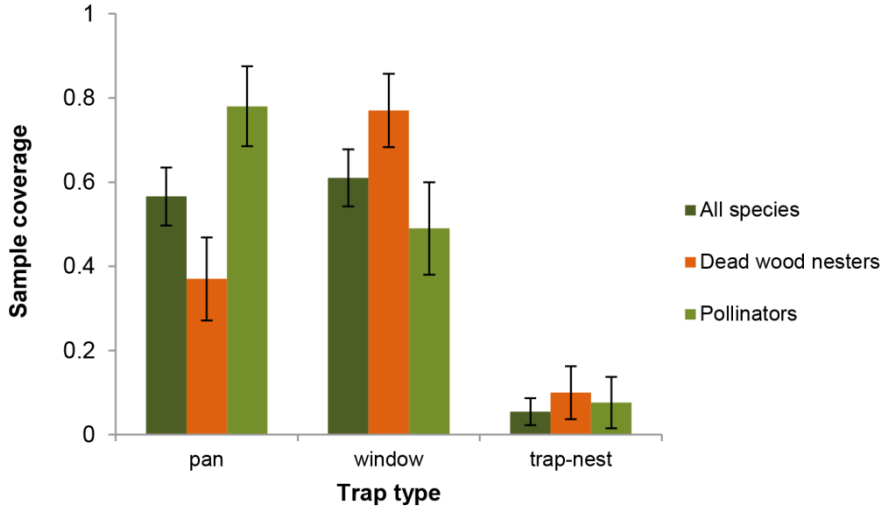

Figure 8. Sample coverage (proportion of collected species per site) of the trap types studied in paper IV for all bee and wasp species, dead wood nesters and pollinators.

5   Conclusions and implications for conservation

In this thesis, I have studied insect diversity patterns and dynamics on clearcuts in managed boreal forests. Specifically, I have aimed to evaluate the importance of resources created during conservation efforts in managed forest for species diversity. The main conclusions and answers to the questions posed in thesis aims are as follows:

I   Habitat quality is important for occurrence of red-listed species on clearcuts, especially the amount of dead wood with suitable characteristics. Species differ in their ability to utilise resources in managed forest landscapes. Specialised species require habitats of high quality, thus conservation planning on landscape level is needed for their preservation.

II Diversity of bees and wasps on clearcuts is increased by high flower richness, large clearcut areas and high proportion of early-successional habitats in the landscape. Species composition differs between landscapes, and regional diversity is predominantly made up by species turnover between different sites and landscapes (beta diversity), while local diversity on each site (alpha diversity) is relatively low.

III Species richness of saproxylic beetles on clearcuts is affected by both local and landscape factors. Dead wood amount on local scale and amount of burned forest land in the landscape are among the most important factors increasing species richness. Effect of prescribed fire on local scale depends on landscape amount of burned habitat for abundance of a red-listed species.

IV Sampling method affects to a high degree which species and how many species of bees and wasps are collected. Window traps are most efficient for collecting dead wood nesting species, while pan traps are most efficient for bee pollinators. A sampling period of four to five weeks during the summer is probably sufficient for obtaining good diversity estimates.

The findings of this thesis indicate that the best way to promote species diversity on clearcuts in managed boreal forest landscapes is to increase habitat characteristics typical for natural early-successional habits. These are large amount and diversity of dead wood, in particular deciduous wood, flower richness, habitat openness and occurrence of fire on local and landscape scale. To ensure sufficient supply of dead wood habitat for saproxylic species, it is necessary to create more dead wood at clearcutting, prevent damage to dead wood caused during forestry operations, and retain trees which will provide substrate in the future. For species associated with early-successional habitats, maintaining habitat openness on clearcuts is important for two reasons: it keeps the dead wood sun-exposed for longer, which is required for species using decayed wood in open habitats, and promotes flowering plant diversity, which benefits mainly bee and wasp species. The open habitat stage could be prolonged by delayed planting of conifers or by allowing natural regeneration on parts of some clearcuts, e.g. surrounding aggregations of dead wood. Using prescribed fire only on clearcuts probably has limited value to biodiversity. However, burning larger areas including clearcuts and patches of forest on landscape scale creates high habitat diversity and large amounts of sun-exposed dead wood, which has positive effect on species diversity. Within current levels of conservation efforts applied in managed forests in Sweden, habitat of high quality cannot be created on all clearcuts. Therefore, it is probably more efficient to modify current conservation management, and focus efforts towards promoting biodiversity on the landscape scale, instead of the local scale. This could be done by prioritising some clearcuts in each landscape with high potential for conservation of early-successional species (e.g., high pre-existing dead wood or tree species diversity, rich flora, proximity to occurrence of threatened species) and concentrating higher levels of conservation efforts there. By such approach, high-quality habitats can be created, which can support specialist species to a larger degree in managed forest landscapes.

6 Acknowledgements

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