From dead trees to landscapes

The role of multifunctional forests in supporting deadwood-dependent biodiversity

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SWEDISH UNIVERSITY
OF AGRICULTURAL
SCIENCES

DOCTORAL THESIS
Umeå 2025

Acta Universitatis Agriculturae Sueciae
2025:33

Cover: Illustration of an ecopark
(Painted by Desirée Guidobaldi Stenbacka)

ISSN 1652-6880
ISBN (print version) 978-91-8046-468-0
ISBN (electronic version) 978-91-8046-518-2
https://doi.org/10.54612/a.7t8tbj18sq

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Print: Original Tryckeri, Umeå 2025

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Abstract

Forests provide critical habitat for a vast number of organisms, including species that rely on deadwood. This thesis investigates the capacity of multifunctional forest landscapes in Sweden, so-called ecoparks, to sustain deadwood-dependent biodiversity compared to conventional production forests. Focusing on saproxylic beetles and wood-inhabiting fungi, I explore how habitat characteristics from the microhabitat to the landscape scale relate to species richness, functional diversity, and community composition. Across nine landscapes in the boreal and boreonemoral zones, I used artificially created high stumps of pine, birch, and aspen to sample saproxylic beetles and eDNA of wood-inhabiting fungi. Combined with field measurements of habitat structures, I analysed diversity and community patterns in relation to deadwood availability, forest types, and high conservation value forests. The results show that ecoparks generally maintain higher structural habitat quality, greater volumes and diversity of deadwood, and more extensive areas of high conservation value forests. These features translate into significantly higher taxonomic and functional diversity of saproxylic beetles, especially red-listed species, with the ecopark Hornsö, known as a hotspot for saproxylic beetles, standing out as a strong driver of these patterns. Both beetles and fungi responded to environmental variables across spatial scales, with local deadwood characteristics, forest composition, and surrounding high conservation value forest all influencing diversity and community structure. The findings underscore the importance of incorporating multi-scale habitat considerations into forest conservation and management.

Keywords: Saproxylic biodiversity, functional traits, community composition, multifunctional forest landscapes, deadwood, conservation, forest management

Från döda träd till levande landskap. Multifunktionella skogars betydelse för dödvedsberoende organismer

Sammanfattning

Skogar utgör livsmiljö för en stor mängd organismer, däribland arter som är beroende av död ved. I denna avhandling undersöks hur väl svenska multifunktionella skogslandskap, så kallade ekoparker, kan bevara vedlevande biologisk mångfald i jämförelse med konventionellt brukade produktionsskogar. Fokus ligger på saproxyla (vedlevande) skalbaggar och vedlevande svampar, och hur habitatkaraktärer från mikrohabitat- till landskapsskala påverkar artrikedom, funktionell mångfald och samhällsstrukturer. I nio landskap i den boreala och boreonemorala zonen användes artificiellt skapade högstubbar av tall, björk och asp för att samla in skalbaggar och eDNA från vedlevande svampar. Tillsammans med fältdata av habitatstrukturer analyserades mönster i mångfald och samhällen i relation till tillgång på död ved, olika skogstyper och förekomst av skogar med höga naturvärden. Resultaten visar att ekoparker generellt har högre strukturell habitatkvalitet, större volym och mångfald av död ved samt mer sammanhängande arealer av skogar med höga naturvärden. Dessa egenskaper hänger samman med en signifikant högre taxonomisk och funktionell mångfald av saproxyla skalbaggar, särskilt rödlistade arter, där ekoparken Hornsö, känd som ett centrum för saproxyla skalbaggar, var en stark drivkraft bakom dessa mönster. Både skalbaggar och svampar svarade på miljövariabler på flera skalor, där lokala dödvedsegenskaper, skogssammansättning och mängden skyddsvärd skog i omgivningen påverkade mångfald och samhällsstruktur. Resultaten betonar vikten av att inkludera ett landskapsperspektiv i skoglig naturvård och förvaltning.

Nyckelord: Vedlevande biodiversitet, funktionell diversitet, samhällen, naturvård, multifunktionella landskap, död ve

Dedication

Till mina fina pojkar Holger och Ivar – må ni växa upp med jord under naglarna, tallbarr i håret och ett hjärta som klappar för skogen och alla dess varelser.

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. Larsson, Ekström, A., Bergmark, P. & Hekkala, A-M. (2021). Can multifunctional forest landscapes sustain a high diversity of saproxylic beetles? Forest Ecology and Management, vol (490), https://doi.org/10.1016/j.foreco.2021.119107

II. Bergmark, P., Hjältén, J., Svensson, J., Neumann, W. & Hekkala, A-M. (2024). Trait-environment interactions of saproxylic beetles as a guide to biodiversity conservation strategies. Journal of Environmental Management, vol (360), https://doi.org/10.1016/j.jenvman.2024.121080

III. Bergmark, P., Dahlberg, A., Hjältén, J., Svensson, J., Neumann, W. & Hekkala, A-M. (2025). Fungal diversity in artificially created deadwood – The interplay between substrate type and landscape composition (manuscript)

IV. Bergmark, P., Larsson, Ekström, A. Hjältén, J. & Hekkala, A-M. (2025). Deadwood drives community structure, while multifunctionality boosts the diversity of longhorn beetles. (Manuscript)

Paper I and II are reproduced with the permission of the publisher or published open access.

The contribution of Paulina Bergmark to the papers included in this thesis was as follows:

I. Co-author. Performed data collection and co-writer of manuscript. Collaborated with main author on idea and analyses.

II. Main author. Performed environmental data collection. Designed the study question, performed the analyses and wrote the manuscript with contribution from co-authors.

III. Main author. Collected environmental data. Designed the study question, performed the analyses and wrote the manuscript with contribution from co-authors.

IV. Main author. Performed environmental data collection. Designed the study question, performed the analyses together with co-authors and wrote the manuscript with contribution from co-authors.

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Abbreviations

BAU	Business as usual
ECO	Ecopark
GLM	Generalized liner mixed effect models
HAH	Habitat amount hypothesis
HCVF	High conservation value forests
HHH	Habitat heterogeneity hypothesis
LMM	Linear mixed effect models
NMDS	Non metric multidimensional scaling
PROD	Production landscape

Photo: Paulina Bergmark

1. Introduction

1.1 The diminishing natural boreal forests

Boreal forests, covering vast areas of the Northern hemisphere, form one of the largest terrestrial biomes on our planet and play a crucial role in maintaining biodiversity (Kayes and Mallik, 2020; Kuuluvainen, 2009), carbon storage (Pan et al., 2011) and ecosystem stability (Bonan, 2008). Historically shaped by natural disturbances such as fire (Niklasson and Granström, 2000), storms and insect outbreaks, these dynamic forest landscapes support a high diversity of species, including many that depend on deadwood and late-successional forest structures.

In Fennoscandia, i.e., the Scandinavian peninsula, Finland, and western part of Russia, the total forested area amounts to >50 million ha of which approximately 47% is situated in Sweden (Esseen et al., 1997). However, over the past century, the expansion of industrial forestry has significantly altered boreal landscapes, leading to the fragmentation and degradation of natural forests (Puettmann et al., 2012). Globally, the decline of natural boreal forests is considered the second most significant forest loss after tropical forest deforestation (Hansen et al., 2013).

The forest landscape in Sweden has changed dramatically during the last 150 years. Before the mid-1900s, Swedish forests were a mosaic of old-growth stands, selectively logged areas, and naturally regenerated forests (Östlund et al., 1997). With the rise of industrial forestry in the mid-20th century, Swedish forest management underwent a dramatic transformation. Clear-cutting, plantation forestry, and the systematic replacement of diverse, uneven-aged forests with monocultures of predominantly coniferous tree species, such as Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), became the dominant management strategy (Linder and Östlund, 1998). This shift was driven by economic incentives to maximize timber yield and efficiency, but with profound negative consequences for forest dwelling species (Felton et al., 2020).

1.2 The crossroad of forest management and biodiversity conservation

As awareness of biodiversity loss and environmental concerns grew in the late 1980s (Jonsson et al., 2019) following the "Our Common Future" report (World Commission on Environmental and Development, 1987), Sweden has taken steps to integrate conservation into forest management. In the early 1990s, the Swedish Forestry Act was revised, shifting its focus from purely production-oriented goals to a dual mandate that emphasized both timber production and environmental considerations (Nylund, 2009). Simultaneously, detailed regulations were removed and a general liberalization and simplification moved the operational mandate closer to forest owners and forestry actors (Enander, 2007). Recognizing environmental conservation as equally important as economic forestry interests marked a significant policy change. Since then, policies promoting set-aside areas, retention forestry, and voluntary conservation measures have been implemented (Gustafsson and Perhans, 2010). During more recent years Sweden has also committed to several policy frameworks aimed at strengthening biodiversity conservation. Nationally, Swedish forest and environmental policies aim to ensure the long-term viability of all naturally occurring species (Angelstam et al., 2011). At the EU level, Sweden has ratified key biodiversity policies, including the EU Biodiversity Strategy for 2030 (European Commission, 2020) and the Green Infrastructure (GI) Strategy, which focus on preserving and restoring natural and semi-natural landscapes to enhance ecological connectivity. Internationally Sweden has signed the Kunming-Montreal Global Biodiversity Framework (CBD, 2022) aligning with the Aichi Biodiversity Targets, including Target #5 , which states that "By 2020, the rate of loss of all natural habitats, including forests, is at least halved and where feasible brought close to zero, and degradation and fragmentation is significantly reduced" (United Nations, 2020). Other relevant targets regarding forest ecosystems include Aichi Target #7 which emphasizes the importance of sustainable forest management in the landscapes surrounding protected areas, with measures such as tree retention helping to maintain biodiversity in managed forests (Angelstam et al., 2020). Target #11 calls for at least 17% of terrestrial ecosystems to be safeguarded through a well-connected and effectively managed network of protected areas and Target #15 calls for restoration of at least 15 percent of degraded ecosystems. Recently, June 2024, the European Commission ratified the EU Nature Restoration Law (European Commission, 2025) which now is a law in Sweden and other member countries. This law further sets requirements of restoration and protection both within Natura 2000 Annex 1 habitats and in forests in general (Svensson & Jonsson 2025).

However, despite implemented policies regarding the protection of habitat and associated biodiversity, the decline of forest biodiversity continues, raising concerns about whether current approaches are sufficient to halt species losses (Eide et al., 2020). Thirty years after a forestry act with the intention to equally support environmental aspects, the Swedish forest governance and management model has resulted in a national failure to meet international, EU and national environmental goals (Angelstam et al., 2020; Swedish Forest Agency, 2023). The challenge remains on how to balance timber production with biodiversity conservation and other values, interests and rights associated with forests and forest landscapes (Lindahl et al., 2017) in a way that maintains ecological functions while meeting commercial forestry demands.

Sweden's forests are thus at a crossroad. The path forward will determine whether biodiversity loss continues or whether more sustainable and multifunctional management strategies can support both ecological and economical goals. This need for change is reflected in recent legislative efforts at the European level, such as the above mentioned EU Restoration Law (European Commission, 2025), which mandates large-scale ecosystem restoration to combat further biodiversity decline and reduction or loss of biodiversity services. How these policies will be implemented in Sweden remains uncertain, but they highlight the urgency of rethinking forest management practices and how to include effective conservation measures within the managed forests.

1.3 Ecoparks - Multifunctional forest landscapes

To implement policies and strategies regarding biodiversity conservation the state-owned forestry company Sveaskog pioneered with the concept of ecoparks in the early 2000s, introducing a model where conservation efforts are embedded within managed forests (Angelstam and Bergman, 2004). By designating large-scale areas where at least 50% of the land is dedicated to nature conservation, ecoparks seek to balance timber production with habitat protection, deadwood retention, and restoration of natural forest dynamics (Bergman and Gustafsson, 2020). These multifunctional forest landscapes represent an effort to move beyond conventional forestry and towards a more holistic approach to forest stewardship, in which biodiversity, recreation, and ecosystem services are integrated into forest management planning. There are today 37 ecoparks strategically distributed across Sweden, from the northern boreal regions to the southern boreonemoral zones. The spatial arrangement of ecoparks ensures to capture the diversity of different type of forest landscapes. Once the ecoparks were established, a landscape analysis was conducted to identify core areas with high conservation value forests and determine the specific forest types associated with these values, e.g., broadleaf-rich areas or old coniferous stands. Based on this analysis, a strategic plan was developed for each ecopark, outlining where and what types of restoration measures should be implemented. Additionally, forestry practices were designed to enhance connectivity between these high conservation value areas, with the long-term goal of creating a more ecologically cohesive landscape. Each ecopark operates under its own management plan, ensuring that conservation and forestry activities are adapted to the specific ecological conditions and objectives of the site.

1.4 Life in dead trees

Deadwood is an essential structural component of forest ecosystems, providing habitat for a diverse array of saproxylic organisms, species that rely on deadwood for at least part of their life cycle (Speight, 1989). Saproxylic organisms include a vast array of insects, fungi, bacteria, lichens, bryophytes, and vertebrates, each contributing to the wood decomposition, nutrient cycling, and structural complexity of deadwood. By breaking down complex organic matter, these organisms contribute to forest regeneration and soil enrichment, reinforcing ecosystem stability and resilience (Parisi et al., 2018; Stokland et al., 2012).

The availability of deadwood in natural boreal forests varies widely depending on forest type, disturbance history and regional conditions, with the highest amounts in late-seral and post-disturbance forests (Siitonen, 2001; Stokland et al., 2012). Different forms of deadwood, ranging from standing snags to fallen logs and buried woody debris, offer diverse ecological niches, allowing a broad spectrum of species to persist. The characteristics of deadwood, such as tree species, decay stage, size and moisture content, determine which organisms can colonize and utilize it (Hägglund and Hjältén, 2018). Recently dead trees with intact bark attract species like bark beetles (Lee et al., 2014), while highly decomposed logs provide habitat for fungi, mosses and detritivorous invertebrates. Environmental factors such as temperature, humidity and light exposure further shape deadwood associated communities (Kriegel et al., 2023; Seibold et al., 2016). This structural and compositional heterogeneity makes deadwood a key resource in boreal forests, sustaining a complex network of interactions across multiple trophic levels, from decomposers to predators and cavity-nesting species. However, the amount of deadwood in production forests is significantly lower compared to old-growth natural forests. Estimates suggest that production forests retain only 10–15% of the deadwood found in natural forests in Northern Europe (Siitonen, 2001), resulting in a considerable loss of habitat for saproxylic species. As a consequence, saproxylic species belong to one of the most threatened organism groups. (Stokland et al., 2012).

In this thesis, I focus on two major groups of deadwood-dependent organisms: saproxylic beetles and wood-inhabiting fungi. These two organism groups represent a large share of the biodiversity linked to deadwood in boreal forests and play essential and complementary roles in wood decomposition and ecosystem functioning (Boddy et al., 2007; Gimmel and Ferro, 2018; Lonsdale et al., 2008). Together, they form the core of the saproxylic community, with fungi initiating the breakdown of lignin and cellulose, and many beetle species further fragmenting the wood, dispersing fungal spores, and creating cavities that serve as microhabitats for other organisms (Löfroth et al., 2023).

Saproxylic beetles is an exceptionally diverse group, with over 1400 species documented in Northern Europe alone, many of which are tightly specialized to particular deadwood conditions, such as decay stage, tree species, or moisture level (Gimmel and Ferro, 2018; Stokland et al., 2012). These beetles occupy various ecological roles, including cambivores, wood borers, fungivores, predators, and detritivores. Their diversity reflects the temporal and structural heterogeneity of deadwood habitats, and their presence can indicate the quality and continuity of forest habitats (Wetherbee et al., 2023). Some species are highly sensitive to forest fragmentation and intensive management, making them important indicators of forest biodiversity and ecological integrity (Nieto and Alexander, 2010).

Wood-inhabiting fungi, particularly polypores and other Basidiomycota, are the primary agents of wood decomposition and play a fundamental role in deadwood dynamics (Dahlberg and Stokland, 2004; Stokland et al., 2012). They vary greatly in their enzymatic abilities, decay strategies (white rot, brown rot, or soft rot), and substrate preferences. Many species are host-tree or substrate-specific, depending on factors like wood diameter, decay stage, and microclimate (Nordén et al., 2013). Fungal communities are also shaped by succession, where early colonizers may alter the substrate in ways that facilitate or inhibit subsequent species, leading to complex and dynamic assemblages over time (Baldrian, 2017). Recent advances in molecular methods, such as DNA metabarcoding, have revealed that the diversity of wood-inhabiting fungi is vastly underestimated, with many species being cryptic or poorly known (Johannesson and Stenlid, 1999; Kubartová et al., 2012). These findings highlight the importance of preserving a wide variety of deadwood substrates to support both known and yet-undescribed fungal species.

1.5 Drivers of biodiversity patterns

Biodiversity is shaped by a complex interplay of ecological, environmental, and evolutionary factors operating at multiple spatial scales. From local habitat conditions to landscape-level processes, a variety of factors influence species richness, community composition, and ecosystem stability. Two key hypotheses, the Habitat Amount Hypothesis (HAH) and the Habitat Heterogeneity Hypothesis (HHH), provide predictions how these factors drive biodiversity patterns. The HAH predicts that species richness and abundance increase with the amount of a given habitat irrespective of its configuration in a local landscape (Fahrig, 2013). In the context of saproxylic species this means that by increasing the amount of deadwood, by retaining more snags, logs, and high stumps, should directly support larger populations and reduce the risk of species extinctions . Positive correlations between the amount of deadwood and species richness has especially been shown in studies of boreal forest systems (Gao et al., 2015; Lassauce et al., 2011). The HHH on the other hand argues that greater structural and compositional diversity within a habitat promotes higher species richness by providing a wider range of ecological niches (Whittaker, 1972). For saproxylic species, this means that not only the total volume of deadwood but also its diversity in tree species, decay stages, size classes, and microhabitats influence community composition and species coexistence (Seibold et al., 2016).

Understanding these determinants is crucial for effective biodiversity conservation, particularly in managed landscapes where human activities alter natural habitats. However, distinguishing between the effects of habitat amount and habitat heterogeneity can be challenging, as these two factors are often correlated (Seibold and Thorn, 2018). Landscapes with higher habitat amounts also tend to be more structurally diverse, making it difficult to isolate their individual contributions to biodiversity. However, both hypotheses provide valuable insights for conservation planning by highlighting the importance of maintaining sufficient habitat area and structural diversity in forested ecosystems (Müller and Bütler, 2010).

1.6 Species diversity and traits: understanding community structure for conservation

To effectively understand biodiversity patterns and guide conservation efforts, it is essential to consider species diversity at multiple spatial scales, i.e., considering α, β and γ diversity (Whittaker, 1960). α diversity reflects local species richness and provides insight into how individual habitat patches support biodiversity. It is influenced by local environmental conditions such as resource availability, microhabitat diversity, and disturbance dynamics. β diversity captures variation in species composition between sites and helps identify the extent of community turnover i.e., species replacement across different substrates, habitats, or management regimes. This component is key to understanding landscape-scale biodiversity and the complementary role of different habitats. γ diversity represents the total regional species richness, shaped by both within-site diversity and among-site differences. It provides an overall measure of conservation value at the landscape or ecosystem level (Ferenčík et al., 2024).

In addition to these diversity measures, integrating species traits—such as feeding guilds, habitat specialization, dispersal ability, and life history traits, allows for a functional perspective on community assembly (Cadotte et al., 2011). Trait-based approaches reveal how organisms respond to environmental gradients and disturbance, and how ecosystem functions may be affected by changes in species composition (Wardle et al., 2011).

Together, these dimensions of biodiversity provide a more complete understanding of community structure and ecosystem functioning. By identifying which habitats support the highest diversity, which traits are filtered by environmental conditions, and how species are distributed across landscapes, we can develop more targeted and efficient conservation strategies.

1.7 Knowledge gaps

Despite decades of research on saproxylic organisms, many knowledge gaps remain, particularly regarding the drivers of diversity and community composition in managed vs. specially designed forest landscapes such as ecoparks. One key limitation in current research is the focus on stand-level comparisons (e.g., nature reserves vs. production forests), often neglecting the landscape context (Sverdrup-Thygeson et al., 2014a). In particular, little is known about how well multifunctional forest landscapes function as biodiversity-supporting systems relative to production-dominated landscapes that typically lack large-scale conservation planning. Adding complexity, recent advances such as trait-based approaches have revealed that different functional groups and life-history strategies (e.g., feeding guilds, decay-stage preferences, wood-type specializations) may respond differently to environmental variables at both the local and landscape scale (Bergmark et al., 2024; Drag et al., 2022; Murray et al., 2017). However, comprehensive studies explicitly linking trait–environment relationships for saproxylic beetles to forest structural characteristics, such as deadwood composition, surrounding forest types, and forest age distributions, remain rare, but see e.g., Johansson et al. (2007a and 2007b) . Our largest knowledge gap is, however, tied to wood-inhabiting fungi, due to the cryptic nature of many species. Traditional survey methods using fruiting bodies often underestimate fungal richness (Rayner and Boddy, 1988), but recent eDNA sampling of deadwood and metabarcoding studies have revealed an unexpectedly high diversity (Rieker et al., 2024), suggesting that much of the fungal biodiversity in deadwood remains undescribed or poorly understood. How this hidden diversity responds to forest structures and management regimes is largely unknown.

Photo: Paulina Bergmark

2. Objectives of this study

The overarching objective of this thesis is to evaluate the role of multifunctional forest landscapes in supporting deadwood-dependent biodiversity by examining how habitat characteristics at different spatial scales, from individual dead trees to landscapes, influence the diversity and distribution of saproxylic beetles and wood-inhabiting fungi in artificially created snags. Specifically, this thesis aims to:

- Evaluate whether habitat structures, both at the local scale (e.g., deadwood amount and diversity) and at the landscape scale (e.g., forest composition and presence of high conservation value forests), differ between ecoparks and production landscapes

- Asses if multifunctional forest landscapes support a higher taxonomic and functional diversity of saproxylic beetles than production forest landscapes.

- Examine how habitat characteristics at different spatial scales influence saproxylic beetle and fungal species richness and community composition, considering factors ranging from microhabitat characteristics (e.g., deadwood type, decay stage) to landscape-scale configuration.

- Provide insights into how conservation strategies in managed forests can be improved to better support deadwood-dependent species under current forestry and policy frameworks.

These overarching aims are addressed through specific research questions and hypotheses explored in each of the four papers comprising this thesis:

Saproxylic beetle diversity in multifunctional vs. production-oriented forest landscapes

By comparing different forest management regimes, I hypothesize that the taxonomic diversity of saproxylic beetles, particularly red-listed species, is higher in ecoparks than in production-oriented forest landscapes, and that these landscapes support distinct beetle community compositions (Paper I and IV). Furthermore, given the expected increase in species richness and habitat heterogeneity in ecoparks, I also hypothesize that the functional diversity of saproxylic beetles is higher in ecoparks compared to production-oriented landscapes (Paper IV).

Effects of local deadwood properties and landscape composition on saproxylic beetles and wood-inhabiting fungi

To understand the environmental drivers of saproxylic biodiversity, I examine how saproxylic beetles respond to local deadwood characteristics, such as volume and diversity (Papers I, II, and IV) as well as landscape composition (Paper II, III and IV). I hypothesize that both increased deadwood volume and diversity as well as the amount of high conservation value forests (HCVF) will translate into increased beetle species richness. I further explore how ecological traits of saproxylic beetles are associated with specific deadwood types and the composition and structure of surrounding forest landscapes (Papers II and IV).

In addition, I assess the relative importance of local microscale factors versus landscape-scale forest structures in shaping communities of wood-inhabiting fungi. Specifically, I ask whether fungal community composition is more strongly influenced by substrate-level features (e.g., tree species, high stump diameter, decay stage) or by the amount (HCVF) in the surrounding landscape, assessed at multiple spatial scales (Paper III).

3. Method

3.1 Study area

A total of nine large forest landscapes have been included in this thesis, spanning across Sweden, covering the middle, southern and boreonemoral vegetation zones (Roberge et al., 2020). Of these, five are ecoparks i.e., multifunctional forest landscapes while four are conventional production landscapes (Table 1). Each ecopark is paired with a nearby production landscape ensuring similarities in forest types and topography, allowing for meaningful comparisons of biodiversity patterns between different management approaches. My paired landscapes (ecopark – production landscape) are thus, starting from the south Hornsö (eco) – Hälleskog (prod), Färna (eco) – Fagersta (prod), Käringberget (eco) – Vindeln (prod) and Rosfors (eco) – Kloken (prod). Ecopark Hornslandet lacks a corresponding production landscape due to challenges in identifying a production forest landscape with comparable forest types and structural characteristics. Each ecopark possesses distinct ecological and structural features, shaped by variations in forest composition, disturbance history, and management approaches (Table 1).

Table 1. Location, climatic information, area distribution to forest management classes and forest types, for each landscape in the study. The size includes all land, productive and non-productive. Other areal distribution information is for productive forest land. Percentages of restoration, set-aside and protected areas are calculated from the total of productive forests. BAU=’*Business as usual’* production landscape. ECO=*Ecopark*.

Area	**Southern Sweden**				**Middle Sweden**	**Northern Sweden**			
Landscape management regime	BAU	ECO	ECO	BAU	ECO	ECO	BAU	ECO	BAU
Name of the area	Hälleskog	Hornsö	Färna	Fagersta	Hornslandet	Käringberget	Vindeln	Rosfors	Kloken
Coordinates	56° 50' N; 15° 39' E	57° 00' N; 16° 09' E	59° 46′ N; 15° 51′ E	60°0′ N; 15°47′ E	61° 67' N; 17° 40' E	64° 04' N; 18° 41' E	64° 03' N; 18° 43' E	65° 38′ N: 21° 10′ E	65°57′ N; 21°0′ E
Mean annual Temperature[1]	7.8 °C	7.8 °C	7.8 °C	6.3°C	5.9 °C	2.5 °C	2.5 °C	2.0 °C	0.4 °C
Mean temperature (June-August)[1]	16.2±1.2	16.2±1.2	15.3±0.7	15.3±0.7	15.4±1.8	13.6±2.3	13.6±2.3	14.4±1.3	13.4±1.3
Mean annual Precipitation[1]	513 mm	513 mm	710 mm	710 mm	675 mm	705 mm	705 mm	646 mm	683 mm
Size (ha)	9144	9242	4004	13500	5479	13963	21181	2662	41518
Production (ha)[2]	8570 (94%)	4438 (53%)	1128 (39%)	12672 (94%)	2944 (54%)	5786 (54%)	20066 (95%)	976 (39%)	36607 (88%)
Conservation concern [2]	574 (6%)	4014 (47%)	1786 (61%)	828 (6%)	2535 (46%)	4989 (46%)	1115 (5%)	1521 (61%)	4911 (12%)

-Restoration	124 (1%)	3227 (38%)	1219 (42%)	118 (<1%)	1831 (33%)	2817 (26%)	18 (<1%)	349 (14%)	126 (<1%)
-Voluntarily set-aside	381 (4%)	485 (6%)	317 (11%)	408 (3%)	357 (7%)	1615 (15%)	331 (2%)	856 (34%)	1941 (5%)
-Protected (Woodland key habitat)	69 (1%)	302 (4%)	251 (9%)	302 (2%)	347 (6%)	557 (5%)	766 (4%)	316 (13%)	2844 (7%)
Pine-dominated forest[3]	45.2%	35%	27.2%	24.1%	54.1%	33.8%	31.1%	28.7%	26.8%
Spruce-dominated forest[3]	10.8%	15.2%	11.8%	13.7%	6.3%	13.9%	14.7%	24.9%	8.6%
Coniferous mixed forest[3]	6%	6.9%	13.7%	17.9%	11%	5%	4.1%	6%	3.7%
Mixed forest[3]	6.6%	19.4%	10.5%	12.5	8.9%	9.2%	10.1%	9%	15.2%
Broadleaf forest[3]	2.8%	12.2%	11.4%	4.5%	2.5%	6.1%	4.3%	8.8%	10%
Clearcut[4]	22.3%	3.7%	8.4%	19.5%	9.6%	18.7%	26.5%	14.8%	22.4%
HCVF[5]	0.08	18.5%	32.4%	0.6%	14.6%	18.3%	2.6%	32.3%	0.6%

[1]Data on mean temperatures and precipitation were from the Swedish Meteorological and Hydrological Institute (2019). [2]Productive forest (FAO, 2012). [3]Forest types according to NMD. Pine-dominated: >70% pine. Spruce-dominated: >70% spruce, Coniferous mixed forest: >70% conifers; Mixed forest: <70% conifers and < 70% of broadleaved trees, Broadleaf forest: >70 % broadleaved trees, [4]Clearcut defined as: Open and re-growing clear-felled, storm-felled or burnt areas outside of wetlands. Trees are less than 5 meters, [5] The percentages of High Conservation Value Forest (HCVF) per landscape are based on the area with the highest probability classification (70–100%) of HCVF presence.

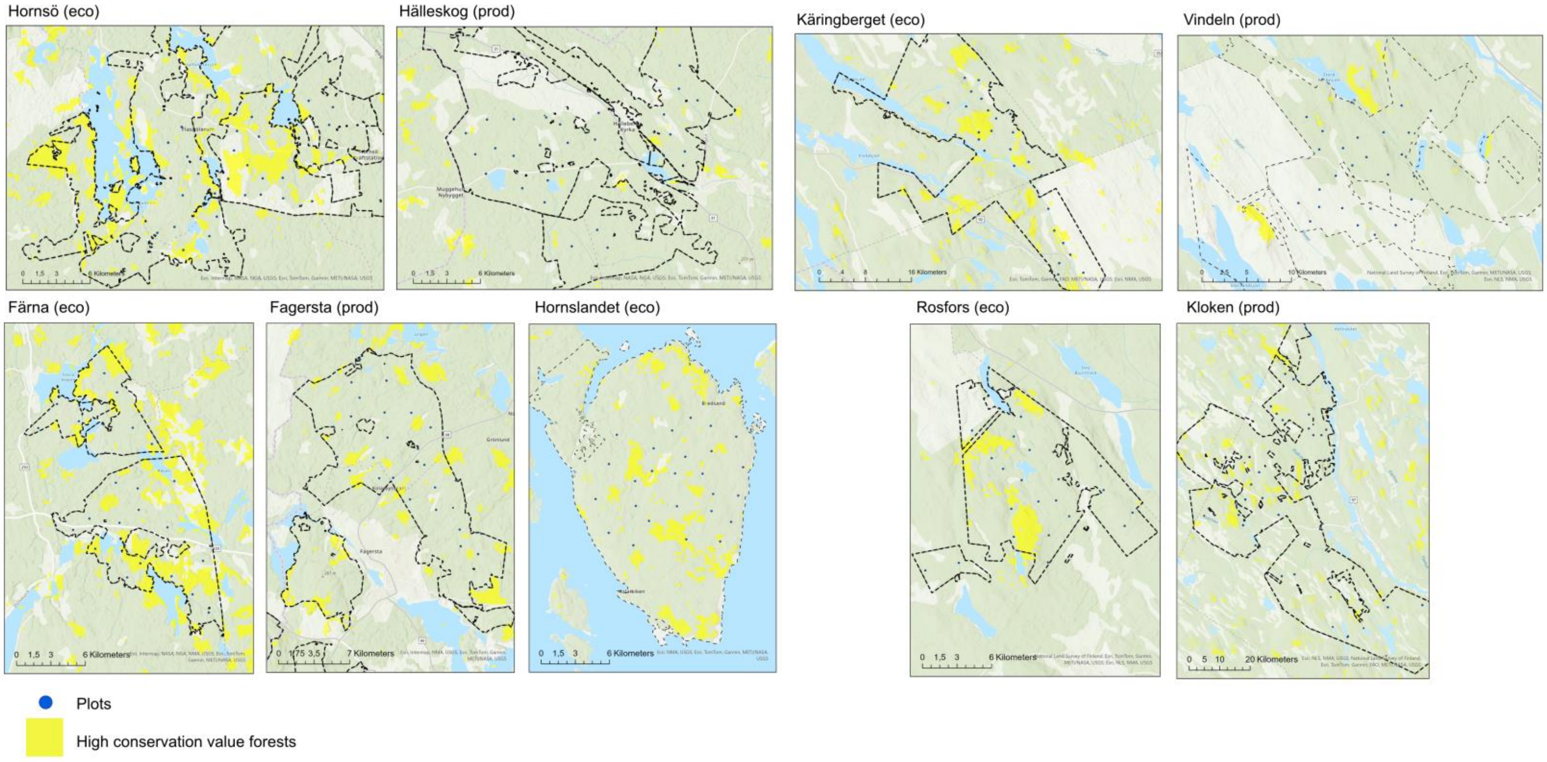

Figure 1. Distribution of highest class (70-100%) of probability of high conservation value forests (HCVF) in ecoparks (eco) and production landscapes (prod).

3.1.1 Ecoparks

Hornsö

Hornsö is characterized by a long history of wildfires, which continued until the early 20th century when large-scale forestry practices began suppressing natural disturbances (Sveaskog, 2008). These fire-adapted forests support many species dependent on burned wood, open-canopy conditions, and post-fire broadleaf regeneration. The area contains extensive old-growth features, including large, veteran trees of oak (*Quercus robur*), beech (*Fagus sylvatica*), and aspen (*Populus tremula)* and is characterized with boulder-rich terrain, rocky outcrops and open, sun-exposed pine forests with old-growth Scots pine (*Pinus sylvestris*). Hornsö is recognized as one of the most species-rich areas for saproxylic insects in northern Europe. Approximately 700 species of wood-living insects have been recorded in the area, including many red-listed species (Lindbladh et al., 2003).

Färna

Färna stands out with its high proportion of key habitats as well as swamp forests and large areas of undrained wetlands with part of them being included in the Natura 2000 network (Sveaskog, 2005a). The landscape is further characterized by boulder-rich spruce forests and the abundance of diverse fire regenerated broadleaf forests, which are especially rich in aspen trees, ranging from young saplings to centuries-old giants.

Hornslandet

Hornslandet is a peninsula along a 20-kilometer long undisturbed coastline. The most ecologically valuable habitats are primarily old coastal pine forests although smaller patches of high value broadleaf, broadleaf-rich and spruce forests are scattered throughout the landscape (Sveaskog, 2004). The area contains wetlands in form of relatively undisturbed mires with flark and string bog formations as well as five designated nature reserves. Just as Hornsö and Färna, Hornslandet is strongly influenced by earlier fire disturbance regimes.

Käringberget

Käringberget is part of a diverse river valley landscape surrounded by steep mountains, hosting a variety of forest types such as old-growth pine and spruce forests, aspen-dominated stands, riparian broadleaf-rich forests, high-elevation spruce forests and sandy pine forests with fire-influenced pine stands (Sveaskog, 2005b).

Rosfors

Rosfors represents a rare example of nutrient-rich forest landscape in a northern setting, which support rapid tree growth and an unusually high diversity of flora and fauna for this latitude (Sveaskog, 2021). The landscape contains old spruce forests and a high abundance of broadleaf trees, especially large aspens. The combination of old-growth characteristics, rich broadleaf content and abundant deadwood creates optimal conditions for many demanding saproxylic insects and forest bird species.

The four papers included in this thesis utilize different combinations of ecoparks and corresponding production landscapes as study areas, depending on the specific research focus of each study. In Paper I, where a comparison was made between ecoparks and production landscapes regarding beetle diversity and community composition, two ecoparks were used, one southern (Hornsö) and one northern (Käringberget) ecopark with its corresponding production landscape. Paper II included three landscapes; two ecoparks, Käringberget and Hornslandet and one production landscape, Vindeln to evaluate potential interactions between functional guilds of saproxylic beetles, and environmental variables. Paper III explored richness and community structures of wood-inhabiting fungi and included five landscapes; Hornsö (eco), Hälleskog (prod), Käringberget (eco), Vindeln (prod) and Hornslandet (eco). Paper IV utilized all ecoparks and corresponding production landscapes except for ecopark Hornslandet, to compare taxonomical and functional diversity of longhorn beetles (Fam: Cerambycidae) between multifunctional forest and production landscapes.

3.2 Study design

The study was set up to primarily sample saproxylic beetles in all ecoparks and corresponding production landscapes (Fig 2). Within each landscape, 26 plots were selected using the following criteria: 1) at least 1000 m distance between plots, 2) plot open from south to west to ensure sun-exposure, 3) includes one pair of high stumps of either pine and birch or birch and aspen. The study was set up twice, using newly created high stumps each time, to sample beetles spanning over two different time periods with the first taking place between years 2010 – 2013 and the second between years 2020 - 2022

The first period involved five of the nine study areas (Hornsö (eco), Hälleskog (prod), Hornslandet (eco), Käringberget (eco) and Vindeln (prod)) where sun-exposed high stumps of pine and birch were artificially created in each plot during the winter of 2010 to serve as trapping stations for saproxylic beetles. The high stump pairs consisted of one pine and one birch with a length of 2.5 m and a diameter range at breast height (DBH) between 13.7–42.2 cm. The majority of plots contained one pine and one birch except for ecopark Hornslandet were several plots consisted of either two pine or two birch high stumps due to difficulties in finding suitable trees following the criteria. In cases where sun-exposure was not satisfactory, the plots were opened manually by removing shadowing trees at the time when the high stumps were created. The cut trees were removed from the plots to not artificially affect local deadwood amount.

The second period involved all nine study areas where high stump pairs were created during winter 2020 and consisted of pine and birch in landscapes Hornsö (eco), Hälleskog (prod), Hornslandet (eco), Käringberget (eco) and Vindeln (prod), and of birch and aspen in landscapes Färna (eco), Fagersta (prod), Rosfors (eco) and Kloken (prod) with a length of 2.5 m and a DBH between 11.8–45.9 cm.

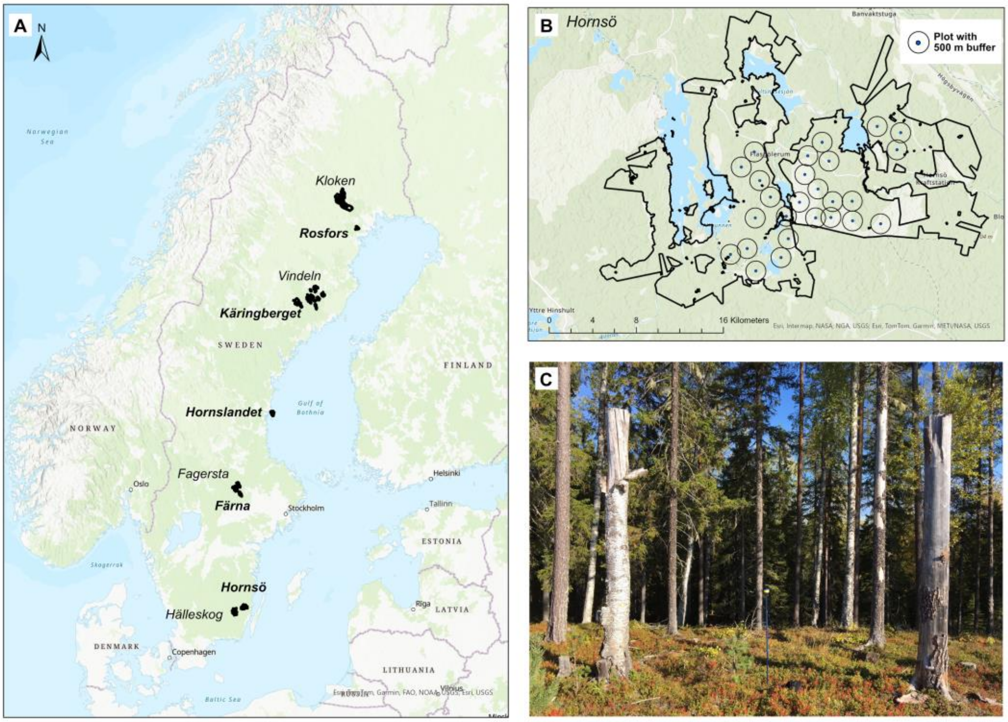

Figure 2. Study design illustrating the distribution of the nine study areas included in this thesis (A), with ecoparks in bold. Each study area contains 26 plots (B), represented as dots within a 500 m radius circle in the Hornsö map. (C) Each plot consists of artificially created high stumps of pine and birch/ birch and aspen

3.3 Data collection

3.3.1 Beetle sampling

During both periods of sampling, two trunk-attached flight-intercept traps were placed on each high stump to collect beetles, totalling 104 traps per study area. A trap consisted of a 10 × 20 cm, 2–3 mm thick, transparent Plexiglas sheet with a 0.5-L aluminium mould beneath the Plexiglas. The moulds were filled with Propylene glycol with a small amount of detergent to remove surface tension. Two traps were placed on the southern side of each high stump, on the heights of 1.1 m and 1.6 m above ground. Beetle sampling went on from early June to early August for three consecutive years after the creation of the high stumps.

Figure 3. Creation of high stumps winter 2020.
Photo: Claes Kindblom

3.3.2 Beetle classification and traits

Collected beetles were sent to taxonomical experts for identification to species or genera level and involved only saproxylic species. During first period of sampling the precision of species identification differed in the southern region (Hornsö – Hälleskog) from Hornslandet (eco), Käringberget (eco) and Vindeln (prod) with fewer genera identified to species level. Thus species counts were compared between ecoparks and production landscapes within the same geographical region in paper I divided into the northern region (Käringberget and Vindeln) and a southern region (Hornsö and Hälleskog). For paper II beetles sampled from period one were further grouped by their ecological traits based on feeding guilds and deadwood habitat preference. Feeding guilds included cambivores, detritivores, fungivores, predators and wood borers, following Koch (Koch, 1992, 1989a, 1989b) and Artdatabanken (Artdatabanken, 2021). For deadwood habitat preference classification, species were classified as either wood-generalists, conifer specialists/generalists or broadleaf specialists/generalists following Artdatabanken (Artdatabanken, 2021) and Ehnström and Axelsson (2002). For paper IV I used a subset of total beetle data collected during the second sampling period (2020-2022), focusing specifically on the longhorn beetles (Fam: Cerambycidae) to study functional diversity. Traits used for calculating functional diversity metrics, included ecological traits such as tree species preference, information regarding specialization, pollination and pyrophilia as well as the number of utilized substrates and the number of larval host plants (Ehnström, 2007; Jeppsson and Forslund, 2014). Life history traits involved generation time (Jeppsson and Forslund, 2014) and morphological traits included information on body size, antenna length, eye area, front femur length and hairiness (Hagge et al., 2021)

Figure 4. Window traps attached to one pine and one birch high stump.

3.3.3 Fungal DNA sampling

During summer and autumn in 2019, fungi were sampled from high stumps cut in 2010 in study areas Hornsö (eco), Hälleskog (prod), Hornslandet (eco), Käringberget (eco) and Vindeln (prod). Sampling was made by drilling high stumps to collect sawdust for later DNA extraction. The samples were collected from each high stump at

50 cm, 100 cm and 150 cm heights in southern, western and northern directions, respectively, and pooled into one collective sample. Before taking the sample, the bark was carefully removed to ensure sampling from the wood itself, and the wood surface was sterilized by burning an area of 3-4 cm in diameter. The samples were taken using a 10 mm diameter drill approximately into the centre of the high stump (Pasanen et al., 2018).

Figure 5. Sampling of fungal DNA from 9 year old high stumps
Photo: Albin Larsson Ekström

The sawdust was collected on an aluminium foil and poured to a zip-lock bag. To prevent cross-contamination, the drill bit was sterilized by burning, using a gas torch, between each high stump. All samples were freeze-dried and send to the Department of Forest Mycology and Plant Pathology in Uppsala, Sweden, for DNA extraction and bioinformatics. Information regarding DNA extraction and bioinformatics procedures can be found in Paper III.

3.3.4 Environmental variables

The environmental variables used across all studies encompassed both local- and landscape-level factors, measured at multiple spatial scales. Each of the four papers incorporated local deadwood variables, focusing on either deadwood amount or diversity, depending on the specific research context. In contrast, the landscape variables and spatial scales differed between studies, depending on the objectives of each study.

3.3.5 Local variables

Field measurements of tree stand structure and deadwood factors were conducted in 2019 using circular plots with a 20-meter radius around each high stump. Due to the slow rate of wood decomposition in boreal forests and the absence of visible large-scale disturbances, the time lag between field measurements and beetle sampling was considered negligible.

All living trees with a DBH ≥ 4.5 cm and a minimum height of 1.3 meters were recorded along with their species identity. *Betula pendula* and *B. pubescens* were classified as birch, and *Q. robur* and *Q. petraea (Matt., Liebl.)* as oak. Canopy closure was assessed by taking hemispherical photographs with a fish-eye lens, which were analysed using ImageJ (Schneider et al., 2012) and the plugin Hemispherical 2.0 (Beckschäfer, 2015) to calculate canopy gap fraction.

For deadwood, both standing and lying dead trees (logs) were recorded, including species, DBH, height, and decay class. Deadwood logs with a diameter ≥ 4.5 cm and a length ≥ 1.3 meters had both top (minimum 4.5 cm) and base diameters measured. Deadwood was categorized into the following types: standing dead tree, snag (standing tree with a broken top), or deadwood log. Logs were assigned to one of four decay classes, based on a system modified from Gibb et al. (Gibb et al., 2005): (1) Hard wood with

>50% intact bark, (2) Hard wood with a smooth, softening surface and <50% bark remaining, (3) Bark-free wood with crevices and holes, soft surface, (4) Very soft wood with indistinct surface and outline, possibly with a remaining hard core. For deciduous logs in advanced decay stages (3–4), classification was based on wood softness (tested with a knife), rather than bark loss, to account for species like birch, which can retain bark despite significant decomposition. Standing dead trees and snags were classified following Jung et al. (Jung et al., 1999) and Thomas (Thomas et al., 1979). To characterize field-layer vegetation, Cajander's vegetation classification system (Cajander, 1926) was used. Dominant vegetation types were recorded, and when vegetation shifted within a plot, the two most dominant types were documented.

Field measurements were repeated in the summer of 2022 around high stumps that were cut in 2020**,** following the same protocols and variables as those used during the 2019 field survey. However, canopy closure and vegetation types were not recorded during the 2022 field survey.

3.3.6 Landscape structures

To study potential relationships between landscape factors and assemblages of beetles and fungi, different landscape variables were assessed for paper II, III and IV. In paper II forest types and forest age classes were used in the analyses, which were obtained from the landowner, and processed by extracting information within 500-meter radius buffers around each plot. The 500 m buffer size was chosen to capture a representative portion of the surrounding landscape, reflecting local forest variability and aligning with previous studies (Ranius et al., 2015). This scale also allowed for the effective use of forest structural data provided by the landowner. Forests were categorized into five forest types based on classifications by the Swedish National Forest Inventory (NFI): pine forest (≥65% *Pinus sylvestris*), spruce forest (≥65% *Picea abies*), mixed coniferous forest (≥65% conifers, without one dominant species), mixed forest (more than 35% but less than 65% broadleaved species), broadleaved forest (≥65% broadleaved species, ≤45% noble hardwoods). Forest age was grouped into five classes: clear-cut (0–2 years), young forest (3–30 years), middle-aged forest (31–80 years), mature forest (81–120 years), old forest (>120 years)

For each buffer, the total area (in hectares) of each forest type and age class was calculated.

In paper III and IV the amount (ha) of high conservation value forests (HCVF) was calculated around each plot within buffers of 300 m, 500 m and 1000 m. In paper IV only the buffer of 500 m was used. Information regarding HCVF was obtained by using a model-based map of relative likelihood of HCVF. This map has been generated by integrating random forest machine learning and open landscape data to predict the relative HCVF probability for all 1 hectare pixels with ≥50% forest cover in Sweden (Bubnicki et al., 2024). Each hectare of forest is assigned a relative likelihood score indicating the HCVF-probability between 0 and 100 percent. Since the HCVF model consists of continuous variables, I classified the probability value to three classes; low probability (0-39 %), medium probability (40-69 %) and high probability (70-100 %) of HCVF. In paper III the probability classes of HCVF were further divided into coniferous or broadleaf-rich forests with data obtained from the Swedish national land cover database (Swedish Environmental Protection Agency, 2020).

3.3.7 Living tree and deadwood calculations

Both living trees and deadwood were categorized into diameter classes to capture size structure and variability across plots. Six diameter classes were used, starting from 4.5–9.9 cm (representing young trees and fine woody debris), followed by 10–19.9 cm, 20–29.9 cm, and so on, up to >50 cm (classes representing older trees and course woody debris). The basal area of living trees and deadwood volumes were calculated and standardized to per-hectare values for each plot.

To quantify structural diversity, diversity indices for both living trees and deadwood were calculated using a method adapted from Siitonen et al. (2000) and Hekkala et al. (2016). Living tree diversity was defined as the number of unique combinations of tree species and diameter class within a plot. Deadwood diversity was calculated as the number of unique combinations of tree species, diameter class, deadwood type (standing tree, snag, or log), and decay class. Volumes of intact standing dead trees in decay classes 3–5 (Thomas et al., 1979) were estimated using tree diameter and height, based on Brandel’s volume equations for pine, spruce, and birch, applicable to both northern and southern Sweden ((Brandel, 1990). For all broadleaved trees taller than 6 m, birch volume functions were applied.

Volumes of logs and snags were calculated as cylinders, using recorded diameters and lengths/heights. For broadleaved deadwood shorter than 6 m, volume was also calculated as a cylinder using DBH.

3.4 Statistical analyses

All statistical analyses were conducted in R (versions 3.5.1 and 3.6.1), and spatial analyses were performed using ArcGIS 10.6 and ArcGIS Pro.

To assess differences in environmental variables between ecoparks and production landscapes such as deadwood variables measured from 20 m radius plots and the amount of HCVF measured from 500 m buffers (Paper I, III and IV), I used a combination of linear models (LM) from the 'lme4' package (Bates et al., 2014) as well as non-parametric tests such as Kruskal-Wallis followed by Dunn's post hoc test with a Bonferroni correction. This non-parametric test is appropriate for comparing differences in distributions among more than two independent groups, particularly when the assumptions of normality and homogeneity of variance are not met (Cleophas and Zwinderman, 2016). In Paper III, I used LMM from the 'lmerTest' package (Kuznetsova et al., 2017) to test for differences in fungal α species richness between pine and birch. To test α richness and explanatory variables between landscapes, I again used the Kruskal-Wallis test followed by Dunn's test. To test for significant associations with environmental variables between fungal α species richness (Paper III), α diversity of saproxylic beetles, red-listed beetles (Paper I) and taxonomic and functional α diversity of longhorn beetles (Paper IV), different types of regression models were applied. Depending on the response variable type (e.g., count or continuous data), I used linear mixed effect models (LMMs), generalized linear models (GLMs) and generalized linear mixed models (GLMMs) from packages 'lme4' (Bates et al., 2014) and 'glmmTMB' (Brooks et al., 2017). Since data was seldom normally distributed I applied a Poisson or negative binomial error distribution. Models included both fixed and random effects to account for hierarchical and nested data structures.

To examine relationships between species traits (e.g., feeding guilds, habitat preferences) and environmental variables at both local (20 m) and landscape scales (500 m) as in paper II, I used a model-based approach to the fourth-corner problem (Legendre et al., 1997). This method integrates three matrices, environmental variables (R), species abundances (L), and species traits (Q), to estimate interaction coefficients describing trait–environment relationships. To calculate the fourth corner I applied a LASSO-penalised negative binomial regression from the R package 'mvabund' (Wang et al., 2012). Prior to all analyses, collinearity among environmental predictors was evaluated using Pearson correlation coefficients (R package 'languageR' (Baayen and Shafaei-Bajestan, 2019)).

To assess functional diversity, I calculated standard metrics such as Functional richness (FRic), Functional evenness (FEve) and Functional divergence (FDiv) with the R package 'FD' (Villéger et al., 2008). These metrics were derived from species trait data.

To explore γ-diversity of saproxylic beetles (Paper I), functional groups of saproxylic beetles (Paper II), longhorn beetles (Paper IV), and wood-inhabiting fungi (Paper III) across forest landscapes and tree species of high stumps, I used sample-size-based and coverage-based rarefaction and extrapolation curves from R package 'iNEXT' (Hsieh et al., 2016).

To analyse differences in community composition (β-diversity) of beetles and fungi across deadwood substrates and forest management regimes as in Paper III and IV, I calculated pairwise dissimilarities using the *vegdist* function from the 'vegan' package (Oksanen et al., 2017). I used the Bray–Curtis dissimilarity index, which is appropriate for species abundance (or presence–absence) data and does not assume normality. To assess whether community composition differed significantly between groups, I performed a permutational multivariate analysis of variance (PERMANOVA) using the *adonis* function when the assumption of homogeneity of variances was met (Paper IV). Differences in community composition were visualised using non-metric multidimensional scaling (NMDS**)** from the 'vegan' package (Paper I and IV). To partion β-diversity of total dissimilarity (Sørensen dissimilarity) into turnover (Simpson dissimilarity) and nestedness-resultant components, the 'betapart' package (Baselga, 2010) was used to test whether community differences were primarily due to species replacement (turnover) or species loss (nestedness). Finally, to identify species that were strongly associated with specific management regimes or substrate types (Paper I and III), I conducted an indicator species analyses using either the 'labdsv' or 'indicspecies' R packages (De Cáceres, 2019; Dufrene and Legendre, 1997).

This helped identify key taxa that contributed most to observed differences in beetle and fungal communities.

Photo: Paulina Bergmark

4. Results and discussion

4.1 Main results

4.1.1 Structural characteristics of ecoparks and production landscapes

In Paper I and III, structural differences were assessed using 20 m plots, where both total deadwood volume and deadwood diversity were found to be significantly higher in ecoparks compared to production landscapes in both regions (Paper I). In southern Sweden, the ecopark Hornsö also had significantly higher living tree diversity than its production counterpart Hälleskog (Paper I). For Paper III, deadwood diversity was categorized into coniferous and broadleaved types. Inventories revealed that the northern ecopark Käringberget had greater diversity of both broadleaved and coniferous deadwood compared to the adjacent production landscape, Vindeln. In the south, ecopark Hornsö contained significantly greater broadleaved deadwood diversity than the nearby production landscape Hälleskog, while diversity of coniferous deadwood were similar between the two.

High conservation value forests (HCVF) were also classified as either broadleaf-rich or coniferous and assessed at spatial scales ranging from 300 to 1000 meters (Paper III). Both types of HCVF were significantly more abundant in the southern and northern ecoparks compared to their respective production landscapes.

In Paper IV deadwood measurements were made around high stumps created in 2020. The study included four ecopark–production landscape pairs, measured at the scale of 500 m radius, HCVF were not divided into forest types as in Paper IV. Here, HCVF amounts were significantly higher in ecoparks Hornsö and Käringberget compared to their corresponding production landscapes, but no differences were found between ecoparks Färna and Rosfors and their respective production counterparts, Fagersta and Kloken. Notably, local deadwood volumes measured in 2022 around newly created high stumps, did not differ significantly between ecoparks and production landscapes in any of the studied regions.

Multifunctional forest landscapes, generally exhibited more diverse structural forest qualities, including higher volumes and diversity of deadwood and larger areas of HCVF, compared to typical production-oriented landscapes. However, the pattern was not consistently observed across all studies in this thesis, especially regarding deadwood volume measurements as observed in Paper IV. When considering the entire landscape (Table 1), ecoparks clearly differ from production-oriented landscapes in their structural composition, particularly in terms of features known to support deadwood-associated biodiversity (Hekkala et al., 2023; Lachat and Müller, 2018; Löfroth et al., 2023; Stokland et al., 2012). Ecoparks contain larger areas of formally protected forests, forest types of conservation concern, and higher proportions of high conservation value forests (HCVF), all of which contribute to greater ecological continuity and structural heterogeneity.

However, in this thesis, differences in habitat characteristics on a local scale (20 m) may have been too fine to capture the full extent of structural differences between ecoparks and production landscapes.

4.1.2 Saproxylic beetles in multifunctional vs. production-oriented forest landscapes

In Paper I, which examined overall saproxylic beetle diversity, two ecoparks with corresponding production landscapes were studied: Hornsö and Hälleskog in the southern boreonemoral region and Käringberget and Vindeln in the northern boreal region. In the south, both α diversity and γ diversity of saproxylic beetles was higher in the ecopark compared to the production landscape, while in the north, diversity levels were similar between the two management regimes (Fig. 6). However, across both regions, the diversity of red-listed species was consistently higher in ecoparks (Fig. 9).

Paper IV added complementary insights by examining taxonomic and functional diversity of longhorn beetles across four ecoparks and their paired production landscapes. Taxonomic richness, Shannon diversity, and functional richness regarding α diversity, were all significantly higher in ecoparks. However, there were no significant differences in longhorn beetle abundance, functional evenness, or functional divergence between the two management regimes. However, ecoparks had both greater taxonomic and functional γ diversity than production landscapes (Fig 7).

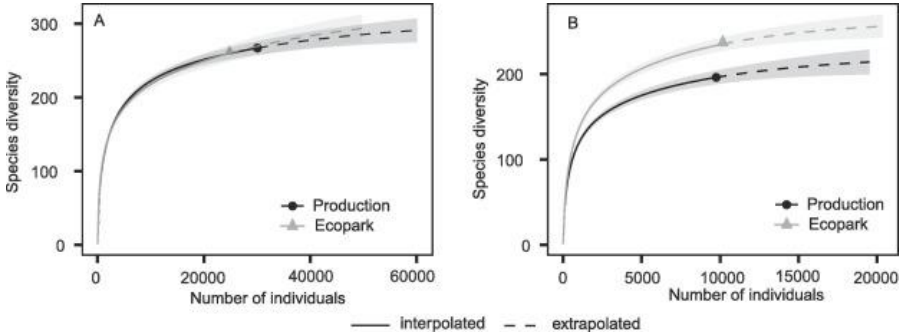

Figure 6. Rarefaction plots with 95% confidence intervals (shaded areas) comparing the γ-diversity of saproxylic beetle in ecoparks and conventional production landscapes. A) Käringberget - Vindeln, B) Hornsö - Hälleskog.

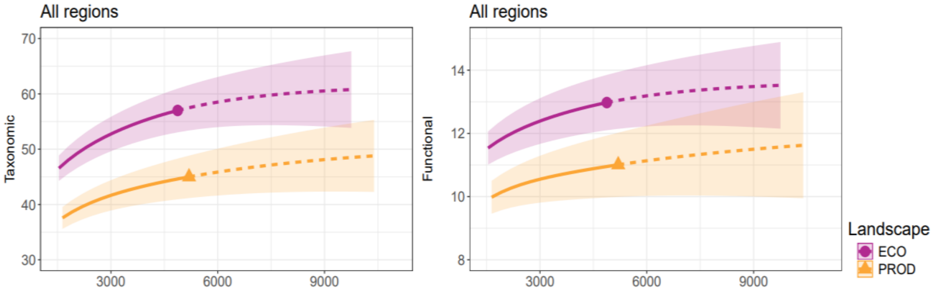

Figure 7. Species rarefaction and extrapolation curves for taxonomic and functional γ-diversity (Hill numbers q=0) between ECO and PROD. Symbols indicate observed values, solid lines rarefied values and dotted lines indicate extrapolated values.

Community composition of saproxylic beetles, i.e., β-diversity, also differed significantly between ecoparks and production forests in both the southern and northern region (Paper I). The differences were more pronounced in the south, where 37 indicator species, including 10 red-listed, were associated with the ecopark, compared to 8 indicator species in the production landscape, none of which were red-listed. In the north, the production landscape was linked to 20 indicator species, including one red-listed species, while only a few indicator species were associated with the ecopark.

For longhorn beetles (Paper IV), ordination analyses showed that species- and trait composition were largely similar between ecoparks and production landscapes (Fig. 8), with substantial overlap across most regions. An exception was observed in the southernmost region (ecopark: Hornsö, production landscape: Hälleskog), where both species and trait compositions showed a slight separation between management types.

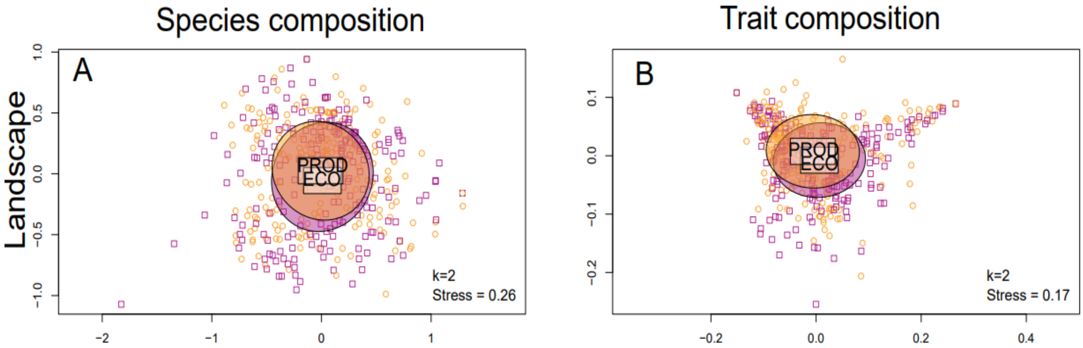

Figure 8. Non metric multidimensional scaling (NMDS) visualising differences in species composition (left column), based on a Bray-Curtis distance matrix, and trait composition (right column), based on a Gower trait matrix, between ecoparks (ECO) and production-oriented landscapes (PROD) Panels A and C are based on the same ordination for species composition and B and D are based on the same ordination for trait composition. Species names in C are based on the weighted average of the site scores for each species along the ordination axes. Vectors in D are based on community-weighted means (CWM) for individual traits with a r^2- >0.5 and were plotted using the *envfit* function.

Ecoparks host greater diversity of red-listed saproxylic beetles (Paper I) as well as greater taxonomic and functional richness of longhorn beetles (Paper IV). These results are in line with previous studies showing of greater diversity of deadwood-dependent species in old-growth compared to managed forests (Jacobsen et al., 2020; Karpiński et al., 2021; Lunde et al., 2025; Stenbacka et al., 2010) and provide compelling evidence that multifunctional forest landscapes support higher levels of saproxylic beetle diversity compared to production-oriented landscapes. In particular, diversity gains were most pronounced in the southern study region, where both α and γ diversity of saproxylic beetles were higher in ecoparks.

However, it is important to note that these differences cannot be attributed solely to the current management regime of ecoparks which includes higher levels of ecological restoration and forestry with enhanced conservation concern (Table 1). Ecoparks were established in areas already rich in natural forest features, such as high volumes of deadwood, old-growth elements, and diverse forest types. As such, the observed higher diversity may in part reflect a legacy of less intensive historical management in forests situated in ecoparks, rather than the effects of current multifunctional forestry practices alone. The broader landscape context appears to play an important role, particularly when considering factors such as the intensity and duration of historical forestry and the potential for successful restoration. For instance, Kouki et al. (2012) found that forests with a shorter history of intensive management supported higher species richness of rare and red-listed species of saproxylic beetles, following restoration, compared to forests with a longer history of forestry. In Sweden, forests in the north have generally experienced a shorter period of intensive management than those in the south, resulting in higher amounts of deadwood and old-growth forests in the north. (Fridman, 2000; Fridman and Walheim, 2000). This helps explain why, in the northern region of this study, there were no significant differences in total saproxylic beetle diversity between ecoparks and production landscapes. Moreover, species assemblages in the northern landscapes were relatively similar between the two management types, whereas in the south, community composition differed more distinctly between the ecopark and the production landscape. This regional variation may reflect differences in forest structure, deadwood availability, and historical land use. It is also worth noting that some saproxylic beetles recorded in our study are known to thrive in recently clear-cut areas, which provide sun-exposed conditions that can temporarily support certain species (Kaila et al., 1997). However, species that depend on well-decayed substrates are likely to respond differently to forest management practices. This highlights the need to consider deadwood diversity when assessing biodiversity impacts.

4.1.3 Effects of local deadwood and landscape properties on saproxylic beetles and wood-inhabiting fungi

Saproxylic beetles

Deadwood volume and diversity was positively associated with α diversity and abundance of saproxylic and red-listed beetles in southern Sweden, while in the north, no such relationships were found (Paper I), partially supporting the Habitat Amount Hypothesis (HAH). The effects of deadwood diversity on saproxylic beetles were inconsistent, varying across years and regions. In the southern study area, deadwood diversity was positively associated with species richness and abundance of saproxylic beetles. However, models including deadwood volume outperformed those with deadwood diversity alone (as indicated by lower AIC values), lending greater support to the HAH over the Habitat Heterogeneity Hypothesis (HHH). Interestingly, in some years, particularly within ecoparks, deadwood diversity was negatively associated with the richness and abundance of red-listed beetles (Fig 9).

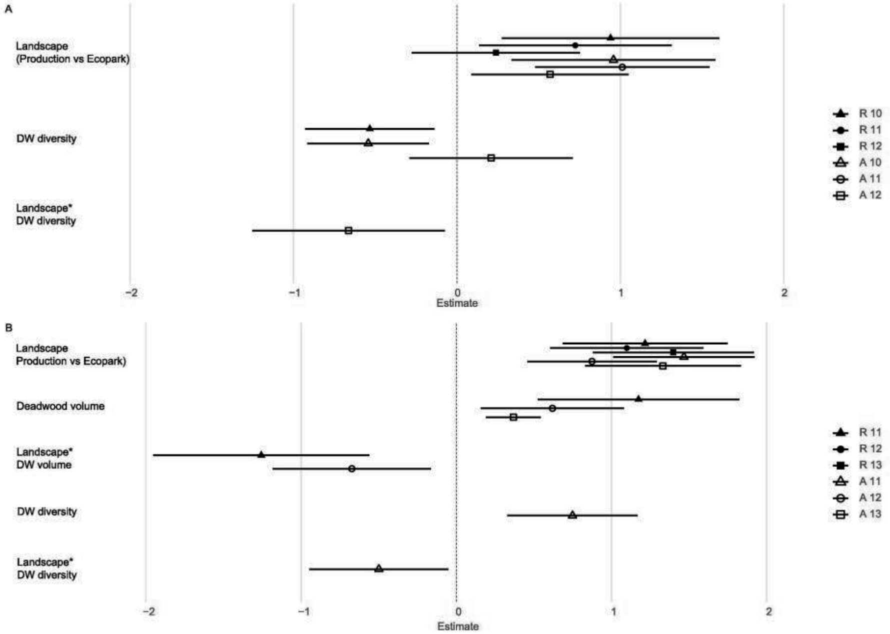

Figure 9. GLM results for red-listed beetles separate for each year of beetle trappings. Only the best performing model for each response variable is shown (Table C.2 for all models in Paper I). For significance, estimate + SE bar must not cross the zero line. The further away from 0, the larger effect. (a) = northern study area, (b) = southern study area. R = richness. A = abundance, number depicts the sampling year (2010–2013).

Paper II further revealed that species traits influenced beetle responses to forest characteristics (Fig. 11 and 12). Specialists (e.g., broadleaf- and conifer-preferring species) responded positively to their matching deadwood types, while generalists showed weaker or mixed responses. Among feeding guilds, wood borers and cambivores were generally associated with coniferous deadwood, whereas fungivores exhibited contrasting responses depending on tree species. Regarding landscape properties, broadleaf generalists showed positive interaction with mixed and broadleaved forests as well as pine forests. Broadleaf generalists showed also positive interactions with mature forests (80-120 years) while fungivores and predators responded positively to the amount of old forests, i.e., forests older than 120 years. Conifer specialists on the other hand responded positively with the amount of clear-cuts and young forests.

While management regime was found to have an effect on taxonomic and functional α and γ diversity of longhorn beetles, with higher diversity in ecoparks (Paper IV), neither deadwood nor the amount of HCVF added to further explain this pattern except in the case of functional richness where deadwood had an additional positive effect on α diversity. Although no significant differences in species or trait composition of longhorn beetles were observed between ecoparks and production landscapes (Paper IV), distinct differences emerged at the substrate level, with pine, birch, and aspen high stumps each supporting unique species and trait compositions. (Fig 10).

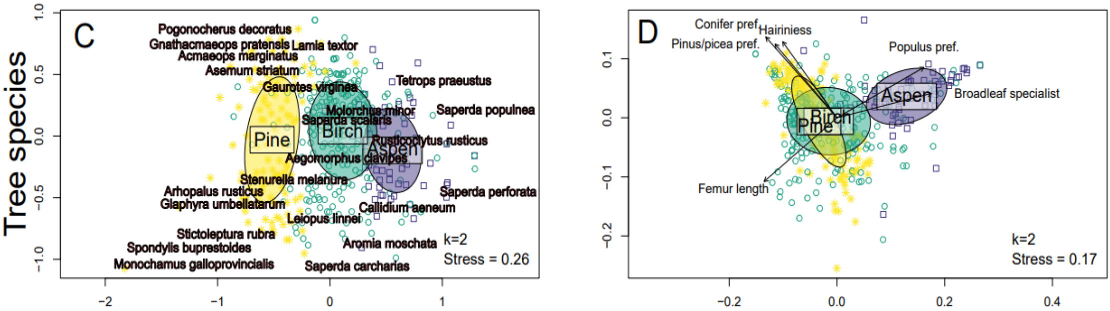

Figure 10. Non metric multidimensional scaling (NMDS) visualising differences in species composition (left column), based on a Bray-Curtis distance matrix, and trait composition (right column), based on a Gower trait matrix, between tree species (C & D). Species names in C are based on the weighted average of the site scores for each species along the ordination axes. Vectors in D are based on community-weighted means (CWM) for individual traits with a r^2- >0.5 and were plotted using the *envfit* function.

Our findings highlight the complex and context-dependent effects of habitat structure on saproxylic beetle communities. In line with the HAH (Fahrig, 2013), deadwood volume was positively associated with α diversity and abundance of saproxylic beetles and red-listed species, but only in the southern region (Paper I). This suggests that habitat amount can enhance local species richness, particularly in landscapes with a longer history of intensive forestry, where deadwood is typically more limiting (Häkkilä et al., 2021; Sandström et al., 2019).

Deadwood diversity showed more inconsistent patterns across regions and years. While it had a positive influence on species richness and abundance of saproxylic beetles in the south, its effects were weaker and less consistent than those of deadwood volume. Moreover, we found unexpected negative associations between deadwood diversity and red-listed beetle richness and abundance in some years, particularly in ecoparks. These patterns suggest that while deadwood heterogeneity can support broader beetle communities by offering a variety of niches (Lassauce et al., 2011; Seibold et al., 2016), it may not always benefit rare or specialist species, which may require specific deadwood types or decay stages (Jonsson et al., 2005).

The fourth-corner analysis (Paper II) added a trait-based dimension to these patterns by revealing that beetle responses to deadwood and landscape characteristics are highly trait-specific. Conifer- and broadleaf-preferring species responded to matching deadwood types, highlighting the need of diversified deadwood substrates. Findings regarding feeding guilds such as fungivores and predators and the association with older forests in the surrounding are patterns consistent with previous studies, (Johansson et al., 2007b; Traylor et al., 2022; Wetherbee et al., 2023) highlighting the need of protecting existing old forests to sustain the full range of saproxylic beetle diversity. The positive interaction between broadleaf generalists and mixed and broadleaved forests has seldom been demonstrated although previous and recent studies have shown positive effects on saproxylic beetle diversity and the amount of broadleaf forests in conifer dominated landscapes (Gran, 2024; Lindbladh et al., 2007; Økland et al., 1996). Since broadleaf-associated species face a higher degree of extinction risk than conifer-associated species (Seibold et al., 2015), due to the disadvantage of broadleaved trees by forestry, there is an urgent need to restore broadleaf-rich habitats.

The higher taxonomic and functional α and γ diversity of longhorn beetles found in ecoparks compared to production landscapes highlights the conservation potential of multifunctional forest landscapes. However, this pattern was not directly explained by local deadwood volume or the surrounding area of HCVF, as these variables were not significant predictors in the models, except in the case of functional richness, which showed a positive association with deadwood amount.

A review by (Sverdrup-Thygeson et al., 2014) highlights that saproxylic beetle responses to spatial scale are highly variable and influenced by species traits, study design, and the surrounding landscape context. Several studies have shown that local (stand-scale) deadwood availability often fails to predict species richness or community composition effectively (Moretti and Barbalat, 2004; Økland et al., 1996). For example, Moretti and Barbalat (2004) found no relationship between deadwood and beetle diversity at a small spatial scale (0.25 ha), whereas diversity patterns at a larger scale (6.25 ha) were associated with broader forest heterogeneity, such as mosaics of fire-created habitats. I found no significant differences in local deadwood amounts between ecoparks and production landscapes from field measurements that took place during the second beetle sampling period. This may help explain the limited predictive power of local-scale habitat variables. Together, these results emphasize the need to account for both landscape-scale processes and the spatial resolution of habitat measurements when evaluating biodiversity responses to forest management.

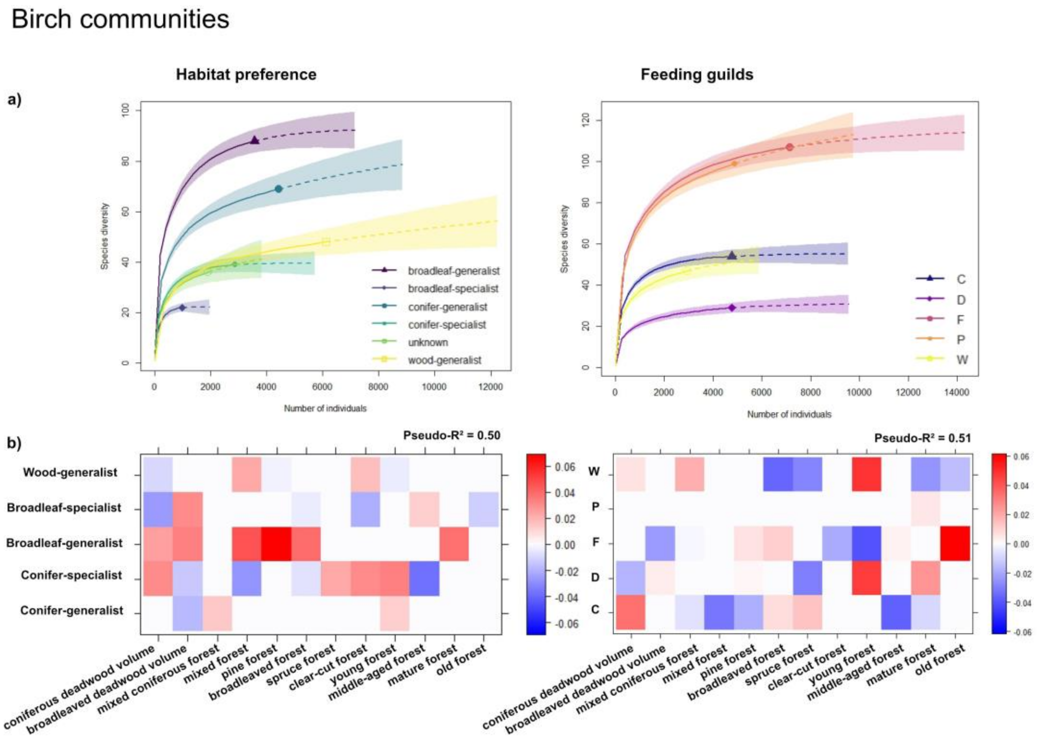

Figure 11. Rarefaction curves for birch communities (a) with 95% confidence intervals (shaded areas) comparing the γ-diversity of ecological traits. Heat maps (b) of interaction coefficients for birch communities between traits (vertical axe) and environmental variables (horizontal axe) showing positive (red), negative (blue) and no associations (white). The intensity of colours refer to the positive (red) and negative (blue) strength of each interaction. Feeding guilds refer to cambivores (C), detritivores (D), fungivores (F), predators (P) and wood borers (W).

Pine communities

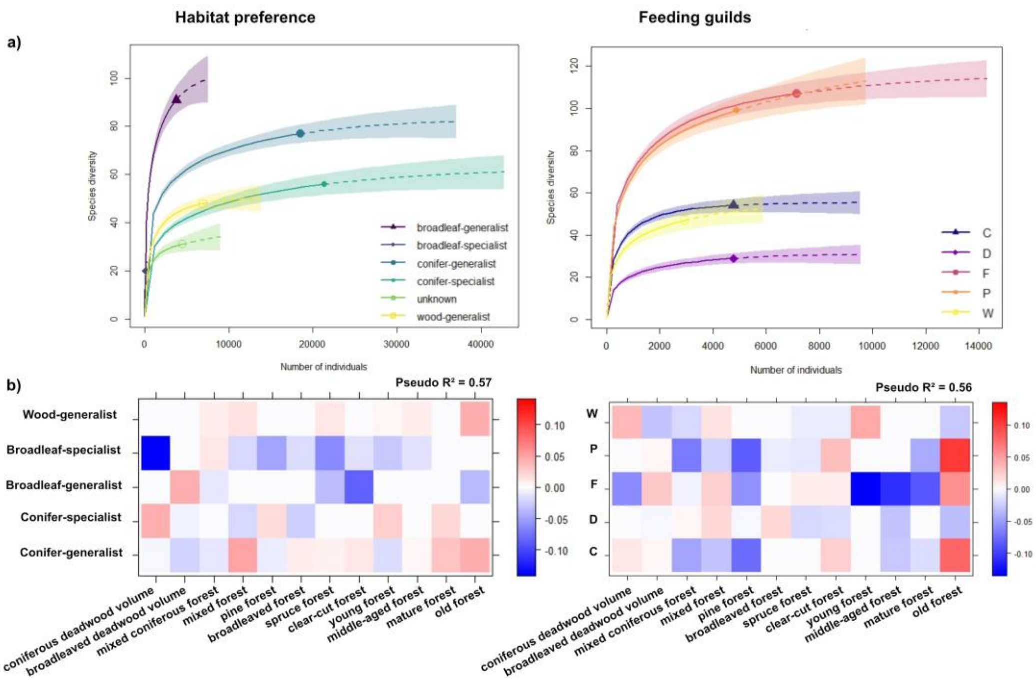

Figure 12. Rarefaction curves for pine communities (a) with 95% confidence intervals (shaded areas) comparing the γ-diversity of ecological traits. Heat maps (b) of interaction coefficients for pine communities between traits (vertical axe) and environmental variables (horizontal axe) showing positive (red), negative (blue) and no associations (white). The intensity of colours refer to the positive (red) and negative (blue) strength of each interaction. Feeding guilds refer to cambivores (C), detritivores (D), fungivores (F), predators (P) and wood borers (W).

Functional trait variation in longhorn beetles

Of the 131 species of longhorn beetles recorded in Sweden, we sampled 61 species in our study (Paper IV) representing a broad spectrum of functional traits. Ordination of species in functional trait space revealed clear structuring by ecological strategies (Fig. 13). Conifer specialists clustered along trait axes characterized by longer generation times and pyrophilia while broadleaf-preferring species were associated with a broader range of larval host plants. Generalists, on the other hand, were more commonly linked to traits such as pollination and body hairiness. Species of conservation concern (Roberge, 2023) were more frequently associated with traits such as larger body size.

These findings underscore the considerable functional variation that exists within a single beetle family, and highlight the risk that losing even a few species could lead to disproportionate reductions in functional diversity. Multiple studies have shown that the ongoing degradation of natural habitats is leading to non-random biodiversity loss, with certain traits or ecological roles disappearing more rapidly than others, ultimately reshaping ecosystem functioning (Eskildsen et al., 2015; Leitão et al., 2016; Newbold et al., 2020). In my study, deadwood substrate identity, specifically the tree species of the high stumps, emerged as the most important factor explaining both taxonomic and functional richness. Different tree species supported distinct suites of traits, indicating that substrate type acts as a strong ecological filter (Ehnström, 2007; Micó et al., 2020; Seibold et al., 2016), shaping the functional composition of beetle communities. These results emphasize the importance of maintaining deadwood from a variety of tree species to preserve a broad range of ecological functions. The observed trait filtering reinforces the need for structurally and compositionally diverse deadwood resources in managed forests. Importantly, this also demonstrates that it is possible to combine production forestry with targeted conservation measures, such as the deliberate creation of deadwood from multiple tree species, as a way to support functionally rich saproxylic communities.

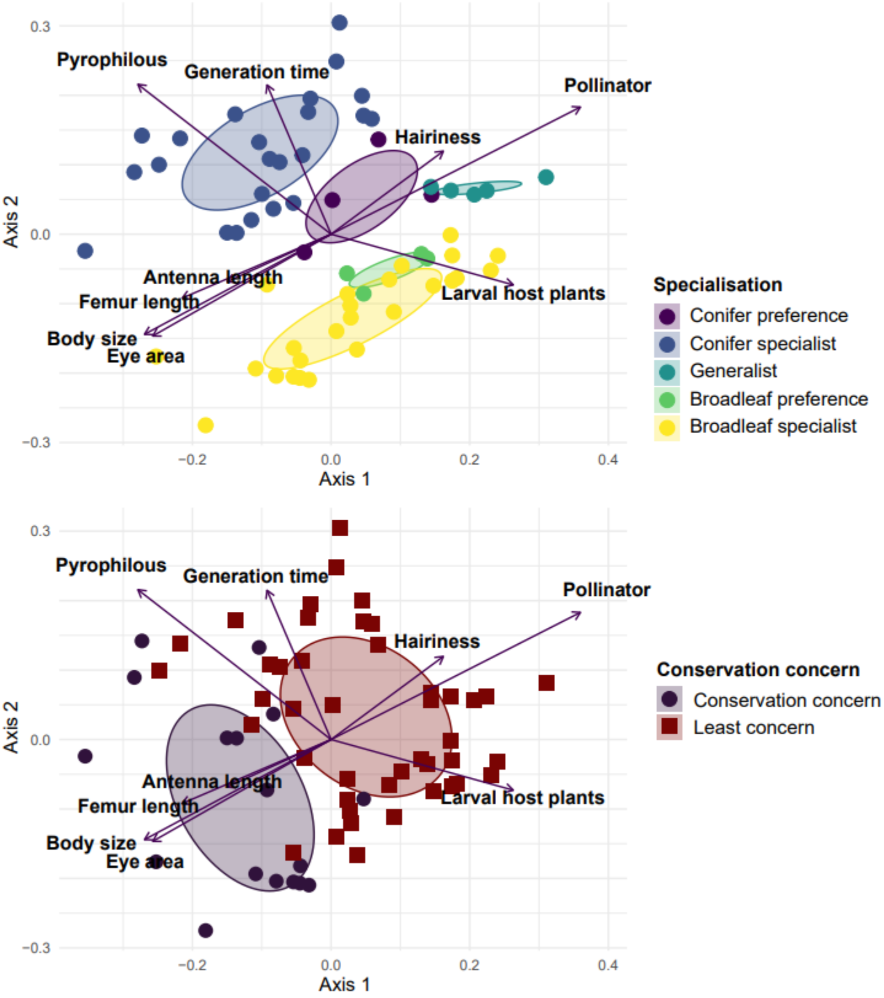

Figure 13. PCoA visualising the grouping of categorical traits (ellipsoids) and of numerical traits (vector arrows). Each point symbolises one morpho-species and its position along the axes represents the composition of traits in relation to the whole community. The top panel groups categorical traits (ellipses and colors) according to tree specialisation. The bottom panel groups categorical traits (ellipses and colors) according to conservation status, being Least concern according to the 2020 red-list of Sweden and Conservation concern being either red-listed (NT,VU,EN,CR) or belonging to the forest agency’s list of indicator species of conservation values (Roberge, 2023)

Responses of wood-inhabiting fungi from micro to macro scales

In Paper III, fungal DNA was sampled from high stumps of pine and birch ten years after their creation, to study community structures and richness of wood-inhabiting fungi. I found distinct communities on the two substrates, with greater α diversity on pine (Fig. 14A), greater β diversity on birch and similar γ diversity between pine and birch (Fig. 14B).

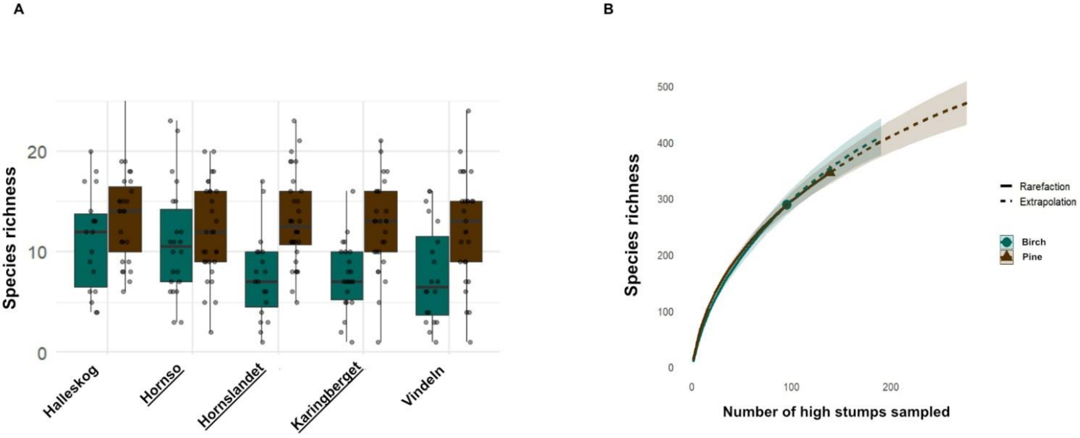

Figure 14. α-diversity (A) in each high stump by study area and tree species. Boxes represent the interquartile range (IQR), the horizontal line indicates the median, and whiskers extend to 1.5×IQR. Individual points represent observed richness per sampling unit. The study areas are ordered from south to north, ecoparks are underlined. γ diversity (B) for total species richness across all landscapes for birch and pine, illustrated with rarefaction and extrapolation curves with 95% confidence intervals.

Species richness was influenced by different environmental variables at the best-performing spatial scales (500 m for birch and 300 m for pine). Fungal richness in birch increased significantly with high stump decay stage and was positively associated with the amount of broadleaf-rich HCVF. Fungal richness in pine was negatively associated with forests of low probability of HCVF.

In terms of community composition, PERMANOVA (Table 2) analyses showed that fungal assemblages were significantly influenced by tree species, landscape, and stump decay stage, with the model explaining 18.9% of the total variation. The dominant driver of β-diversity was species turnover, both within and between pine and birch high stumps, indicating that different species replaced one another rather than species being lost.

Table 2. PERMANOVA results testing environmental variables on fungal community composition. Run on Bray-Curtis dissimilarity with 999 permutations

Factor	Df	SumOfSqs	R²	F	p
Tree species	1	11.745	0.118	34.248	**0.001**
High stump DBH	1	0.402	0.004	1.1725	0.223
High stump decay	1	0.919	0.009	2.6795	**0.001**
Local deadwood diversity	1	0.25	0.003	0.7299	0.821
Landscape	4	3.911	0.039	2.8509	**0.001**
Residual	235	80.59			
Total	243	99.403			

The indicator species analysis identified 25 significant indicator species for pine and 14 for birch. The strongest indicator for pine was *Variabilispora* sp. (Indicator value 0.85, p=0.005), and *Fomes fomentarius* (0.68, p=0.005) for birch (Fig. 15).

This study investigated how microhabitat, local, and landscape-scale factors influence fungal richness and communities in artificially created high stumps of pine and birch, a practice commonly used in northern Europe as restoration and conservation measure to benefit wood-inhabiting organisms at clearcutting in large scale (Lindbladh et al., 2007). Our results showed that fungal richness on birch stumps increased with surrounding broadleaf-rich HCVF, suggesting that landscape connectivity supports colonization, consistent with findings on spore dispersal limitations (Berglund and Jonsson, 2008; Norros et al., 2014). However, local deadwood diversity had no effect.

The higher β diversity of fungal communities in birch stumps compared to pine stumps is likely driven by multiple factors. A key explanation is the greater variation in decay stages observed among the birch high stumps. Although all stumps were created simultaneously and placed in similarly sun-exposed environments (Larsson Ekström et al., 2021), some birch stumps remained alive and sprouted new shoots, while others were already soft, decayed, and close to collapse. As decomposition advances, fungal communities shift continuously, leading to increased α diversity over time as indicated by the positive link between decay stage and species richness and greater community turnover between individual stumps. These findings underscore the importance of deadwood heterogeneity, particularly in terms of tree species and decay stages, in shaping fungal diversity. They also support earlier research highlighting how wood properties influence fungal colonization (Hoppe et al., 2016; Krah et al., 2018; Ottosson et al., 2014), while suggesting that birch high stumps may serve as more short-lived habitats for fungi.

In pine stumps, richness was unrelated to nearby coniferous HCVF but declined with increasing surrounding low-quality coniferous forests, likely reflecting broader pine-fungi distributions in conifer-dominated landscapes. Tree species was the strongest driver of fungal community structure with pine and birch supporting distinct assemblages.

The indicator species analysis for frequently occurring taxa provided valuable ecological insights. Several indicator species were identified for both birch and pine, including both well-known fungi and little-known or rarely recorded taxa. For example, *Leptodontidium trabinellum* and *Vexillomyces fraxinicola* were indicators for birch, while *Rhinocladiella atrovirens* and *Carcinomyces polyporinus* were among the indicators for pine. These findings demonstrate how DNA-based methods can help uncover the occurrence and potential host associations of both known and overlooked fungal species.

Despite the frequent use of high stumps in retention forestry, studies on their fungal communities are still rare, and we know little about how well they function as conservation substrates for wood-inhabiting fungi. This is important, as a recent review by Lunde et al. (2025), highlights that wood-inhabiting fungi are particularly negatively affected by intensive forestry practices such as clear-cutting. Our findings underscore the need to evaluate the effectiveness of artificial deadwood in supporting fungal diversity and to promote varied deadwood creation in forest management strategies.

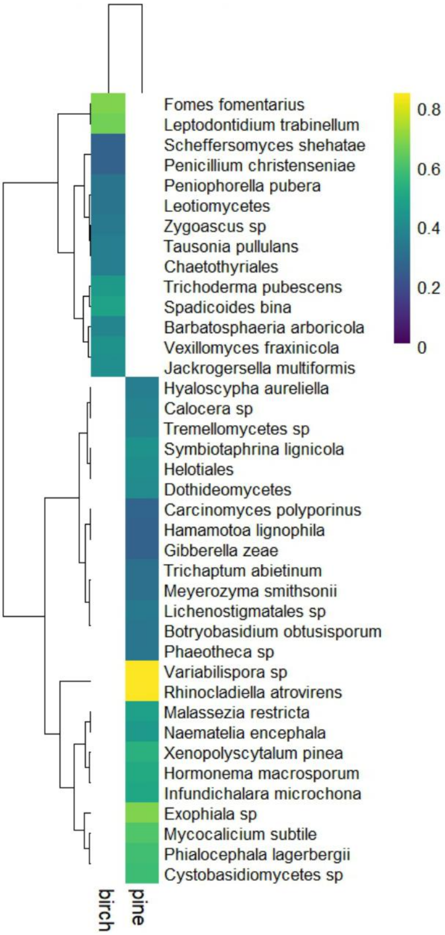

Figure 15. Heat map of indicator species analysis for fungal communities associated with pine high stumps and birch high stumps pooled across landscapes. The colour gradient represents the strength of the association (indicator value increasing from blue to yellow). Only species with a significant indicator value at α = 0.05 are shown.

5. Conclusions

The results presented in this thesis underscore the conservation value of multifunctional forest landscapes in supporting deadwood-dependent biodiversity. By integrating protected areas with active restoration and continuity of deadwood structures, ecoparks offer important refugia for saproxylic species and promote functionally diverse communities, features often lacking in intensively managed production forests.

While higher taxonomic and functional diversity, including greater occurrences of red-listed species, was found in ecoparks, these patterns cannot be fully explained by current management practices alone. The legacy of past land use and forest composition clearly plays a role. Still, my findings show that species closely associated with specific deadwood habitats were more abundant where relevant resources, such as broadleaf tree species and deadwood, were available, both locally and in the surrounding landscape. For example, broadleaf-associated species responded positively to the presence of mature broadleaf forest and broadleaf-rich deadwood.

One major conservation strategy within ecoparks is the restoration and promotion of broadleaf-dominated habitats. My results support the importance of such efforts and suggest that ongoing management actions, if maintained and scaled, have the potential to support long-term population growth for saproxylic species of conservation concern of which many are associated with broadleaved deadwood.

Throughout this thesis, a consistent and clear message emerges, diversifying deadwood is key to effective conservation. In several of the studies, the tree species of the high stump itself explained most of the variation in community structure and species richness, particularly with regard to functional diversity. Different deadwood substrates not only supported distinct species assemblages but also structured the functional trait space, indicating that various tree species provide habitat for species with different ecological roles and functions.

This provides a strong argument that conservation efforts can be significantly strengthened by actively restoring and maintaining a diversity of deadwood types within managed forests. By ensuring the presence of both coniferous and broadleaved substrates, across various sizes and decay stages, forest managers can support a wider range of saproxylic organisms and help sustain the ecological functions they provide.

Finally, this thesis underscores the importance of adopting a landscape perspective. While many valuable actions can be taken at the local scale, the spatial arrangement of habitats and the composition of the surrounding matrix are crucial. To truly support biodiversity, conservation and restoration planning must extend beyond individual stands and consider the configuration of production forests between areas of high conservation value.

In this broader context, multifunctional forest landscapes like ecoparks can play a central role. Not only do they combine ecological restoration with forestry objectives, but they also have the potential to act as dispersal nodes, harbouring source populations of deadwood-dependent species that can spread into surrounding areas, provided that enough suitable habitat is available in the landscape. By integrating these principles into forest planning, we can build more resilient forest ecosystems that support biodiversity in the long term.

6. Future perspectives

Ongoing research in ecoparks offers a valuable opportunity to deepen our understanding of how forestry and biodiversity conservation can be integrated in practice. These landscapes represent a unique arena where ambitious conservation goals are combined with active forest management, allowing researchers to evaluate the ecological outcomes of various restoration measures. The ability to study how, where, and what types of habitats that should be restored, across both local and landscape scales, is essential for developing more targeted and effective conservation strategies.

Ecoparks stand out in this thesis as landscapes that support richer and more functionally diverse communities of deadwood-dependent species compared to production landscapes. However, we still lack a comprehensive understanding of how ecoparks perform in the long term relative to large, continuous tracts of high conservation value forests, such as national parks. These areas, shaped by different histories and degrees of management, may support different species pools or ecological functions that are not fully captured within multifunctional landscapes. Future studies should therefore focus on long-term monitoring of species and functional diversity across a broader spectrum of forest types, from intensively managed areas to ecoparks and fully protected forests. Such comparative approaches will be critical for evaluating the full conservation potential of multifunctional forest landscapes and for guiding restoration efforts that not only mitigate past losses but also build ecological resilience for the future.

By continuing to explore the role of ecoparks as living laboratories for restoration ecology, we can better inform forest policy and management in the face of ongoing biodiversity decline.

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Photo: Paulina Bergmark

Popular science summary

Nothing in the forest is as alive as a dead tree. Countless fungi, beetles, and other organisms depend on deadwood for food, shelter, and reproduction. Yet, in modern production forests, deadwood has become a scarce resource and as a result, many species that rely on it are now threatened. This thesis investigates whether *ecoparks*, forest landscapes managed with both conservation and forestry in mind, can better support these deadwood-dependent species compared to conventional production forests. I used artificially created high stumps to study deadwood dependent beetles and fungi across five ecoparks and four conventional production forest landscapes. I examined how factors from the scale of an individual dead tree to the broader landscape influenced species richness and community composition of these two organism groups. I found that ecoparks typically host higher diversity of deadwood and support richer and more functionally diverse communities of beetles, especially red-listed species. One ecopark, Hornsö, known as a biodiversity hotspot, stood out as particularly important. Moreover, my study shows that both beetles and fungi respond to environmental factors at multiple scales—meaning that conservation efforts should consider not just local habitat features, but also the wider forest matrix. A recurring message throughout the thesis is the importance of *diversifying deadwood*. Different tree species and decay stages support different sets of organisms, and increasing this diversity can be a powerful and practical way to strengthen biodiversity in managed forests.

Photo: Paulina Bergmark

Populärvetenskaplig sammanfattning

Inget i skogen är så levande som ett dött träd**.** Otaliga svampar, skalbaggar och andra organismer är helt beroende av död ved för föda, skydd och fortplantning. Men i dagens moderna produktionsskogar har död ved blivit en bristvara, och som en följd är många av de arter som är beroende av den nu hotade. I denna avhandling undersöker jag om ekoparker, skogslandskap där både naturvård och skogsbruk kombineras, bättre kan bevara dessa vedlevande arter jämfört med konventionella produktionsskogar. Med hjälp av kapade högstubbar studerade jag vedlevande skalbaggar och svampar i fem ekoparker och fyra produktionslandskap. Jag undersökte hur faktorer från enstaka döda träd till landskapsnivå påverkade artrikedom och samhällssammansättning hos dessa två organismgrupper. Resultaten visar att ekoparker generellt hyser en större mångfald av död ved och stödjer rikare och mer funktionellt varierade skalbaggssamhällen, särskilt bland rödlistade arter. Min forskning visar också att både skalbaggar och svampar påverkas av miljöfaktorer på flera rumsliga skalor, vilket innebär att naturvårdsåtgärder bör ske med ett större landskapsperspektiv. Ett återkommande budskap i avhandlingen är vikten av att diversifiera död ved. Olika trädslag gynnar olika arter, och att öka denna variation kan vara ett kraftfullt och praktiskt sätt att stärka den biologiska mångfalden i brukade skogar.

Acknowledgements

I would like to begin by thanking my supervisors for your guidance and support throughout these years. Jocke, Johan, and Wiebke, thank you for challenging me, encouraging me to think critically, and always pushing me to do my best.

But above all, I want to extend my deepest thanks to you, Anne. I couldn’t have wished for a better supervisor. Your open communication, honesty, unwavering support, sharp scientific eye, and, most of all, your enormous passion for science, have truly inspired me and made me really enjoy this PhD ride.

I would also like to thank all my fantastic colleges for making me love to come to work every day, for great talks, many good laughs, enormous support each time I’ve doubted myself. Many of you have a special place in my heart, you know who you are!

Peter and Malin, thank you for always showing such enthusiasm and curiosity. Each meeting with you has left me with a feeling that this research matters and can contribute to further knowledge of how to best work with nature conservation.

Last but not least I want to thank my family for keeping my feet on the ground always reminding me of what truly matters.

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Forest Ecology and Management 490 (2021) 119107

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Can multifunctional forest landscapes sustain a high diversity of saproxylic beetles?

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ARTICLE INFO

Keywords:
Habitat amount hypothesis
Habitat heterogeneity hypothesis
Landscape ecology
Coleoptera
Forest management
Boreal forest

ABSTRACT

Intensive forestry practices have led to fragmentation of habitats that have high conservation value and has reduced the availability of deadwood in forests. This has in turn, led to a decline in species associated with deadwood (e.g. saproxylic beetles). Conservation measures have been developed in order to halt the negative trend in forest biodiversity, both at local and landscape scales. Ecoparks are large forest landscapes, with at least 50% of the forestland being managed with enhanced conservation concern including legal and voluntary protection or restoration of forests. Ecoparks aim to combine production, nature conservation and recreation (e.g. berry picking, hiking, hunting, fishing) and thereby represent multifunctional forest landscapes. The purpose of this study was to evaluate whether ecoparks can sustain greater diversity of saproxylic beetles than conventionally managed production landscapes, and whether the local habitat amount and diversity can have an additional effect on species assemblages. Two ecoparks and two representative conventional production landscapes, which implement a rotation forestry with general nature consideration, were selected for the study. Beetles were collected during three years in sun-exposed plots, where local (20 m radius) forest structures were measured. We found that both ecoparks sustained greater abundance and richness of nationally red-listed beetles (IUCN classes NT, VU, EN) and contained different beetle assemblages in comparison with conventional landscapes. Local deadwood volume had a positive relationship with the richness and abundance of saproxylic and red-listed beetles in the southern study area (long history of land-use), but not in the north (short history of land-use), partially supporting habitat amount hypothesis (HAH) at the local scale. Instead, the responses of beetles to deadwood diversity showed inconclusive results, varying between years and study areas. Our results highlight the potential of multifunctional forests in conserving biodiversity of saproxylic beetle species, especially red-listed species, as well as the importance of local deadwood availability.

1. Introduction

Fragmentation and degradation of boreal forests are severely threatening the biodiversity and function of boreal forest ecosystems (Ceballos et al., 2015; Cyr et al., 2009; Maxwell et al., 2016; Thorn et al., 2020). While natural forest ecosystems exhibit highly variable structures and dynamics, intensively managed production forests are managed in a way to produce the highest economic profit. This, in turn results in simplification of structures towards lower variation in tree sizes, as well as a more homogenous tree species composition, by favoring economically interesting trees (Cyr et al., 2009; Östlund et al., 1997; Shorohova et al., 2011). Changes in structures have, directly or indirectly caused a decline and extinction threat to hundreds of species dependent on natural forest structure and composition (ArtDatabanken, 2020; Hyvärinen et al., 2019). A straightforward solution to halt the decline of species dependent on forests would be to protect valuable habitats (such as national parks, large-scale nature reserves). However, to efficiently conserve a diversity of focal forest species, management practices must include consideration of biodiversity both within and outside formally protected forest landscapes (Lindenmayer et al., 2006).

The new integrated forestry model gives equal emphasis on production and environmental goals, and emphasizes forest management planning from a landscape perspective, to sustain the full complement of forest biota and their supporting natural systems (Gustafsson and Perhans, 2010; Poiani et al., 2000; Puettmann et al., 2012). This includes the implementation of retention forestry (Franklin, 1989; Gustafsson et al., 2012) and restoration measures such as prescribed burning and deadwood enrichment (Halme et al., 2013; Koivula & Vanha-Majamaa,

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https://doi.org/10.1016/j.foreco.2021.119107
Received 11 December 2020; Received in revised form 22 February 2021; Accepted 24 February 2021

2020) within a matrix of production landscapes. Also, Green Infrastructure planning (European Commission, 2013) calls specifically for the implementation of landscape planning when dealing with activities that exploit nature, *i.e.* manage forests in such a way that enhances connectivity between high conservation value forests (Angelstam et al., 2020). A multiscale conservation approach aims to maintain connectivity, landscape heterogeneity, structural complexity and implementation of natural disturbance regimes (Angelstam and Bergman, 2004; Lindenmayer et al., 2006). A landscape approach can also sustain a higher variability of valuable habitats and maintain the multifunctionality of forests, where the forests are simultaneously used for timber and non-timber production, conservation and recreation (Gustafsson and Perhans, 2010; Kruys et al., 2013).

To implement a landscape perspective in their forest management, the state-owned forest company Sveaskog (owning 14% of forests in Sweden and being the largest forest owner in Europe), established large forest landscapes, called ecoparks, with the goal of combining production forestry with biodiversity conservation (Angelstam and Bergman, 2004; Dawson et al., 2017). Today, there are 37 ecoparks located throughout Sweden from north to south, and by covering ca. 170,000 ha of productive forestland it is thus the second biggest GI project in Sweden after Natura 2000. The management plan of an ecopark, aimed at recreating and maintaining a high quality matrix, includes restoration activities such as prescribed burnings, restoration of wetlands, and recreation of deciduous stands (Angelstam and Bergman, 2004). Protected or unmanaged areas have been stated to be more species-rich than surrounding areas or managed forests (Coetzee et al., 2014; see also Halme et al., 2010; Paillet et al., 2010), but similar comparisons between multifunctional forest landscapes and conventionally managed forest landscapes are still lacking.

The literature on the effects of landscape configuration on biodiversity is still limited (Sverdrup-Thygeson et al., 2014), and no consensus has been reached for the relative importance of local- versus landscape-scale determinants on forest biodiversity (Fahrig, 2013; Hanski, 2015; Komonen & Müller, 2018; Ranius et al., 2019). Few studies have examined the importance of landscape properties for beetle species communities. Landscapes richer in old forests (Gibb et al., 2006; Olsson et al., 2012) and suitable habitats (Bergman et al., 2012; Rubene et al., 2017), or with shorter forest management history (Kouki et al., 2012) play an important role for saproxylic beetles. The importance of connectivity between high quality habitats seems especially important for red-listed saproxylic species due to their specific habitat requirements and higher sensitivity to fragmentation attributable to their lower dispersal abilities (Henle et al., 2004; Nordén et al., 2013; Siitonen, 2001). In addition to landscape configuration, local resources play a vital role in focal species populations, and should not be disregarded in landscape scale studies. The habitat amount hypothesis (HAH) predicts that species richness and abundance increase with the amount of a given habitat irrespective of its configuration in a local landscape (Fahrig, 2013), *i.e.* as long as the amount of habitat is not reduced within a given landscape, the effects of fragmentation should have only negligible effects on species communities. Habitat amount hypothesis has been supported by studies examining several taxonomic groups (Gao et al., 2015; Haeler et al., 2021; Seibold et al., 2017; Watling et al., 2020). However, there are studies rejecting this hypothesis as well (Evju and Sverdrup-Thygeson, 2016; Haddad et al., 2017). Furthermore, Saura (2020) suggests that the hypothesis has been misinterpreted and "erroneously viewed as negating or diminishing the relevance of fragmentation effects," thereby emphasizing the importance of including landscape in assessments of local resources.

The habitat heterogeneity hypothesis (HHH, Whittaker, 1972) states that with increased habitat heterogeneity, species richness increases, and the hypothesis has gained support in many biological communities (González-Megías et al., 2011; Hamm and Drossel, 2017; Seibold et al., 2016). Diversity of deadwood, considering the different species, decay stages, sizes and postures (i.e. lying, standing) of dead trees and type of deadwood, has shown to be an important driver of saproxylic beetle richness in a number of studies, stating the importance of habitat heterogeneity (Bouget et al., 2013; Brin et al., 2011; Gao et al., 2015; Similä et al., 2003).

The assemblages of saproxylic beetles are thus related to both local habitat and landscape configuration, and the effects of landscape and local scales can be intermixed (Saura, 2020; Bergman et al., 2012). In this study, the aim is to evaluate the importance of multifunctional forest landscapes for saproxylic beetles while accounting for the effects of local habitat availability and heterogeneity (deadwood volume and diversity). We use two large (~10,000 ha) ecoparks and their respective conventional production landscapes as our study system to analyse the effects of land use on a landscape level and local habitat amount (deadwood volume) and heterogeneity (deadwood diversity) on saproxylic beetles (Coleoptera). We created 26 permanent sun-exposed sampling plots including high stumps of one Scots pine and one Silver birch in each of the four landscapes, and sampled beetles from the same plots for three consecutive years. First, we examined the general effect of the landscape on the richness and abundance of saproxylic and red-listed beetles. Second, we determined if there was an interaction between landscape and local resources, applying the habitat amount (HAH) and habitat heterogeneity hypotheses (HHH) in these different landscapes.

We hypothesized that (I) ecoparks hold higher species richness and abundance of saproxylic and red-listed beetles than their respective reference conventional production sites, (II) species richness and abundance of saproxylic and red-listed beetles increase with increasing deadwood diversity (HHH) regardless of landscape management regime, (III) species richness and abundance of saproxylic and red-listed beetles increase with increasing volumes of deadwood (HAH) regardless of landscape management regime, and (IV) ecoparks contain different beetle community assemblages than conventional production landscapes.

Our study is unique in its assessment of multifunctional landscapes (ecoparks) and is the first step in a long-term project exploring the importance of such landscapes and their effects on biodiversity. Our study contributes to landscape management of forests and supports the aim to reach the United Nations sustainable development goal 15 to "halt and reverse land degradations and halt biodiversity loss" (United Nations, 2020).

2. Materials and methods

2.1. Study area and sites

The study was conducted in two ecoparks and two conventionally managed production landscapes in Sweden. Each ecopark is paired with a conventionally managed production landscape to minimize environmental and management variations. Thus, the pairs are close in vicinity, have similar forest types and topographies, are continuous landscapes and are owned by the same forest company. In northern Sweden, ecopark Käringberget with its production landscape Vindeln in the central boreal zone (Ahti et al., 1968) were selected as study areas (Fig. 1). In southern Sweden, Ecopark Hornsö with production landscape Hälleskog in the hemiboreal zone (Ahti et al., 1968) were selected as study areas (Fig. 1). Ecopark Käringberget was established in 2005, having a long history of fire. It is dominated by Scots pine and Norway spruce (*Picea abies L. H.Karst)* with some elements of birch (*Betula pendula Roth., Betula pubescens Ehrh.)* and aspen (*Populus tremula L.)* (Sveaskog, 2005). Ecopark Hornsö was established in 2004 to preserve and restore valuable habitats, such as old-growth pine and deciduous stands. It is mainly dominated by Scots pine (*Pinus sylvestris L.)* with pedunculate oak (*Quercus robur L.)* and beech (*Fagus sylvatica L.)* occurring frequently as well. Up until the 1900′s, fire was a frequent disturbance in this landscape, which has greatly affected the state of the landscape (Sveaskog, 2008). Both ecoparks have similar distributions of forests of conservation concern and production forests, with a majority of conservation

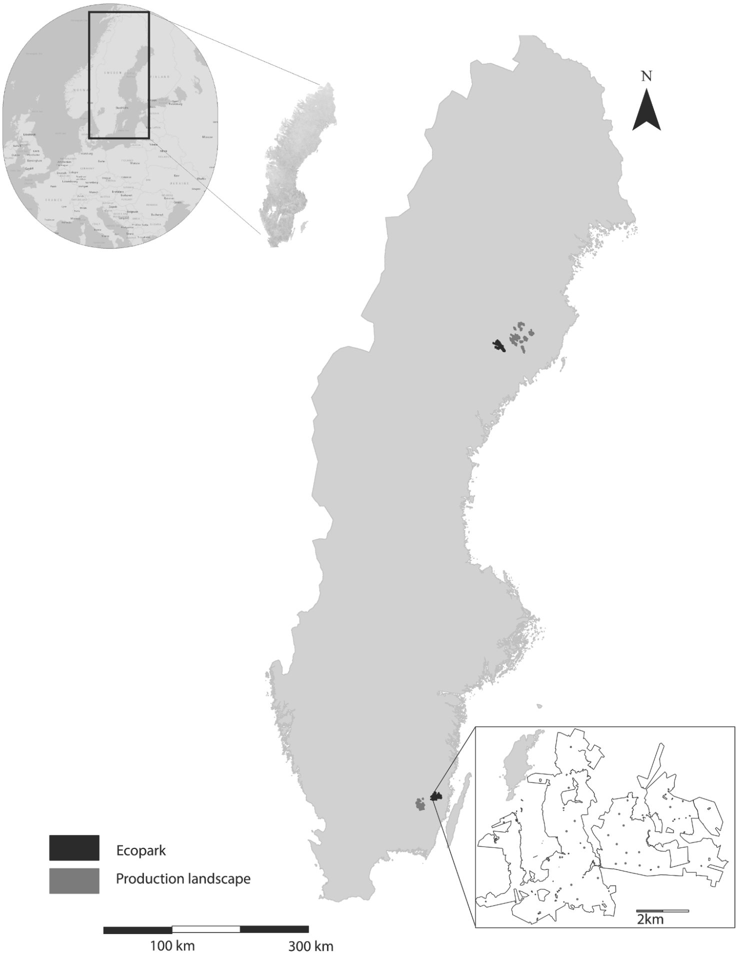

Fig. 1. Location of the study areas in the Northern (ecopark = Käringberget, conventional production landscape Vindeln) and Southern (ecopark = Hornsö, conventional production landscape = Hälleskog) Sweden, and an example of the distribution of study plots within a study area (dots in inset map).

forests being restoration sites, whereas the conventional production landscapes are highly dominated by production forest sites (Table 1). Both ecoparks also consist of greater proportions of forests in higher age classes than their respective production landscapes (Appendix A, Fig. A.1). Production forests refer to productive forestland (growth more than 1 m^3/ha/a) that are subject to forestry (thinning, rotation cutting, soil scarification etc.); conservation concern refers to all productive forestland exempted from forestry. Within forests of conservation concern there are three further classifications: 1) Restoration, where measures are being taken to restore natural values or structures by prescribed fires, deadwood enrichment and, as an example, benefiting deciduous trees through removal of spruce; 2) Set-aside, areas that are voluntarily set-aside from forestry; and 3) Protected, areas that are legally protected from exploitation.

2.2. Sampling design

The aim was to sample beetles from similar conditions in each of the landscapes. Therefore, “trapping stations” (hereafter ‘plots’) that consist of two sun-exposed high stumps of similar diameter and tree species across the landscapes were developed. In this way, trapping effectiveness was ensured to be equal between landscapes and to catch species of similar successional stages. The target species were early successional beetle species dependent on deadwood. In each landscape, 26 plots were chosen according to following criteria: 1) plots must be at least 1000 m from each other, to ensure independent sampling units within a landscape, 2) the plot contains at least one living pine and one living birch with a diameter of approximately 25 cm and which are located two to five meters from each other, 3) the plot is easily accessible from gravel roads, 4) the plot is sun-exposed towards south-west (edges were preferred). In each plot, the selected birch and pine trees were cut into 2.5 m high stumps in 2010 in northern Sweden and 2011 in southern Sweden. In a few cases, two pines or two birches were chosen when suitable trees were not found, and were not included in the analyses of this study, resulting in 18–19 plots per landscape in the final analysis in southern Sweden and 25 in northern Sweden. The selected stumps were sun-exposed by removing shading trees from south and west. The removed trees were not left in the stands, in order to not artificially

Table 1

Location, area distribution and dominating vegetation for each landscape in the study. The size includes all land, productive and non-productive. Other areal distribution information is productive forestland. Percentages of restoration, set-aside and protected areas are calculated from the total of conservation concern areas.

Area	Northern Sweden		Southern Sweden	
Landscape	ECOPARK	PRODUCTION	ECOPARK	PRODUCTION
Site name	Käringberget	Vindeln	Hornsö	Hälleskog
Coordinates	64° 04′ N;18° 41′ E	64° 03′ N;18° 43′ E	57° 00′ N;16° 09′ E	56° 50′ N;15° 39′ E
Mean annual Temperature[1]	2.5 °C	2.5 °C	7.8 °C	7.8 °C
Mean temperature (June-August)[1]	13.6 ± 2.3	13.6 ± 2.3	16.2 ± 1.2	16.2 ± 1.2
Mean annual Precipitation[1]	705 mm	705 mm	513 mm	513 mm
Size (ha)	13,963	21,181	9242	9144
Production (ha)[2]	5786 (53.7%)	20,066 (94.7%)	4438 (52.5%)	8570 (93.7%)
Conservation concern[2]	4989 (46.3%)	1115 (5.3%)	4014 (47.5%)	574 (6.3%)
-Restoration	2817 (26.1%)	18 (0.1%)	3227 (38.2%)	124 (1.4%)
-Set-aside	1615 (15%)	331 (1.6%)	485 (5.7%)	381 (4.2%)
-Protected	557 (5.2%)	766 (3.6%)	302 (3.6%)	69 (0.8%)
Dominating Vegetation[3]	VT (38%),MT (27%)	VT (46%),MT (27%)	CT (38%),MT (35%)	CT (46%),MT (12%)

[1] Data on mean temperatures and precipitation were from the Swedish Meteorological and Hydrological Institute (2019).

[2] Productive forest (FAO, 2012).

[3] Vegetation classes according to Cajander (1926) as follows: VT – Vaccinium type. Dwarf shrub vegetation dominated by *Vaccinum vitis idaea.* MT – Myrtillus type. Dwarf shrub vegetation dominated by *Vaccinium myrtillus* accompanied by *V. vitis idaea.* CT – Calluna type. Dwarf shrub vegetation dominated by *Calluna vulgaris.*

affect the local deadwood availability. Thus, due to partial tree removal from the plots, the local tree stand structure is not a representative sample describing the whole landscape.

2.3. Beetle sampling and classification

The beetles were sampled using two small flight-intercept traps per high stump, similar to Kaila (1993). The traps consisted of a 10 × 20 cm, 2 mm thick, transparent Plexiglas sheet that was attached to the trunk of each high stump, with a 0.5-liter aluminium mould beneath the Plexiglas to capture insects. Propylene glycol diluted to ca 60 percent with a small amount of detergent to decrease the surface tension was used as preserving liquid in the traps. The traps were placed at the heights of 1.1 and 1.6 m from the ground, facing south. The traps were set at the end of May or the beginning of June and removed at the end of July, covering the main flight period of beetles (June-July). The traps were emptied twice in each sampling season for three consecutive years, 2010–2012 in northern and 2011–2013 in southern Sweden. The beetles were then identified to species or genera level, separate for each high stump, by expert taxonomists (same experts throughout the years, one in the southern region and another in the northern region). The main purpose of species identification was to identify saproxylic beetles with high conservation value, thus some families known not to be deadwood dependent were ignored. Conservation status was determined by the national red-list of Sweden in 2010 (Gärdenfors, 2010), because the findings of this project may have affected the later threat statuses of red-list assessment in 2015 and 2020.

Precision of species identification was higher in the northern than in the southern region (Appendix E for the full species lists in both regions). Thus, species counts in northern and southern regions are not comparable. However, comparisons between production landscape and ecopark within the same geographical regions are valid.

2.4. Field measurements

Measurements on tree stand structure were carried out in circular sample plots (20 m radius) around the high stumps in 2019. Since the wood decomposition in boreal forests is a slow process, and since we saw no traces of major disturbances, we deemed the time lag between beetle trapping and field measurements to be of negligible importance, and the relative differences between landscapes to be valid. Living tree diameters at breast height (1.3 m, DBH) were recorded for each tree with a DBH $\geq$ 4.5 cm and a height of $\geq$1.3 m as well as their respective tree species. *Betula pendula* and *B. pubescens* were classified as birch, and *Q. robur and Q. petraea (Matt., Liebl.)* as oak.

In order to measure canopy closure, hemispherical images were taken using a fish-eye lens. These images were then processed in ImageJ (Schneider et al., 2012) using the plugin Hemispherical 2.0 (Beckschäfer, 2015) to obtain values for canopy gap fraction.

The species, DBH, height and decay class was recorded for standing and lying dead trees (logs). For deadwood logs $\geq$4.5 cm in diameter and at $\geq$1.3 m in length two diameters were measured; the top (to a minimum value 4.5 cm) and base diameters. Tree types were classified into; standing dead tree, snag (standing tree with a broken top) or deadwood log.

Four decay classes were used to describe the decomposition stage of deadwood logs, adjusted from Gibb et al. (2005): (1) Hard wood with intact bark $>$50%, (2) Hard wood with smooth surface beginning to soften, $<$50% bark remaining, (3) crevices and holes, soft wood surface, free of bark, (4) soft wood, possibly with a hard core remaining, hard to define surface and outline. The deciduous trees in later decay stages (3–4) were classified by judging by the softness of the wood, and not the percentage of bark, by using a knife. Some deciduous trees such as birch might maintain most of its bark even though most of the wood is decomposed. Standing trees and snags were classified according to Jung et al. (1999) and Thomas (1979). Cajander's vegetation classification was used in order to categorize the field vegetation (Cajander, 1926). Vegetation was classified according to the dominating type, in cases where the vegetation type was shifting, the two most dominating types were chosen.

2.5. Calculations

Both living trees and all deadwood were divided into diameter classes, starting from 4.5 to 9.9 (saplings and fine woody debris), 10–19.9, 20–29.9 and so on up to $>$50 cm (coarse woody debris), to a total of six different diameter classes. Basal area of living trees and deadwood volumes were converted to per hectare values for each plot. Living tree and deadwood diversity index was calculated, modified by Siitonen et al. (2000) and Hekkala et al. (2016). Living tree diversity in a plot was defined as a number of unique combinations of tree species and diameter class. Deadwood diversity was defined as a number of unique combinations of tree species, diameter class, type of deadwood (standing/snag/log) and decay stage.

Volumes of intact standing dead trees classes 3–5 (Thomas, 1979) were calculated based on diameter and height. Brandel's functions for pine, spruce and birch for Northern and Southern Sweden were used (Brandel, 1990). Birch functions were used for all broadleaves $>$6 m (Brandel, 1990). Volumes of logs and snags were calculated as cylinders based on diameter and height/length. Broadleaves $<$6 m were calculated as cylinders using DBH (see Appendix B. for the formulas of calculating volumes).

2.6. Data analyses

All beetle catches were pooled for each plot (four traps per plot), per landscape and year. Plots with missing traps or stump pairs of the same tree species were dropped from the analyses. Species richness and abundance for all saproxylic and red-listed beetles were used as response variables. R version 3.5.1 was used for all analysis (R development core team, 2018).

Linear models (LM) were used to test differences between ecoparks and production landscapes in tree stand structure measured from 20 m radius plots. Generalised linear models (GLMs) and generalised linear mixed effect models (GLMMs) using the lme4-package (Bates et al., 2014) with Poisson error distribution for count data were used to explore relationships and differences in species richness (α-diversity) and abundance between deadwood volume (HAH) and diversity (HHH) as well as between landscapes. Deadwood volumes were log-transformed prior to testing. Normality of residuals and homogeneity of error variance were checked with diagnostic plots.

The differences in total saproxylic species richness (γ-diversity) between ecopark and production landscape were compared by using rarefaction and extrapolation curves based on equal sample sizes (abundance) per landscape (package iNEXT (Hsieh et al., 2016)). GLMM was used to test landscape and deadwood effects on saproxylic beetle richness and abundance, using plotID and Year as random factors to account for repeated measures from the same plots and yearly variations (due to weather conditions and assemblage change during decay succession). When the variation of Year was small (less than 0.01), it was excluded as redundant variable from the analyses, and only plotID was used. PlotID is a unique factor value for each plot, so each plotID was sampled three times. When testing landscape and deadwood effects for red-listed beetles, GLM was used for each year of collected insect data separately, to ensure model convergence. The richness and abundance of saproxylic and red-listed beetles were modelled using three sets of explanatory variables 1) landscape only, 2) landscape*deadwood volume, and 3) landscape*deadwood diversity. The best model was selected by using the Akaike Information Criteria (AIC), integrated in bbmle-package (Bolker, 2020), the models with ΔAIC ranging between 0 and 2 were considered the best models (Anderson et al., 1998; Burnham and Anderson, 2004). The model with lowest AIC is given in the results, and the other best models are given in Appendix (Table C1.)

Beetle community assemblages were visualized by non-metric multidimensional scaling (NMDS) using the vegan package (Oksanen et al., 2017), and then analysed with Permutational Multivariate Analysis of Variance Using Distance Matrices (Adonis), using year as stratified variable (Species ~ landscape, strata = Year. Permutations = 1000). Northern and southern study areas were treated separately.

In order to test hypothesis I, landscape was used as fixed explanatory variable. To test hypothesis II, the landscape and deadwood diversity were used as fixed explanatory variables (landscape * deadwood diversity, when no interaction was detected, the interaction term was removed). To test hypothesis III, landscape and deadwood amount were used as fixed explanatory variables, similarly as with deadwood diversity. To test hypothesis IV, NMDS was used to illustrate the community assemblages and Adonis was used to test the differences in assemblages. An indicator species analysis (Dufrêne and Legendre, 1997) was conducted using the multipatt-function in the indicspecies package (De Cáceres, 2019), to reveal the most influential species in different landscapes. Landscape was used as a variable for site groups, with 999 permutations.

3. Results

In total, 54,916 individuals of 303 saproxylic beetle species and 224 individuals of 24 red-listed beetle species were found in the northern study area. In the southern study area, respective numbers were 19, 463 individuals of 261 saproxylic beetle species and 449 individuals of 48 red-listed beetle species (Table E.1). Ecoparks were characterized by a higher local deadwood volume and diversity in both the northern and southern study areas, living tree diversity and basal area was greater in the southern ecopark compared to production landscape (Table 2). The stump diameters were greater in the ecopark in the south but not in the north (Table 2).

3.1. Hypothesis I ecoparks vs production landscapes

In the northern study area, the rarefied γ-diversity and α-diversity of saproxylic beetles were similar in ecopark and production landscape (Figs. 2a and 3a). The beetle abundance was significantly lower in the northern ecopark (Fig. 3a). On the contrary, in the southern study area the rarefied γ-diversity was higher in the ecopark (Fig. 2b). In addition, the α-diversity was higher in the southern ecopark in comparison with the production landscape (Table C.1A1, $p = 0.008$). Richness and abundance of red-listed beetles were higher in the ecopark in comparison with conventional management in both northern and southern areas (Fig. 3).

3.2. Hypothesis II (Habitat heterogeneity)

According to model comparisons, deadwood diversity had no additional effect on the richness or abundance of saproxylic beetle species in the north, as the inclusion of deadwood diversity in addition to landscape did not improve the models of saproxylic richness or abundance (Fig. 3, Table C.1). However, deadwood diversity had a negative relationship with richness and abundance of red-listed beetles during the first year in the northern area (Fig. 4a, Table C.2). Furthermore, there was an interaction between landscape and deadwood diversity, meaning that during the third sampling year in the northern ecopark, deadwood diversity had negative relationships with the abundance of red-listed species.

In the southern study area, deadwood diversity had positive effects on saproxylic species richness ($p = 0.008$) and abundance ($p = 0.009$) (Table C.1), but the model including deadwood diversity had higher predictive error (higher AIC) in comparison to the model including deadwood volume. During the first sampling year, the abundance of red-listed beetles and deadwood diversity had positive relationships, and the interaction between landscape and deadwood diversity revealed a negative relationship between red-listed species abundance and deadwood diversity in the ecopark (Fig. 4b).

3.3. Hypothesis III (Habitat amount hypothesis)

In general, local deadwood volume had no relationship with saproxylic beetles in the north, but positive in the south where it best explained the variation in α-diversity of saproxylic beetles (Fig. 3, Table C.1). In addition, the richness and abundance of red-listed species had a positive relationship with deadwood volume in the southern study area (Fig. 4b). There was an interaction between deadwood volume and landscape, meaning that the deadwood volume had negative relationship with the richness (first year) and abundance (second year) of red-listed beetles in the southern ecopark (Fig. 4b, Table C.2).

3.4. Hypothesis IV saproxylic beetles' assemblage structure

The beetle assemblages differed between the landscapes both in the northern, (Adonis: $F = 3.16$, $p \leq 0.001$, Fig. 5a), and southern study areas (Adonis: $F = 6.94$, $p \leq 0.001$, Fig. 5b), but the difference was more clear in the south. Indicator species analysis showed that in the northern landscapes, more species were found to be indicators to conventional landscape (20 significant indicators, Table D.1), than to ecopark (9

Table 2
Stand structure in study areas. Mean ± S.E. given. P-values are based on linear models (LM). Numbers highlighted as bold hold significance, $p < 0.05$.

Landscape	**Southern Sweden**		**p**	**Northern Sweden**		**p**
	PRODUCTION	ECOPARK		PRODUCTION	ECOPARK	
N (plots)	19	18		25	25	
Stump diameter (cm)	Pine 27.4 ± 5.3	32.4 ± 4.8	**0.004**	29 ± 6.3	25.9 ± 5.4	0.073
	Birch 22.8 ± 2.9	27.2 ± 5.5	**0.004**	23.5 ± 5.6	23 ± 5.3	0.75
Basal area of living trees (m^2/ha)	9.4 ± 0.5	14.6 ± 0.7	**0.001**	10 ± 0.8	12.7 ± 0.6	0.05
Living tree Diversity	8.3 ± 0.3	12.2 ± 0.4	**<0.001**	7.6 ± 0.4	9 ± 0.3	0.1
Deadwood volume (m^3/ha)	4.4 ± 0.2	9.3 ± 0.6	**0.02**	6.6 ± 0.6	11.6 ± 1.7	**0.047**
Deadwood Diversity	7 ± 0.3	9.5 ± 0.5	**0.02**	7.6 ± 0.5	12.2 ± 0.8	**0.004**
Canopy closure (%)	27 ± 0.01	37 ± 0.02	**0.001**	40 ± 0.02	38 ± 0.01	0.5

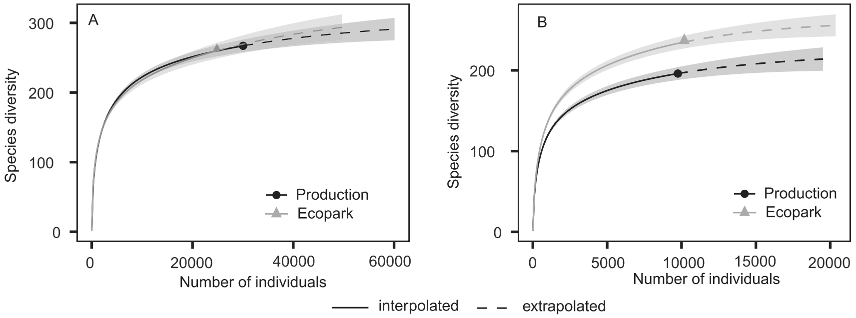

Fig. 2. Rarefaction plots with 95% confidence intervals (shaded areas) comparing the γ-diversity of saproxylic beetle in ecoparks and conventional production landscapes. A) Northern study area, B) Southern study area.

species, one being red-listed). In the southern landscapes, the ecopark had 37 significant indicator species, of which 10 red-listed species and conventionally managed forests had eight significant indicator species/genera, without any red-listed species (Table D.1).

4. Discussion

We found that ecoparks host a greater diversity and abundance of red-listed beetles compared to conventionally managed production landscapes supporting our first hypothesis. In southern Sweden, also the species richness of all saproxylic species was higher in the ecopark. We

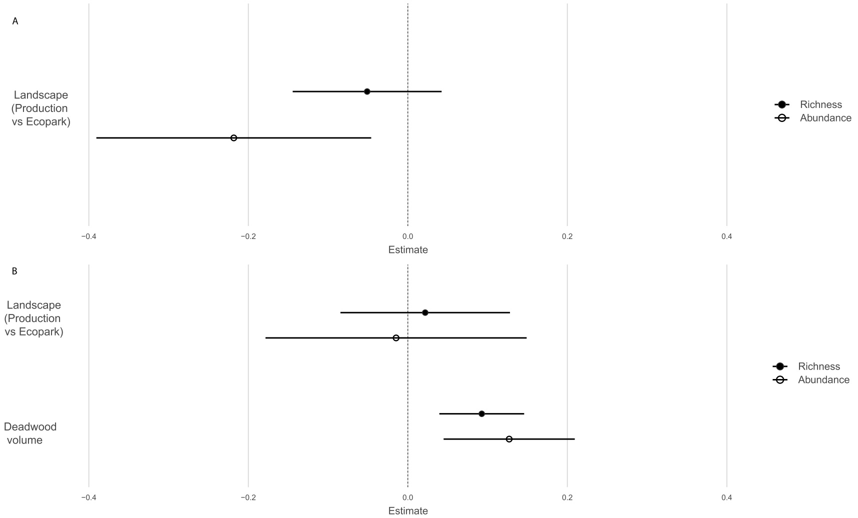

Fig. 3. GLMER results for saproxylic beetles. For significance, estimate + SE bar must not cross the 0.0 line. The further away from 0, the larger effect. Only the best performing model results for each response variable is shown (see Appendix C for all models). (a) = northern study area. (b) = southern study area.

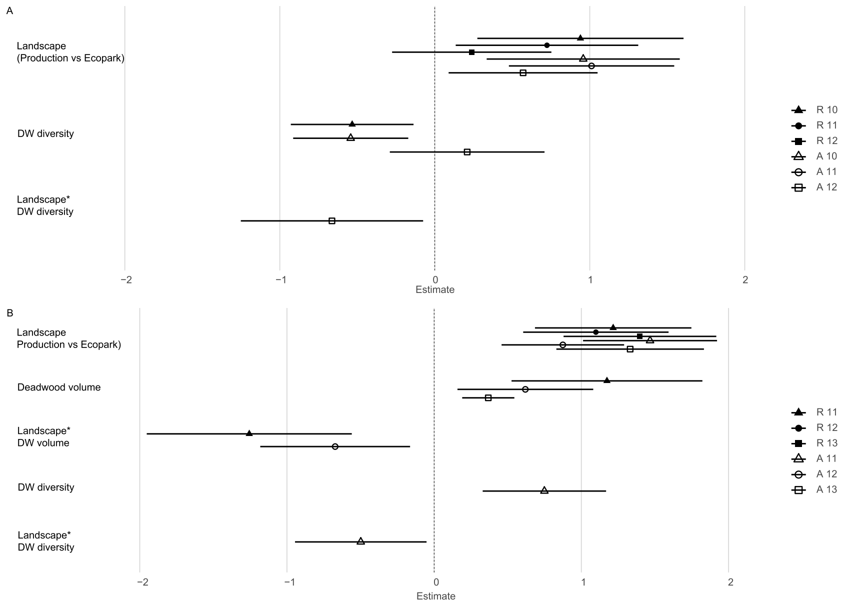

Fig. 4. GLM results for red-listed beetles separate for each year of beetle trappings. Only the best performing model for each response variable is shown (Table C.2 for all models). For significance, estimate + SE bar must not cross the zero line. The further away from 0, the larger effect. (a) = northern study area, (b) = southern study area. R = richness. A = abundance, number depicts the sampling year (2010–2013).

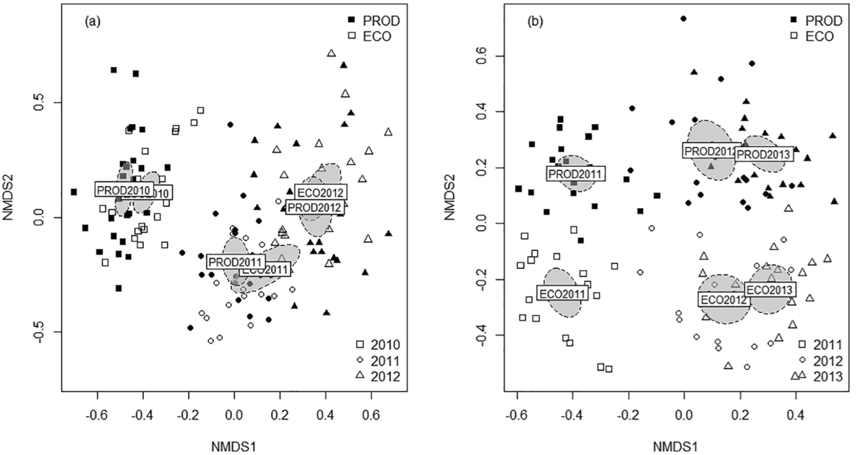

Fig. 5. NMDS plot visualizing differences in beetle community assemblages between landscapes and years in (a) northern study area, stress = 0.18 and (b) southern study area, stress = 0.19. Ellipsoids visualize the centroids of landscapes and years with standard error, conf = 0.95. Mind differences in axis scales. All saproxylic beetles are included.

also found that species assemblages differed between ecoparks and conventional landscapes, supporting our hypothesis IV. These results support adapting a landscape perspective for the conservation of beetles. It should however, be stated that, although these ecoparks might do better than conventionally managed landscapes, we do not know how well they fare compared to large natural forest landscapes, such as national parks. Our results also give partial support to the habitat amount hypothesis (HAH) as the local volume of deadwood had a positive relationship with saproxylic and red-listed beetle abundance and richness in southern Sweden. We only found weak support for the habitat heterogeneity hypothesis (HHH) and can therefore neither accept nor reject this hypothesis.

4.1. Ecopark versus conventionally managed landscapes

Our result showing that ecoparks contain higher richness and abundance of red-listed beetles in comparison to production landscapes can be due to a generally higher local deadwood volume and diversity as well as to the management of the landscapes. The difference in γ-diversity of beetles in the southern region can indicate higher habitat heterogeneity between plots in the ecopark, as the ecopark contained more diverse species assemblages. The local structural differences between ecopark and its respective production landscape (e.g. living tree variables, stump diameters, canopy closure and deadwood volume) are more pronounced in the south, while they are more similar in the north. This may be a result of a more intensive land-use and a longer history of exploitation in the southern production landscape in comparison to northern Sweden (Fridman, 2000; Fridman and Walheim, 2000). During the second and third year of trapping, richness of red-listed species was best explained by the landscape (as a whole), emphasizing the importance of the management regime of landscapes in addition to local resources. These results are in line with other studies showing the importance of landscape composition for threatened species and the general species richness (Coetzee et al., 2014; Hallinger et al., 2018; Ranius et al., 2019; Ranius and Fahrig, 2006). In our study, we did not explicitly investigate the deadwood availability or habitat configuration at larger spatial scales, limiting our possibilities to extinguish the variables causing this effect. The ecoparks, however, contain larger forest areas of conservation concern, including woodland key habitats (WKH, defined as an area with high conservation value in which red-listed species occur or are likely to occur (see e.g. Timonen et al., 2010), and an age structure with higher proportions of old (>120 years) forests (Table 2 and Fig. A.1), which probably have had a positive effect on species assemblages therein. This argument is supported by, for example, Götmark et al. (2011), who concluded that the area of WKHs within a radius of 1 km had great positive effect on oak beetles. Spatially explicit data analyses are needed in order to ensure the cause of the effects (Bergmark et al, unpublished).

In contrast to red-listed species, the α-diversity (richness) and abundance of all saproxylic species was similar or even lower in the ecopark in comparison to the production landscape. Saproxylic beetles are often found in great amounts after disturbances where dying and dead trees are created; including clearcutting (Hyvärinen et al., 2005; Toivanen and Kotiaho, 2007) and it is therefore not surprising to find a similar number of species in the ecopark and conventionally managed landscape in the north.

Both ecoparks however, hold distinguished assemblages of saproxylic beetles in comparison to their respective production landscape, which indicates that ecoparks house species assemblages that are not found to the same extent in the managed landscape, also shown in our indicator species analysis.

The indicator species for the southern ecopark are largely confined to specific broadleaf tree species or to broadleaves in general, contrasting its reference site having only generalist species as indicators. Furthermore, there is a great abundance of red-listed indicator species in the southern ecopark, all being niched to either large or small diameter deadwood and with many of them being only found in that part of the country (e.g. *Xylotrechus antelope* (Schöenherr, 1817)*, Strangalia attenuata* (Linnaeus, 1758)*, Poecilium alni* (Linnaeus, 1767)). This goes well in line with the distinguished species communities between ecopark and conventional production landscape in southern Sweden (Fig. 5). This further emphasizes the importance of maintaining an array of available substrates, such as deadwood of varying sizes (Brin et al., 2011; Lindhe and Lindelöw, 2004; Similä et al., 2003). We did not find the same distinction between indicator species in the two northern sites. For example, most of the red-listed species (13/24, Table E.) were found from both landscapes, but in greater abundance in ecopark. Although forestry activities are performed within the ecoparks, there are still large areas that are exempted from forestry and possibly host species not found in intensively managed landscapes.

4.2. Deadwood diversity in relation to saproxylic species

Several previous studies have shown a positive relationship between diversity of local deadwood (Bouget et al., 2013; Seibold et al., 2016; Similä et al., 2003) or stand structure (Janssen et al., 2009; Joelsson et al., 2018) and the diversity or richness of beetle species. In our results, the relationship between deadwood diversity and beetle diversity or abundance was somewhat inconclusive. In the models that did show a positive relationship between red-listed species and deadwood diversity, there was also an interaction with the landscape indicating a negative relationship within ecoparks (see Tables C.1, C.2). Deadwood volume seemed to have a better explanatory power in our models, however, giving less significance to deadwood diversity in our study. Therefore, we can neither give full support to nor disregard the habitat heterogeneity hypothesis in this study. It should also be stated that the volume and diversity of deadwood can be strongly correlated, and difficult to separate (Kunttu et al., 2015; Seibold et al., 2016).

4.3. Deadwood volume in relation to saproxylic species (HAH)

Results of this study partially supported the habitat amount hypothesis, that increasing local habitat (deadwood) amount positively affects species richness, as in the southern region the deadwood volume was a better predictor of the α-diversity of beetles than the landscape. As deadwood diversity and volume was tested separately, and deadwood volume showed more conclusive results, our results are in support of deadwood amount as being an important driver of saproxylic beetle richness. This goes in line with several previous studies of habitat amount, among a range of organism groups (Fahrig, 2013; Haeler et al., 2021; Melo et al., 2017; Percel et al., 2019, 2018; Seibold et al., 2017; Watling et al., 2020). However, as noted by Seibold et al. (2016), abiotic factors may have combined effects with biotic factors as shown by their finding that deadwood volume was more important than deadwood diversity in sun-exposed habitats, similar to this study. Several studies also dictate that not only one factor of deadwood or habitat characteristics matter, but rather several, or a combination of several different characteristics (Kunttu et al., 2015; Lassauce et al., 2011; Martin, 2018; Similä et al., 2003), which seems to be the case in our study as well.

4.4. Management of the forest landscape

In some cases, we found negative relationships between beetle species richness or abundance and deadwood volume or diversity, especially in the ecoparks (Fig. 4). There is a plausible explanation for this, which however requires further investigations beyond this study. The intermediate landscape-complexity hypothesis, mainly with support from agricultural landscapes (Tscharntke et al., 2012) suggests that the complexity of the landscape dictates the effectiveness of conservation and restoration work. In complex landscapes with more than 20% non-crop areas, local conservation work would have a lower effect due to the overall high biodiversity in the landscape. In intermediate complex landscapes, local conservation work would have a large effect, due to the overall lack of complexity or biodiversity (Jonsson et al., 2015). If an ecopark represents a more complex landscape, with approximately 50% forests exempt from forestry, then production sites represent intermediate complexity, with their 5–6% forests exempted from forestry. Our results showing negative (or no) relationships between local deadwood and richness and abundances of saproxylic beetles in ecoparks, and positive relationships in the production landscapes, is in line with the intermediate landscape-complexity hypothesis, which, although originating from agricultural systems, has had some support in forest systems (Mori et al., 2017; Pardini et al., 2010; Rubene et al., 2017). Landscape complexity could also explain why the differences in community assemblages and red-listed species richness and abundance between ecopark and production landscape is greater in southern Sweden than in northern Sweden, and why deadwood have shown relationships to the community assemblages there and not in northern Sweden. Northern Sweden generally has larger amounts of deadwood in the landscape (Fridman and Walheim, 2000) and a greater proportion of old-growth forests (Fridman, 2000). Although the northern ecopark does differ from its production landscape and from other surrounding landscapes (Bergmark et al, unpublished), it does not differ as drastically as in southern Sweden.

Southern and central Sweden has a long history of extensive land-use, where natural forests containing broadleaves, large and old trees have been converted into dense, coniferous (spruce) forests of young ages and short rotations (Axelsson and Östlund, 2001; Björse and Bradshaw, 1998; Esseen et al., 1997; Lindbladh et al., 2014; Linder and Östlund, 1998). This has led to fragmented remnants of species confined to small, unmanaged patches, indicating extinction debts (Bommarco et al., 2014; Dahlström et al., 2006; Nilsson and Franzén, 2006). The southern ecopark house species confined to varying habitat and substrates that are increasingly rare in the managed forest landscape, such as large diameter trees, broadleaf species such as oak etc. Although there are indications of extinction debts in northern Sweden as well (Berglund and Jonsson, 2008, 2005), this might not have had as much of an effect yet as in southern Sweden, thus explaining the differences in results in southern and northern Sweden.

4.5. Implications for management

Loss of biodiversity is a pressing matter and it is of great importance globally. Sweden's goals for sustainable forests have not been met by 2020 (Swedish environmental protection agency, 2020), and the state of red-listed species in Swedish forests show a continuing negative trend (ArtDatabanken, 2020), a trend that is not exclusive for Sweden (Almond et al., 2020). Therefore, the need to understand how to tackle this trend is vital. Green Infrastructure planning and multiscale conservation, where the connectivity of a landscape is emphasized, as well as multifunctional forestry, where forests are managed in a less intensive manner to preserve higher biodiversity and allow recreation, are possible solutions to tackle the decline, but our study emphasizes also the importance of local structures. In areas where the history of land-use is short, we may not see the importance of landscape planning as clearly as in areas with higher rates of fragmentation and a greater extinction debt. In order to counteract future extinctions of forest-dwelling species, landscape planning should be implemented already, in all forest management.

Author contributions

ALE: Conceptualization, Methodology, Formal analysis, Investigation, Writing original draft, Visualization. **AMH:** Conceptualization, Data curation, Writing-Review and editing, Visualization, Supervision, Project administration, Funding acquisition. **PB**: Conceptualization, Methodology, Investigation, Writing-Review and editing, Visualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Peter Bergman and Malin Norderman from Sveaskog AB for providing the beetle monitoring data and information on data sampling, Dr. Anita Norman for correcting the language and two anonymous reviewers for constructive comments that improved the manuscript. This study was funded by Sveaskog AB and WWF (Forest foundation), grant number: 178-241086 to AMH and the Foundation for Oscar and Lili Lamms minne, grant number: DO2018-0033 to PB.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119107.

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Appendix A. Forest type by age class

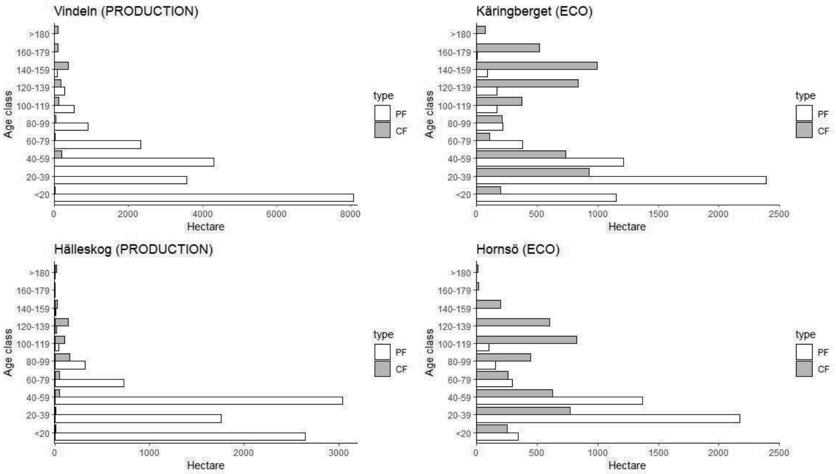

Fig. A.1. Production and nature forest area per age class for different sites. PF = Production forests. CF = Conservation forests. Note the different axis-scales.

Appendix B. Formulas

H = Height of tree from ground surface to the top branch of the crown.
D = Diameter at breast height, 1,3 m (DBH).
L = Length of log.

Volume formula (dm3) for pine in southern Sweden, H>=4 m, D>=4,5 cm, south of 60° (Brandel 1990)

$10^{-1,38903} \times D^{1,84493} \times (D+20,0)^{0,06563} \times H^{2,02122} \times (H-1,3)^{-1,01095}$

Volume formula (dm3) for spruce in southern Sweden, H>=4 m, D>=4,5 cm, south of 60° (Brandel 1990)

$10^{-1,02039} \times D^{2,00128} \times (D+20,0)^{-0,47473} \times H^{2,87138} \times (H-1,3)^{-1,61803}$

Volume formula (dm3) for birch in southern Sweden, latitude -56,9°, H>=6 m, D>=4,5 cm (Brandel 1990)

$10^{-0,89363} \times D^{2,23818} \times (D+20,0)^{-1,06930} \times H^{6,02015} \times (H - 1,3)^{-4,51472}$

Volume formula (dm3) for pine in northern Sweden, H>=4 m, D>=4,5 cm, north of 60° (Brandel 1990)

$10^{-1,20914} \times D^{1,94740} \times (D+20,0)^{-0,05947} \times H^{1,40958} \times (H-1,3)^{-0,45810}$

Volume formula (dm3) for spruce in northern Sweden, H>=4 m, D>=4,5 cm, north of 60° (Brandel 1990)

$10^{-0,79783} \times D^{2,07157} \times (D+20,0)^{-0,73882} \times H^{3,16332} \times (H-1,3)^{-1,82622}$

Volume formula (dm3) for birch in northern Sweden, latitude 59,0°-, H>=6 m, D>=4,5 cm (Brandel 1990)

$10^{-0,84627} \times D^{2,23818} \times (D+20,0)^{-1,06930} \times H^{6,02015} \times (H - 1,3)^{-4,51472}$

Basal area per tree

pi*(D/200)^2)

Formula to calculate logs

D1/2*D2/2*pi*L

Appendix C. model results and dAIC

Table C.1. GLMER (generalized linear mixed effect model) results of saproxylic beetles in northern and southern Sweden. Log-mean higher than 0 shows positive effects vs intercept, lower than 0 is negative effect. Numbers highlighted as bold hold significance, p <0,05. GLMER = x=y~(Landscape ,Landscape+DW volume/DW diversity)+(1|plotid)+(1|Year), Poisson/negative binomial (nb). Bracketed letters () next to model name shows which models were compared for dAIC, models with the same letters were compared to each other. Lowest dAIC highlighted in yellow, models within 2 dAIC highlighted in orange. DW diversity =deadwood diversity, DW volume =log-transformed deadwood volume. ECO = Ecopark, compared to conventional production landscapes.

Northern Sweden							
Model	Predictors	Log-mean	SE	p	Random effect (year)	dAIC	weight
Saproxylic richness Landscape (a)	Landscape (ECO)	-0.05	0.05	0.284	σ² = 0.02 τ00 = 0.02 plotid ICC = 0.55	0.0	0.51
Saproxylic richness Landscape+DW volume (a)	Landscape (ECO)	-0.04	0.05	0.384	σ² = 0.02	1.7	0.22
	DW volume	-0.02	0.03	0.555	τ00 = 0.02 plotid ICC = 0.55		
Saproxylic richness Landscape+DW diversity (a)	Landscape (ECO)	-0.07	0.05	0.179	σ² = 0.02	1.3	0.27
	DW diversity	0.00	0.00	0.386	τ00 = 0.02 plotid ICC = 0.55		
Saproxylic abundance Landscape (nb) (b)	Landscape (ECO)	-0.22	0.09	**0.013**	σ² = 0.14 τ00 = 0.05 plotid 0.24 Year ICC = 0.68	0.0	0.54
Saproxylic abundance Landscape+DW volume (nb) (b)	Landscape (ECO)	-0.22	0.09	**0.017**	σ² = 0.14 τ00 = 0.05 plotid	2.0	0.20
	DW volume	0.00	0.06	0.969	0.24 Year ICC = 0.68		
Saproxylic abundance Landscape+DW diversity (nb) (b)	Landscape (ECO)	-0.25	0.10	**0.010**	σ² = 0.14 τ00 = 0.04 plotid	1.5	0.26
	DW diversity	0.01	0.01	0.483	0.24 Year		

					ICC = 0.68		

Southern Sweden

Model	Predictors	Log-mean	SE	p	Random effect (year)	dAIC	weight
Saproxylic richness Landscape (e)	Landscape (ECO)	0.13	0.05	**0.008**	σ^2 = 0.02 τ00 = 0.02 plotid ICC = 0.41	8.1	0.015
Saproxylic richness Landscape+DW volume (e)	Landscape (ECO)	0.02	0.05	0.688	σ^2 = 0.02	0.0	0858
	DW volume	0.16	0.05	**0.001**	τ00 = 0.01 plotid ICC = 0.31		
Saproxylic richness Landscape+DW diversity (e)	Landscape (ECO)	0.10	0.05	**0.041**	σ^2 = 0.02	3.8	0.127
	DW diversity	0.02	0.01	**0.008**	τ00 = 0.01 plotid ICC = 0.35		
Saproxylic abundance Landscape (nb) (f)	Landscape (ECO)	0.14	0.08	0.068	σ^2 = 0.01 τ00 = 0.05 plotid ICC = 0.90	6.2	0.032
Saproxylic abundance Landscape+DW volume (nb) (f)	Landscape (ECO)	-0.01	0.08	0.860	σ^2 = 0.08	0.0	0.705
	DW volume	0.21	0.07	**0.002**	τ00 = 0.01 plotid ICC = 0.11		
Saproxylic abundance Landscape+DW diversity (nb) (f)	Landscape (ECO)	0.08	0.07	0.241	σ^2 = 0.09	2.0	0.263
	DW diversity	0.02	0.01	**0.009**	τ00 = 0.01 plotid ICC = 0.12		

*Table C.2. GLM (generalized linear model) model results of red-listed beetles in northern and southern Sweden separated for each year. Log-mean higher than 0 shows positive effects vs intercept, lower than 0 is negative effect. Numbers highlighted as bold hold significance, p <0,05. GLM = x=y~(Landscape,Landscape*DW volume/DW diversity,Landscape+DW volume/DW diversity), Poisson. Bracketed letters () next to model name shows which models were compared for dAIC, models with the same letters were compared to each other. Lowest dAIC highlighted in yellow, models within 2 dAIC highlighted in orange. DW diversity =deadwood diversity, DW volume =log-transformed deadwood volume. ECO = Ecopark, compared to conventional production landscapes.*

Northern Sweden

Model	Predictors	Log-mean	SE	p	dAIC	weight
Richness '10 Landscape (a)	Landscape (ECO)	0.59	0.32	0.068	6.1	0.0321
Richness '10	Landscape (ECO)	0.89	0.78	0.255	8.9	0.0078

Landscape*DW volume (a)	DW volume	-0.11	0.35	0.740		
	Landscape (ECO)*DW volume	-0.13	0.42	0.764		
Richness '10 Landscape+DW volume (a)	Landscape (ECO)	0.68	0.33	**0.042**	7.0	0.0203
	DW volume	-0.20	0.19	0.301		
Richness '10 Landscape*DW diversity (a)	Landscape (ECO)	1.04	0.69	0.131	2.0	0.2551
	DW diversity	-0.08	0.07	0.290		
	Landscape (ECO)*DW diversity	-0.01	0.08	0.871		
Richness '10 Landscape+DW diversity (a)	Landscape (ECO)	0.94	0.34	**0.006**	0.0	0.6846
	DW diversity	-0.09	0.03	**0.008**		
Abundance '10 Landscape (b)	Landscape (ECO)	0.60	0.30	**0.047**	7.6	0.0160
Abundance '10 Landscape*DW volume (b)	Landscape (ECO)	0.93	0.75	0.214	10.9	0.0030
	DW volume	-0.02	0.32	0.948		
	Landscape (ECO)*DW volume	-0.16	0.39	0.690		
Abundance '10 Landscape+DW volume (b)	Landscape (ECO)	0.66	0.31	**0.035**	9.1	0.0076
	DW volume	-0.13	0.18	0.476		
Abundance '10 Landscape*DW diversity (b)	Landscape (ECO)	0.93	0.64	0.149	2.0	0.2620
	DW diversity	-0.09	0.07	0.188		
	Landscape (ECO)*DW diversity	0.00	0.08	0.956		
Abundance '10 Landscape+DW diversity (b)	Landscape (ECO)	0.96	0.32	**0.003**	0.0	0.7112
	DW diversity	-0.09	0.03	**0.004**		
Richness '11	Landscape (ECO)	0.72	0.30	**0.016**	0.0	0.335

Landscape (c)						
Richness '11 Landscape*DW volume (c)	Landscape (ECO)	0.87	0.72	0.232	3.3	0.065
	DW volume	-0.11	0.35	0.753		
	Landscape (ECO)*DW volume	-0.04	0.40	0.912		
Richness '11 Landscape+DW volume (c)	Landscape (ECO)	0.79	0.31	**0.011**	1.3	0.175
	DW volume	-0.14	0.17	0.406		
Richness '11 Landscape*DW diversity (c)	Landscape (ECO)	0.48	0.68	0.483	1.9	0.133
	DW diversity	-0.08	0.08	0.314		
	Landscape (ECO)*DW diversity	0.05	0.09	0.525		
Richness '11 Landscape+DW diversity (c)	Landscape (ECO)	0.88	0.32	**0.006**	0.3	0.292
	DW diversity	-0.03	0.03	0.203		
Abundance '11 Landscape (d)	Landscape (ECO)	1.01	0.27	**<0.001**	0.1	0.328
Abundance '11 Landscape*DW volume (d)	Landscape (ECO)	0.89	0.66	0.176	3.9	0.048
	DW volume	-0.12	0.33	0.711		
	Landscape (ECO)*DW volume	0.09	0.37	0.803		
Abundance '11 Landscape+DW volume (d)	Landscape (ECO)	1.04	0.28	**<0.001**	2.0	0.127
	DW volume	-0.05	0.14	0.739		
Abundance '11 Landscape*DW diversity (d)	Landscape (ECO)	0.78	0.62	0.208	1.6	0.156
	DW diversity	-0.08	0.08	0.313		
	Landscape (ECO)*DW diversity	0.05	0.08	0.520		
Abundance '11 Landscape+DW diversity (d)	Landscape (ECO)	1.15	0.29	**<0.001**	0.0	0.341
	DW diversity	-0.03	0.02	0.161		

Richness '12 Landscape (e)	Landscape (ECO)	0.24	0.26	0.363	0.0	0.37
Richness '12 Landscape*DW volume (e)	Landscape (ECO)	1.15	0.70	0.098	1.5	0.17
	DW volume	0.38	0.26	0.145		
	Landscape (ECO)*DW volume	-0.50	0.34	0.136		
Richness '12 Landscape+DW volume (e)	Landscape (ECO)	0.20	0.27	0.454	1.8	0.15
	DW volume	0.07	0.16	0.643		
Richness '12 Landscape*DW diversity (e)	Landscape (ECO)	1.02	0.57	0.071	1.5	0.17
	DW diversity	0.05	0.04	0.228		
	Landscape (ECO)*DW diversity	-0.08	0.05	0.116		
Richness '12 Landscape+DW diversity (e)	Landscape (ECO)	0.27	0.29	0.339	1.9	0.14
	DW diversity	-0.01	0.02	0.764		
Abundance '12 Landscape (f)	Landscape (ECO)	0.49	0.21	**0.019**	20.6	<0.001
Abundance '12 Landscape*DW volume (f)	Landscape (ECO)	1.87	0.55	**0.001**	16.0	<0.001
	DW volume	0.33	0.22	0.136		
	Landscape (ECO)*DW volume	-0.74	0.28	**0.007**		
Abundance '12 Landscape*DW diversity (f)	Landscape (ECO)	1.69	0.50	**0.001**	0.0	1
	DW diversity	0.03	0.04	0.412		
	Landscape (ECO)*DW diversity	-0.11	0.05	**0.027**		
Southern Sweden						
Model	Predictors	Log-mean	SE	p	dAIC	weight
Richness '11 Landscape (g)	Landscape (ECO)	1.52	0.26	**<0.001**	8.7	0.01

Richness '11 Landscape*DW volume (g)	Landscape (ECO)	4.80	1.07	**<0.001**	0.0	0.81
	DW volume	1.96	0.55	**<0.001**		
	Landscape (ECO)*DW volume	-2.10	0.59	**<0.001**		
Richness '11 Landscape*DW diversity (g)	Landscape (ECO)	2.68	0.72	**<0.001**	3.0	0.18
	DW diversity	0.19	0.07	**0.004**		
	Landscape (ECO)*DW diversity	-0.15	0.07	**0.036**		
Abundance '11 Landscape (h)	Landscape (ECO)	1.61	0.22	**<0.001**	16.7	<0.001
Abundance '11 Landscape*DW volume (h)	Landscape (ECO)	4.62	0.92	**<0.001**	0.4	0.45
	DW volume	2.13	0.47	**<0.001**		
	Landscape (ECO)*DW volume	-2.14	0.50	**<0.001**		
Abundance '11 Landscape*DW diversity (h)	Landscape (ECO)	2.56	0.61	**<0.001**	0.0	0.55
	DW diversity	0.20	0.06	**<0.001**		
	Landscape (ECO)*DW diversity	-0.13	0.06	**0.011**		
Richness '12 Landscape (i)	Landscape (ECO)	1.10	0.25	**<0.001**	0.7	0.267
Richness '12 Landscape*DW volume (i)	Landscape (ECO)	1.37	0.93	0.141	3.5	0.065
	DW volume	0.44	0.52	0.399		
	Landscape (ECO)*DW volume	-0.27	0.57	0.629		
Richness '12 Landscape+DW volume (i)	Landscape (ECO)	0.95	0.30	**0.001**	1.7	0.158
	DW volume	0.21	0.21	0.329		
Richness '12 Landscape*DW diversity (i)	Landscape (ECO)	0.95	0.67	0.157	2.0	0.137
	DW diversity	0.04	0.07	0.585		
	Landscape (ECO)*DW diversity	0.01	0.08	0.945		

Richness '12 Landscape+DW diversity (i)	Landscape (ECO)	1.00	0.26	**<0.001**	0.0	0.372
	DW diversity	0.04	0.03	0.099		
Abundance '12 Landscape (j)	Landscape (ECO)	1.12	0.19	**<0.001**	3.1	0.07
Abundance '12 Landscape*DW volume (j)	Landscape (ECO)	2.79	0.73	**<0.001**	0.0	0.32
	DW volume	1.03	0.39	**0.008**		
	Landscape (ECO)*DW volume	-1.11	0.43	**0.010**		
Abundance '12 Landscape*DW diversity (j)	Landscape (ECO)	1.65	0.51	**0.001**	0.2	0.29
	DW diversity	0.11	0.05	**0.028**		
	Landscape (ECO)*DW diversity	-0.08	0.06	0.166		
Abundance '12 Landscape+DW diversity (j)	Landscape (ECO)	1.01	0.20	**<0.001**	0.0	0.32
	DW diversity	0.05	0.02	**0.023**		
Richness '13 Landscape (k)	Landscape (ECO)	1.40	0.26	**<0.001**	0.0	0.33
Richness '13 Landscape*DW volume (k)	Landscape (ECO)	2.59	1.02	**0.011**	1.1	0.20
	DW volume	0.95	0.56	0.091		
	Landscape (ECO)*DW volume	-0.87	0.61	0.153		
Richness '13 Landscape+DW volume (k)	Landscape (ECO)	1.25	0.31	**<0.001**	1.1	0.19
	DW volume	0.20	0.21	0.335		
Richness '13 Landscape*DW diversity (k)	Landscape (ECO)	2.36	0.70	**0.001**	1.6	0.15
	DW diversity	0.12	0.07	0.109		
	Landscape (ECO)*DW diversity	-0.12	0.08	0.112		
Richness '13 Landscape+DW diversity (k)	Landscape (ECO)	1.38	0.27	**<0.001**	1.9	0.13
	DW diversity	0.01	0.03	0.800		

Abundance '13 Landscape (l)	Landscape (ECO)	1.79	0.23	**<0.001**	14.1	<0.001
Abundance '13 Landscape*DW volume (l)	Landscape (ECO)	2.21	0.88	**0.012**	0.9	0.3932
	DW volume	1.12	0.50	**0.023**		
	Landscape (ECO)*DW volume	-0.56	0.52	0.282		
Abundance '13 Landscape+DW volume (l)	Landscape (ECO)	1.33	0.26	**<0.001**	0.0	0.6031
	DW volume	0.61	0.15	**<0.001**		
Abundance '13 Landscape*DW diversity (l)	Landscape (ECO)	2.72	0.61	**<0.001**	11.3	0.0021
	DW diversity	0.15	0.06	**0.015**		
	Landscape (ECO)*DW volume	-0.12	0.06	0.056		
Abundance '13 Landscape+DW diversity (l)	Landscape (ECO)	1.71	0.23	**<0.001**	12.7	0.0010
	DW diversity	0.04	0.02	0.061		

Appendix D. Indicator species list

Table D.1. Indicator species list (northern Sweden). Result list from indicator species analysis indicspecies. Indicator species for ecopark or conventional production landscapes with p-value <0.05 indicated with bold numbers. A = Mean occurrence of species in landscape-type. 1 meaning that it only occurs in that landscape-type (ecopark or conventional production landscapes). B = Relative occurrence frequency in sites belonging to landscape-type. 1 Meaning that it occurs in all sites belonging to landscape-type (ecopark or conventional production landscapes). NT = Near threatened. VU = Vulnerable. EN = Endangered. multipatt(abund, landscape, func = "IndVal.g", control = how(nperm=999).

Northern Sweden species	**Red-list**	**A**	**B**	**stat**	**p-value**	**Landscape**
Anthaxia quadripunctata		0.88011	0.61111	0.733	**0.001 *****	PROD
Glischrochilus hortensis		0.87614	0.48611	0.653	**0.001 *****	PROD
Endomychus coccineus		0.92120	0.37500	0.588	**0.001 *****	PROD
Anisotoma castanea		0.86596	0.34722	0.548	**0.001 *****	PROD
Anisotoma humeralis		0.85755	0.29167	0.500	**0.002 ****	PROD
Aspidiphorus orbiculatus		0.94872	0.18056	0.414	**0.004 ****	PROD
Tetropium castaneum		0.79896	0.25000	0.447	**0.006 ****	PROD
Agathidium seminulum		1.00000	0.09722	0.312	**0.011 ***	PROD
Pocadius ferrugineus		0.89157	0.11111	0.315	**0.013 ***	PROD
Philonthus politus		1.00000	0.08333	0.289	**0.015 ***	PROD
Mycetochara flavipes		0.80435	0.16667	0.366	**0.016 ***	PROD
Platycerus caprea		0.82222	0.12500	0.321	**0.027 ***	PROD
Platysoma angustatum		0.75510	0.20833	0.397	**0.029 ***	PROD
Magdalis duplicata		0.80435	0.16667	0.366	**0.030 ***	PROD
Malthodes pumilus		1.00000	0.06944	0.264	**0.030 ***	PROD
Anastrangalia sanguinolenta		0.72958	0.22222	0.403	**0.033 ***	PROD
Selatosomus nigricornis		0.89157	0.08333	0.273	**0.043 ***	PROD
Cis punctulatus		0.68452	0.16667	0.338	**0.044 ***	PROD
Quedius maurus		0.80435	0.11111	0.299	**0.044 ***	PROD
Leptura quadrifasciata		0.73267	0.18056	0.364	**0.050 ***	PROD
Cerylon ferrugineum		0.79143	0.51351	0.638	**0.001 *****	ECO
Mycetophagus multipunctatus		0.76707	0.35135	0.519	**0.002 ****	ECO
Soronia punctatissima		0.74162	0.43243	0.566	**0.004 ****	ECO
Trypodendron laeve		0.86643	0.18919	0.405	**0.009 ****	ECO
Mycetochara obscura	NT	0.77576	0.21622	0.410	**0.013 ***	ECO
Anaspis arctica		0.76656	0.21622	0.407	**0.016 ***	ECO
Agathidium nigripenne		1.00000	0.08108	0.285	**0.027 ***	ECO
Lordithon trimaculatus		1.00000	0.08108	0.285	**0.028 ***	ECO
Crypturgus pusillus		0.73544	0.20270	0.386	**0.038 ***	ECO

Table D.2. Indicator species list (southern Sweden). Result list from indicator species analysis indicspecies. Indicator species for ecopark or conventional production landscapes with p-value <0.05 indicated with bold numbers. A = Mean occurrence of species in landscape-type. 1 meaning that it only occurs in that landscape-type (ecopark or conventional production landscapes). B = Relative occurrence frequency in sites belonging to landscape-type. 1 Meaning that it occurs in all sites belonging to landscape-type (ecopark or conventional production landscapes). NT = Near threatened. VU = Vulnerable. EN = Endangered. multipatt(abund, landscape, func = "IndVal.g", control = how(nperm=999).

Southern Sweden species	**Red-List**	**A**	**B**	**stat**	**p-value**	**Landscape**
Melanotus castanipes		0.79807	0.81356	0.806	**0.001** ***	PROD
Agathidium sp		0.87389	0.52542	0.678	**0.001** ***	PROD
Hylis sp		0.84426	0.52542	0.666	**0.001** ***	PROD
Pityogenes chalcographus		0.90965	0.45763	0.645	**0.001** ***	PROD
Hadreule elongatula		0.76210	0.47458	0.601	**0.001** ***	PROD
Crypturgus sp		0.89174	0.22034	0.443	**0.007** **	PROD
Latridius sp		0.85919	0.22034	0.435	**0.008** **	PROD
Atomaria sp		0.80891	0.30508	0.497	**0.013** *	PROD
Megatoma undata		0.75899	0.81481	0.786	**0.001** ***	ECO
Stephostethus sp		0.92459	0.66667	0.785	**0.001** ***	ECO
Rhyncolus sculpturatus		0.83765	0.61111	0.715	**0.001** ***	ECO
Scolytus sp		0.78287	0.44444	0.590	**0.001** ***	ECO
Stenocorus meridianus		0.93864	0.35185	0.575	**0.001** ***	ECO
Xylotrechus antilope	NT	0.97816	0.33333	0.571	**0.001** ***	ECO
Latridius hirtus		0.90769	0.35185	0.565	**0.001** ***	ECO
Tragosoma depsarium	VU	1.00000	0.27778	0.527	**0.001** ***	ECO
Ctesias serra		0.83319	0.33333	0.527	**0.001** ***	ECO
Agrilus sulcicollis		0.91982	0.29630	0.522	**0.001** ***	ECO
Rhyncolus ater		0.96941	0.27778	0.519	**0.001** ***	ECO
Cartodere nodifer		0.89335	0.27778	0.498	**0.001** ***	ECO
Pedostrangalia (Etorofus) pubescens	VU	0.83742	0.27778	0.482	**0.001** ***	ECO
Agrilus biguttatus	NT	1.00000	0.20370	0.451	**0.001** ***	ECO
Corticeus unicolor		1.00000	0.16667	0.408	**0.001** ***	ECO
Glischrochilus hortensis		0.76068	0.55556	0.650	**0.002** **	ECO
Carphacis striatus	VU	1.00000	0.22222	0.471	**0.002** **	ECO
Rutpela maculata		0.96327	0.20370	0.443	**0.002** **	ECO
Dircaea australis	VU	1.00000	0.18519	0.430	**0.002** **	ECO
Pyrrhidium sanguineum	NT	1.00000	0.14815	0.385	**0.002** **	ECO
Trachys minuta		1.00000	0.12963	0.360	**0.002** **	ECO
Strangalia attenuata	VU	1.00000	0.16667	0.408	**0.003** **	ECO
Selatosomus aeneus		0.73201	0.35185	0.508	**0.008** **	ECO
Ptinus rufipes		1.00000	0.11111	0.333	**0.008** **	ECO
Agrilus angustulus		1.00000	0.11111	0.333	**0.010** **	ECO
Rhizophagus bipustulatus		0.78667	0.25926	0.452	**0.011** *	ECO

Anobium rufipes		0.83603	0.20370	0.413	**0.011 ***	ECO
Phymatodes (Poecilium) alni	NT	1.00000	0.11111	0.333	**0.011 ***	ECO
Tritoma bipustulata		1.00000	0.11111	0.333	**0.013 ***	ECO
Anaesthetis testacea	VU	1.00000	0.09259	0.304	**0.018 ***	ECO
Melasis buprestoides		1.00000	0.09259	0.304	**0.023 ***	ECO
Phymatodes testaceus		0.88437	0.12963	0.339	**0.025 ***	ECO
Scraptia sp		1.00000	0.09259	0.304	**0.030 ***	ECO
Sulcacis sp		0.81379	0.18519	0.388	**0.037 ***	ECO
Plegaderus caesus		1.00000	0.07407	0.272	**0.040 ***	ECO
Leiopus linnei		0.88437	0.11111	0.313	**0.048 ***	ECO
Hadrobregmus pertinax		0.74448	0.22222	0.407	**0.050 ***	ECO

Appendix E. Species list

Table E.1. Species list. Total abundance of saproxylic and red-listed species for each site. Red-listed species displayed further down separately. NT = Near threatened. VU = Vulnerable. EN = Endangered.

Saproxylic species	**Hälleskog (PROD)**	**Hornsö (ECO)**	**Vindeln (PROD)**	**Käringberget (ECO)**	**Total**
Aderidae					
Anidorus nigrinus	16	6			22
Euglenes oculatus	18	22			40
Euglenes pygmaeus	1		21	7	29
Anaspidae					
Anaspis marginicollis			38	40	78
Anthribidae					
Allandrus undulatus	1	1			2
Anthribus nebulosus	55	36	1	1	93
Enedreytes (Pseudeuparius) sepicola		1			1
Gonotropis dorsalis	2		1	3	6
Platyrhinus resinosus	1				1
Bostrichidae					
Stephanopachys substriatus			1	1	2
Buprestidae					
Agrilus angustulus		6			6
Agrilus betuleti	4	2			6
Agrilus biguttatus		18			18
Agrilus populneus	1				1
Agrilus sulcicollis	2	21			23
Agrilus viridis	13	6	8	4	31
Anthaxia quadripunctata	132	46	150	21	349
Anthaxia similis		4			4
Buprestis novemmaculata		2			2
Buprestis octoguttata		3			3
Buprestis rustica	8	1	2		11
Chrysobothris affinis	1	3			4
Chrysobothris chrysostigma	5	3	15	5	28
Dicerca furcata				1	1
Phaenops cyanea	89	402		1	492
Trachys minuta		11	2	1	14
Cantharide					

Saproxylic species	**Hälleskog (PROD)**	**Hornsö (ECO)**	**Vindeln (PROD)**	**Käringberget (ECO)**	**Total**
Absidia schoenherri			269	185	454
Malthinus biguttatus			3	1	4
Malthodes brevicollis			21	19	40
Malthodes crassicornis			5		5
Malthodes flavoguttatus			1	3	4
Malthodes fuscus			7	2	9
Malthodes guttifer			3	4	7
Malthodes marginatus			4		4
Malthodes minimus			2	1	3
Malthodes pumilus			5		5
Malthodes sp			87	94	181
Matlthodes maurus			4		4
Carabidae					
Dromius agilis			3	5	8
Pterostichus oblongopunctatus				2	2
Tachyta nana		1	2	6	9
Cerambycidae	-	-	-	-	-
Acanthocinus aedilis			12	16	28
Acmaeops septentrionis			3	7	10
Aegomorphus clavipes	32	58			90
Alosterna tabacicolor	2	3	1		6
Anaesthetis testacea		5			5
Anastrangalia reyi	19	15	45	22	101
Anastrangalia sanguinolenta	240	82	21	8	351
Anoplodera sexguttata		3			3
Arhopalus rusticus	74	133	12	15	234
Asemum striatum	10	3	89	56	158
Callidium coriaceum		1			1
Callidium violaceum			2	2	4
Clytus arietis	45	110			155
Exocentrus adspersus		1			1
Gaurotes virginea	3		1		4
Gnathacmaeops pratensis			1		1
Judolia sexmaculata	2	2	3	1	8
Leiopus linnei	1	7			8
Leptura quadrifasciata	138	89	16	6	249
Lepturobosca virens				1	1
Molorchus minor	12	26	11	26	75
Monochamus galloprovincialis	1	1			2
Monochamus sutor	2		3		5
Necydalis major	19	15	2	1	37
Oxymirus cursor	4	2	11	7	24
Pachyta lamed			7	5	12

Saproxylic species	Hälleskog (PROD)	Hornsö (ECO)	Vindeln (PROD)	Käringberget (ECO)	Total
Pedostrangalia (Etorofus) pubescens	7	33			40
Phymatodes (Poecilium) alni		14			14
Phymatodes testaceus	1	7			8
Plagionotus arcuatus	5	9			14
Pogonocherus decoratus			3	2	5
Pogonocherus fasciculatus	14	4	88	57	163
Pyrrhidium sanguineum		11			11
Rhagium inquisitor	127	121	496	668	1412
Rhagium mordax	16	46	88	156	306
Rutpela maculata	1	24			25
Saperda perforata		1			1
Saperda populnea	1				1
Saperda scalaris	14	24	3	1	42
Spondylis buprestoides	33	96			129
Stenocorus meridianus	2	28			30
Stenurella melanura	100	81	3	2	186
Stenurella nigra		1			1
Stictoleptura maculicornis	20	13	1	1	35
Stictoleptura rubra	13	5			18
Strangalia attenuata		13			13
Tetropium castaneum	6	4	58	15	83
Tragosoma depsarium		20			20
Xylotrechus antilope	1	41			42
Xylotrechus rusticus	66	133	34	30	263
Cerylonidae					
Cerylon deplanatum		1			1
Cerylon ferrugineum			20	78	98
Cerylon histeroides			520	328	848
Ciidae					
Cis alter			1		1
Cis bidentatus			4	9	13
Cis boleti	38	54	428	149	669
Cis castaneus				1	1
Cis comptus			82	114	196
Cis dentatus			2	2	4
Cis glabratus			10	12	22
Cis hispidus			28	76	104
Cis jacquemartii			9	7	16
Cis lineatocribratus			1	2	3
Cis punctulatus			19	9	28
Cis setiger				7	7
Cis sp	43	55	4		102
Ennearthron cornutum			1	5	6

Saproxylic species	Hälleskog (PROD)	Hornsö (ECO)	Vindeln (PROD)	Käringberget (ECO)	Total
Ennearthron laricinum				2	2
Hadreule elongatula	47	14	22	12	95
Orthocis alni	8	7	43	34	92
Orthocis festivus			1	1	2
Orthocis sp	2				2
Sulcacis affinis			4	2	6
Sulcacis sp	3	12			15
Cleridae					
Thanasimus femoralis	18	21	84	79	202
Thanasimus formicarius	168	264	452	529	1413
Tillus elongatus		1			1
Colydiidae					
Lasconotus jelskii				1	1
Corylophidae					
Orthoperus sp			10	14	24
Cryptophagidae					
Atomaria sp	34	8	150	177	369
Cryptophagus pubescens		2			2
Cryptophagus sp	18	9	78	92	197
Henoticus sp	1	1			2
Micrambe abietis			6		6
Micrambe sp	11	4	11	17	43
Cucujidae					
Pediacus fuscus			4	8	12
Curculionidae					
Cryphalus saltuarius				1	1
Cryptorhynchus lapathi			1		1
Crypturgus cinereus			34	40	74
Crypturgus hispidulus			23	21	44
Crypturgus pusillus			7	20	27
Crypturgus sp	27	3			30
Crypturgus subcribrosus			12	18	30
Dendroctonus micans			1		1
Dryocoetes autographus			314	191	505
Dryocoetes hectographus			11	6	17
Dryocoetes sp	29	12			41
Hylastes brunneus			4465	3192	7657
Hylastes cunicularius			1180	982	2162
Hylastes opacus			34	26	60
Hylastes sp	229	261			490
Hylobius abietis	326	205	242	244	1017
Hylobius piceus			1	1	2
Hylobius pinastri	3	2	8		13

Saproxylic species	Hälleskog (PROD)	Hornsö (ECO)	Vindeln (PROD)	Käringberget (ECO)	Total
Hylurgops glabratus			4	8	12
Hylurgops palliatus			96	88	184
Hylurgops sp	36	259			295
Ips typographus	3		62	51	116
Magdalis carbonaria			7	13	20
Magdalis duplicata			20	5	25
Magdalis frontalis			5	1	6
Magdalis phlegmatica			2	1	3
Magdalis ruficornis			1	1	2
Magdalis sp	41	16			57
Magdalis violacea			50	34	84
Orthotomicus laricis			1	1	2
Orthotomicus proximus			8	5	13
Orthotomicus sp	6	6			12
Orthotomicus suturalis			8		8
Phloeotribus sp	1				1
Phloeotribus spinulosus			4		4
Pissodes castaneus	1				1
Pissodes harcyniae			2	1	3
Pissodes pini	136	36	41	28	241
Pissodes piniphilus	7	6	6	12	31
Pityogenes bidentatus			56	31	87
Pityogenes chalcographus	106	10	571	394	1081
Pityogenes quadridens			3	2	5
Pityogenes sp	39	21	163	87	310
Pityophthorus micrographus			11	3	14
Polygraphus poligraphus			28	13	41
Polygraphus punctifrons			5		5
Polygraphus sp	1				1
Polygraphus subopacus			51	45	96
Rhyncolus ater	1	29	9	9	48
Rhyncolus sculpturatus	17	85	11	11	124
Scolytus ratzeburgii	333	319	92	253	997
Scolytus sp	20	66			86
Tomicus minor			9	4	13
Tomicus piniperda			574	473	1047
Tomicus sp	30	45			75
Trypodendron domesticum			14	39	53
Trypodendron laeve			6	40	46
Trypodendron lineatum			3502	2916	6418
Trypodendron signatum			13	6	19
Trypodendron sp	63	131			194
Trypophloeus sp			1		1

Saproxylic species	**Hälleskog (PROD)**	**Hornsö (ECO)**	**Vindeln (PROD)**	**Käringberget (ECO)**	**Total**
Xyleborinus saxesenii		2			2
Xyleborus monographus		4			4
Xylechinus pilosus				1	1
<u>Dasytidae</u>					
Aplocnemus impressus		1			1
Dasytes aeratus		1			1
Dasytes fusculus				1	1
<u>Dermestidae</u>					
Anthrenus museorum	30	37	27	13	107
Attagenus pellio	8	4			12
Ctesias serra	5	32			37
Dermestes palmi			1	1	2
Globicornis emarginata	3	8	35	49	95
Megatoma undata	31	98	30	20	179
<u>Elateridae</u>					
Ampedus balteatus	577	433	148	142	1300
Ampedus cinnabarinus	8	6			14
Ampedus nigrinus	30	12	571	293	906
Ampedus nigroflavus	2	2			4
Ampedus pomonae	5	8			13
Ampedus pomorum	10	16			26
Ampedus praeustus		1			1
Ampedus sanguineus	5	6			11
Ampedus sanguinolentus	4	6			10
Ampedus tristis	10	5	119	113	247
Anostirus castaneus	3				3
Athous subfuscus	134	70	67	58	329
Cardiophorus ruficollis	139	77	41	17	274
Danosoma conspersum			4	2	6
Danosoma fasciatus			8	11	19
Denticollis borealis	4	7	26	53	90
Denticollis linearis	2		6	3	11
Drapetes mordelloides	4	1			5
Ectinus aterrimus		1			1
Harminius undulatus			2	4	6
Lacon fasciatus			8	12	20
Melanotus castanipes	187	44	735	437	1403
Melanotus villosus	150	100			250
Selatosomus (Paraphotistus) impressus	35	19	46	26	126
Selatosomus aeneus	8	20	60	35	123
Selatosomus impressus				2	2
Selatosomus nigricornis			8	1	9
Stenagostus rufus		2			2

Saproxylic species	**Hälleskog (PROD)**	**Hornsö (ECO)**	**Vindeln (PROD)**	**Käringberget (ECO)**	**Total**
Endomychidae					
Endomychus coccineus	77	105	182	16	380
Mycetina cruciata	3	1			4
Erotylidae					
Dacne bipustulata	56	87	139	128	410
Triplax aenea	3		22	48	73
Triplax rufipes		23			23
Triplax russica	26	62	43	149	280
Triplax scutellaris			9	15	24
Tritoma bipustulata		14			14
Eucnemidae					
Hylis sp	74	13			87
Melasis buprestoides		11			11
Microrhagus lepidus		1			1
Histeridae					
Acritus nigricornis	2				2
Dendrophilus pygmaeus			3		3
Gnathoncus buyssoni			38	25	63
Gnathoncus communis			1		1
Gnathoncus nannetensis		1	13	11	25
Paromalus flavicornis		1			1
Platysoma (Eblisia) minus		2	6	13	21
Platysoma angustatum			24	8	32
Platysoma deplanatum	2	6			8
Platystomus albinus	18	25	21	33	97
Plegaderus caesus		5			5
Plegaderus vulneratus	22	50	513	594	1179
Hydrophilidae					
Megasternum concinnum			9	2	11
Laemophloeidae					
Cryptolestes abietis				3	3
Cryptolestes corticinus	2	2			4
Cryptolestes ferrugineus				5	5
Cryptolestes(Leptophloeus) alternans	2		7	9	18
Latridiidae					
Cartodere nodifer	3	23			26
Cartodere sp	7	6			13
Corticaria sp	20	14	105	110	249
Corticarina sp	3	2			5
Cortinicara gibbosa	12	23	170	202	407
Enicmus fungicola				1	1
Enicmus rugosus	652	1242	791	1054	3739
Enicmus sp	13	9		4	26

Saproxylic species	**Hälleskog (PROD)**	**Hornsö (ECO)**	**Vindeln (PROD)**	**Käringberget (ECO)**	**Total**
Latridius hirtus	4	36	23	56	119
Latridius minutus			17	18	35
Latridius sp	20	3	1		24
Stephostethus pandellei			15	45	60
Stephostethus rugicollis			54	69	123
Stephostethus sp	7	101			108
Leiodidae					
Agathidium nigripenne				6	6
Agathidium seminulum			14		14
Agathidium sp	48	7	151	102	308
Amphicyllus globus			1	1	2
Anisotoma axillaris			500	235	735
Anisotoma castanea			44	7	51
Anisotoma glabra			393	269	662
Anisotoma humeralis			41	7	48
Lucanidae					
Platycerus caprea			9	2	11
Platycerus caraboides		1			1
Sinodendron cylindricum	3	6			9
Lycidae					
Dictyoptera aurora			10	13	23
Lygistopterus sanguineus	24	11	4	5	44
Platycis minutus				1	1
Pyropterus nigroruber	3	2			5
Lymexylidae					
Hylecoetus dermestoides	1	6	63	138	208
Malachiidae					
Malachius bipustulatus		7			7
Melandryidae					
Abdera (Wanachia) triguttata	11	27	24	30	92
Abdera affinis			2	4	6
Dircaea australis		11			11
Hallomenus binotatus	2		1	2	5
Orchesia fasciata		1	3		4
Orchesia micans	10	5	13	13	41
Osphya bipunctata		2			2
Phloiotrya rufipes		1			1
Serropalpus barbatus	2	1			3
Xylita laevigata	6	3	103	108	220
Zilora ferruginea			1	1	2
Melyridae					
Aplocnemus nigricornis	12	8			20
Aplocnemus tarsalis			2		2

Saproxylic species	**Hälleskog (PROD)**	**Hornsö (ECO)**	**Vindeln (PROD)**	**Käringberget (ECO)**	**Total**
Dasytes niger	136	153	19	31	339
Dasytes obscurus	15	9	211	82	317
Dasytes plumbeus	134	318	2		454
Dolichosoma lineare			3		3
Nepachys cardiacae			5	9	14
Monotomidae					
Monotoma sp				1	1
Rhizophagus bipustulatus	8	27	17	23	75
Rhizophagus cribratus			2	1	3
Rhizophagus fenestralis	2	6			8
Rhizophagus ferrugineus	110	113	2068	1146	3437
Rhizophagus parvulus			136	168	304
Rhizophagus dispar	26	15	58	55	154
Rhizophagus nitidulus	6	21			27
Mordellidae					
Curtimorda maculosa	13	1	16	8	38
Mordella sp	20	24	17	7	68
Mordellistena humeralis			2		2
Tomoxia bucephala	219	227			446
Mycetophagidae					
Litargus connexus	4	13	12	11	40
Mycetophagus decempunctatus		1			1
Mycetophagus fulvicollis				3	3
Mycetophagus multipunctatus			13	44	57
Mycetophagus piceus		2			2
Mycetophagus populi	1	2	3	2	8
Nitidulidae					
Amphotis marginata		1			1
Carpophilus marginellus			8	12	20
Cryptarcha strigata		1			1
Cryptarcha undata		2			2
Epuraea sp	126	105	1806	1795	3832
Glischrochilus hortensis	20	64	117	17	218
Glischrochilus quadripunctatus	18	12	378	706	1114
Glischrochilus quadrisignatus		1			1
Ipidia binotata	1	3			4
Pityophagus ferrugineus	43	18	724	357	1142
Pocadius ferrugineus			8	1	9
Soronia grisea	30	35	55	117	237
Soronia punctatissima	16	10	20	59	105
Oedemeridae					
Calopus serraticornis				1	1
Chrysanthia geniculata			1		1

Saproxylic species	**Hälleskog (PROD)**	**Hornsö (ECO)**	**Vindeln (PROD)**	**Käringberget (ECO)**	**Total**
Chrysanthia viridissima				1	1
Ischnomera caerulea		2			2
Ptiliidae					
Ptiliidae sp			269	94	363
Ptinidae					
Anobium punctatum	2				2
Anobium rufipes	3	14	7	1	25
Anobium thomsoni		2	8	3	13
Dorcatoma dresdensis	7	10	2	4	23
Dorcatoma punctulata			1		1
Dorcatoma robusta	11	26	17	19	73
Dryophilus pusillus	3				3
Ernobius explanatus				2	2
Ernobius nigrinus			1		1
Ernobius sp	16	20			36
Gastrallus immarginatus	2				2
Hadrobregmus pertinax	6	16	40	37	99
Hedobia (Ptinomorphus) imperialis		1			1
Microbregma emarginata				1	1
Ptilinus pectinicornis		1			1
Ptinus dubius		3			3
Ptinus rufipes		10			10
Ptinus subpilosus			5	3	8
Stagetus borealis		1	1		2
Xyletinus fibyensis		2			2
Xyletinus hanseni	1	2			3
Pyrochroidae					
Pyrochroa coccinea	11	21			32
Schizotus pectinicornis	4	6	5	14	29
Pythidae					
Pytho depressus			17	17	34
Salpingidae					
Rabocerus gabrieli			4	7	11
Salpingus ruficollis	49	31	52	73	205
Sphaeriestes bimaculatus				1	1
Sphaeriestes castaneus	1	2			3
Sphaeriestes stockmanni	1				1
Scarabaeidae					
Cetonia aurata	65	139			204
Protaetia cuprea	1458	698	1983	1551	5690
Trichius fasciatus	114	61		1	176
Scraptiidae					
Anaspis arctica			8	27	35

Saproxylic species	Hälleskog (PROD)	Hornsö (ECO)	Vindeln (PROD)	Käringberget (ECO)	Total
Anaspis rufilabris			41	30	71
Anaspis sp	185	148			333
Scraptia sp		6			6
Scydmaenidae					
Microscydmus minimus				1	1
Stenichnus bicolor			2		2
Silvanidae					
Dendrophagus crenatus	1			4	5
Silvanoprus fagi	9	2	6	4	21
Silvanus bidentatus		3	4	1	8
Sphaeritidae					
Sphaerites glabratus			5	1	6
Sphindidae					
Aspidiphorus orbiculatus	11	11	18	1	41
Sphindus dubius	78	145	29	23	275
Staphylinidae					
Acidota crenata			22	34	56
Atrecus affinis				1	1
Atrecus longiceps			5	5	10
Atrecus pilicornis			1	2	3
Bibloporus sp			14	14	28
Bisnius puella			5	3	8
Bisnius subuliformis			1		1
Carphacis striatus		22			22
Euplectus sp			170	162	332
Eutheia plicata	1				1
Lordithon lunulatus		1	130	71	202
Lordithon speciosus			1		1
Lordithon thoracicus			1		1
Lordithon trimaculatus				7	7
Nudobius lentus			119	135	254
Othius subuliformis				1	1
Philonthus addendus			1		1
Philonthus marginatus			4		4
Philonthus politus			11		11
Phyllodrepa (Dropephylla) clavigera				3	3
Phyllodrepa melanocephala			2		2
Quedius brevis			1		1
Quedius maurus			8	2	10
Quedius mesomelinus			4		4
Quedius plagiatus			50	50	100
Quedius tenellus			25	7	32
Scaphisoma sp			165	213	378

Saproxylic species	**Hälleskog (PROD)**	**Hornsö (ECO)**	**Vindeln (PROD)**	**Käringberget (ECO)**	**Total**
Sepedophilus littoreus			6		6
Sepedophilus sp			7	7	14
Tachinus subterraneus			1		1
Trichophya pilicornis			1		1
Tyrus mucronatus			2	3	5
Velleius dilatatus		2			2
Xantholinus tricolor			1	1	2
Tenebrionidae					
Bolitophagus reticulatus	1	1	4	6	12
Corticeus bicolor				2	2
Corticeus linearis	9	2	72	42	125
Corticeus unicolor		20			20
Diaperis boleti	437	644			1081
Mycetochara axillaris	1		1		2
Mycetochara flavipes	15	26	12	3	56
Mycetochara linearis (maura)		4			4
Mycetochara obscura			9	32	41
Palorus depressus	1	6			7
Pseudocistela ceramboides	4	4			8
Uloma rufa		1			1
Tetratomidae					
Tetratoma ancora			8	15	23
Trogossitidae					
Grynocharis oblonga		2			2
Nemozoma elongatum	1				1
Ostoma ferruginea	1			3	4
Thymalus limbatus	1	2			3
Zopheridae					
Bitoma crenata	39	20	3		62
Colydium elongatum		10			10
Synchita humeralis	12	15	8	3	38
Grand Total	9279	10184	30060	24856	74379

Red-listed species	**Hälleskog (PROD)**	**Hornsö (ECO)**	**Vindeln (PROD)**	**Käringberget (ECO)**	**Total**
Anthribidae					
Enedreytes (Pseudeuparius) sepicola		1			1
Gonotropis dorsalis	2		1	3	6
Platyrhinus resinosus	1				1
Buprestidae					
Agrilus biguttatus		18			18
Buprestis novemmaculata		2			2
Dicerca furcata				1	1

Red-listed species	**Hälleskog (PROD)**	**Hornsö (ECO)**	**Vindeln (PROD)**	**Käringberget (ECO)**	**Total**
Carabidae					
Tachyta nana		1	2	6	9
Cerambycidae					
Acmaeops septentrionis			3	7	10
Aegomorphus clavipes	32	58			90
Anaesthetis testacea		5			5
Anoplodera sexguttata		3			3
Exocentrus adspersus		1			1
Monochamus galloprovincialis	1	1			2
Necydalis major	19	15	2	1	37
Pedostrangalia (Etorofus) pubescens	7	33			40
Phymatodes (Poecilium) alni		14			14
Pyrrhidium sanguineum		11			11
Saperda perforata		1			1
Strangalia attenuata		13			13
Tragosoma depsarium		20			20
Xylotrechus antilope	1	41			42
Cerylonidae					
Cerylon deplanatum		1			1
Chrysomelidae					
Cryptocephalus distinguendus	1		1		2
Cryptocephalus sexpunctatus				1	1
Ciidae					
Cis dentatus			2	2	4
Ennearthron laricinum				2	2
Colydiidae					
Lasconotus jelskii				1	1
Curculionidae					
Xyleborinus saxesenii		2			2
Xyleborus monographus		4			4
Dasytidae					
Aplocnemus impressus		1			1
Dermestidae					
Dermestes palmi			1	1	2
Elateridae					
Ampedus cinnabarinus	8	6			14
Ampedus nigroflavus	2	2			4
Ampedus praeustus		1			1
Ampedus sanguinolentus	4	6			10
Danosoma conspersum			4	2	6
Denticollis borealis	4	7	26	53	90
Drapetes mordelloides	4	1			5
Harminius undulatus			2	4	6

Red-listed species	**Hälleskog (PROD)**	**Hornsö (ECO)**	**Vindeln (PROD)**	**Käringberget (ECO)**	**Total**
Lacon fasciatus			8	12	20
Stenagostus rufus		2			2
Erotylidae					
Triplax rufipes		23			23
Eucnemidae					
Microrhagus lepidus		1			1
Histeridae					
Platysoma (Eblisia) minus		2	6	13	21
Platysoma deplanatum	2	6			8
Melandryidae					
Dircaea australis		11			11
Orchesia fasciata		1	3		4
Osphya bipunctata		2			2
Phloiotrya rufipes		1			1
Zilora ferruginea			1	1	2
Mordellidae					
Mordellistena humeralis			2		2
Mycetophagidae					
Mycetophagus decempunctatus		1			1
Mycetophagus fulvicollis				3	3
Nitidulidae					
Amphotis marginata		1			1
Glischrochilus quadrisignatus		1			1
Ipidia binotata	1	3			4
Oedemeridae					
Ischnomera caerulea		2			2
Ptinidae					
Stagetus borealis		1	1		2
Staphylinidae					
Carphacis striatus		22			22
Phyllodrepa (Dropephylla) clavigera				3	3
Tenebrionidae					
Corticeus bicolor				2	2
Mycetochara obscura			9	32	41
Uloma rufa		1			1
Zopheridae					
Colydium elongatum		10			10
Grand Total	89	360	74	150	673

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Journal of Environmental Management 360 (2024) 121080

Contents lists available at ScienceDirect

Journal of Environmental Management

journal homepage: www.elsevier.com/locate/jenvman

Research article

Trait-environment interactions of saproxylic beetles as a guide to biodiversity conservation strategies

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ARTICLE INFO

Keywords:
Coleoptera
Landscape
Deadwood
Forest management
Biodiversity
Functional traits

ABSTRACT

Conservation of biodiversity requires in-depth knowledge of trait-environment interactions to understand the influence the environment has on species assemblages. Saproxylic beetles exhibit a wide range of traits and functions in the forest ecosystems. Understanding their responses to surrounding environment thus improves our capacity to identify habitats that should be restored or protected. We investigated potential interactions between ecological traits in saproxylic beetles (feeding guilds and habitat preferences) and environmental variables (deadwood, type and age of surrounding forest). We sampled beetles from 78 plots containing newly created high stumps of Scots pine and Silver birch in boreal forest landscapes in Sweden for three consecutive years. Using a model based approach, our aim was to explore potential interactions between ecological traits and the surrounding environment at close and distant scale (20 m and 500 m radius). We found that broadleaf-preferring beetle species are positively associated with the local broadleaf-originated deadwood and broadleaf-rich forests in the surrounding landscapes. Conifer-preferring species are positively associated with the local amount of coniferous deadwood and young and old forests in the surrounding landscape. Fungivorous and predatory beetles are positively associated with old forests in the surrounding landscapes. Our results indicate that both local amounts of deadwood and types of forests in the landscape are important in shaping saproxylic beetle communities. We particularly highlight the need to increase deadwood amounts of various qualities in the landscape, exempt older forests from production and to increase broadleaf-rich habitats in order to meet different beetle species' habitat requirements. Trait responses among saproxylic beetles provide insights into the significance of broadleaf forest and dead wood as essential attributes in boreal forest restoration, which helps conservation planning and management in forest landscapes.

1. Introduction

Studying assemblages of different guilds of species is essential to understand the effects of biotic and abiotic changes on biodiversity (Fountain-Jones et al., 2015). While species richness and abundance may provide useful information of general ecosystem conditions, species traits and niche requirements add to the understanding of the functional roles of species in a given ecosystem (Dawson et al., 2021; Flynn et al., 2009; Hekkala and Roberge, 2018). These traits represent morphological, physiological, biochemical or life-history differences between species and species groups regarding e.g. habitat preferences and feeding strategies. Especially ecological traits have shown to be a good way of explaining species' responses to changes in their environment (Drag et al., 2022).

The use of morphological and life-history traits has a long tradition in studies of e.g. birds and plant species (Chelli et al., 2019; Cormont et al., 2011), but have in recent years gained popularity among ecologists working on more cryptic and species-rich taxa (Cadotte et al., 2011; Rodríguez et al., 2021). In forest ecosystems, saproxylic *i.e.,* deadwood-dependent, beetles (Coleoptera) is a species-rich organism group that exhibits a wide diversity of traits (Stokland et al., 2012; Ulyshen and Šobotník, 2018). Saproxylic beetles have a relatively short life cycle, high reproductive capacity, good dispersal ability and they respond fast to environmental changes (Hjältén et al., 2017; Hyvärinen et al., 2006; Müller et al., 2010). They have evolved a wide range of adaptations and strategies regarding deadwood habitats, making deadwood quantity and diversity important factors for their survival (Stokland et al., 2012; Seibold et al., 2017). Saproxylic beetles' general

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https://doi.org/10.1016/j.jenvman.2024.121080
Received 5 February 2024; Received in revised form 15 April 2024; Accepted 2 May 2024

functional role in forests is related to the decomposition of wood (Seibold et al., 2021; Stokland et al., 2012), and through their different feeding guilds they also provide conditions suitable for other organisms to establish. Cambivores depend on weakened or newly dead trees to feed on the energy-rich phloem or cambium where the feeding contributes to positive feedbacks for a diverse community of bacteria, fungi and other invertebrates (Stokland et al., 2012). Wood borers (xylophages) burrow into the heartwood and feed on the wood itself, and create a range of cavities for other organisms to occupy once the beetles leave their larval stage (Buse et al., 2008; Hammond et al., 2001). Fungivores appear usually in later stages of wood decay, they feed on fungi and act as vectors for fungal dispersal (Lunde et al., 2023). Predators feed on other invertebrates and have thus an important ecosystem function in forest pest insect control (Reeve, 1997).

In addition to the feeding guilds, saproxylic beetles exhibit great variation in their niche selection, being generalists or specialists on woody material of different origins (Dahlberg and Stokland, 2004). The communities of beetles are therefore dependent on resource availability, but also on resource heterogeneity, connectivity and habitat continuity at different spatial scales, which in turn is influenced by forest-use intensity and legacies (Bouget and Parmain, 2016; Kouki et al., 2012; Seibold et al., 2017). Today, approximately 11 % of saproxylic beetles in Europe, consisting of hundreds of species, are threatened due to the lack of suitable deadwood habitats (ArtDatabanken, 2020; Hyvärinen et al., 2019; Nieto and Alexander, 2010; Siitonen, 2001). The main reason for this is large-scale forestry practices that have degraded the forest structures by simplifying the tree layering and species composition, decreasing deadwood volumes and reducing structural heterogeneity – factors known to be important for forest biodiversity (Gao et al., 2015; Hämäläinen et al., 2024; Hekkala et al., 2023; Seibold et al., 2017), ecosystem functionality (Eriksson and Hammer, 2006) and ecosystem services (Pohjanmies et al., 2017).

In North European boreal forests, the amount of deadwood in production forests is estimated to be 10–15 % of that normally found in old-growth forests (Siitonen, 2001; Stokland et al., 2012) with long continuity. Remaining deadwood-rich habitats are rare and highly fragmented throughout the forest landscape. To avoid further fragmentation of essential habitats for species, spatial considerations including protection and restoration of habitat connectivity and continuity (Moor et al., 2022; Svensson et al., 2023), is highly needed. For example, as a result of a systematic removal of broadleaf trees to favour coniferous trees in the Swedish forestry model (Svensson et al., 2023), there is paucity of old-growth broadleaf-rich habitats in Sweden (Mikusiński et al., 2021), habitats known to be one of the most species-rich types in boreal Fennoscandia (Esseen et al., 1997). This is reflected in the Swedish Red-list (ArtDatabanken, 2020) with a higher proportion of threatened saproxylic beetles being associated with broadleaved deadwood (Jonsell et al., 2004). Thus, conservation actions aimed at promoting broadleaf trees and broadleaved deadwood might be a neat way forward to benefit broadleaf associated beetles, including species on the red-list (Bell et al., 2015).

To understand trait-environment interactions, consideration of spatial scale is crucial (Hedenås and Ericson, 2008), as many important ecological processes operate at a landscape scale (Hansen et al., 1991; Rubene et al., 2017). Although the significance of deadwood for forest biodiversity is well established (Gao et al., 2015; Lassauce et al., 2011) there is still a lack of knowledge and understanding regarding the relationship between deadwood-dependent taxa and spatial scales (Sverdrup-Thygeson et al., 2014). While several studies highlight the importance of local habitat quality, such as the amount and diversity of habitat (Larsson Ekström et al., 2021; McGeoch et al., 2007; Seibold et al., 2017) recent studies also point on the importance of landscape configuration and its influence on species assemblages (Hämäläinen et al., 2023; Kouki et al., 2012; Pilskog et al., 2018).

Increased knowledge on beetle assemblage responses to forest structural variables at different spatial scales would enable a deeper understanding on the factors that influences saproxylic species community composition and function. This information is, in turn, crucial for strengthening functional and resilient ecosystems in managed boreal forest landscapes as input to forest restoration at stand- and landscape scale forest management and conservation planning.

The aim with this study was to evaluate potential interactions between functional guilds of saproxylic beetles, and environmental variables at different spatial scales in boreal forest ecosystems. We approached the potential interactions by analysing communities of saproxylic beetles, and their relationship with local deadwood availability, and age and type of forests in the surrounding landscape in 78 plots scattered in boreal forest landscapes in Sweden.

2. Material and methods

2.1. Study areas and sampling design

The study was performed in 78 plots in three boreal forest landscapes in Sweden (Fig. 1). Two of these landscapes (Käringberget and Hornslandet) are among the 37 Ecoparks set aside by the state owned forestry company Sveaskog. The ecoparks are characterized by higher ambitions regarding nature conservation (Bergman and Gustafsson, 2020) with at least 50 percent of the area being managed only for conservation purposes. The rest of the area is managed with silvicultural practices (Table 1). The third landscape (Vindeln) is a conventionally managed production landscape with 5 % nature consideration according to Swedish forestry legal standards. All three landscapes have a stand-level management planning with Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), Silver and Downy birch (*Betula pubescens)/pendula*) and to some extent Aspen (*Populus tremula*) as dominating tree species (Table 1.).

Within each landscape, 26 plots were selected (Fig. 1) using the following criteria: 1) at least 1000 m distance between plots, 2) plot open from south to west to ensure sun-exposure, 3) includes one Scots pine and Silver birch in diameters 20–30 cm, standing close to each other. During the winter of 2010, sun-exposed high stumps of one Scots pine and one Silver birch were created in in each plot, to serve as trapping stations for saproxylic beetles. The length of the high stumps are 2.5 m and have a diameter range at breast height between 14 and 42 cm. The majority of plots contained one Scots pine and one Silver birch high stump, but in one of the landscapes (Hornslandet), several plots contained either two Scots pine or two Silver birch high stumps due to difficulties in finding suitable trees following the criteria. Finally, 86 pine and 70 birch high stumps were included in the study. In cases where sun-exposure was not satisfactory, the plots were opened manually by removing shadowing trees at the time when the stumps were created. The cut trees were removed from the plots to not artificially affect local dead wood amount.

2.2. Beetle sampling and classification

Two trunk-attached flight-intercept traps were placed on each high stump to collect beetles, totalling 104 traps per landscape. A trap consisted of a 10 × 20 cm, 2–3 mm thick, transparent Plexiglas sheet with a 0.5-L aluminium mould beneath the Plexiglas. The moulds were filled with Propylene glycol with a small amount of detergent to remove surface tension (Fig. 1C). Two traps were placed on the southern side of each high stump, on the heights of 1.1 m and 1.6 m above ground. Beetle sampling went on from early June to early August for three consecutive years after the creation of high stumps (2010, 2011 and 2012). The beetles were sent to a taxonomic expert for identification to species or genera level (see Appendix Table S2 for full species list). Only saproxylic beetles (see definition in Stokland et al., 2012) were considered in the analyses.

The beetles were grouped by their ecological traits regarding feeding guilds and habitat preference. Feeding guilds were divided into

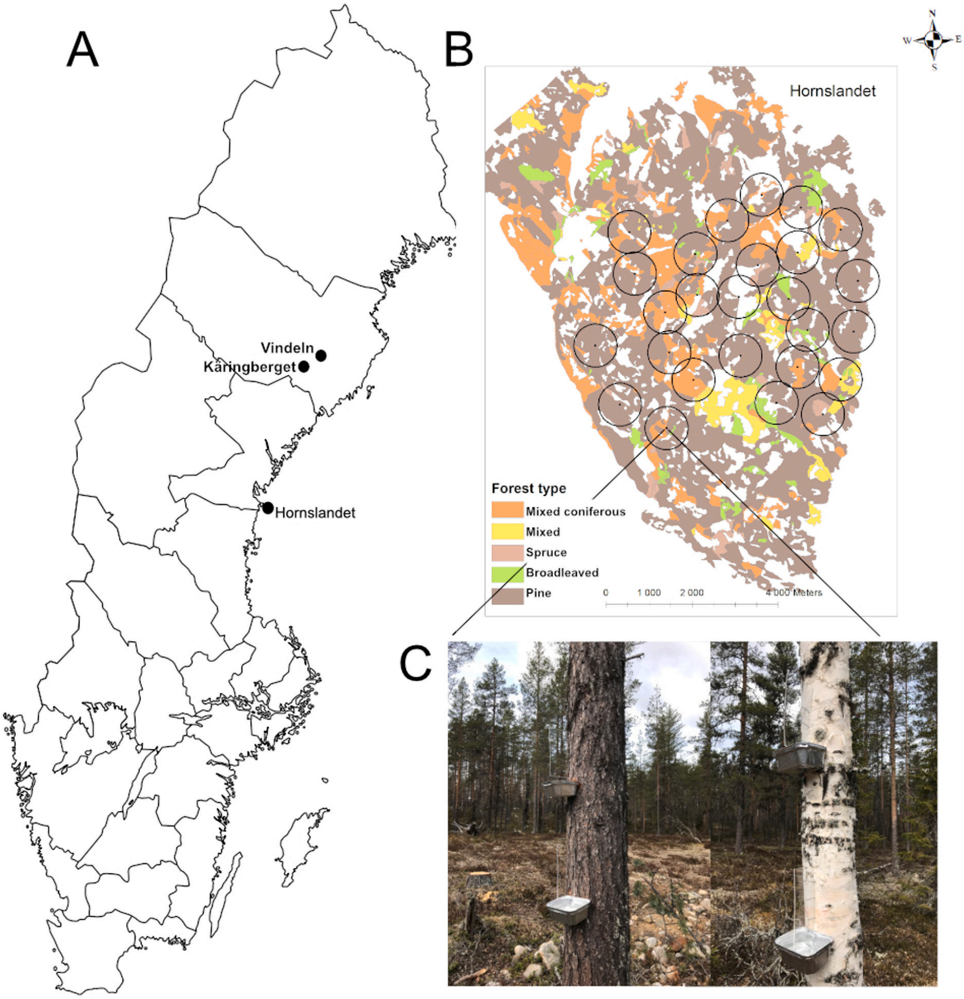

Fig. 1. A map of the locations of study landscapes in Sweden (A). An example of the placement of the plots in the landscapes (black dot), with 500 m radius buffer (B). Each plot contain one pair of high stumps of Scots pine and Silver birch, with two flight intercept traps per high stump (C).

cambivores, detritivores, fungivores, predators and wood borers, following Koch (Koch, 1989a,b, 1992) and Artdatabanken (2021). For habitat preference classification, each saproxylic species was also classified as wood-generalist, conifer-specialist or -generalist and broadleaf-specialist or –generalist (Artdatabanken, 2021; Ehnström and Axelsson, 2002).

2.3. Field measurements and environmental data collection

Local environmental variables were measured within 20 m radius circles around each high stump sampling point. Twenty meter radius gives a good representation of the local habitat and is a time effective scale for manual measurements. Local environmental variables were collected during summer and autumn in 2019. Data were collected on all deadwood over 4.5 cm in diameter, considering tree species, posture (*i.e.* standing or lying), height/length, diameter and stage of decay. For standing dead trees, diameter was measured at breast height (DBH), for deadwood logs two diameters were measured, the top (to a minimum of 4.5 cm) and the basal diameter. Only the part inside the 20 m radius plot of a deadwood log was measured. The decay degree for lying dead wood was classified to four stages according to Gibb et al. (2005): (1) Hard wood with intact bark >50%, (2) Hard wood with smooth surface beginning to soften, <50% bark remaining, (3) Crevices and holes, soft wood surface, free of bark, (4) Soft wood, possibly with a hard core remaining, hard to define surface and outline. Broadleaved trees were in later decay stages (2–4) defined only by softness, not by remaining bark. Standing dead trees were classified to decay degrees according to Thomas (1979). For calculations of dead wood volumes and dead wood diversity, see Larsson Ekström et al. (2021).

Landscape data regarding types and ages of forests were obtained from the landowner, a state forest company Sveaskog AB, and prepared by extracting information from 500 m radius buffers around each plot. We chose 500 m buffers as it captures the variability of forests in large part of the landscape surrounding the plots (Ranius et al., 2015) and

Table 1
A summary of location, management, climate, vegetation types and distribution of forest types and age classes for the three study landscapes.

Landscape	Käringberget	Hornslandet	Vindeln
Coordinates	64° 04′ N; 18° 41′ E	61° 67′ N; 17° 44′ E	64° 03′ N; 18° 43′ E
Management regime	ecopark	ecopark	production landscape
Size (ha)	10,775	5479	12,528
Mean temperature (June–August) (∘C)[a]	13.5	14.9	13.5
Mean annual precipitation (mm)[a]	552	516	552
Vegetation type[b]	VT (38%), MT (27%)	VT (50%), CT (31%)	VT (46%), MT (27%)
Forest types (proportion of the landscape)			
Pine forest (≥65% pine)	57	70	52
Spruce forest (≥65% spruce)	8	3	17
Coniferous mixed forest (≥65% conifers)	22	18	23
Mixed forest (more than 35% but less than 65% broadleaves)	8	5	7
Broadleaved forest (≥65% broadleaves)	6	4	2
Forest age classes (proportion of the landscape)			
Clear-cuts (0–2 years)	3	3	13
Young (3–30)	34	22	30
Middle-aged (31–80)	29	31	31
Mature (81–120)	11	40	16
Old (>120)	23	5	10

[a] Data on mean temperatures and precipitation were from the Swedish Metrological Institute (Swedish Meteorological and Hydrological Institute, 2019).

[b] Vegetation classes according to Cajander (1926) as follows: VT – Vaccinium type. Dwarf shrub vegetation dominated by Vaccinum vitis idaea. CT – Calluna type. Dwarf shrub vegetation dominated by *Calluna vulgaris*. MT – Myrtillus type. Dwarf shrubs dominated by *Vaccinium myrtillus*.

allows the use of forest owner's data on forest structures (see Fig. 1.). Forests were classified into five different forest types according to the definitions by the Swedish National Forest Inventories (NFI): pine forest (≥65% pine), spruce forest (≥65% spruce), mixed coniferous forest (≥65% conifers), mixed forest (more than 35% but less than 65% broadleaves) and broadleaved forest (≥65% broadleaves, ≤45% noble broadleaves). Forest age was classified into five classes: clear-cut (0–2 years), young (3–30 years), middle-aged (31–80 years), mature (81–120) and old (>120). Each forest type and age class was calculated as the total amount of hectares (10,000 m^2) within each 500 m radius buffer.

2.4. Statistical analyses

For statistical analyses, all saproxylic beetles collected from one high stump were pooled over the whole sampling period (2010–2012). The unit of replication is thus one high stump on a sampling plot. The analyses were carried out for pooled landscapes but separately for pine and birch traps and separately for feeding guilds and habitat preference. In plots with two pines or two birches, only one of these high stumps was randomly chosen for the analyses, and stumps with lost trap collections were omitted from analyses ($N_{Birch} = 65$, $N_{Pine} = 73$).

To compare gamma diversity of beetles between different functional guilds, total species richness (pooled landscapes) per ecological trait group was calculated for pine and birch high stumps *i.e.*, one regarding feeding guilds and one regarding habitat preference by using rarefaction and extrapolation curves (R-package 'iNEXT' (Hsieh et al., 2016)) with 95% confidence intervals (Cumming et al., 2007).

To examine associations between different feeding guilds or habitat preferences and environmental variables, we used a model-based approach to the fourth corner problem (Legendre et al., 1997). The fourth corner problem is specifically designed to studying environment – trait associations (Brown et al., 2014). The model uses a set of three matrices, environmental data (R), species abundance data (L) and species trait data (Q) to produce a fourth matrix with interaction coefficients between traits and environmental variables. The size of coefficients are a measure of importance, and are interpreted as the amount by which a unit (1 SD) change in the trait variable changes the slope of the relationship between abundance and a given environmental variable. To estimate these coefficients, we used a LASSO-penalised negative binomial regression (R package 'mvabund' (Wang et al., 2012)). The LASSO penalty aids in interpretation as it completes model selection by setting to zero any terms in the model which do not explain any variation in species response *i.e.*, do not reduce BIC (Brown et al., 2014). A species effect is included in the model (*i.e.* a different intercept term for each species), so that traits are used to explain patterns in relative abundance across taxa, not patterns in absolute abundance. For model evaluation i.e., to measure the amount of variance explained by the regression models, pseudo-R^2 was calculated as the R^2 of the predicted against the observed abundance values for each species at each site with the function 'predict.traitglm' (R package 'mvabund' (Wang et al., 2012)). Prior to the analysis, local and landscape environmental variables were checked for collinearity with Pearson correlations (R package 'languageR' (Baayen and Shafaei-Bajestan, 2019)). Due to high sensitivity for collinearity within the environmental variables in the fourth corner analysis, deadwood diversity was removed from the analysis due to moderately high correlation with deadwood volume (Appendix, Fig. S3.)

All spatial analyses were done in in ArcGIS version 10.6 and data preparation, handling, visualization and statistical analyses were carried out in R Studio (R-version 3.6.1).

3. Results

3.1. Species diversity among functional guilds

We sampled in total 75,053 individuals of 353 different saproxylic beetle species (302 species of 19,894 individuals on birch, and 323 species of 55,223 individuals on pine). The rarefaction curves were beginning to saturate (reach the asymptote) in all cases except for broadleaf-generalists and -specialists sampled from pine stumps, indicating that we have sampled most of the species and can rely on our results.

Among beetle communities collected from birch stumps, broadleaf-generalist species had the highest rarefied species diversity, followed by conifer-generalist (Fig. 2a). Species abundance was the highest among wood-generalists. Among the feeding guilds, fungivores and predators had significantly the highest rarefied diversity, and detritivores the lowest.

Among beetle communities collected from pine stumps, the rarefied species diversity was the highest for broadleaf-generalist species and conifer-generalist species (Fig. 3a). Conifer-specialists had the highest species abundance. Regarding feeding guilds, cambivores had significantly the highest species diversity, followed by fungivores. Both cambivores and fungivores were also the most abundant feeding guild groups among pine communities.

3.2. Trait – environment interactions

The fourth corner models generated different environmental responses across traits with both positive and negative interactions of varying strengths (Figs. 2b & 3b). While highlighting the strongest interactions in sections 3.2.1 and 3.2.2, all interaction coefficients (IC) can be found in the APPENDIX (Table S1a-d). The models had Pseudo-R^2 values above 0.5 (Figs. 2 and 3), indicating that the predictors of the models, i.e., the environmental variables, explains a substantial proportion of the variation in the response variable, i.e., the abundance of

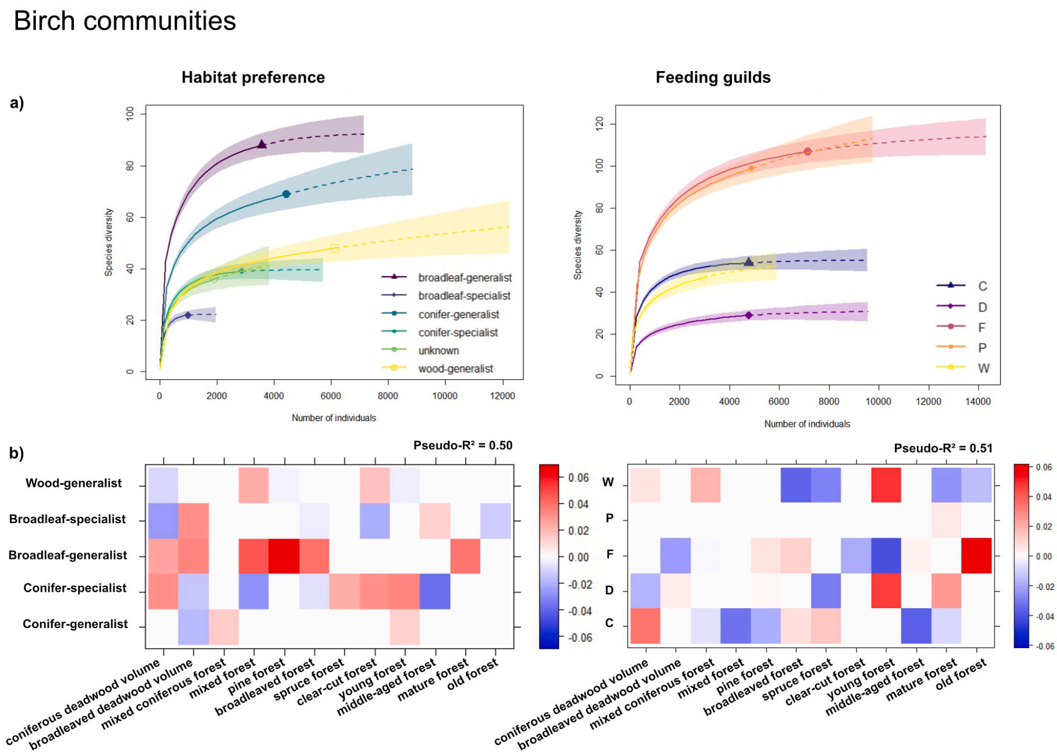

Fig. 2. Rarefaction curves for birch communities (a) with 95% confidence intervals (shaded areas) comparing the γ-diversity of ecological traits. Heat maps (b) of interaction coefficients for birch communities between traits (vertical axe) and environmental variables (horizontal axe) showing positive (red), negative (blue) and no associations (white). The intensity of colours refer to the positive (red) and negative (blue) strength of each interaction. Feeding guilds refer to cambivores (C), detritivores (D), fungivores (F), predators (P) and wood borers (W). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

different trait groups.

3.2.1. *Trait responses to local deadwood amounts*

Among beetle communities collected from birch stumps (Fig. 2b), the strongest positive interactions were found for broadleaf-preferring species and local amount of broadleaf originated deadwood (IC = 0.034 for broadleaf-generalists and 0.031 for broadleaf-specialists) as well as for conifer-specialists and local amount of coniferous deadwood (IC = 0.030). The strongest negative interaction among birch communities was found for broadleaf-specialists and the amount of coniferous deadwood (IC = −0.027). Regarding feeding guilds, a positive interaction was found for cambivores and local amount of coniferous deadwood (IC = 0.034) and a negative interaction for fungivores and local amount of broadleaved deadwood (IC = −0.024).

Among beetle communities collected from pine stumps (Fig. 3b), the strongest positive interactions were found for conifer-specialists and local amount of coniferous deadwood (IC = 0.044), and for broadleaf-generalists and local amount of broadleaved deadwood (IC = 0.042). A negative interaction was found for broadleaf-specialists and local amount of coniferous deadwood (IC = −0.141). Regarding feeding guilds, a positive interaction was found for wood borers and local amount of coniferous deadwood (IC = 0.036), but a negative interaction with local amount of broadleaved deadwood (IC = −0.031). Contrary to birch communities, fungivores from pine traps had a positive interaction with local amount of broadleaved deadwood (IC = 0.027) and a negative interaction with local amount of coniferous deadwood (IC = −0.059).

3.2.2. *Trait responses to forest structures in the surrounding landscapes*

Among beetle communities collected from birch high stumps, broadleaf-generalists and conifer-specialists had the strongest interactions with landscape variables. For broadleaf generalists, there was a positive interaction with the amount of mixed forests (IC = 0.046), broadleaved forests (IC = 0.039) and the amount of pine forests (IC = 0.069). Regarding forest age, broadleaf-generalists had a positive interaction with the amount of mature forests in the surrounding landscape. On the other hand, conifer-specialists had positive interactions with the amount of clear-cut- and young forests (IC = 0.031 and 0.033) and a negative interaction with middle-aged forests (IC = −0.038).

Regarding feeding guilds among birch communities, interactions with landscape variables were found for all guilds except for predators. Cambivores had negative interactions with the amount of mixed forests (IC = −0.032) and the amount of middle-aged forests (IC = −0.037). Detritivores had a positive interaction with young forests (IC = 0.046) and a negative interaction with spruce forests (IC = −0.030). Fungivores had strongest positive interactions with the amount of old forests (IC = 0.061) and a negative interaction with young forests (IC = −0.042). Wood borers had the strongest positive interaction with young forests (IC = 0.049) and a negative interaction with the amount of broadleaved forests (IC = −0.036).

Among beetle communities sampled from pine stumps, conifer

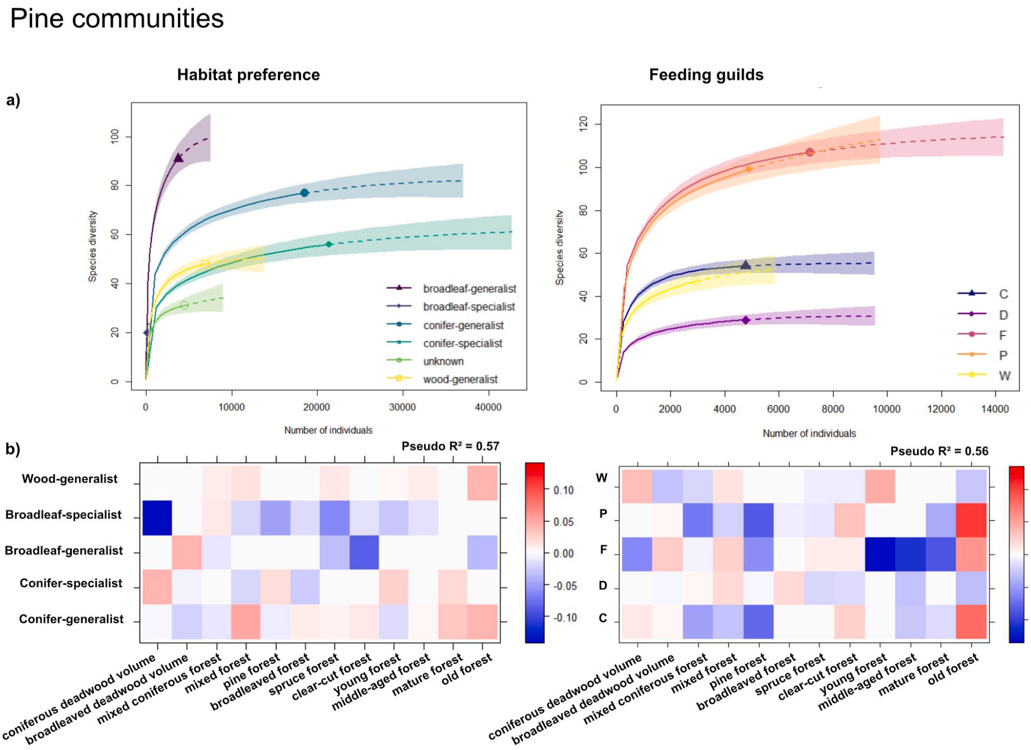

Fig. 3. Rarefaction curves for pine communities (a) with 95% confidence intervals (shaded areas) comparing the γ-diversity of ecological traits. Heat maps (b) of interaction coefficients for pine communities between traits (vertical axe) and environmental variables (horizontal axe) showing positive (red), negative (blue) and no associations (white). The intensity of colours refer to the positive (red) and negative (blue) strength of each interaction. Feeding guilds refer to cambivores (C), detritivores (D), fungivores (F), predators (P) and wood borers (W). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

generalists had the strongest positive interactions with the amount of mixed forests (IC = 0.050) and the amount of old forests (IC = 0.044). Wood-generalists also had the strongest interaction with the amount of old forests (IC = 0.042). For broadleaf-generalists negative interactions were found with the amount of spruce forests (IC = −0.035), clear-cut forests (IC = −0.085) and the amount of old forests (IC = −0.036). Broadleaf-specialists had negative interactions with the amount of pine-forests (IC = −0.047), the amount of spruce forests (IC = −0.064) and the amount of young-forests (IC = −0.029).

4. Discussion

With this study, we assessed interactions between ecological traits of saproxylic beetles and local deadwood amounts and forest types in the landscape. We found significant trait-environment interactions at both local and landscape scales, indicating that multiple spatial scales need to be considered when planning for conservation actions. Our results can be summarized in three main findings that can provide direct recommendations regarding ecological restoration and protection in boreal forests. First, broadleaf-preferring beetle species are positively associated with both the local amount of broadleaf-originated deadwood and broadleaf-rich forests in the surrounding landscape. This suggests that measures should target both the increase of deadwood and ‘broadleafication’ within forest stand composition at larger scales. Second, conifer-associated species have the strongest positive relationships with local coniferous deadwood and surrounding young and old forests. This finding supports the importance of local deadwood, but also the relevance of increasing diversity in age structure across forest stands in the surrounding landscape. Third, both predatory and fungivorous beetles are strongly associated with old forests, emphasizing the significance of this habitat type on guild level. These findings increase our knowledge on saproxylic guild and habitat responses to boreal forest management and restoration, thus improving our ability to produce efficient conservation strategies.

4.1. *Local deadwood and its significance for beetle communities*

We found a clear positive interaction between local deadwood volumes/qualities and beetles with preferences or specialization to either coniferous or broadleaved deadwood. Earlier studies have highlighted the significance of local deadwood amount, diversity, or substrate type in relation to the total species richness of saproxylic beetles or red-listed species (e.g., Larsson Ekström et al., 2021; McGeoch et al., 2007; Seibold et al., 2017; Ulyshen and Hanula, 2009). However, our findings deepen this knowledge by elucidating the relationships between deadwood types (broadleaf/conifer) and respective species assemblages.

Specifically in Swedish forests, deadwood occurs at low abundance; around 8.7 m^3 deadwood per hectare is estimated within high productive forests outside protected areas (Swedish University of Agricultural Sciences (SLU), 2023). This is far from deadwood quantities in natural boreal conditions where volumes can be 50–80 m^3 per hectare (Siitonen, 2001) and far from estimated thresholds for maintaining red-listed species (20 m^3/ha) (Hekkala et al., 2023).

The moderately high correlation between deadwood volume and diversity in our study implies that an increase in deadwood quantity within our plots corresponds to a higher diversity of deadwood (including tree species, decay stages, postures of trees, associated fungal communities etc.). Deadwood diversity is known to be important for deadwood-dependent biodiversity (Hägglund and Hjältén, 2018; Økland et al., 1996; Seibold et al., 2016; Similä et al., 2003; Yang et al., 2021). These results suggest that forest management must consider not only the amount of deadwood but also the origin and diversity of deadwood, and therefore diversify the qualities of dead trees retained at harvesting or specifically created as part of restoration management. Since late 1990s, a common practice in Swedish silviculture is to create high stumps during clear-felling operations to increase the amount of deadwood substrates (Gustafsson et al., 2020). These man-made high stumps have shown to support a relatively rich saproxylic beetle fauna (Andersson et al., 2015; Hjältén et al., 2010, 2012) that vary considerably between tree species (Jonsell et al., 2004; Lindhe and Lindelöw, 2004), which we also confirm in this study. However, the overwhelming part of the high stumps that are created consist of coniferous trees with spruce as the dominating tree species (83%), while birch and aspen high stumps make up only approximately 4% at logging sites (Lindhe and Lindelöw, 2004). Our research emphasizes the importance of creating high stumps of broadleaved trees, to maintain the broadleaf-associated beetle assemblages.

Regarding feeding guilds, wood borers and cambivores had positive interactions with local amount of coniferous deadwood. Cambivores were mainly represented by conifer-specialists, and wood borers were mainly conifer-generalists (Table S2). Most cambivores are early successional species such as bark beetles (Curculionidae:Scolytinae), specialised on weakened or freshly killed trees. They are known to have good dispersal abilities since they are adapted to an ephemeral habitat (Hanski, 1987), which suggests that cambivores are less sensitive to habitat fragmentation than other feeding guilds of saproxylic beetles. Local amount of deadwood is thus an important factor for early successional species as they are able to find and disperse to deadwood hot-spots in the landscape. Both cambivores and wood borers contribute important ecosystem functions by shaping deadwood habitats in a way that enables other organism groups to utilize the same resource (Stokland et al., 2012).

4.2. Importance of forest structures in the landscape

Our study revealed several ecological interactions between beetle occurrence and forest structures in the landscape, emphasizing that not only local variables determine the beetle communities.

The finding of a positive relationship between the amount of broadleaf-rich habitats (broadleaved and mixed forests) and broadleaf-related beetles is particularly interesting, since the proportion of those habitats is relatively low (ranging approximately between 2 and 8 percent) in the three studied landscapes (see Table 1). This implies that landscape composition is of importance for broadleaf-associated species, something that has seldom been demonstrated. An earlier study by Økland et al. (1996) showed a positive correlation between saproxylic beetles associated with birch and aspen and the amount of broadleaved trees and broadleaf-originated deadwood in the surrounding landscapes. Also Abrahamsson (2007) found in his study that the amount of broadleaved forest in the surrounding of clear-cuts explained a significant amount of variation in beetle species composition on high stumps but did not include information regarding habitat preference of species.

The positive relationship of broadleaf-generalist species with mature forests (81–120 years) further implies the need of setting aside older broadleaf-rich habitats from exploitation. At the same time, the current negative trend with decreasing area of older broadleaf-rich forests in Northern Sweden (SLU, 2020) and that such forests are already rare in boreal Sweden (Mikusiński et al., 2021) could further threaten the communities related to broadleaf-rich habitats. Favouring broadleaf-rich forests are therefore urgently needed, especially since broadleaf-associated species face a higher degree of extinction risk than conifer-associated species (Seibold et al., 2015) due to the disadvantage of broadleaved trees by forestry. In order to mitigate the negative trend, many forest companies are actively restoring forests with focus on broadleaves, with positive results (Bell et al., 2015; Bergman and Gustafsson, 2020). However, it takes many decades before the restored stands reach mature age, which often is a prerequisite before other conservation actions can take place, e.g., retention of large diameter broadleaf deadwood (Hof and Hjältén, 2018). Also, older forests usually contain greater amounts of deadwood (Bujoczek et al., 2021; Martin et al., 2021; Šēnhofa et al., 2020). As the time of writing, both deadwood and broadleaf-rich forests have low abundance on boreal stand- and landscape scale and are identified as critical restoration themes in Sweden (Svensson et al., 2023; Mikusiński et al., 2021). Both these themes are also elevated as critical to reach the national environmental goal targets on sustainable forests (Swedish Forest Agency, 2023).

The positive interaction regarding broadleaf-generalists with pine forests in the landscape might be explained by the fact that all three landscapes in our study are highly pine-dominated (more than 50 % of each landscape consist of pine stands, see Table 1.). In other words, many broadleaf-rich habitats are surrounded by a large amount of pine forests (Fig. S1.). It could also be due to the fact that pine forests, especially mature or older pine forests, are more open than spruce- or mixed-coniferous forests. Previous studies have shown that many broadleaf-associated beetles are often positively correlated with open habitats, including clear-cut forests if only a sufficient number of suitable host trees is retained (Martikainen, 2001; Ranius and Jansson, 2000; Sverdrup-Thygeson and Ims, 2002). Since the broadleaf tree species in our landscapes consists mainly of birch and aspen, so called pioneer species that grow after a major disturbance such as fire, storm or clear-cut, it is expected that beetle species dependent on birch and aspen are favoured by canopy openness. However, the negative interaction between broadleaf-associated species and clear-cuts may indicate that there is an insufficient number of broadleaved trees or deadwood retained on clear-cuts in our study areas. It is also worth mentioning that many shade-tolerant species of saproxylic beetles utilize dead birches (Bell et al., 2015; Lindhe et al., 2005) which proposes that birch can host both shade-tolerant and open-preferring species. This highlights the importance of restoring broadleaf-originated deadwood in both open and more closed forests. Even though we found one of the strongest associations between broadleaf-generalists and the amount of broadleaf-rich habitats in communities sampled from birch stumps, we did not observe the same in pine stumps. At the same time, the rarefaction curve revealed that we had not sampled enough broadleaf-preferring species from pine stumps to make reliable conclusions (Fig. 3a.)

We found a positive interaction between fungivores and forests older than 120 years and a negative interaction with younger forests. These interactions were found for both pine and birch samples making them the strongest in our study. Fungivores often specialize on certain fungi growing on specific tree species (Stokland et al., 2012). Old forests with a long continuity tend to accumulate greater amounts of deadwood and contain a higher biodiversity of deadwood-dependent fungi compared to younger forests (Edman et al., 2004; Esseen et al., 1997). Given that fungivores play a crucial role as dispersal agents for fungal spores and form a species-rich group, it is imperative to preserve older forests in a landscape context. This is because maintaining deadwood continuity, specifically having deadwood in various decay stages, is challenging to restore, primarily due to the essential factor of time (Vrška et al., 2015). In our study, twice as many fungivores were broadleaf-preferring in comparison to conifer-preferring species, highlighting the need for the protection of older, broadleaf-rich forests to ensure a continuous presence of deadwood originating from broadleaf trees.

We also found a strong positive interaction between predators and old forests in pine samples. Predators form the most generalist group as their prey is ubiquitous. However, larvae and pupae of detritivores and fungivores constitute the main prey source for predators (Stokland et al., 2012). Our results are also in line with Wetherbee et al. (2023) who found a higher proportion of predatory saproxylic beetles in near natural forests compared to managed forests. However, despite the high diversity and abundance of predatory beetles caught in birch traps, we did not detect any interactions, neither positive nor negative, except for a weak positive interaction with mature forests. This implies the generalist nature of predatory beetles but also the complex relationships with their prey and the environment (Johansson et al., 2007).

By utilizing a combination of one pine and one birch high stumps in plots with varying local and landscape habitat composition, we were able to assess the significance of local and landscape scale habitats for various beetle guilds. Although our study considered boreal forests, we argue that our results could potentially represent other forest types in different climatic regions, as we focus on trait responses to environmental variables rather than single species responses. Similarly as in boreal forests, broadleaf-associated beetles face a higher extinction risk in temperate forests, due to the replacement of broadleaved forests by conifer-dominated stands (Seibold et al., 2015). Regarding our study design, the pairs of high stumps in our plots were situated close to each other, which can potentially result in spill over of species between traps on birch and pine high stumps, which is the reason to examine also broadleaf-associated species sampled from pine stumps, and conifer-associated species from birch stumps. The abundances of different trait groups on birch vs pine high stumps has to be kept in mind when interpreting the interactions. In regards to the time-lag between beetle sampling (2010–2012) and field measurements (2019), we argue that local deadwood data collected in the field are valid due to the very slow processes regarding for example deadwood decay in the boreal zone, and the fact that no major disturbances such as bark beetle outbreaks, fires or windfalls had taken place in our study sites during that time (Larsson Ekström et al., 2021).

5. Conclusions

Significant trait-environment interactions were found at both local and landscape scales, emphasizing the importance of considering multiple spatial scales in conservation planning. The findings suggest three main recommendations for ecological restoration and protection in boreal forests. First, increasing both the amount of deadwood and promoting broadleaf-rich forests at larger scales benefits broadleaf-preferring beetle species. Second, local coniferous deadwood and diverse age structures (both young and old) across forest stands positively influence conifer-associated species. Third, old forests play a crucial role for both predatory and fungivorous beetles at the guild level. These insights enhance our understanding of saproxylic guild and habitat responses, contributing to more effective conservation strategies in boreal forest management and restoration. The Swedish forestry model need to become more diversified to meet diverse habitat requirements of saproxylic beetles. Shifting away from a systematic, stand-oriented clear-cut forestry approach to forest management with broad system boundaries is essential. This approach should recognize restoration as a key component within these boundaries.

Further, our study suggests that considering traits in biodiversity assessments is a promising approach to determine which types of habitats need to be prioritized when undertaking restoration and conservation actions in boreal forest landscapes.

CRediT authorship contribution statement

Paulina Bergmark: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Joakim Hjältén:** Writing – review & editing, Funding acquisition, Conceptualization. **Johan Svensson:** Writing – review & editing, Conceptualization. **Wiebke Neumann:** Writing – review & editing. **Anne-Maarit Hekkala:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We thank Sveaskog AB for providing us with study areas and beetle data,Albin Larsson Ekström for his help with data collection and three anonymous reviewers for constructive comments that improved the manuscript. This study was funded by the Foundation for Oscar and Lili Lamms minne, grant number: DO2018-0033 to PB.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2024.121080.

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APPENDIX

Table S1. *Interaction coefficients from the trait.glm models for (a) pine communities feeding guilds, (b) pine communities habitat preference, (c) birch communities feeding guilds and (d) birch communities habitat preference. Note that many coefficients are set to zero due to the lasso penalty, which acts as model selection. The size of coefficients is a measure of importance, and are interpreted as the amount by which a unit (1 SD) change in the trait variable changes the slope of the relationship between abundance and a given environmental variable.*

a) Birch communities, habitat preference. Overall Pseudo-$R^2 = 0.50$

Trait	**Coniferous deadwood volume**	**Broadleaved deadwood volume**	**Mixed coniferous forest**	**Mixed forest**	**Pine forest**	**Broadleaved forest**	**Spruce forest**	**Clear-cut forest**	**Young forest**	**Middle-aged forest**	**Mature forest**	**Old forest**
Wood-generalist	-0.009	0.000	0.000	0.022	-0.002	0.000	0.000	0.017	-0.004	0.000	0.000	0.000
Broadleaf-specialist	-0.027	0.031	0.000	0.000	0.000	-0.004	0.000	-0.021	0.000	0.013	0.000	-0.013
Broadleaf-generalist	0.026	0.034	0.000	0.046	0.069	0.039	0.000	0.000	0.000	0.000	0.038	0.000
Conifer-specialist	0.030	-0.015	0.000	-0.028	0.001	-0.007	0.023	0.031	0.033	-0.038	0.000	0.000
Conifer-generalist	0.000	-0.018	0.014	0.000	0.000	0.000	0.000	0.000	0.012	0.000	0.000	0.000

b) Birch communities, feeding guilds. Overall Pseudo-$R^2 = 0.51$

Trait	**Coniferous deadwood volume**	**Broadleaved deadwood volume**	**Mixed coniferous forest**	**Mixed forest**	**Pine forest**	**Broadleaved forest**	**Spruce forest**	**Clear-cut forest**	**Young forest**	**Middle-aged forest**	**Mature forest**	**Old forest**
Wood-borer	0.006	0.000	0.018	0.000	0.000	-0.036	-0.029	0.000	0.049	0.000	-0.000	-0.015
Predator	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.000
Fungivore	0.000	-0.024	-0.001	0.000	0.007	0.012	0.000	-0.020	-0.042	0.003	0.000	0.061
Detritivore	-0.017	0.004	0.000	0.000	0.001	0.000	-0.030	0.000	0.046	0.000	0.024	0.000
Cambivore	0.034	0.000	-0.006	-0.032	-0.019	0.007	0.014	0.000	0.000	-0.037	-0.009	0.000

c) Pine communities, habitat preference. Overall Pseudo $R^2 = 0.57$

Trait	**Coniferous deadwood volume**	**Broadleaved deadwood volume**	**Mixed coniferous forest**	**Mixed forest**	**Pine forest**	**Broadleaved forest**	**Spruce forest**	**Clear-cut forest**	**Young forest**	**Middle-aged forest**	**Mature forest**	**Old forest**
Wood-generalist	0.000	0.000	0.009	0.013	0.000	0.000	0.012	0.000	0.004	0.008	0.000	0.042
Broadleaf-specialist	-0.141	0.000	0.010	-0.021	-0.047	-0.016	-0.064	-0.015	-0.029	-0.013	0.000	0.000
Broadleaf-generalist	0.000	0.042	-0.011	0.000	0.000	0.000	-0.035	-0.085	0.000	0.000	-0.001	-0.036
Conifer-specialist	0.044	-0.006	0.000	-0.021	0.018	-0.026	0.000	0.000	0.026	0.000	0.021	0.000
Conifer-generalist	-0.003	-0.022	-0.010	0.050	-0.009	0.010	0.007	0.012	-0.016	0.004	0.032	0.044

d) Pine communities, feeding guilds. Overall Pseudo $R^2 = 0.56$

Trait	**Coniferous deadwood volume**	**Broadleaved deadwood volume**	**Mixed coniferous forest**	**Mixed forest**	**Pine forest**	**Broadleaved forest**	**Spruce forest**	**Clear-cut forest**	**Young forest**	**Middle-aged forest**	**Mature forest**	**Old forest**
Wood-borer	0.036	-0.031	-0.018	0.013	0.000	0.001	-0.009	-0.009	0.043	0.000	0.001	-0.027
Predator	0.000	0.002	-0.069	-0.022	-0.086	-0.008	-0.012	0.033	0.000	0.000	-0.045	0.104
Fungivore	-0.059	0.027	-0.005	0.024	-0.057	0.001	0.008	0.007	-0.135	-0.108	-0.087	0.058
Detritivore	0.000	-0.003	0.002	0.018	-0.003	0.018	-0.020	-0.015	0.000	-0.031	0.000	-0.033
Cambivore	0.012	0.002	-0.046	-0.031	-0.077	0.000	0.000	0.025	0.000	-0.026	-0.016	0.079

Table S2. *Saproxylic beetle species sampled from birch and pine traps over three consecutive years. Feeding guilds refer to cambivore (C), detritivore (D), fungivore (F), herbivore (H), predator (P) and wood-borer (W). Red-list status refer to least concern (LC), near threatened (NT) and vulnerable (VU)*

Family	Species	Feeding guild	Habitat preference	Red-list	Total abundance
Aderidae	*Anidorus nigrinus* (Germar, 1842)	D,F	broadleaf-generalist	LC	6
Aderidae	*Euglenes pygmaeus* (De Geer, 1775)	F	broadleaf-generalist	LC	104
Anthribidae	*Anthribus nebulosus* (Forster, 1770)	P	conifer-generalist	LC	16
Anthribidae	*Gonotropis dorsalis* (Thunberg, 1796)	C, F	broadleaf-specialist	NT	4
Anthribidae	*Platystomos albinus* (Linnaeus, 1758)	W,F	broadleaf-generalist	LC	64
Bostrichidae	*Stephanopachys substriatus* (Paykull, 1800)	C	conifer-specialist	LC	2
Buprestidae	*Agrilus viridis* (Linnaeus, 1758)	C	broadleaf-specialist	LC	17
Buprestidae	*Anthaxia quadripunctata* (Linnaeus, 1758)	C	conifer-generalist	LC	325
Buprestidae	*Anthaxia similis* (Saunders, 1871)	H	conifer-specialist	LC	6
Buprestidae	*Buprestis haemorrhoidalis* (Herbst, 1780)	D	conifer-specialist	LC	2
Buprestidae	*Buprestis rustica* (Linnaeus, 1758)	W	conifer-generalist	LC	5
Buprestidae	*Chalcophora mariana* (Linnaeus, 1758)	D	conifer-generalist	LC	1
Buprestidae	*Chrysobothris chrysostigma* (Linnaeus, 1758)	C	conifer-generalist	LC	22
Buprestidae	*Dicerca furcata* (Thunberg, 1787)	F	broadleaf-generalist	NT	1
Buprestidae	*Phaenops cyaneus* (Fabricius, 1775)	H	conifer-specialist	LC	92
Buprestidae	*Trachys minuta* (Linnaeus, 1758)	H	broadleaf-generalist	LC	5
Cantharidae	*Malthinus biguttatus* (Linnaeus, 1758)	H,P	unknown	LC	4
Cantharidae	*Malthinus flaveolus* (Herbst, 1786)	P	broadleaf-generalist	LC	4
Cantharidae	*Malthodes brevicollis* (Paykull, 1798)	H,P	broadleaf-generalist	LC	76
Cantharidae	*Malthodes crassicornis* (Mäklin, 1846)	P	broadleaf-generalist	LC	10
Cantharidae	*Malthodes flavoguttatus* (Kiesenwetter, 1852)	P	unknown	LC	4
Cantharidae	*Malthodes fuscus* (Waltl, 1838)	P	unknown	LC	13
Cantharidae	*Malthodes guttifer* (Kiesenwetter, 1852)	P	broadleaf-generalist	LC	14
Cantharidae	*Malthodes marginatus* (Latreille, 1806)	P	broadleaf-generalist	LC	9
Cantharidae	*Malthodes maurus* (Laporte de Castelnau, 1840)	P	unknown	LC	4
Cantharidae	*Malthodes minimus* (Linnaeus, 1758)	P	unknown	LC	7
Cantharidae	*Malthodes pumilus* (Brébisson, 1835)	P	unknown	LC	10
Cantharidae	*Malthodes sp*	P	unknown	LC	25
Cantharidae	*Malthodes spathifer* (Kiesenwetter, 1852)	P	broadleaf-generalist	LC	3
Cantharidae	*Podistra schoenherri* (Dejean, 1837)	P	conifer-generalist	LC	461
Carabidae	*Dromius agilis* (Fabricius, 1787)	P	conifer-generalist	LC	11
Carabidae	*Tachyta nana* (Gyllenhal, 1810)	P	broadleaf-generalist	NT	9

Cerambycidae	*Acanthocinus aedilis* (Linnaeus, 1758)	C	conifer-specialist	LC	53
Cerambycidae	*Acmaeops septentrionis* (Thomson, 1866)	C,W	conifer-specialist	NT	10
Cerambycidae	*Aegomorphus clavipes* (Schrank, 1781)	D	broadleaf-generalist	NT	4
Cerambycidae	*Alosterna tabacicolor* (De Geer, 1775)	W	broadleaf-generalist	LC	3
Cerambycidae	*Anastrangalia reyi* (Heyden, 1889)	W	conifer-generalist	LC	74
Cerambycidae	*Anastrangalia sanguinolenta* (Linnaeus, 1761)	W	conifer-generalist	LC	71
Cerambycidae	*Arhopalus rusticus* (Linnaeus, 1758)	C,W	conifer-specialist	LC	119
Cerambycidae	*Asemum striatum* (Linnaeus, 1758)	C,W	conifer-generalist	LC	164
Cerambycidae	*Callidium coriaceum* (Paykull, 1800)	C,W	conifer-specialist	LC	1
Cerambycidae	*Callidium violaceum* (Linnaeus, 1758)	H	conifer-specialist	LC	4
Cerambycidae	*Gaurotes virginea* (Linnaeus, 1758)	C	conifer-specialist	LC	3
Cerambycidae	*Gnathacmaeops pratensis* (Laicharting, 1784)	C,W	conifer-generalist	LC	2
Cerambycidae	*Judolia sexmaculata* (Linnaeus, 1758)	C,W	conifer-generalist	LC	7
Cerambycidae	*Leptura quadrifasciata* (Linnaeus, 1758)	W	wood-generalist	LC	33
Cerambycidae	*Lepturobosca virens* (Linnaeus, 1758)	W	wood-generalist	LC	2
Cerambycidae	*Molorchus minor* (Linnaeus, 1758)	C,W	conifer-generalist	LC	40
Cerambycidae	*Monochamus sutor* (Linnaeus, 1758)	C,W	conifer-specialist	LC	7
Cerambycidae	*Necydalis major* (Linnaeus, 1758)	W	wood-generalist	NT	7
Cerambycidae	*Oxymirus cursor* (Linnaeus, 1758)	W	conifer-generalist	LC	18
Cerambycidae	*Pachyta lamed* (Linnaeus, 1758)	C	conifer-specialist	LC	12
Cerambycidae	*Pogonocherus decoratus* (Fairmaire, 1855)	C,W	conifer-specialist	LC	5
Cerambycidae	*Pogonocherus fasciculatus* (De Geer, 1775)	C,W	conifer-specialist	LC	172
Cerambycidae	*Rhagium inquisitor* (Linnaeus, 1758)	C,W	conifer-generalist	LC	1709
Cerambycidae	*Rhagium mordax* (De Geer, 1775)	C	broadleaf-generalist	LC	282
Cerambycidae	*Rusticoclytus rusticus* (Linnaeus, 1758)	C,W	broadleaf-generalist	LC	64
Cerambycidae	*Saperda scalaris* (Linnaeus, 1758)	C,W	broadleaf-generalist	LC	5
Cerambycidae	*Stenurella melanura* (Linnaeus, 1758)	W	wood-generalist	LC	7
Cerambycidae	*Stictoleptura maculicornis* (De Geer, 1775)	D,W	wood-generalist	LC	3
Cerambycidae	*Tetropium castaneum* (Linnaeus, 1758)	C	conifer-specialist	LC	81
Cerambycidae	*Tragosoma depsarium* (Linnaeus, 1767)	D	conifer-specialist	VU	60
Cerylonidae	*Cerylon deplanatum* (Gyllenhal, 1827)	F	broadleaf-specialist	NT	3
Cerylonidae	*Cerylon ferrugineum* (Stephens, 1830)	F	broadleaf-generalist	LC	115
Cerylonidae	*Cerylon histeroides* (Fabricius, 1792)	F	wood-generalist	LC	898
Ciidae	*Cis bidentatus* (Olivier, 1790)	F	wood-generalist	LC	16
Ciidae	*Cis boleti* (Scopoli, 1763)	F	broadleaf-generalist	LC	603
Ciidae	*Cis castaneus* (Herbst, 1793)	F	broadleaf-generalist	LC	3
Ciidae	*Cis comptus* (Gyllenhal, 1827)	F	broadleaf-generalist	LC	222
Ciidae	*Cis dentatus* (Mellié, 1848)	F	conifer-generalist	NT	8
Ciidae	*Cis festivus* (Panzer, 1793)	F	broadleaf-generalist	LC	2
Ciidae	*Cis glabratus (*Mellié, 1848)	F	conifer-generalist	LC	32
Ciidae	*Cis jacquemartii* (Mellié, 1848)	F	broadleaf-specialist	LC	17

Ciidae	*Cis lineatocribratus* (Mellié, 1848)	F	conifer-generalist	LC	5
Ciidae	*Cis micans* (Fabricius, 1792)	F	broadleaf-generalist	LC	110
Ciidae	*Cis punctulatus* (Gyllenhal, 1827)	F	conifer-generalist	LC	32
Ciidae	*Cis villosulus* (Marsham, 1802)	F	broadleaf-specialist	LC	7
Ciidae	*Dolichocis laricinus* (Mellié, 1848)	F	wood-generalist	NT	2
Ciidae	*Ennearthron cornutum* (Gyllenhal, 1827)	F	wood-generalist	LC	14
Ciidae	*Hadreule elongatula* (Gyllenhal, 1827)	F	wood-generalist	LC	37
Ciidae	*Orthocis alni* (Gyllenhal, 1813)	F	broadleaf-generalist	LC	90
Ciidae	*Orthocis vestitus* (Mellié, 1848)	F	broadleaf-generalist	LC	1
Ciidae	*Rhopalodontus strandi* (Lohse, 1969)	F	broadleaf-generalist	LC	2
Ciidae	*Sulcacis nitidus* (Fabricius, 1792)	F	wood-generalist	LC	11
Cleridae	*Thanasimus femoralis* (Zetterstedt, 1828)	P	conifer-generalist	LC	190
Cleridae	*Thanasimus formicarius* (Linnaeus, 1758)	P	conifer-generalist	LC	1743
Corylophidae	*Orthoperus sp*	P	unknown	LC	35
Cryptophagidae	*Atomaria sp*	F	unknown	LC	361
Cryptophagidae	*Cryptophagus sp*	F	unknown	LC	186
Cryptophagidae	*Henoticus serratus* (Gyllenhal, 1808)	F	broadleaf-generalist	LC	1
Cryptophagidae	*Micrambe abietis* (Paykull, 1798)	F	wood-generalist	LC	10
Cryptophagidae	*Micrambe sp*	F	unknown	LC	8
Cucujidae	*Pediacus fuscus* (Erichson, 1845)	F	wood-generalist	LC	12
Curculionidae	*Cryphalus saltuarius* (Weise, 1891)	C	conifer-specialist	LC	1
Curculionidae	*Cryptorhynchus lapathi* (Linnaeus, 1758)	H	broadleaf-specialist	LC	1
Curculionidae	*Crypturgus cinereus* (Herbst, 1793)	C	conifer-specialist	LC	76
Curculionidae	*Crypturgus hispidulus* (Thomson, 1870)	C	conifer-specialist	LC	88
Curculionidae	*Crypturgus pusillus* (Gyllenhal, 1813)	C	conifer-specialist	LC	32
Curculionidae	*Crypturgus subcribrosus* (Eggers, 1933)	C	conifer-specialist	LC	38
Curculionidae	*Dendroctonus micans* (Kugelann, 1794)	C	conifer-specialist	LC	1
Curculionidae	*Dryocoetes autographu*s (Ratzeburg, 1837)	C	conifer-specialist	LC	526
Curculionidae	*Dryocoetes hectographus* (Reitter, 1913)	C	conifer-specialist	LC	17
Curculionidae	*Hylastes brunneus* (Erichson, 1836)	C	conifer-specialist	LC	12234
Curculionidae	*Hylastes cunicularius* (Erichson, 1836)	C	conifer-specialist	LC	2544
Curculionidae	*Hylastes opacus* (Erichson, 1836)	C	conifer-specialist	LC	160
Curculionidae	*Hylobius abietis* (Linnaeus, 1758)	C,W	wood-generalist	LC	1267
Curculionidae	*Hylobius excavatus* (Laicharting, 1781)	C	conifer-generalist	LC	2
Curculionidae	*Hylobius pinastri* (Gyllenhal, 1813)	C,W	conifer-specialist	LC	13
Curculionidae	*Hylurgops glabratus* (Zetterstedt, 1828)	C	conifer-specialist	LC	15
Curculionidae	*Hylurgops palliatus* (Gyllenhal, 1813)	C	conifer-generalist	LC	584
Curculionidae	*Ips typographus* (Linnaeus, 1758)	C	conifer-generalist	LC	113
Curculionidae	*Magdalis carbonaria* (Linnaeus, 1758)	H	broadleaf-specialist	LC	25
Curculionidae	*Magdalis duplicata* (Germar, 1819)	C	conifer-generalist	LC	33
Curculionidae	*Magdalis frontalis* (Gyllenhal, 1827)	W	conifer-generalist	LC	11
Curculionidae	*Magdalis linearis* (Gyllenhal, 1827)	W	conifer-generalist	LC	2
Curculionidae	*Magdalis phlegmatica* (Herbst, 1797)	W	conifer-generalist	LC	11

Curculionidae	*Magdalis ruficornis* (Linnaeus, 1758)	C	broadleaf-generalist	LC	4
Curculionidae	*Magdalis violacea* (Linnaeus, 1758)	C	conifer-specialist	LC	94
Curculionidae	*Orthotomicus laricis* (Fabricius, 1792)	C	conifer-specialist	LC	3
Curculionidae	*Orthotomicus proximus* (Eichhoff, 1868)	C	conifer-specialist	LC	30
Curculionidae	*Orthotomicus suturalis* (Gyllenhal, 1827)	C	conifer-specialist	LC	10
Curculionidae	*Phloeotribus spinulosus* (Rey, 1883)	C	conifer-specialist	LC	6
Curculionidae	*Pissodes harcyniae* (Herbst, 1795)	C	conifer-specialist	LC	3
Curculionidae	*Pissodes pini* (Linnaeus, 1758)	C	conifer-specialist	LC	197
Curculionidae	*Pissodes piniphilus* (Herbst, 1797)	C	conifer-specialist	LC	37
Curculionidae	*Pityogenes bidentatus* (Herbst, 1783)	C	conifer-specialist	LC	156
Curculionidae	*Pityogenes chalcographus* (Linnaeus, 1761)	C	conifer-specialist	LC	1191
Curculionidae	*Pityogenes quadridens* (Hartig, 1834)	C	conifer-specialist	LC	84
Curculionidae	*Pityophthorus micrographus* (Linnaeus, 1758)	C	conifer-specialist	LC	17
Curculionidae	*Polygraphus poligraphus* (Linnaeus, 1758)	C	conifer-specialist	LC	49
Curculionidae	*Polygraphus punctifrons* (Thomson, 1886)	C	conifer-specialist	LC	5
Curculionidae	*Polygraphus subopacus* (Thomson, 1871)	C	conifer-specialist	LC	98
Curculionidae	*Rhyncolus ater* (Linnaeus, 1758)	W	conifer-generalist	LC	31
Curculionidae	*Rhyncolus sculpturatus* (Waltl, 1839)	W	wood-generalist	LC	48
Curculionidae	*Scolytus ratzeburgii* (Janson, 1856)	C	broadleaf-specialist	LC	674
Curculionidae	*Tomicus minor* (Hartig, 1834)	C,F	conifer-specialist	LC	19
Curculionidae	*Tomicus piniperda* (Linnaeus, 1758)	C	conifer-specialist	LC	1393
Curculionidae	*Trachodes hispidus* (Linnaeus, 1758)	D	broadleaf-specialist	LC	10
Curculionidae	*Trypodendron domesticum* (Linnaeus, 1758)	F	broadleaf-generalist	LC	83
Curculionidae	*Trypodendron laeve (*Eggers, 1939)	F	conifer-generalist	LC	356
Curculionidae	*Trypodendron lineatum* (Olivier, 1795)	F	conifer-generalist	LC	8373
Curculionidae	*Trypodendron signatum* (Fabricius, 1792)	F	broadleaf-specialist	LC	19
Curculionidae	*Trypophloeus sp*	C	broadleaf-specialist	LC	2
Curculionidae	*Xylechinus pilosus* (Ratzeburg, 1837)	C	conifer-specialist	LC	1
Dasytidae	*Aplocnemus nigricornis* (Fabricius, 1792)	P	wood-generalist	LC	13
Dasytidae	*Aplocnemus tarsalis* (Sahlberg, 1822)	P	conifer-generalist	LC	3
Dasytidae	*Dasytes fusculus* (Illiger, 1801)	P	broadleaf-generalist	LC	9
Dasytidae	*Dasytes niger* (Linnaeus, 1760)	P	broadleaf-generalist	LC	55
Dasytidae	*Dasytes obscurus* (Gyllenhal, 1813)	P	conifer-generalist	LC	399
Dasytidae	*Dasytes plumbeus* (Müller, 1776)	P	broadleaf-generalist	LC	57
Dasytidae	*Dolichosoma lineare* (Rossi, 1792)	P	conifer-generalist	LC	3
Dasytidae	*Trichoceble memnonia* (Kiesenwetter, 1861)	P	broadleaf-generalist	LC	1
Dermestidae	*Anthrenus museorum* (Linnaeus, 1760)	D	broadleaf-generalist	LC	46
Dermestidae	*Anthrenus scrophulariae* (Linnaeus, 1758)	D	broadleaf-generalist	LC	1
Dermestidae	*Dermestes palmi (*Sjöberg, 1950)	D	broadleaf-generalist	VU	2
Dermestidae	*Globicornis emarginata* (Gyllenhal, 1808)	D	wood-generalist	LC	97
Dermestidae	*Megatoma undata* (Linnaeus, 1758)	P	wood-generalist	LC	98

Elateridae	*Ampedus balteatus* (Linnaeus, 1758)	P,W	conifer-generalist	LC	720
Elateridae	*Ampedus cinnabarinus* (Eschscholtz, 1829)	P	broadleaf-generalist	NT	1
Elateridae	*Ampedus nigrinus* (Herbst, 1784)	P,W	wood-generalist	LC	976
Elateridae	*Ampedus pomonae* (Stephens, 1830)	P,W	broadleaf-generalist	LC	1
Elateridae	*Ampedus pomorum* (Herbst, 1784)	P,W	broadleaf-generalist	LC	3
Elateridae	*Ampedus suecicus* (Palm, 1976)	P	wood-generalist	LC	3
Elateridae	*Ampedus tristis* (Linnaeus, 1758)	P,W	conifer-generalist	LC	239
Elateridae	*Athous subfuscus* (Müller, 1764)	P	wood-generalist	LC	173
Elateridae	*Cardiophorus ruficollis* (Linnaeus, 1758)	D,W	conifer-generalist	LC	187
Elateridae	*Danosoma conspersum* (Gyllenhal, 1808)	P	wood-generalist	NT	7
Elateridae	*Danosoma fasciatum* (Linnaeus, 1758)	P	wood-generalist	NT	22
Elateridae	*Denticollis borealis* (Paykull, 1800)	P,W	broadleaf-generalist	NT	92
Elateridae	*Denticollis linearis* (Linnaeus, 1758)	P,W	broadleaf-generalist	LC	9
Elateridae	*Diacanthous undulatus* (De Geer, 1774)	P,W	broadleaf-generalist	NT	6
Elateridae	*Melanotus castanipes* (Paykull, 1800)	P,W	conifer-generalist	LC	1324
Endomychidae	*Endomychus coccineus* (Linnaeus, 1758)	F	broadleaf-specialist	LC	224
Endomychidae	*Leiestes seminiger* (Gyllenhal, 1808)	F	broadleaf-generalist	LC	1
Erotylidae	*Dacne bipustulata* (Thunberg, 1781)	F	broadleaf-generalist	LC	344
Erotylidae	*Triplax aenea* (Schaller, 1783)	F	broadleaf-generalist	LC	83
Erotylidae	*Triplax rufipes* (Fabricius, 1787)	F	broadleaf-generalist	NT	3
Erotylidae	*Triplax russica* (Linnaeus, 1758)	F	broadleaf-generalist	LC	254
Erotylidae	*Triplax scutellaris* (Charpentier, 1825)	F	broadleaf-generalist	LC	24
Histeridae	*Dendrophilus pygmaeus* (Linnaeus, 1758)	P	unknown	LC	6
Histeridae	*Eblisia minor* (Rossi, 1790)	P	broadleaf-generalist	NT	10
Histeridae	*Gnathoncus buyssoni* (Auzat, 1917)	P	broadleaf-generalist	LC	99
Histeridae	*Gnathoncus communis* (Marseul, 1862)	P	wood-generalist	LC	1
Histeridae	*Gnathoncus nannetensis* (Marseul, 1862)	P	broadleaf-generalist	LC	34
Histeridae	*Platysoma angustatum* (Hoffmann, 1803)	P	conifer-generalist	LC	32
Histeridae	*Plegaderus vulneratus* (Panzer, 1797)	P	conifer-generalist	LC	1327
Hydrophilidae	*Megasternum concinnum* (Marsham, 1802)	D,H,P	unknown	LC	14
Laemophloeidae	*Cryptolestes abietis* (Wankowicz, 1865)	P	conifer-generalist	LC	3
Laemophloeidae	*Cryptolestes ferrugineus* (Stephens, 1831)	F	wood-generalist	LC	6
Laemophloeidae	*Leptophloeus alternans* (Erichson, 1846)	F	conifer-generalist	LC	23
Latridiidae	*Cartodere nodifer* (Westwood, 1839)	F	broadleaf-generalist	LC	2
Latridiidae	*Corticaria sp*	F	unknown	LC	266
Latridiidae	*Corticarina minuta* (Fabricius, 1792)	F	broadleaf-generalist	LC	3
Latridiidae	*Corticarina similata* (Gyllenhal, 1827)	F	unknown	LC	13
Latridiidae	*Cortinicara gibbosa* (Herbst, 1793)	F	conifer-generalist	LC	459
Latridiidae	*Enicmus fungicola (*Thomson, 1868)	F	wood-generalist	LC	1

Latridiidae	*Enicmus rugosus* (Herbst, 1793)	F	wood-generalist	LC	2575
Latridiidae	*Enicmus transversus* (Olivier, 1790)	F	wood-generalist	LC	1
Latridiidae	*Latridius hirtus (*Gyllenhal, 1827)	F	broadleaf-generalist	LC	102
Latridiidae	*Latridius minutus* (Linnaeus, 1767)	F	wood-generalist	LC	36
Latridiidae	*Stephostethus pandellei* (Brisout de Barneville, 1863)	F	wood-generalist	LC	62
Latridiidae	*Stephostethus rugicollis* (Olivier, 1790)	F	conifer-generalist	LC	131
Leiodidae	*Agathidium nigripenne* (Fabricius, 1792)	F	broadleaf-generalist	LC	7
Leiodidae	*Agathidium seminulum* (Linnaeus, 1758)	F	wood-generalist	LC	15
Leiodidae	*Agathidium sp*	F	unknown	LC	117
Leiodidae	*Amphicyllis globu*s (Fabricius, 1792)	F	broadleaf-specialist	LC	2
Leiodidae	*Anisotoma axillaris (*Gyllenhal, 1810)	F	broadleaf-generalist	LC	855
Leiodidae	*Anisotoma castanea* (Herbst, 1792)	F	wood-generalist	LC	67
Leiodidae	*Anisotoma glabra* (Kugelann, 1794)	F	wood-generalist	LC	742
Leiodidae	*Anisotoma humeralis* (Fabricius, 1792)	F	broadleaf-generalist	LC	127
Leiodidae	*Nemadus colonoides* (Kraatz, 1851)	D	broadleaf-generalist	LC	5
Lucanidae	*Platycerus caprea* (De Geer, 1774)	W	broadleaf-specialist	LC	11
Lycidae	*Dictyoptera aurora* (Herbst, 1784)	P	conifer-generalist	LC	26
Lycidae	*Lygistopterus sanguineus* (Linnaeus, 1758)	P	broadleaf-generalist	LC	16
Lycidae	*Platycis minutus* (Fabricius, 1787)	P	wood-generalist	LC	1
Lycidae	*Pyropterus nigroruber* (De Geer, 1774)	P	wood-generalist	LC	1
Lymexylidae	*Elateroides dermestoides* (Linnaeus, 1760)	F	broadleaf-generalist	LC	230
Malachiidae	*Nepachys cardiacae* (Linnaeus, 1760)	P	conifer-generalist	LC	17
Melandryidae	*Abdera affinis* (Paykull, 1799)	F	broadleaf-specialist	LC	7
Melandryidae	*Orchesia fasciata* (Illiger, 1798)	F	conifer-generalist	NT	6
Melandryidae	*Orchesia micans* (Panzer, 1793)	F	broadleaf-generalist	LC	30
Melandryidae	*Orchesia minor* (Walker, 1837)	F	wood-generalist	LC	1
Melandryidae	*Serropalpus barbatus* (Schaller, 1783)	W	conifer-generalist	LC	1
Melandryidae	*Wanachia triguttata* (Gyllenhal, 1810)	F	conifer-generalist	LC	62
Melandryidae	*Xylita laevigata* (Hellenius, 1786)	F	conifer-generalist	LC	243
Melandryidae	*Zilora ferruginea* (Paykull, 1798)	F	conifer-generalist	NT	4
Monotomidae	*Monotoma sp*	D	unknown	LC	1
Monotomidae	*Rhizophagus bipustulatus* (Fabricius, 1792)	P,F	broadleaf-generalist	LC	102
Monotomidae	*Rhizophagus cribratus* (Gyllenhal, 1827)	P	broadleaf-specialist	LC	4
Monotomidae	*Rhizophagus depressus* (Fabricius, 1792)	F	broadleaf-generalist	LC	826
Monotomidae	*Rhizophagus dispar* (Paykull, 1800)	P	wood-generalist	LC	136
Monotomidae	*Rhizophagus fenestralis* (Linnaeus, 1758)	F	wood-generalist	LC	334
Monotomidae	*Rhizophagus ferrugineus* (Paykull, 1800)	P	conifer-specialist	LC	4398
Mordellidae	*Curtimorda maculosa* (Naezen, 1794)	F	conifer-generalist	LC	24
Mordellidae	*Mordella aculeata* Linnaeus, 1758	F	broadleaf-specialist	LC	3
Mordellidae	*Mordella holomelaena (*Apfelbeck, 1914)	F	broadleaf-generalist	LC	6

Mordellidae	*Mordella sp*	D,F,H	unknown	LC	24
Mordellidae	*Mordellistena humeralis* (Linnaeus, 1758)	H	broadleaf-specialist	NT	2
Mordellidae	*Tomoxia bucephala* (Costa, 1854)	W	broadleaf-generalist	LC	28
Mycetophagidae	*Litargus connexus* (Geoffroy, 1785)	F	broadleaf-generalist	LC	43
Mycetophagidae	*Mycetophagus decempunctatus* (Fabricius, 1801)	F	broadleaf-generalist	VU	6
Mycetophagidae	*Mycetophagus fulvicollis* (Fabricius, 1792)	F	broadleaf-generalist	NT	3
Mycetophagidae	*Mycetophagus multipunctatus (*Fabricius, 1792)	F	broadleaf-generalist	LC	98
Mycetophagidae	*Mycetophagus populi (*Fabricius, 1798)	F	broadleaf-generalist	LC	6
Nitidulidae	*Carpophilus marginellus (*Motschulsky, 1858)	D, F	broadleaf-specialist	LC	26
Nitidulidae	*Cychramus luteus* (Fabricius, 1787)	F	broadleaf-generalist	LC	1
Nitidulidae	*Epuraea sp*	F,D	unknown	LC	3931
Nitidulidae	*Glischrochilus hortensis* (Geoffroy, 1785)	D,F	broadleaf-generalist	LC	343
Nitidulidae	*Glischrochilus quadripunctatus* (Linnaeus, 1758)	F,P	conifer-generalist	LC	1139
Nitidulidae	*Ipidia binotata* (Reitter, 1875)	F	wood-generalist	NT	8
Nitidulidae	*Pityophagus ferrugineus* (Linnaeus, 1760)	P	conifer-generalist	LC	1299
Nitidulidae	*Pocadius ferrugineus* (Fabricius, 1775)	F	broadleaf-generalist	LC	10
Nitidulidae	*Soronia grisea* (Linnaeus, 1758)	D	broadleaf-generalist	LC	211
Nitidulidae	*Soronia punctatissima* (Illiger, 1794)	D,F	broadleaf-generalist	LC	137
Oedemeridae	*Calopus serraticornis* (Linnaeus, 1758)	W	conifer-generalist	LC	4
Oedemeridae	*Chrysanthia geniculata* (Heyden, 1877)	W	conifer-generalist	LC	4
Oedemeridae	*Chrysanthia viridissima* (Linnaeus, 1758)	W	conifer-generalist	LC	1
Ptiliidae	*Ptiliidae sp*	F	unknown	LC	367
Ptinidae	*Cacotemnus rufipes* (Fabricius, 1792)	D	broadleaf-specialist	LC	25
Ptinidae	*Cacotemnus thomsoni* (Kraatz, 1881)	D	conifer-specialist	LC	54
Ptinidae	*Dorcatoma dresdensis* (Herbst, 1792)	F	conifer-generalist	LC	10
Ptinidae	*Dorcatoma punctulata* (Mulsant & Rey, 1864)	F	conifer-generalist	LC	1
Ptinidae	*Dorcatoma robusta (*Strand, 1938)	F	broadleaf-generalist	LC	55
Ptinidae	*Dryophilus pusillus* (Gyllenhal, 1808)	H	conifer-specialist	LC	1
Ptinidae	*Episernus angulicollis* (Thomson, 1863)	W	conifer-specialist	LC	1
Ptinidae	*Ernobius abietinus* (Gyllenhal, 1808)	D	conifer-specialist	LC	2
Ptinidae	*Ernobius abietis* (Fabricius, 1792)	D	conifer-generalist	LC	30
Ptinidae	*Ernobius explanatus* (Mannerheim, 1843)	W	conifer-specialist	LC	2
Ptinidae	*Ernobius mollis* (Linnaeus, 1758)	W	conifer-generalist	LC	20
Ptinidae	*Ernobius nigrinus* (Sturm, 1837)	W	conifer-specialist	LC	4
Ptinidae	*Hadrobregmus pertinax* (Linnaeus, 1758)	W	conifer-generalist	LC	88
Ptinidae	*Microbregma emarginatum* (Duftschmid, 1825)	C	conifer-specialist	LC	1
Ptinidae	*Ptinus dubius* (Sturm, 1837)	D	conifer-generalist	LC	2
Ptinidae	*Ptinus subpillosus* (Sturm, 1837)	C	broadleaf-generalist	LC	11
Ptinidae	*Stagetus borealis* (Israelson, 1971)	F,W	conifer-generalist	NT	3
Pyrochroidae	*Schizotus pectinicornis* (Linnaeus, 1758)	C	broadleaf-generalist	LC	20

Pythidae	*Pytho depressus* (Linnaeus, 1767)	C	conifer-generalist	LC	49
Salpingidae	*Rabocerus gabrieli* (Gerhardt, 1901)	P	broadleaf-specialist	LC	11
Salpingidae	*Salpingus ruficollis* (Linnaeus, 1760)	P	broadleaf-generalist	LC	232
Salpingidae	*Sphaeriestes bimaculatus* (Gyllenhal, 1810)	P	conifer-specialist	LC	1
Salpingidae	*Sphaeriestes castaneus* (Panzer, 1796)	F	conifer-generalist	LC	7
Scarabaeidae	*Cetonia aurata* (Linnaeus, 1758)	D	broadleaf-generalist	LC	7
Scarabaeidae	*Protaetia metallica* (Fabricius, 1775)	D	wood-generalist	LC	4921
Scarabaeidae	*Trichius fasciatus* (Linnaeus, 1758)	W	broadleaf-generalist	LC	9
Scraptiidae	*Anaspis arctica* (Zetterstedt, 1828)	P	broadleaf-generalist	LC	74
Scraptiidae	*Anaspis marginicollis* (Lindberg, 1925)	P	wood-generalist	LC	120
Scraptiidae	*Anaspis rufilabris* (Gyllenhal, 1827)	P	broadleaf-generalist	LC	187
Scraptiidae	*Anaspis thoracica* (Linnaeus, 1758)	P	broadleaf-generalist	LC	24
Silvanidae	*Dendrophagus crenatus* (Paykull, 1799)	F	conifer-generalist	LC	4
Silvanidae	*Silvanoprus fagi* (Guérin-Ménéville, 1844)	F	conifer-generalist	LC	11
Silvanidae	*Silvanus bidentatus* (Fabricius, 1792)	F	wood-generalist	LC	5
Sphaeritidae	*Sphaerites glabratus* (Fabricius, 1792)	P	unknown	LC	6
Sphindidae	*Aspidiphorus orbiculatus* (Gyllenhal, 1808)	F	broadleaf-generalist	LC	26
Sphindidae	*Sphindus dubius* (Gyllenhal, 1808)	F	conifer-generalist	LC	137
Staphylinidae	*Acidota crenata* (Fabricius, 1792)	P	unknown	LC	67
Staphylinidae	*Atrecus affinis* (Paykull, 1789)	P	conifer-generalist	LC	2
Staphylinidae	*Atrecus longiceps* (Fauvel, 1873)	P	conifer-generalist	LC	10
Staphylinidae	*Atrecus pilicornis* (Paykull, 1790)	P	wood-generalist	LC	3
Staphylinidae	*Bibloporus sp*	P	unknown	LC	38
Staphylinidae	*Bisnius puella* (Nordmann, 1837)	P	unknown	LC	10
Staphylinidae	*Bisnius subuliformis* (Gravenhorst, 1802)	P	wood-generalist	LC	10
Staphylinidae	*Dropephylla clavigera* (Luze, 1906)	P	conifer-generalist	NT	4
Staphylinidae	*Euconnus claviger* (Müller & Kunze, 1822)	P	wood-generalist	LC	1
Staphylinidae	*Euplectus sp*	P	unknown	LC	349
Staphylinidae	*Haploglossa villosula* (Stephens, 1832)	P	broadleaf-generalist	LC	6
Staphylinidae	*Lordithon lunulatus* (Linnaeus, 1760)	P	broadleaf-generalist	LC	207
Staphylinidae	*Lordithon speciosus* (Erichson, 1839)	P	broadleaf-generalist	LC	1
Staphylinidae	*Lordithon thoracicus* (Fabricius, 1777)	P	broadleaf-generalist	LC	1
Staphylinidae	*Lordithon trimaculatus* (Fabricius, 1793)	P	broadleaf-generalist	LC	8
Staphylinidae	*Lordithon trinotatus* (Erichson, 1839)	P	unknown	LC	3
Staphylinidae	*Microscydmus minimus* (Chaudoir, 1845)	P	broadleaf-generalist	LC	1
Staphylinidae	*Mycetoporus sp*	P	unknown	LC	48
Staphylinidae	*Nudobius lentus* (Gravenhorst, 1806)	P	conifer-generalist	LC	251
Staphylinidae	*Othius subuliformis* (Stephens, 1833)	P	unknown	LC	2
Staphylinidae	*Philonthus addendus* (Sharp, 1867)	P	unknown	LC	2
Staphylinidae	*Philonthus marginatus* (O. Müller, 1764)	P	unknown	LC	4
Staphylinidae	*Philonthus politus* (Linnaeus, 1758)	P	unknown	LC	22

Staphylinidae	*Phyllodrepa melanocephala* (Fabricius, 1787)	P	broadleaf-generalist	LC	3
Staphylinidae	*Quedionuchus glaber* (O. Müller, 1776)	P	wood-generalist	LC	103
Staphylinidae	*Quedius brevis* (Erichson, 1840)	P	unknown	LC	3
Staphylinidae	*Quedius fuliginosus* (Gravenhorst, 1802)	P	unknown	LC	1
Staphylinidae	*Quedius maurus* (Sahlberg, 1830)	P	broadleaf-generalist	LC	12
Staphylinidae	*Quedius mesomelinus* (Marsham, 1802)	P	broadleaf-generalist	LC	11
Staphylinidae	*Quedius tenellus* (Gravenhorst, 1806)	P	wood-generalist	LC	32
Staphylinidae	*Scaphisoma sp*	F	unknown	LC	426
Staphylinidae	*Sepedophilus littoreus* (Linnaeus, 1758)	F	broadleaf-generalist	LC	7
Staphylinidae	*Sepedophilus sp*	F	unknown	LC	14
Staphylinidae	*Sepedophilus testaceus* (Fabricius, 1793)	F	wood-generalist	LC	3
Staphylinidae	*Stenichnus bicolor* (Denny, 1825)	P	wood-generalist	LC	3
Staphylinidae	*Stenichnus collaris* (Müller & Kunze, 1822)	P	wood-generalist	LC	3
Staphylinidae	*Tachinus subterraneus* (Linnaeus, 1758)	P	unknown	LC	1
Staphylinidae	*Trichophya pilicornis* (Gyllenhal, 1810)	P	unknown	LC	1
Staphylinidae	*Trimium brevicorne* (Reichenbach, 1816)	D	broadleaf-generalist	LC	1
Staphylinidae	*Tyrus mucronatus* (Panzer, 1805)	P	wood-generalist	LC	9
Staphylinidae	*Xantholinus tricolor* (Fabricius, 1787)	P	conifer-generalist	LC	3
Tenebrionidae	*Bolitophagus reticulatus* (Linnaeus, 1767)	F	broadleaf-specialist	LC	14
Tenebrionidae	*Corticeus bicolor* (Olivier, 1790)	F	broadleaf-specialist	NT	2
Tenebrionidae	*Corticeus linearis* (Fabricius, 1790)	P	conifer-generalist	LC	121
Tenebrionidae	*Diaperis boleti* (Linnaeus, 1758)	F	broadleaf-generalist	LC	162
Tenebrionidae	*Mycetochara axillaris* (Paykull, 1799)	D	broadleaf-specialist	LC	2
Tenebrionidae	*Mycetochara flavipes* (Fabricius, 1792)	D	broadleaf-generalist	LC	30
Tenebrionidae	*Mycetochara obscura* (Zetterstedt, 1840)	D	conifer-generalist	NT	52
Tenebrionidae	*Palorus depressus* (Fabricius, 1790)	D	broadleaf-generalist	LC	1
Tenebrionidae	*Pseudocistela ceramboides* (Linnaeus, 1758)	D	broadleaf-generalist	LC	4
Tenebrionidae	*Uloma rufa* (Piller & Mitterpacher, 1783)	D	conifer-generalist	NT	2
Tetratomidae	*Hallomenus binotatus* (Quensel, 1790)	F	wood-generalist	LC	5
Tetratomidae	*Tetratoma ancora* (Fabricius, 1790)	F	wood-generalist	LC	24
Trogossitidae	*Nemozoma elongatum* (Linnaeus, 1760)	P	conifer-generalist	LC	9
Trogossitidae	*Peltis ferruginea* (Linnaeus, 1758)	F	wood-generalist	LC	3
Trogossitidae	*Thymalus limbatus* (Fabricius, 1787)	D,F	broadleaf-generalist	LC	2
Zopheridae	*Bitoma crenata* (Fabricius, 1775)	P	wood-generalist	LC	26
Zopheridae	*Lasconotus jelskii* (Wankowicz, 1867)	P	conifer-generalist	VU	1
Zopheridae	*Synchita humeralis* (Fabricius, 1792)	D,F	broadleaf-specialist	LC	21

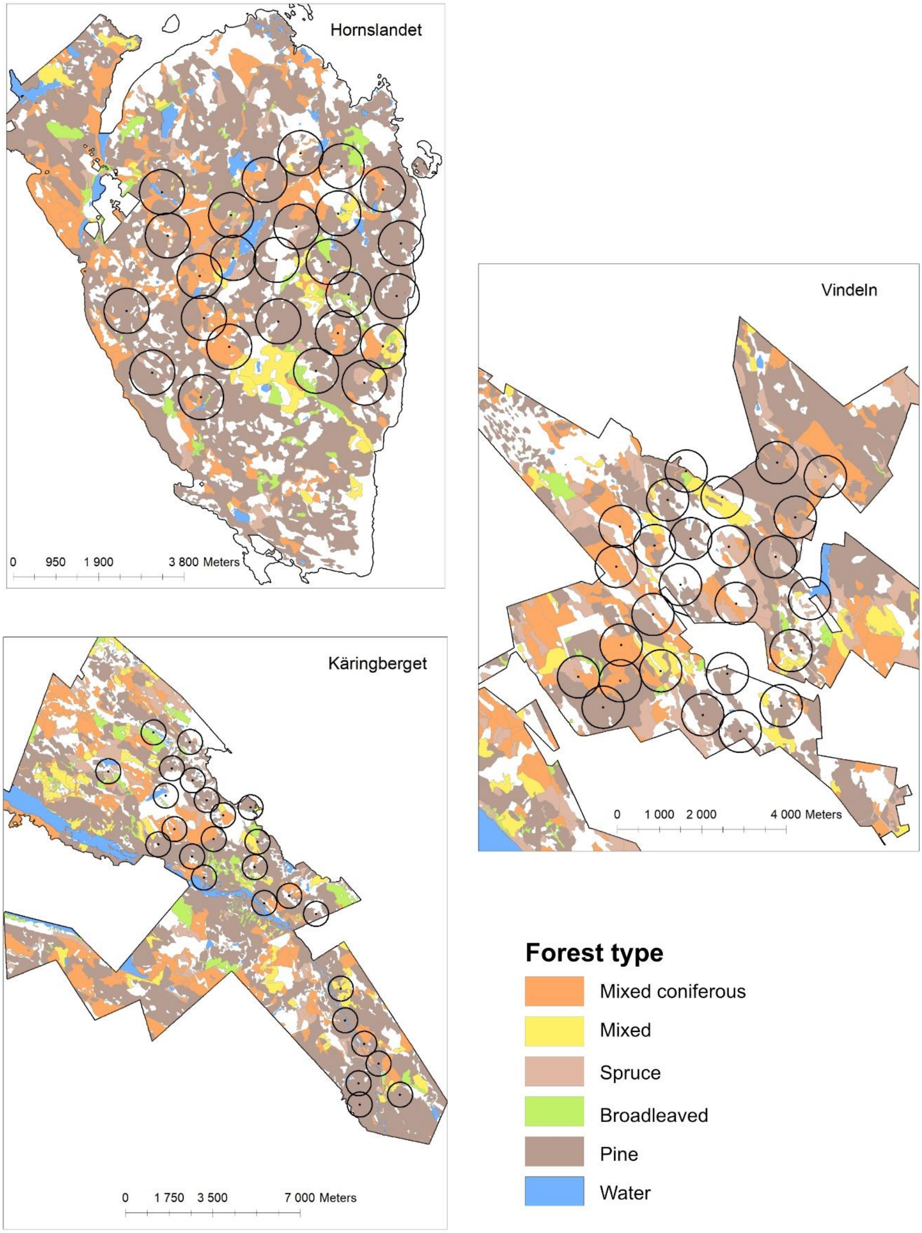

Fig. S1. Representation of forest type cover in the three studied landscapes Hornslandet, Käringberget and Vindeln. Mixed coniferous (≥65% conifers), mixed (more than 35% but less than 65% broadleaves), spruce (≥65% spruce), broadleaved (≥65% broadleaves) and pine (≥65% pine).

Fig. S2. Representation of forest age-classes in the three studied landscapes Hornslandet, Käringberget and Vindeln. Circle radius is 500m. Age-classes clear-cut (0-2 years), young (3-30 years), middle-aged (31-80 years), mature (81-120) and old (>120 years).

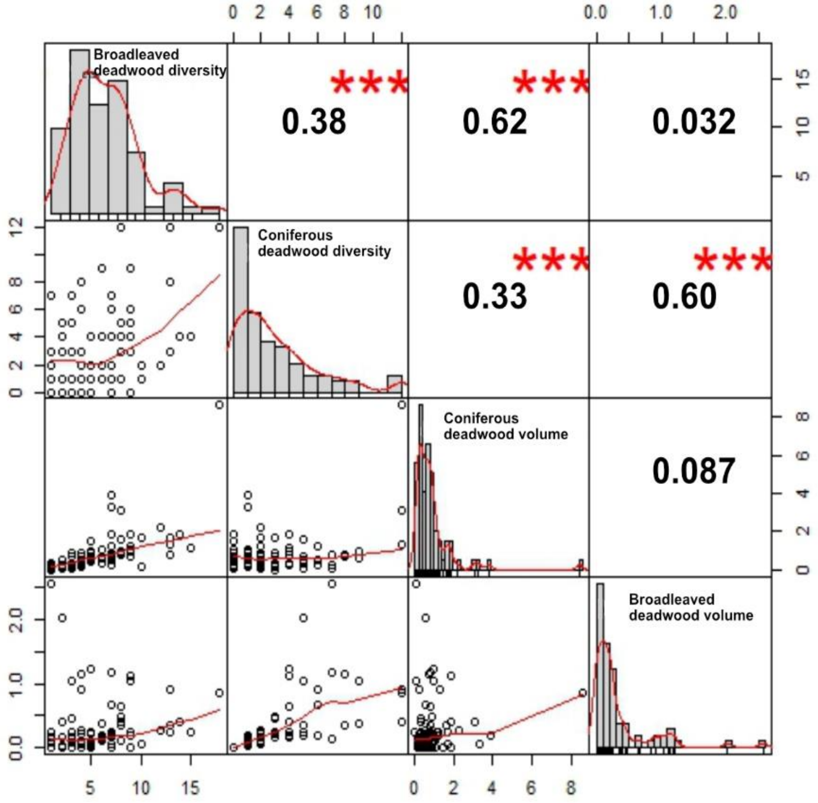

Fig. S3. Pearson correlations between deadwood diversity and deadwood volume. *** indicate p level ≤0.001