



Boreal Beetle Communities: Importance of Tree Continuity and Structural Complexity

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Abstract

Understanding the underlying processes that maintain biodiversity, such as habitat amount and dispersal possibilities, is essential for successful biodiversity conservation. Forest-dwelling beetles (Coleoptera) in boreal forests are negatively impacted by clear-cut forestry, but to what extent this pattern results from a disrupted tree continuity or from changes in structural complexity is poorly understood. This thesis aims to clarify whether beetle abundance, diversity and community composition differ in relation to tree continuity and structural complexity, and how such relations differ with time since tree continuity is broken. Beetles were sampled with flight intercept traps in twenty boreal pine forests in northern Sweden. Half of the forest stands had been clear-cut and half had an undisrupted tree continuity, and both stand types included a range of structural complexity measured as dead wood volume and diversity, habitat tree abundance and richness, and basal area. Beetle abundance was significantly higher in long tree continuity stands than in clear-cut stands, a pattern primarily driven by low abundance in old clear-cut stands. Beetle diversity was positively associated with structural complexity, indicating that the abundance and diversity of microhabitats on dead wood and living tree is important in determining beetle diversity at any given site. Across the forest landscape, stands with a long tree continuity hosted a wider range of beetle species than clear-cut stands. Old clear-cut stands had a higher basal area and exhibited a lower abundance of beetles belonging to a smaller but distinct species assembly, probably due to these stands growing denser and having a lower sun exposure. Young clear-cut stands had a beetle community composition that virtually was a subset of the long tree continuity beetle community. My results suggest that to maintain beetle abundance and diversity, forests with undisrupted continuity and forest harboring a wide diversity of habitats on living or dead wood should be prioritized as set-asides, and that a high abundance and diversity of such habitats should be ensured across the landscape.

Keywords: Beetles, Coleoptera, biodiversity, community composition, tree continuity, structural complexity, dead wood, habitat trees.

Table of contents

1. Introduction	5
1.1 Forestry History in Sweden and its Impact on Forest Habitat and Landscape	6
1.2 Impacts of Altered Forest Habitats and Landscapes on Beetle Communities	7
1.3 Beta Diversity in Assessing Community Structure.....	8
1.4 Research Gaps and Study Aims.....	9
2. Materials and Methods	11
2.1 Study Sites	11
2.2 Beetle Sampling	13
2.3 Dead Wood Survey	14
2.4 Pre-Analysis	16
2.5 Statistical Analyses	17
3. Results	21
3.1 Dead Wood Survey.....	21
3.2 Beetle Abundance, Species Richness and Diversity	22
3.3 Beetle Community Composition.....	26
4. Discussion	30
4.1 Decoupling the Effects of Tree Continuity and Structural Complexity	30
4.2 Beetle Abundance	31
4.3 Beetle Species Richness and Diversity	32
4.4 Beetle Community Composition.....	33
4.5 Management Implications	34
4.6 Conclusions.....	35
References	37
Popular science summary	49
Acknowledgements	51
Appendix 1 – Supplementary information	52
Appendix 2 – Species list	65

1. Introduction

Understanding the processes that maintain biodiversity is essential for successful conservation of biodiversity (Sutherland et al. 2013). Ecosystems tend to be limited in the number of species that can coexist through the availability and diversity of suitable habitats (Hutchinson 1957; Mac Arthur & Wilson 1967; Janssen et al. 2016). Further, species diversity can be constrained by dispersal limitation (Janssen et al. 2016; MacArthur and Wilson 1967; Pulliam 2000). The relative importance of habitat limitation and dispersal limitation is important for developing effective conservation strategies, yet it is still a debated question (Hodgson et al. 2011).

Many insect populations around the globe are in decline (Sánchez-Bayo & Wyckhuys 2019; Wagner 2019; Cardoso et al. 2020). Beetles (Coleoptera; Linnaeus, 1758) are a diverse and functionally important group in forest ecosystems (Gimmel & Ferro 2018). In Sweden more than a thousand beetle species are saproxylic (Ehnström 2001), meaning that they are directly or indirectly dependent upon dead wood during some part of their life cycle (Speight 1989). The importance of dead wood as insect habitat has been known since the late 19th century (see Thorn et al. 2020). Dead wood is a varying substrate with hundreds of different microhabitats (Siitonen 2001). Certain qualities of dead wood, including tree species, stage of decay, diameter, sun exposure, position (lying, standing or stump), tree growth rate, whether the wood has burned, fungal flora decaying the wood, and beetle species already present, determines the beetle species composition that utilizes the wood (Berg et al. 1994; Siitonen 2001; Lindhe & Lindelöw 2004; Gibb et al. 2006; Brin et al. 2011; Weslien et al. 2011; Hjältén et al. 2012; Runnel et al. 2021). 85 % of red-listed forest-dwelling beetle species in Sweden are saproxylic and these species, in particular, often show a strong association with specific dead wood characteristics (Jonsell et al. 1998).

Dispersal ability varies among beetles and impacts their response to changing environmental conditions (Lassau et al. 2005; Janssen et al. 2016). Even for species with a high dispersal ability, there may remain species-specific requirements to establish a population in a new habitat (Janssen et al. 2016). Species with a low dispersal ability would be unable to establish viable populations in new areas when the landscape changes, such as when tree continuity is disrupted. The relative importance of dead wood and other habitat structures (structural complexity) and forest spatiotemporal continuity (tree continuity) for forest-dwelling beetles thus depends on the interplay of habitat and dispersal limitation within this group.

1.1 Forestry History in Sweden and its Impact on Forest Habitat and Landscape

Globally, boreal forests contribute to approximately one-third of the Earth's forest cover and are a large contributor to global forest goods production (see e.g. Brandt et al. 2013; Gauthier et al. 2015; Mery et al. 2010). Covering more than 20 million hectares, boreal forests account for almost half of the land area in Sweden (Statistics Sweden 2023). Swedish boreal forests host a large proportion of the nation's threatened forest species of international importance, i.e., species either endemic to the Nordics or with a majority of the population in Sweden (Berg et al. 1994). Given that biodiversity preservation cannot rely solely on existing reserve networks (Hansen et al. 1991), forest management necessitates careful consideration of its impacts on biodiversity.

Large-scale utilization of the Swedish boreal forest started in the 1800s, with industrial exploitation successively increasing in intensity and clear-cutting of forest stands becoming a predominant harvest method from the 1940s (Östlund et al. 1997; Linder & Östlund 1998). Forest management in Swedish boreal forests has, both on the level of landscape and habitat, decreased ecosystem heterogeneity, which is closely linked to biodiversity (Haila & Kouki 1994). During the 20th century, the share of Swedish boreal forests that is 150 years or older has decreased drastically (Linder & Östlund 1992; Hellberg et al. 2009; Ahlström et al. 2022). Old growth-forests have become severely fragmented in the boreal landscape (Kouki et al. 2001). Further, intensive management, together with fire suppression, has led to an increased stand homogenization of boreal forests (Gauthier et al. 2015). Stands have, for example, become much more even aged and one layered since the 1870s (Linder & Östlund 1992; Östlund et al. 1997). Anthropogenic interventions in boreal forests in Fennoscandia have also decreased tree species diversity, especially by decreasing the presence of deciduous trees (Nilsson 1997; Vanha-Majamaa et al. 2007; Lachat & Müller 2018).

The dead wood dynamics of natural and managed forests are very different. In natural boreal forests dead wood is created through background mortality and in sudden large input events after natural disturbances such as storms or fire, while in managed forests most of the wood is removed from the site after harvest, often leading to a lower in-site dead wood input (Siitonen 2001; Seibold & Thorn 2018). Dead wood volumes in Swedish boreal forests has drastically decreased since the 1870s due to forest management measures, including thinning, clear-cut harvesting, forest fire prevention, and salvation logging (Linder & Östlund 1992; Siitonen et al. 2000). Removal of logging residue for fuel after clear-cut harvesting further decreases available dead wood volumes (Jonsell 2007). In the boreal zone of Fennoscandia, dead wood in managed forests has been heavily reduced by 90 % compared to natural forests (see Siitonen 2001). Managed forests in the boreal forest landscape are today deprived of dead wood (> 10 cm in diameter) (Kyaschenko et al. 2022). Forest degeneration through the decline in forest structural complexity has often been overlooked in favor of the more widely discussed issue of deforestation (Thorn et al. 2020). Removal of dead and dying trees was historically seen as an economically sound approach (Östlund et al. 1997)

and is to some extent still today considered preferable for conservation than removal of healthy trees, as pointed out by Müller et al. (2016).

Habitat trees are often ancient trees, large living trees or trees with special characteristics (tree-related microhabitats, TreMs; Larrieu et al. 2018), that presumably have a high conservation value and are important for maintaining high forest biodiversity (Swedish Forest Agency 2020). Habitat trees are characteristic of old growth forests and contribute to the forest structural complexity by increasing the diversity of TreMs and providing a supply of dead wood (Ranius et al. 2009; Lachat & Müller 2018). Forest management prevents trees from aging and reaching senescence and habitat trees are often missing in managed forests (Lachat & Müller 2018). In Sweden, the long history of intense forestry since the 1870s has led to a dramatic decline of both old and large diameter (> 30 cm) trees (Linder & Östlund 1992). Managed forests are today deprived of large diameter trees compared to natural forests (Kyaschenko et al. 2022).

1.2 Impacts of Altered Forest Habitats and Landscapes on Beetle Communities

Saproxylic beetle species richness tends to be higher in boreal forests with a long tree continuity than in managed forests (Martikainen et al. 2000; Similä et al. 2003; Olsson et al. 2012; Jacobsen et al. 2020; Burner et al. 2021). Certain beetle species may be more sensitive to the disruptions of tree continuity caused by clear-cut forestry; little is known for most individual species. (Burner et al. 2021). Saproxylic beetle community composition also differs between forest stands with a long tree continuity and managed stands (Martikainen et al. 2000; Jacobsen et al. 2020), with threatened species usually missing from managed stands (Similä et al. 2003).

Beetles are negatively affected both by forestry measures that decrease tree continuity and measures that decrease structural complexity. Tree continuity and structural complexity are often correlated (Sippola et al. 1998; Siitonen et al. 2000), making it challenging to discern between the effects of tree continuity and structural complexity. Saproxylic beetle abundance and richness tends to increase with stand age (Irmeler et al. 2010; Stenbacka et al. 2010) and forests with long tree continuity can act as refuges for species with limited dispersal ability, such as *Pytho kolwensis* Sahlberg (Pythidae), that has high requirements for old-growth habitats that now are isolated in the forest landscape (Siitonen & Saaristo 2000). Saproxylic beetle abundance and richness is well known to exhibit a positive correlation with dead wood volume (Martikainen et al. 2000; Similä et al. 2003; Lassauce et al. 2011; Seibold et al. 2017; Hämäläinen et al. 2018; Haeler et al. 2021). The literature is, however, not unanimous; Gran (2022) for example, found no effect of dead wood volume and diversity on beetle alpha-diversity. Dead wood diversity has been found to be more important than dead wood volume for beetle species diversity (Similä et al. 2003; Janssen et al. 2016), although dead wood volume and diversity often are correlated (Økland et al. 1996; Similä et al. 2003). The spatiotemporal continuity of dead wood is a field that has received limited attention (see Sverdrup-Thygeson

et al. 2014), yet studies indicate that connectivity between dead wood is more important than dead wood amount or diversity (Schiegg 2000a; b). Promoting a continuous input of diverse dead wood is, therefore, essential for enhancing saproxylic beetle diversity (Similä et al. 2003).

1.3 Beta Diversity in Assessing Community Structure

To understand structures and processes at the community level, it is important to consider measures beyond specimen abundance and local species diversity (alpha diversity). The term *beta diversity* was introduced by Whittaker (1960) as “the extent of change of community composition, or degree of community differentiation”. A commonly used beta diversity measure is the Sørensen measure, expressed as a pairwise comparison between two communities: $\beta_{sør} = \frac{b+c}{2a+b+c}$, where a is the number of species existing in both communities, b is the number of species present in the first but not the second community and c is the number of species present in the second but not the first community (Dice 1945; Sørensen 1948; Koleff et al. 2003; Baselga 2010) (Figure 1a).

Beta diversity can reflect two separate processes: species turnover (replacement) and nestedness (species loss) (Baselga 2010; Villéger et al. 2013). Simpson (1943) introduced a turnover measure to account for only the replacement of species between two sites, later formulated as $\beta_{sim} = \frac{\min(b,c)}{a+\min(b,c)}$ (Lennon et al. 2001; Baselga 2010). Baselga (2010) proposed the nestedness component of beta diversity to be $\beta_{nes} = \beta_{sør} - \beta_{sim} = \frac{b+c}{2a+b+c} - \frac{\min(b,c)}{a+\min(b,c)} = \frac{\max(b,c)-\min(b,c)}{2a+\min(b,c)+\max(b,c)} \times \frac{a}{a+\min(b,c)}$. Using these formulations, turnover, nestedness and total beta diversity take a value between zero and one. Turnover equals zero when one community is a subset of the other ($b = 0$ or $c = 0$; Figure 1b) and equals one when no species are shared between the communities ($a = 0$; Figure 1c), while nestedness equals zero when two communities have the same number of species ($b = c$; Figure 1d) or when no species are shared between the communities ($a = 0$; Figure 1c) (Villéger et al. 2013). All situations in which two communities are not identical (Figure 1e) can be explained by turnover, nestedness or a combination of both (Baselga 2010). A high beta diversity can thus be a result from (1) a low proportion of shared species between two communities with a similar number of species (high turnover, low nestedness; low a and high b and c ; Figure 1f), (2) a species richness difference between the two communities with similar species (low turnover, high nestedness; low $\min(b, c)$, high $\max(b, c)$; Figure 1g), or (3) a combination of both (Figure 1h) (Villéger et al. 2013). Whether turnover or nestedness is the dominant contributor to beta diversity would influence management and conservation decisions: preserving the widest range of different sites would be appropriate when turnover is dominant, while preserving the most species rich sites would be appropriate when nestedness is dominant (Baselga 2010). It should be noted that in most situations, turnover is the dominant contributor in a pairwise comparison of beta diversity and

that a lower total beta diversity not necessarily means that the pair of sites have a lower conservation value (compare Figure 1g-i).

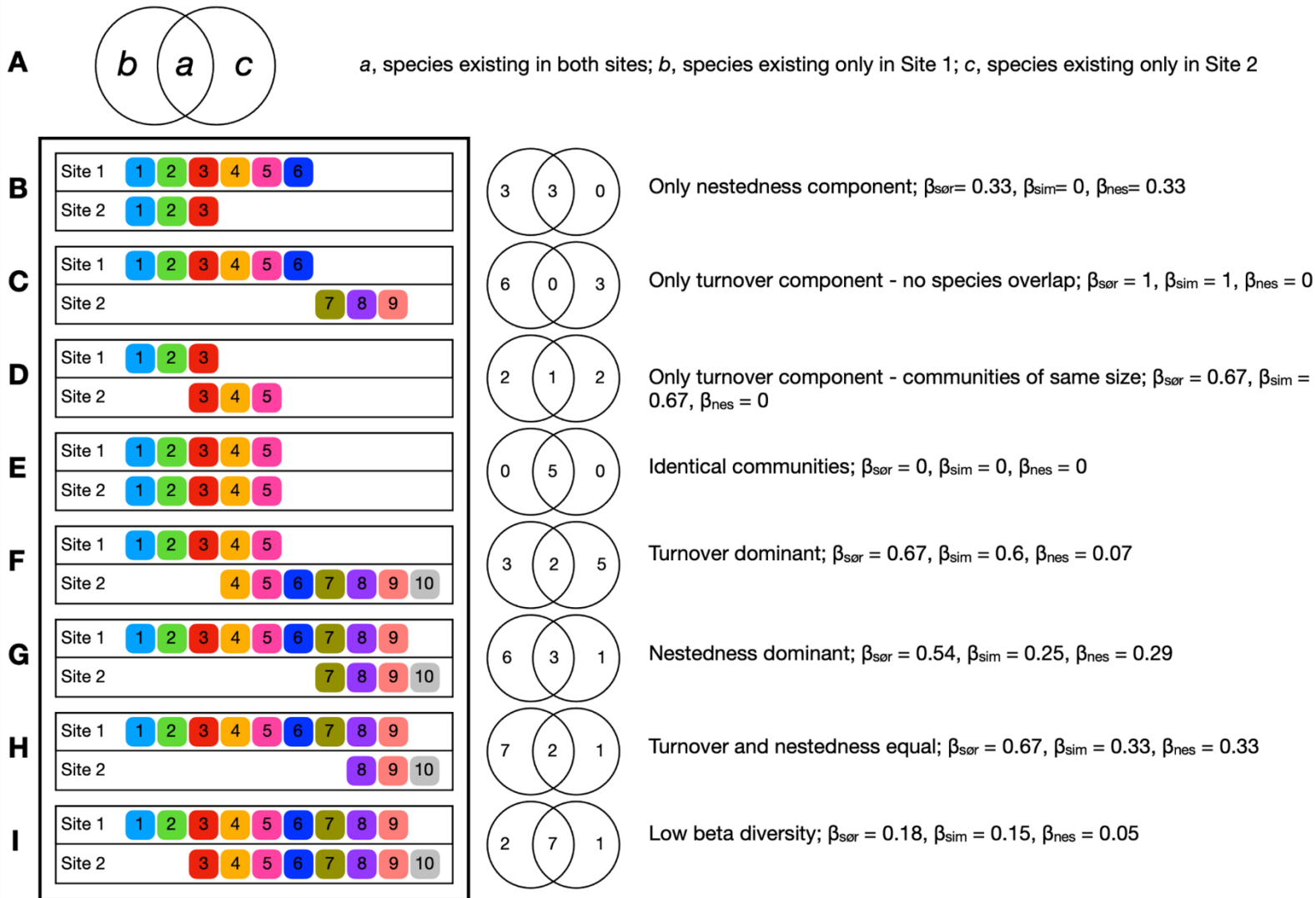


Figure 1. *A*, possible distribution of species between two sites; *B-I*, hypothetical examples of pairwise beta diversity and turnover and nestedness components between two sites. β_{sor} , Sørensen pairwise dissimilarity; β_{sim} , Simpson pairwise dissimilarity; β_{nes} , nestedness-fraction of Sørensen pairwise dissimilarity. Loosely based on Baselga (2010).

1.4 Research Gaps and Study Aims

A challenge in the existing literature (see e.g. Haeler et al. 2021; Hämäläinen et al. 2018; Martikainen et al. 2000; Seibold et al. 2017; Similä et al. 2003; Stenbacka et al. 2010) on beetle abundance, diversity, and community composition is distinguishing whether the observed patterns, when disrupting tree continuity, result from the alterations in continuity itself or from changes in structural

complexity. If tree continuity is an influential factor this indicates dispersal limitation while if structural complexity is an influential factor this indicates habitat limitation.

In my study design I explicitly attempt to include sites representing a range of structural complexity, both for stands with and without disrupted tree continuity. I hence expect to be able to decouple the effects of tree continuity and structural complexity. The main aim of this study is to clarify whether, and if so why, abundance, diversity (local alpha diversity) and community composition (beta diversity and community assemblages) of forest-dwelling coleopterans differ in relation to tree continuity and forest structural complexity. More specifically, I investigate whether beetle abundance, diversity, and community composition differ between forests with long undisrupted tree continuity and forests where the tree continuity has been disrupted by clear-cut forestry. I also investigate whether beetle abundance, diversity and community composition differ with time since a stand has been clear-cut. I further assess whether beetle abundance, diversity and community composition is best predicted by tree continuity (stand age) or by forest structural complexity, i.e., volume and diversity of dead wood, amount and richness of habitat trees, and stand basal area. Finally, I assess which forest structural complexity variables best can predict beetle abundance, diversity, and community composition.

2. Materials and Methods

2.1 Study Sites

The study was conducted at twenty study sites (Figure 2) in northern Västerbotten county and southern Norrbotten county, Sweden (64°98' – 65°99' N, 17°18' – 19°13' E). Altitude at the study sites ranges between 270 and 448 m above sea level ($\mu = 365$, S.E. = 12, $n = 20$). The study area is located in the boreal zone; average temperature during June and July at the study sites is 12.7 ± 0.1 °C (S.E., $n = 20$), average daily minimum temperature during the same months is 7.7 ± 0.1 °C (S.E., $n = 20$), and average daily maximum temperature is 17.7 ± 0.1 °C (S.E., $n = 20$; SMHI). Average monthly precipitation in June and July is 72.8 ± 0.6 mm (S.E., $n = 20$; SMHI).

The sites were selected with the aim to represent a range of tree continuity and structural complexity. Ten of the selected sites have a long tree continuity and have never been clear-cut. These stands have an average tree age of 150 ± 4 years (“long tree continuity”; S.E., $n = 10$, Table 1), with single trees being considerably older. The other ten study sites had shorter tree continuity, five of which were harvested by clear-cutting 61 ± 3 years ago (“young clear-cut”; S.E., $n = 5$; Table 1), and five of which were harvested by clear-cutting 78 ± 3 years ago (“old clear-cut”; S.E., $n = 5$; Table 1). The sites were selected to represent a range of structural complexity. The study sites were selected in consultation with Sweden’s largest forest company, state-owned Sveaskog, that also own and manage the forest at all study sites. None of the study sites are formally protected, but the ten stands with long tree continuity are voluntarily set aside by the landowner and are today either unmanaged or managed solely for nature conservation. All sites have historically to some degree been exposed to forestry interventions in the form of selective logging, but none of the ten sites selected to have long tree continuity have been exposed to clear-cut forestry. Four of the long tree continuity sites are classified as woodland key habitats and registered by the Swedish Forest Agency (www.skogsstyrelsen.se/en/). Woodland key habitats are sites of particular value for nature conservation, with the potential to harbor a proportionally large share of endangered, vulnerable, rare, care-demanding, or red-listed species due to their habitat structure, stand history, species composition, or physical environment (Timonen et al. 2010). The study sites were dominated by Scots pine (*Pinus sylvestris* L.) with elements of Norway spruce (*Picea abies* (L.) H. Karst) and birch (*Betula pendula* Roth and *Betula pubescens* Ehrh.; Table 1). However, one stand had an almost equal mixture of pine

and spruce (Table 1). Data on stand age, stand area, tree species mixture, and basal area of living trees were provided by the landowner (Table 1).

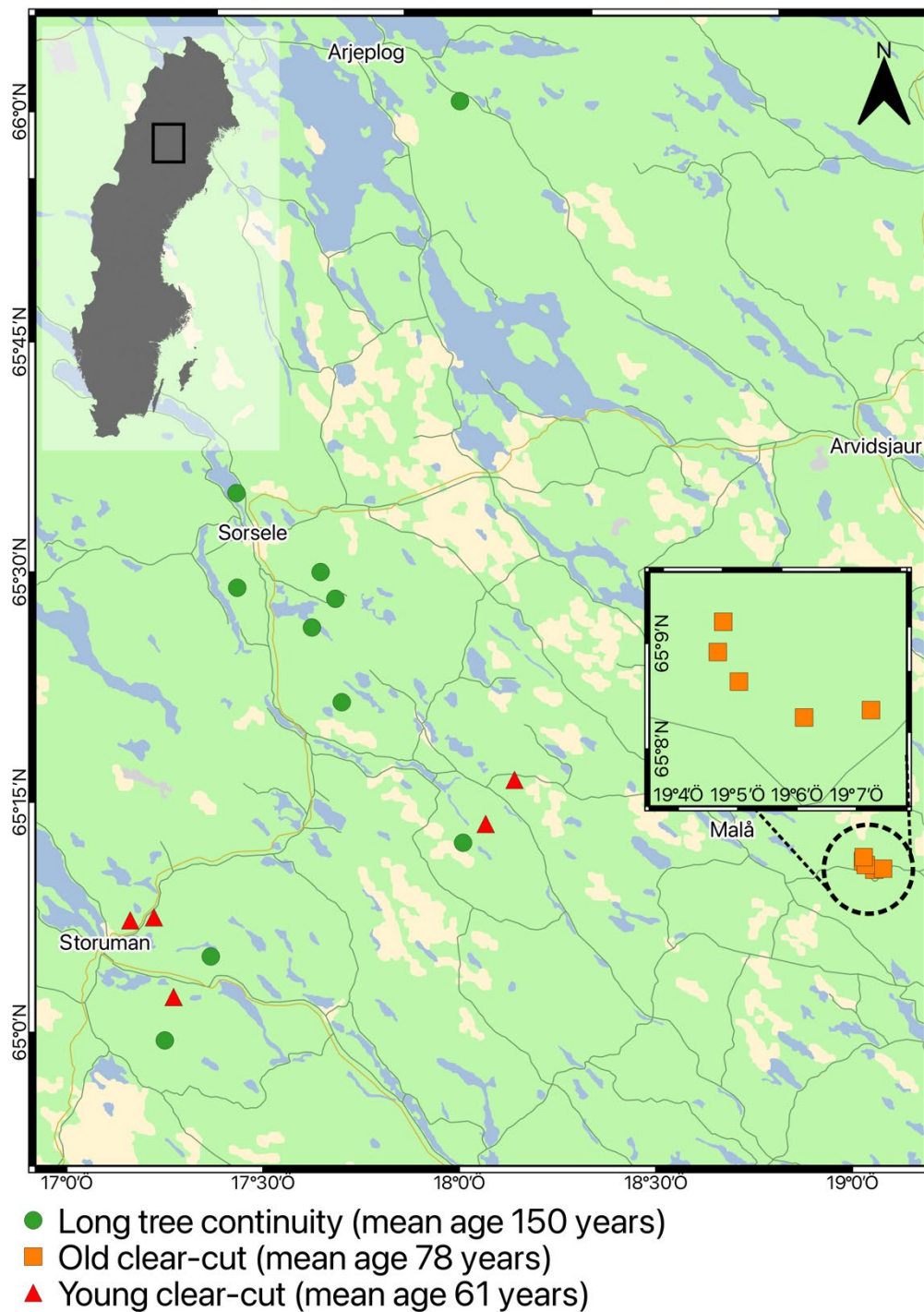


Figure 2. Map of the study area with the study sites for beetle sampling and dead wood survey marked.

Table 1. Stand properties of forest stands where beetles were sampled. *YCC*, young clear-cut (mean 61 years); *OCC*, old clear-cut (mean 78 years); *LTC*, long tree continuity (mean 150 years). Percentage of tree species based on basal area to nearest 10 %.

Stand	Percentage Scots pine	Percentage Norway spruce	Percentage broadleaf	Stand area (ha)	Stand age (mean tree age in years)	Mean basal area of living trees (m ² /ha)
YCC1	100	0	0	58.8	65	20.8
YCC2	100	0	0	77.4	69	16.6
YCC3	90	10	0	3.64	55	18.8
YCC4	100	0	0	28.2	58	16.4
YCC5	90	0	10	18.1	57	22.1
OCC1	90	0	0	10.5	92	27.2
OCC2	100	0	0	12.6	86	31.0
OCC3	100	0	0	11.3	78	26.0
OCC4	100	0	0	15.9	78	25.0
OCC5	100	0	0	9.7	88	27.0
LTC1	100	0	0	18.8	171	13.9
LTC2	90	10	0	19.1	113	19.8
LTC3	90	10	0	13.9	148	16.1
LTC4	90	10	0	6.7	130	19.9
LTC5	90	0	0	25.7	130	20.2
LTC6	90	10	0	2.1	210	19.1
LTC7	80	20	0	19.8	147	17.0
LTC8	80	10	0	38.2	155	21.1
LTC9	80	20	0	40.6	146	23.2
LTC10	60	40	10	11.2	147	25.1

2.2 Beetle Sampling

In each study sites three flight intercept traps were placed evenly spaced within the stand, at least 100 m apart and 100 m from the stand edge, aiming to form an approximately equilateral triangle. In a few cases where stand size or shape or suitable trap locations were limited, adjustments had to be made in the distance and positioning of the traps. The traps were made of a 30 cm wide and 50 or 60 cm long transparent Plexiglass sheet which was secured between two trees. Below the plexiglass sheet a 2-liter metal tray was fastened to capture insects. The tray was filled about halfway with a preservation liquid made of propylene glycol diluted to approximately 50% with water, and a small amount of detergent to decrease surface tension. The traps were placed so that the tray was at a height of approximately 110 cm (Figure 3b) and so that there would be a free flight path for insects to collide with the trap. All traps were put up between 5 and 15 June 2023, emptied once between 26 and 30 June 2023 and emptied a second time and taken down between 24 July and 3 August 2023. This period was chosen as June and July are the most

effective months in capturing a large saproxylic beetle species richness (Wikars et al. 2005). All traps were active for 49 days. The caught insects were stored in the preservation liquid until they were identified. The beetles were identified to species level by an expert taxonomist. Beetles were identified to species pairs or to genus level in cases where determination to species was impossible, for example due to specimens being damaged or only female specimens being found of species which only can be determined by preparation of the male genitalia.

2.3 Dead Wood Survey

Dead wood volume and diversity was surveyed using line and band transects between 14 July and 29 August 2023. At each site three transects were made. The first transect started at the position of one of the insect traps and was drawn in the direction of another trap. The next two transects were then placed at a 60° angle to the first transect, forming an equilateral triangle, but being adjusted to ensure that transects did overlap. Each transect had a length of 75 m (Figure 3a). At a few sites the positioning of the transects had to be adjusted due to the size or shape of the stand. Lying dead wood with a length ≥ 130 cm and a maximum diameter ≥ 10 cm was measured at the point where the line transects crossed the wood, according to the line transect method presented by Van Wagner and Wilson (1976). Lying dead wood was split into two categories according to their maximum diameter: ≥ 10 cm, < 20 cm; and ≥ 20 cm. Within a band transects extending 5 m to either side of the line transects the diameter at breast height (130 cm; DBH) and height of all standing dead wood with a height ≥ 130 cm and a maximum diameter ≥ 10 cm was measured. The average diameter and average height of tree stumps (standing dead wood with a height ≥ 40 cm, < 130 cm and a diameter ≥ 10 cm) were measured within the band transect.

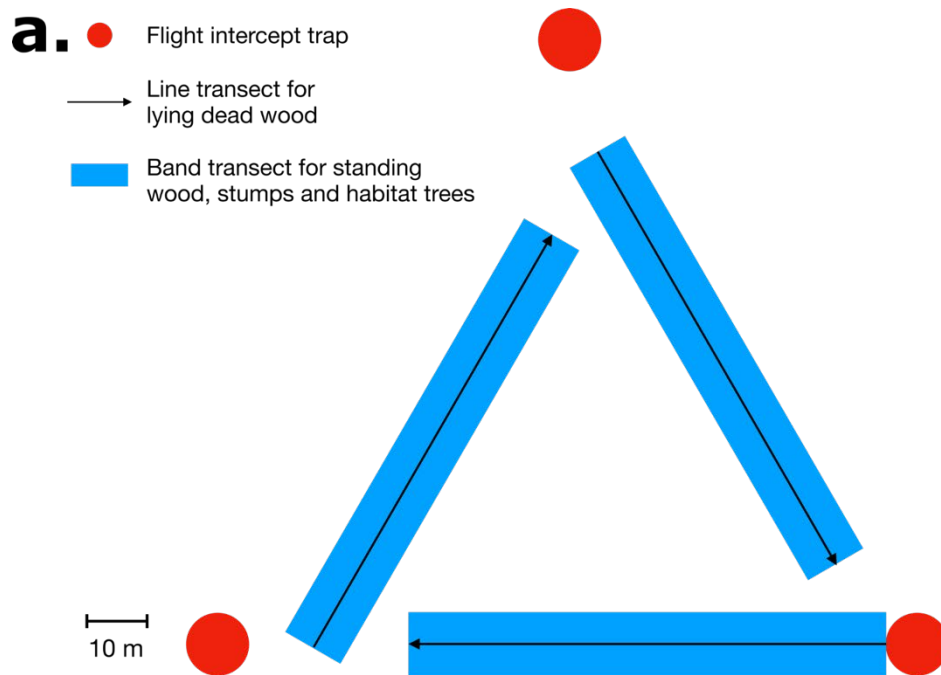


Figure 3. Schematic illustration demonstrating how beetle sampling and dead wood survey were performed within a site. The top panel (a) shows positioning of flight intercept traps and transects for dead wood survey. The bottom panel (b) shows one of the flight intercept traps used to sample beetles.

The tree species of the dead wood objects were identified when possible. Signs of fire damage were noted on standing dead wood and tree stumps. Four decay classes were used to describe the decomposition stage of the dead wood objects following the description made by the Swedish National Forest Inventory (2023): (1) Hard dead wood, when the trunk volume consists of more than 90 % hard dead wood; (2) Partially decomposed wood, when the trunk volume consists of 10-25 % soft wood; (3) Decomposed wood, when the trunk volume consists of 26-75 % soft wood; (4) Very decomposed wood, when the trunk volume consists of 76-100 % soft wood. The wood softness was determined by probing the dead wood objects with a knife, caliper of similar object.

Habitat trees within the band transect were recorded. Habitat trees were identified using the following criteria from the Swedish Forest Agency (2020): (1) DBH of at least 7 cm and (2) any of the following: (a) special characters including polypores on the trunk, cavities, nesting holes or canopy nests, signs of fire damage, bark with diverging structure such as cracked or coarse bark, branches with diverging structure such as coarse, twirled or hanging branches, diverging canopy shape and clearly late-grown trees; (b) Unusual tree species (in this study only goat willow (*Salix caprea* L.) was identified in this category); (c) DBH \geq 50 cm for Norway spruce and Scots pine, DBH \geq 40 cm for birch, and DBH \geq 30 cm for aspen (*Populus tremula* L.); or (d) Old age (I did not determine the exact age of trees in this study; age alone was therefore never the sole reason for a tree being classified as a habitat tree).

The storm *Hans* swept across Sweden in the beginning of August 2023, causing widespread wind damage (Sveaskog 2023). Two of the five old clear-cut stands, included in the beetle inventory, had extensive wind damage, and could not be surveyed for dead wood. Trees with raw wood, i.e., fresh windthrows with a raw cambium and usually living needles or leaves were not considered in the survey since these fell after the beetles were sampled.

2.4 Pre-Analysis

Beetle specimens that were not determined to species level were included in the abundance calculation and their treatment in the richness and diversity calculations followed the following rules: (1) if none of the specimens in a species pair or genus were determined to species level, all specimens were kept at species pair or genus level and the species pair or genus was treated as a species in richness and diversity analysis; (2) if some of the specimens in a genus were determined to species level and only one of these species was found in a particular stand, all undetermined specimens of the genus were assigned to that species in the stand; (3) if some of the specimens in a genus were determined to species level and multiple of these species were found in a particular stand, all undetermined specimens of that genus in the stand were excluded from richness and diversity analysis; and (4) if some of the specimens in a genus were determined to species level and only undetermined specimens of the genus were found in one or several stands, all specimens of the genus were collapsed to genus level for the richness and diversity analysis. The

rules were made conservatively to rather underestimate than overestimate species richness and diversity, while not affecting the abundance. Specimens that were so poorly damaged that determination to genus level was impossible were excluded from the study. The beetle species were divided into feeding guilds.

The beetle samples from the three traps were pooled for each stand and the abundance per stand was calculated. Abundance per catch effort was calculated to accommodate for the differently sized window traps by dividing the beetle abundance by the total area of the plexiglass sheets for the traps in each stand. Calculating abundance per catch effort also accommodates for two cases where traps had to be excluded from analysis due to wrong placement and damage. Beetle species richness and the Shannon diversity index ($H = -\sum_i p_i \ln p_i$, where p_i is the proportional abundance of species i ; Shannon, 1948) were calculated for each stand (alpha-diversity) using the vegan package (Oksanen et al. 2022) in R (R Core Team 2023). Effective species number was calculated based on the Shannon diversity index (e^H) to get a more comparable value for species diversity, as recommended by Jost (2006).

Volume of lying dead wood was estimated for each stand using the line transect method introduced by Van Wagner and Wilson (1976) and Van Wagner (1982). Volume of standing dead wood was calculated using functions introduced by Brandel (1990). Stumps were treated as cylinders when calculating volume. A detailed description of the dead wood volume calculations is found in Table S1. To quantify dead wood diversity the dead wood objects were categorized using a method similar to Siitonen *et al.* (2000). The following categorization was used: position (lying, standing, stump), species (pine, spruce, birch, goat willow), decay class (1, 2, 3, 4), diameter (<20 cm, ≥20 cm; the diameter measurements of the different positions differs: for lying dead wood it is maximum diameter, for standing dead wood it is DBH and for stumps it is the average diameter, but for the purpose of categorizing this difference is of minor importance) and signs of fire damage (yes, no; measured only on stumps and standing dead wood). This gives 192 possible combinations of characters that a dead wood object can be classified by. Effective species number was calculated based on the Shannon diversity index, calculated by treating each distinct character combination as a species.

The abundance of habitat trees was calculated for each stand. Habitat tree richness was quantified by adding the number of distinct characters (polypores; cavities, nests and woodpecker feeding marks; signs of fire; diverging bark; diverging stems or branches; diverging canopy; late grown trees; dead branches) found on habitat trees within the stand to the number of distinct habitat tree species found in the stand.

2.5 Statistical Analyses

Welch two-sample t -tests were performed to compare the mean stand age and forest structural complexity variables (dead wood volume, dead wood diversity, habitat tree abundance, habitat tree richness, and living tree basal area) between long tree

continuity stands and stands that have been clear-cut. Analyses of Variance (ANOVA) and Tukey Honest Significant Difference post hoc tests (TukeyHSD) were performed to compare the mean stand age and forest complexity variables between long tree continuity stands, old clear-cut stands (mean 78 years) and young clear-cut stands (mean 61 years). Welch two-sample *t*-tests and ANOVA were employed in the same way to the mean beetle abundance, species richness and species diversity. Venn diagrams were made to visualize the occurrence of beetle species in young clear-cut stands, old clear-cut stands and long tree continuity stands. Additional Venn diagrams were generated after excluding species occurring only once in the dataset (singletons) to assess the impact of singletons on the occurrence pattern of beetle species across the stand types. Beetle abundance, richness and diversity analyses were performed on all beetle species and on only saproxylic species.

Prior to analyses, data was checked so that the underlying assumptions of the tests were met by visual inspection of histograms and by performing Shapiro-Wilk normality tests. As beetle abundance, richness and diversity distributions demonstrated normality, multiple linear regression models were applied to examine beetle abundance, species richness and species diversity, using stand age, dead wood volume, dead wood diversity habitat tree abundance, habitat tree richness, and basal area of living trees as independent variables. To explore alternative models, given the limited sample size, the following modeling approach was used. Models were first fitted with only one predictor at the time. Models with predictors that at least tended towards being statistically significant ($p < 0.1$) were kept and models were built upon these by adding one additional predictor, with and without interactions. Models in which the added predictor or interaction terms at least tended towards being statistically significant ($p < 0.1$) were kept. To avoid overfitting the data, models were not fitted with more than two predictors. Collinearity was avoided by not including the correlated predictors habitat tree abundance and habitat tree richness in the same model (using $r > |0.7|$ as a guideline for severe collinearity (Dormann et al. 2013), see Figure S1). The model residuals were checked using diagnostic plots.

Selection among the models identified as described above was based on Akaike's information criterion corrected for small sample sizes (AICc; Hurvich and Tsai 1989). The criteria was calculated using the MuMIn package (Bartoń, 2023) in R (R Core Team 2023). The best models were considered those with significant or near significant ($p < 0.1$) predictor or interaction terms and within two AICc units of the model with the lowest AICc. AICc is not reliable for direct model comparison when sample sizes differ and, in such cases, the AICc values were compared independently. The best models are presented in the result and all models considered after the initial exploration process are found in Table S2. Models were made for all beetle species and only saproxylic species.

Analyses of beta diversity between clear-cut stands and long tree continuity stands, and between young clear-cut stands, old clear-cut stands and long tree continuity stands were performed based on the occurrence of beetle species. Beta diversity was partitioned into a turnover (replacement) and nestedness (species loss) fraction. Simpson pairwise dissimilarity was used to account for turnover, the nestedness-

fraction of Sørensen pairwise dissimilarity was used to account for nestedness, and Sørensen pairwise dissimilarity was used to account for total beta diversity. Distance matrices were calculated using the `beta.pair` function in the `betapart` package (Baselga et al. 2023). Turnover, nestedness and total beta diversity were then calculated as the average Euclidean distances (computed using the dissimilarity indices above reduced to principle coordinate axes) between the group (stand category) members and the spatial median of the group in multivariate space, as proposed by Anderson (2006) and Anderson et al. (2006). Bias resulting from unequal sample sizes was addressed using a bias correction of $\sqrt{\frac{n}{n-1}}$, where n is sample size, to the estimated distances to the spatial median of each group, as proposed by Stier et al. (2013). The calculations of turnover, nestedness and total beta diversity were performed using the `betadisper` function in `vegan` (Oksanen et al. 2022). Welch two-sample t -tests and ANOVA were used to test for differences in turnover, nestedness, and total beta diversity between the two groups (clear-cut, long tree continuity) and three groups (young clear-cut, old clear-cut, long tree continuity), respectively. Analyses of beta diversity were performed on all beetle species and on only saproxylic beetle species.

A rank-abundance curve was made to visualize the overall community composition of the inventoried beetles. Community assemblages were visualized by non-metric multidimensional scaling (NMDS) using the `vegan` package (`metaMDS` function; Oksanen et al. 2022). A scree plot was made to determine the minimum number of dimensions needed to not underfit the dissimilarity data, using a stress of 0.2 as a guideline for maximum acceptable stress. Bray-Curtis dissimilarity was used as dissimilarity index and a minimum of 20 and maximum of 100 random starts were used. The effect of environmental variables (in addition to the environmental variables included in the regression models: volume standing dead wood, volume lying dead wood, volume stumps, volume dead wood with signs of fire, volume dead pine wood, volume dead birch wood, volume dead spruce wood, and volume of wood in decay class 1-4, respectively) on community composition was tested using the `envfit` function. Permutational multivariate analysis of variance using distance matrices (`permanova`) was performed using the `adonis2` function (`permutations = 999`) to analyze the difference in beetle community composition between long tree continuity stands and clear-cut stands. A separate `permanova` was used to clarify the potential difference between young and old clear-cut stands. Pairwise comparisons between the group levels was performed with corrections for multiple testing and FDR-adjusted p -values using the `RVAideMemoire` package (Herve, 2023). An indicator species analysis was performed using the `multipatt` function in the `indicspecies` package (Cáceres & Legendre 2009) to reveal the most influential species for long tree continuity stands, old clear-cut stands, and young clear-cut stands. The analyses were performed with all beetle species and on saproxylic species separately. Species of which there only was one specimen present in the dataset (singletons) can have disproportionate influence on the NMDS and were therefore excluded from the NMDS analyses.

Statistical analyses were performed using the statistical programming language R (R Core Team 2023). The packages `dplyr` (Wickham et al. 2023a), `NCmisc` (Cooper

2022), reshape2 (Wickham 2007), tibble (Müller & Wickham 2023), and tidyr (Wickham et al. 2023b) were used for data manipulation, and BiodiversityR (Kindt & Coe 2005), ggcorrplot (Kassambara 2023), ggplot2 (Wickham 2016), ggvenn (Yan 2023), jtools (Long 2022), patchwork (Pedersen 2023), sjPlot (Lüdecke 2023), and stringr (Wickham 2022) were used for data visualization.

3. Results

3.1 Dead Wood Survey

Dead wood volume ranged between 1.6 and 46.2 m³/ha ($\mu = 11.6$, S.E. = 2.5, $n = 18$) for the surveyed forest stands. Overall, 31 % of the possible 192 dead wood character combinations were found: between 2 and 9 % for any individual stand ($\mu = 5.7$, S.E. = 0.4, $n = 18$). Dead wood diversity (effective “species” number) ranged from 3.6 and 15.7 ($\mu = 8.9$, S.E. = 0.2, $n = 18$). In total 61 habitat trees were identified. The number of habitat trees per hectare ranged between 0 and 31 ($\mu = 10.4$, S.E. = 2.3, $n = 18$). Habitat tree richness ranged between 0 and 8 distinct habitat tree characters and species per stand ($\mu = 3.6$, S.E. = 0.7, $n = 18$).

Dead wood volume (t -test, $t_{10.36} = 2.7$, $p = 0.03$), habitat tree abundance, (t -test, $t_{16.00} = 2.8$, $p = 0.02$), and habitat tree richness (t -test, $t_{16.00} = 2.8$, $p = 0.02$) was higher in long tree continuity stands than clear-cut stands (Figure S2). No difference in dead wood diversity was found between stands with long tree continuity and stands exposed to clear-cutting (t -test, $t_{15.68} = 1.2$, $p = 0.3$; Figure S2). When separating the clear-cut stands into young (mean 61 years) and old (mean 78 years), habitat tree richness differed among the three stand types (ANOVA, $F_{2,17} = 6.0$, $p = 0.02$). Post hoc comparisons revealed that the richness was significantly different between long tree continuity stands than the young clear-cut stands (Tukey HSD, $p = 0.02$), but that the differences between old clear-cut stands and long tree continuity stands ($p = 0.2$) and between young and old clear-cut stands ($p = 0.7$) were not statistically significant (Figure 4f). However, there was no significant difference in dead wood volume (ANOVA, $F_{2,17} = 2.8$, $p = 0.1$; Figure 4b), dead wood diversity (ANOVA, $F_{2,17} = 0.6$, $p = 0.6$; Figure 4e), nor habitat tree abundance (ANOVA, $F_{2,17} = 3.5$, $p = 0.06$; Figure 4c) between young clear-cut stands, old clear-cut stands and long tree continuity stands. Stand age was higher in the long tree continuity stands (t -test, $t_{13.52} = 8.2$, $p < 0.001$; Figure S2), but a statistically significant difference could only be ascertained between the long tree continuity stands and the clear-cut stands (ANOVA, $F_{2,19} = 40$, $p < 0.001$; Tukey HSD, $p < 0.001$, $p < 0.001$ and $p = 0.2$ for old clear-cut vs long tree continuity, young clear-cut vs old tree continuity, and young vs old clear-cut, respectively; Figure 4a). Basal area tended to be higher in the clear-cut stands than the long tree continuity stands (t -test, $t_{15.70} = 1.9$, $p = 0.08$, Figure S2). This was primarily due to the higher basal area in the old clear-cut stands (ANOVA, $F_{2,19} = 4.0$, $p < 0.001$; Tukey HSD, $p < 0.001$, $p > 0.9$, and $p < 0.001$ for old clear-cut vs long tree continuity, young clear-cut vs long tree

continuity, and young vs old clear-cut, respectively; Figure 4d). Significant positive correlations were found between habitat tree abundance and richness, and between the two habitat tree variables and stand age and dead wood volume (Figure S1).

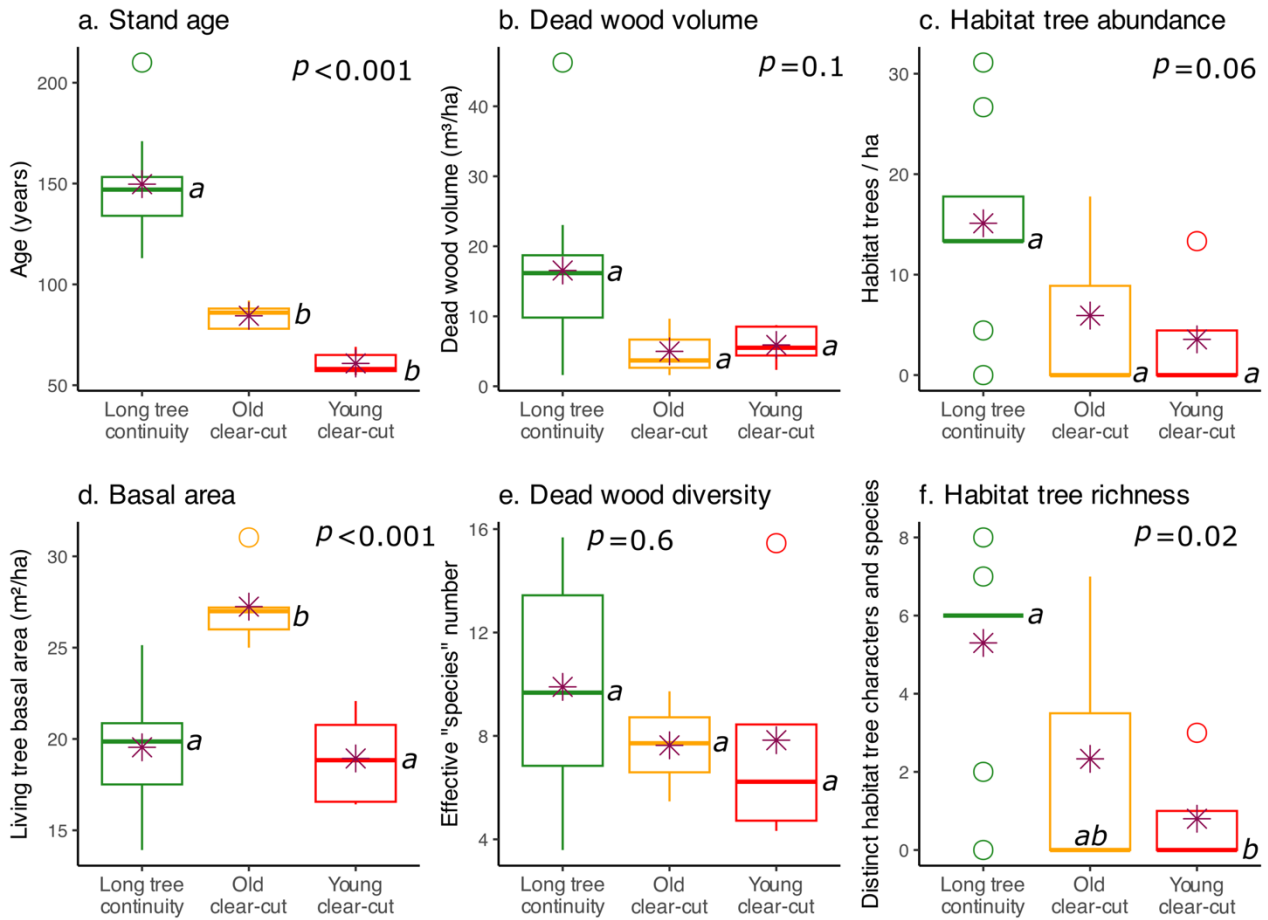


Figure 4. Stand age and forest structural complexity variables in forest stands with long tree continuity (mean 150 years) and forest stands that have been clear-cut. The clear-cut stands are divided into young (mean 61 years) and old (mean 78 years) clear-cuts. The asterisk indicates the mean. Letters indicate which stand categories statistically differ from each other, with the p-value from the analysis of variance (ANOVA) shown. Dead wood survey was not possible in two of the old clear-cut stands due to wind damage.

3.2 Beetle Abundance, Species Richness and Diversity

3,159 specimens of 182 species, representing 43 families, were collected. A full species list is provided in Table S6. An unknown quantity of beetles had decomposed before species identification was possible. Beetle abundance (per catch effort, i.e., total window trap area per stand) ranged between 147 and 496 beetles/m² ($\mu = 309$, S.E. = 24, $n = 20$). The abundance of saproxylic species ranged

between 45 and 296 beetles/m² ($\mu = 166$, S.E. = 16, $n = 20$). The beetle richness ranged between 22 and 59 species per stand ($\mu = 43$, S.E. = 2, $n = 20$); and for saproxylic beetles the richness ranged between 11 and 35 species per stand ($\mu = 24$, S.E. = 1.4, $n = 20$). Beetle diversity (effective species numbers) ranged between 8 and 35 ($\mu = 22$, S.E. = 1.4, $n = 20$); for saproxylic species it ranged between 3.6 and 21 ($\mu = 13$, S.E. = 1.1, $n = 20$).

Beetle abundance was significantly higher in forest stands with long tree continuity than in stands that have been clear-cut, both for all species (t-test, $t_{16.17} = 3.0$, $p = 0.008$), and for saproxylic species (t-test, $t_{17.62} = 3.6$, $p = 0.003$; Figure S3). For richness there was no difference between stands with long tree continuity and clear-cut stands, neither for all species (t-test, $t_{15.98} = 1.8$, $p = 0.2$) nor for saproxylic species (t-test, $t_{17.58} = 1.0$, $p = 0.4$; Figure S3). This was also the case for species diversity, with no differences neither for all beetle species (t-test, $t_{17.97} = 1.2$, $p = 0.3$), nor for saproxylic species (t-test, $t_{16.19} = 1.5$, $p = 0.2$; Figure S3). The lower abundance in the clear-cut stands was due to a lower abundance in the old clear-cut stands, which significantly differed from the long tree continuity stands but not the young clear-cut stands, both for all species (ANOVA, $F_{2, 19} = 7.6$, $p = 0.005$; TukeyHSD, $p = 0.004$, $p = 0.4$, and $p = 0.2$ for old clear-cut vs long tree continuity, young clear-cut vs long tree continuity, and young vs old clear-cut, respectively; Figure 5a) and for saproxylic species (ANOVA, $F_{2, 19} = 11$, $p < 0.001$; TukeyHSD, $p < 0.001$, $p = 0.2$, and $p = 0.06$ for old clear-cut vs long tree continuity, young clear-cut vs long tree continuity, and young vs old clear-cut, respectively; Figure 5d). There was no statistically significant difference in beetle species richness between long tree continuity, old clear-cut and young clear-cut stands for all species (ANOVA, $F_{2, 19} = 2.4$, $p = 0.2$; Figure 5b), nor saproxylic species (ANOVA, $F_{2, 19} = 2.7$, $p = 0.1$; Figure 5e), neither was a difference found for species diversity of all (ANOVA, $F(2, 19) = 0.7$, $p = 0.5$; Figure 5c) nor saproxylic species (ANOVA, $F_{2, 19} = 1.1$, $p = 0.1$; Figure 5f).

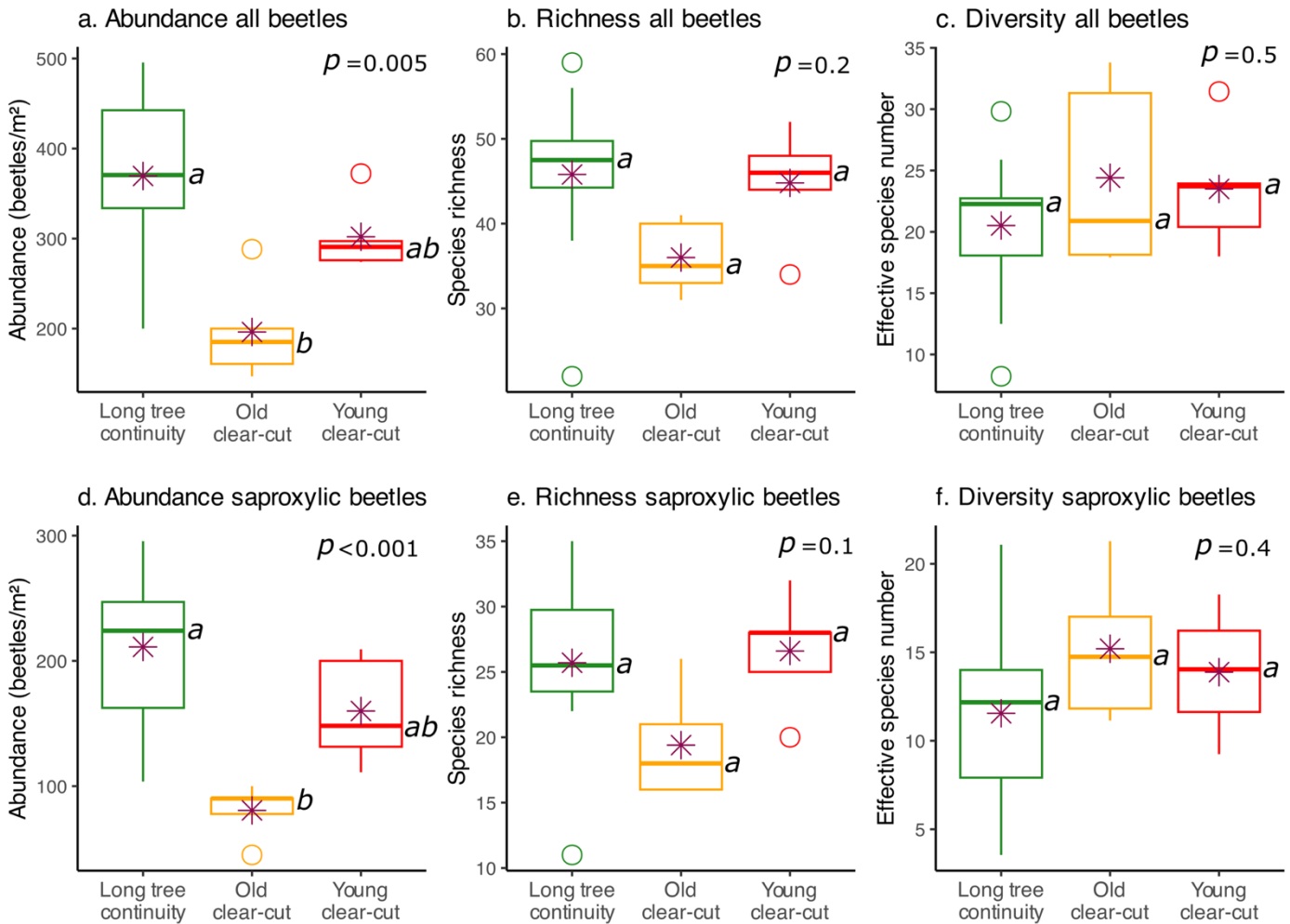


Figure 5. Abundance per catch effort (per m² of trap window), richness and diversity of beetles in forest stands with long tree continuity (mean 150 years) and forest stands that have been clear-cut. The clear-cut stands are divided into young (mean 61 years) an old (mean 78 years) clear-cuts. The asterisk indicates the mean. Letters indicate which stand categories statistically differ from each other, with the p-value from the analysis of variance (ANOVA) shown.

Among the best linear regression models explaining beetle abundance, some showed a positive association between abundance and stand age and others a negative association between abundance and basal area (Figure 6a). These patterns were similar for both all beetle species and for saproxylic species. Alternative models indicated a positive association between habitat tree abundance and richness on the abundance of all beetle species. These models had a negative interaction between the abundance and richness of habitat trees and the basal area. Abundance of saproxylic species were also positively associated with dead wood volume. The best models for beetle species richness indicate positive relationships with habitat tree abundance and richness, but no such pattern was found for the richness of only saproxylic species (Figure 6b). One model found a negative interaction between habitat tree abundance and basal area. Beetle diversity was negatively associated

with stand age, and positively with dead wood diversity, habitat tree abundance and habitat tree richness (Figure 6c). For saproxylic beetle diversity, the best models indicated a negative association with stand age and a positive association with habitat tree richness. Not all predictors were significant at $\alpha = 0.05$, and all model effect sizes were small, apart for two of the abundance models with relatively large model effect sizes for habitat tree abundance and richness.

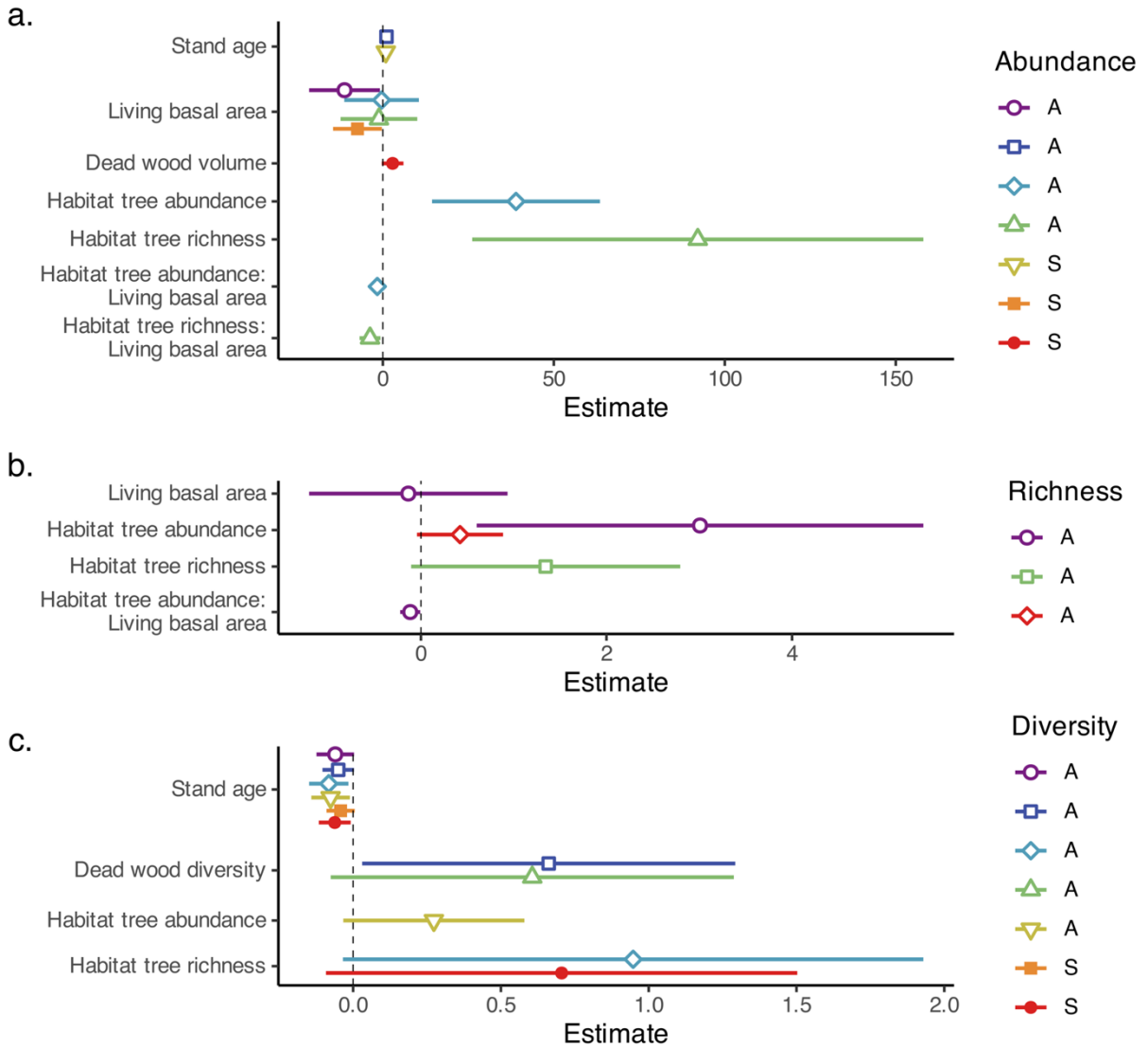


Figure 6. Model estimates (95% confidence intervals) for multiple linear regression models of beetle abundance, species richness and species diversity. A, model with all beetle species; S, model with saproxylic beetle species.

3.3 Beetle Community Composition

About 56 % of the identified beetle species were present both in long tree continuity stands and clear-cut stands (Figure 7a). About 28 % were only found in long tree continuity stands, and about 16 % of species were only found in clear-cut stands. About 9 % of species were unique to young clear-cut stands and only 5.5 % of species were unique to the old clear-cut stands. The pattern was remarkably similar when only saproxylic beetle species were considered (Figure 7b). Excluding singletons from the Venn diagram did not notably affect the observed patterns between the stand types (Figure S4). Few species contributed to a large proportion of the total beetle abundance (Figure S5).

a. All beetle species

b. Saproxylic beetle species

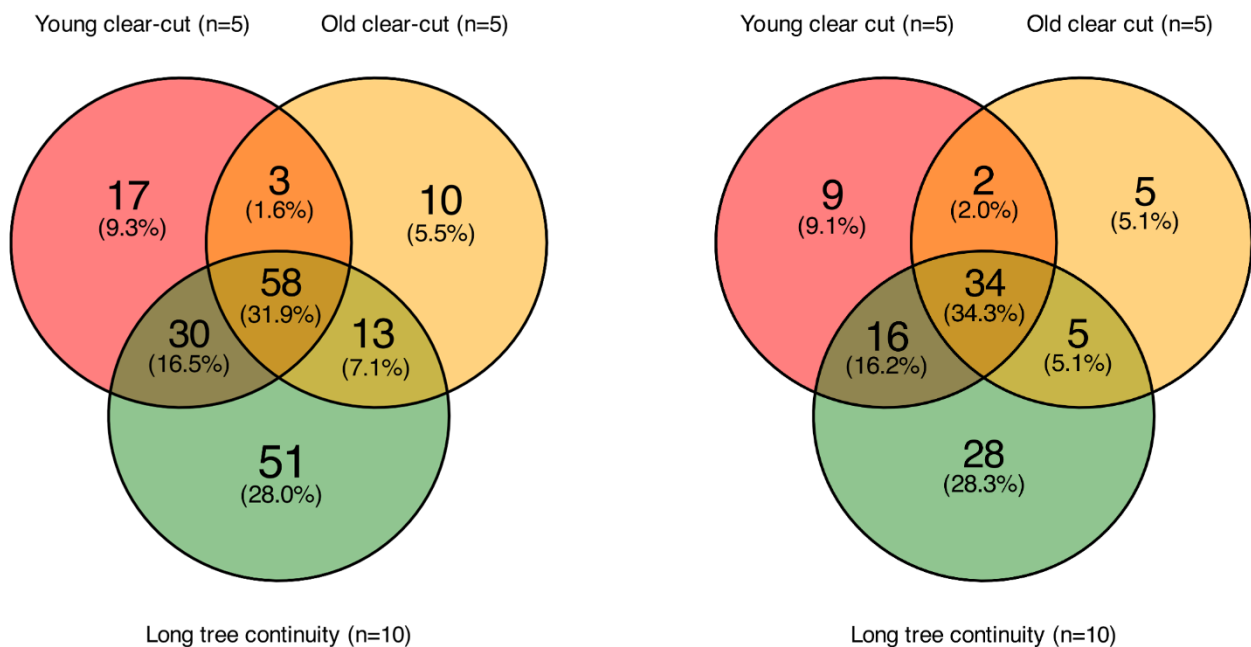


Figure 7. Venn diagrams showing the occurrence of beetle species in forest stands with long tree continuity (mean 150 years) and forest stands that have been clear-cut. The clear-cut stands are divided into young (mean 61 years) and old clear-cuts (mean 78 years).

Beta diversity of beetle species ranged from 0.27 and 0.62 ($\mu = 0.38$, S.E. = 0.02, $n = 20$), with the turnover component ranging from 0.24 and 0.50 ($\mu = 0.34$, S.E. = 0.02, $n = 20$), and the nestedness component ranging from 0.00 and 0.18 ($\mu = 0.04$, S.E. = 0.01, $n = 20$). For saproxylic beetle species beta diversity ranged from 0.28 and 0.66 ($\mu = 0.38$, S.E. = 0.02, $n = 20$), with the turnover component ranging from 0.24 and 0.56 ($\mu = 0.34$, S.E. = 0.02, $n = 20$) and the nestedness component ranging from 0.00 and 0.17 ($\mu = 0.05$, S.E. = 0.01, $n = 20$). Turnover was the dominant component of beta diversity for all sites. No statistically significant differences were observed in beta diversity, nor in the turnover or nestedness components, between long tree continuity stands and clear-

cut stands, nor between the three stand types when the clear-cut stands were divided into young and old clear-cuts (Figure 8). However, there was a noticeable trend indicating a higher turnover in stands with long tree continuity, especially when considering all beetle species (Figure 8a). There was also a tendency for old clear-cut stands to exhibit a lower total beta diversity compared to young clear-cut stands and long tree continuity stands (Figure 8c). Nestedness did not differ much between stands or across stand types (Figure 8b,e). For detailed statistical results, see Table S3.

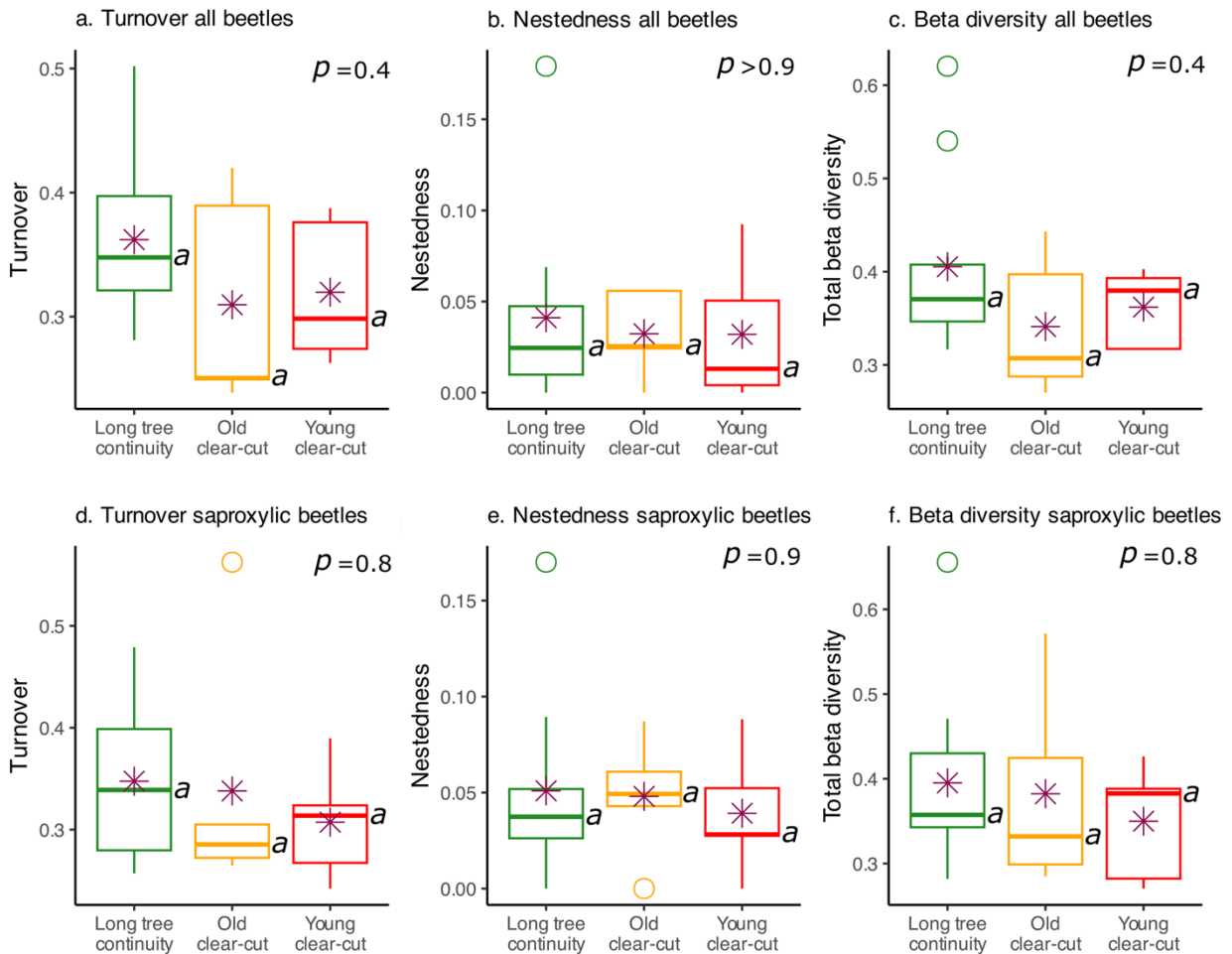


Figure 8. Turnover, nestedness and total beta diversity of beetle species in forest stands with long tree continuity (mean 150 years) and forest stands that have been clear-cut. The clear-cut stands are divided into young (mean 61 years) and old (mean 78 years) clear-cuts. The asterisk indicates the mean. Letters indicate which stand categories statistically differ from each other, with the p -value from the analysis of variance (ANOVA) being shown..

The beetle species assemblages differed between long tree continuity stands and clear-cut stands, both when considering all beetle species (permanova, $F_{1, 19} = 1.9$, $p = 0.02$) and saproxylic beetle species (permanova, $F_{1, 19} = 2.1$, $p = 0.02$). This difference was, however, caused by the distinct community composition of the old clear-cut stands (permanova, $F_{2,19} = 2.0$, $p = 0.004$). The beetle community

assemblages of the old clear-cut stands differed significantly from the young clear-cut stands (pairwise comparison, $p = 0.04$), and the long tree continuity stands (pairwise comparison, $p = 0.006$), while there was no statistically significant difference in community composition between young clear-cut stands and long tree continuity stands (pairwise comparison, $p = 0.5$; Figure 9). The same pattern was found for saproxylic beetle species (permanova, $F_{2, 19} = 2.6$, $p = 0.001$; pairwise comparisons, $p = 0.04$, $p = 0.003$, and $p = 0.4$, for old vs young clear-cut, old clear-cut vs long tree continuity, and young clear-cut vs long tree continuity, respectively; Figure 9). The environmental variables that were significant or near significant ($p < 0.1$) in explaining the community composition, were basal area ($p = 0.03$), dead birch wood volume ($p = 0.07$ and $p = 0.06$ for all beetle species and saproxylic species, respectively), and stand age ($p = 0.08$); stand age not being significant ($p > 0.1$) when only considering saproxylic beetle species ($p = 0.2$; Figure 9). All vectors of the environmental variables and their associated p -values can be found in Table S4. Indicator species are shown in Figure 9 and the full result from the indicator species analysis can be found in Table S5.

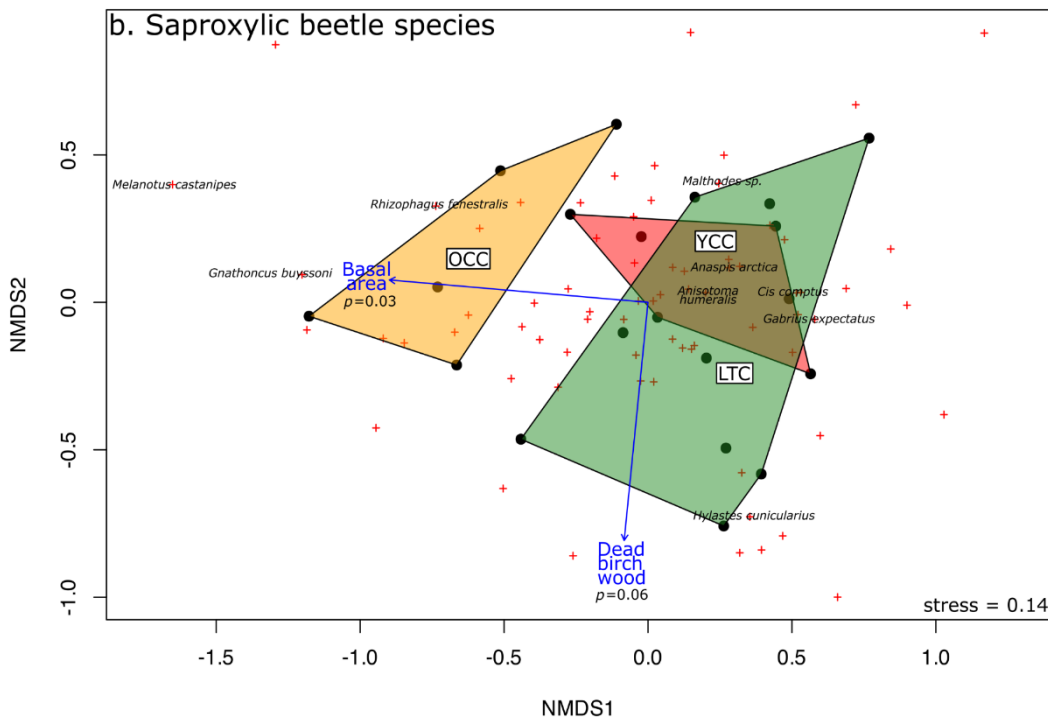
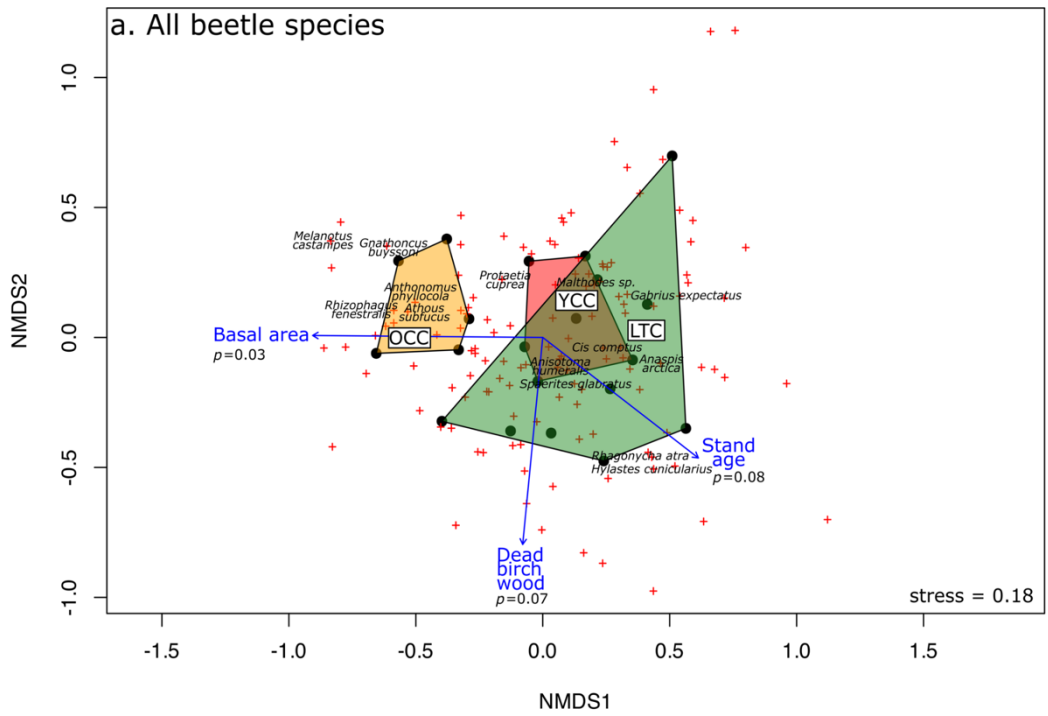


Figure 9. NMDS plots visualizing beetle community assemblages. Colored polygons outline the different stand types. LTC, long tree continuity (mean 150 years); YCC, young clear-cut (mean 61 years); OCC, old clear-cut (mean 78 years). Vectors show direction of environmental predictors significant at $p < 0.1$, with the p -values indicated. Indicator species are displayed. Both NMDS analyses are performed with two dimensions.

4. Discussion

4.1 Decoupling the Effects of Tree Continuity and Structural Complexity

Structural complexity in the form of dead wood and other habitat structures is often higher in stands with a long tree continuity than in stands that have been regenerated after clear-cutting (see e.g. Siitonen 2001; Siitonen et al. 2000; Sippola et al. 1998). A challenge in the currently available literature on the effect of disrupting tree continuity is the difficulty to determine to what extent it is the continuity itself or changes in the structural complexity that creates the observed patterns in invertebrate communities. Many studies only investigate either continuity, or structural complexity (e.g. Hämäläinen et al. 2018; Seibold et al. 2017), or cannot clearly differentiate between the two (e.g. Martikainen et al. 2000; Similä et al. 2003; Stenbacka et al. 2010). A number of studies, however, on saproxylic invertebrates in general (Kouki et al. 2001) and beetles specifically (Økland et al. 1996; Janssen et al. 2016; Kraut et al. 2016; Haeler et al. 2021) indicate that availability of suitable habitat structures is the limiting factor for these organisms and that dispersal limitation plays little or no effect, even for low-dispersal species. Økland et al. (1996), e.g., found stronger relationships between saproxylic beetle diversity and structural complexity than tree continuity in the landscape, Janssen et al. (2016) found that saproxylic beetle diversity was associated with stand maturity but not forest continuity, and Kraut et al. (2016) found that forests with disrupted tree continuity were suitable saproxylic beetle habitats as long as dead wood was abundant. Irmeler et al. (2010) did, in contrast, find indications of dispersal limitation for the least mobile beetle species. Despite the lack of support for dispersal limitation for most forest dwelling beetles, forests with long tree continuity may host a greater richness of saproxylic beetles regardless of study substrate (Jacobsen et al. 2020). Furthermore, enhancing habitat quality through the addition of dead wood in heavily managed landscapes may not consistently yield successful outcomes (Kouki et al. 2001), and maintained tree continuity is a commonly recommended management practice even in studies where there are no indications of dispersal limitation (Økland et al. 1996; Kraut et al. 2016).

I was able to, at least partly, separate the effects of tree continuity and structural complexity by explicitly choosing sites with a range of structural complexity, both for clear-cut and long tree continuity stands. Although dead wood volume, and habitat tree abundance and richness were significantly higher in the long tree

continuity stands (Figure S2), the range of these variables covered by the long tree continuity stands was high (Figure 4). Thus, the structural complexity of the least complex long tree continuity stands resembles that of the clear-cut stands. Dead wood diversity, which probably is a more important structural complexity variable than dead wood volume for saproxylic beetles (Similä et al. 2003; Janssen et al. 2016), did not differ significantly between the stand types (Figure 4e), and stand age was only significantly correlated with the habitat tree variables, and not to the dead wood variables (Figure S1), which indicates that the effects of tree continuity and structural complexity at least partly were separated in this study.

4.2 Beetle Abundance

In accordance with earlier findings (Martikainen et al. 2000; Olsson et al. 2012), my study demonstrates that stands with long tree continuity harbor a higher abundance of beetles than stands where the tree continuity had been disrupted by clear-cutting (Figure S3a). Saproxylic beetle species are driving this pattern (Figure S3d), which suggests that forests might lose part of the ecological functions, including decomposition and energy recycling, provided by saproxylic beetles if beetle abundances decrease after tree continuity is disrupted by clear-cut harvesting. When separating young (mean 61 years) and old (mean 78 years) clear-cut stands I found that it is primarily the old clear-cut stands that give rise to the significant difference in beetle abundance between long tree continuity stands and clear-cut stands (Figure 5a,d). One reason for this could be the significantly higher basal area of living trees in the old clear-cut stands (Figure 4d). The basal area in the other stands is likely lower due to thinner tree diameter in the young clear-cut stands and a lower tree density in the long tree continuity stands. Basal area and canopy cover are positively correlated (Korhonen et al. 2007), and hence the old clear-cut stands likely have less sun exposure than the other stand types. Many beetle species are favored by sun exposure (Lindhe et al. 2005; Sebek et al. 2016), which can explain the low abundance in the old clear-cut stands. In addition, beetles tend to be more active at higher temperatures (Hannigan et al. 2023), leading to a higher capture rate in more sun exposed stands.

Multiple linear regression models for beetle abundance indicated a positive association with stand age and habitat tree abundance and richness, and a negative association with basal area (Figure 6a). The negative association with basal area is likely due to the high basal areal in the old clear-cut stands, as described above. Although the effect size of the model is small, the association with stand age may point to that tree continuity contributes to a higher beetle abundance rather than structural complexity. However, since there was a trend for the old clear-cut stands to have a lower beetle abundance than the young clear-cut stands (Figure 5a), stand age can likely only explain part of the variation in beetle abundance between long tree continuity stands and clear-cut stands and possible among long tree continuity stands, but not among clear-cut stands.

The model effect size for habitat tree abundance and richness was considerably larger than the effect sizes in any of the models identified in this study, suggesting

that beetle abundance is strongly associated with habitat tree abundance and richness. However, the associations between beetle abundance and habitat tree abundance and richness was only present when the model included an interaction between the habitat tree variables and basal area, highlighting the previously mentioned importance of basal area. The negative interaction can be interpreted as that the positive relationship with beetle abundance and habitat tree abundance or richness is larger in stands with a lower basal area. There was no significant difference in basal area between stands with long tree continuity and young clear-cut stands, but basal area was significantly higher in old clear-cut stands, and abundance and richness of habitat trees was significantly higher in long tree continuity stands than in clear-cut stands. This suggests that although habitat trees have some importance, their effect is not independent of the effect of basal area and stand type.

The positive, although weak, relationship between dead wood volume and saproxylic beetle abundance indicates that structural complexity, and especially access to dead wood, is important to host a higher abundance of saproxylic beetles. This relationship was, however, only marginally statistically significant ($p = 0.08$); the saproxylic beetle dataset collected in this study might be too small to obtain robust results. That this trend only occurred for saproxylic species is not surprising as dead wood amount has a stronger influence on saproxylic than non-saproxylic species (see e.g. Martikainen et al. 2000).

4.3 Beetle Species Richness and Diversity

While saproxylic beetle diversity commonly is higher in stands with long tree continuity (Martikainen et al. 2000; Similä et al. 2003; Jacobsen et al. 2020; Burner et al. 2021), I found no significant difference in beetle richness and diversity between clear-cut and long tree continuity stands. Hence, long tree continuity alone is insufficient in explaining the variation in beetle diversity. Lindhe et al. (2005) found that out of the half of the investigated species that were significantly affected by sun exposure, more than two thirds were favored by sun exposure rather than shade. This can explain the trend of a lower beetle species richness in the old clear-cut stands that was observed in the present study (Figure 5b,e), as these stands had a high basal area and thus a denser canopy cover. Nevertheless, basal area was not a significant predictor in the multiple linear regression models for beetle species richness or diversity.

Some of the models of beetle diversity indicated a minor negative association between stand age and beetle species diversity, which contradicts earlier studies (Siitonen et al. 2000; Irmeler et al. 2010; Stenbacka et al. 2010). Beetle species richness showed indications of a positive association with abundance and richness of habitat trees. Beetle diversity showed indications of positive association with dead wood diversity, habitat tree abundance and richness. Although not all these variables were statistically significant, the trends indicate that, at the stand level, structural complexity may be more important for beetle richness and diversity than tree continuity, especially when considering the variation in structural complexity

among stands with a long tree continuity. For instance, the second oldest stand had a very low structural complexity and the lowest beetle species richness among all stands. Surprisingly, dead wood diversity emerged as a predictor only in models with all beetle species, not in those with only saproxylic species, likely indicating that the relatively low number of saproxylic beetle trapped in this study limits the possibility to detect differences.

My results also indicate that habitat trees are important structural components for beetle species richness and diversity. The importance of habitat trees for beetle diversity has not been given the same attention as that of dead wood (but see Bouget et al. 2014; Pilskog et al. 2020), especially in boreal ecosystems. Since stand age and the habitat tree variables were correlated, their contrasting effects on beetle diversity may indicate that habitat trees provide an important structural component for beetles rather than only being indicators for suitable habitats. More research is needed to discern which types of tree related microhabitats on habitat trees are key structures for beetles in boreal forest ecosystems.

4.4 Beetle Community Composition

Both for clear-cut and long tree continuity stands, a small number of common species contributed to much of the total abundance (Figure S5). These common species were present in most stands and were more abundant in the stands with long tree continuity, indicating that the lower beetle abundance in clear-cut stands mainly is due to a lower abundance of common species, especially in the old clear-cut stands where they may be less frequent or less active due to lower sun exposure. More beetle species were found exclusively in long tree continuity stands than exclusively in clear-cut stands (Figure 7). The long tree continuity stands thus seem able host a wider range of less common species compared to clear-cut stands on a landscape level, despite that I found no significant differences in species richness at a stand level between the stand types. The pattern persisted when species of which only one specimen was found in the total dataset (singletons) were removed (Figure S4), suggesting that these findings are not merely a result of random occurrences in specific stands, but rather indicative of an ecological distinction between the stand types.

The difference in beetle community composition between long tree continuity stands and clear-cut stands was caused by the distinct community composition of the old clear-cut stands. This pattern was largely driven by the saproxylic beetle species assemblage. It should be noted that the old clear-cut stands were geographically near each other and separate from the other stands (see Figure 2), which could contribute to their distinct community composition. Nevertheless, my results indicate that stands regenerated after clear-cutting may develop a distinct beetle community of more shade-tolerant species that differ from forests that have not been exposed to clear-cutting.

The beetle communities of young clear-cut stands and long tree continuity stands had a large overlap in species composition, and the young clear-cut beetle

community was largely a subset of the long tree continuity beetle community (Figure 9). The NMDS analysis revealed stand age as an environmental variable that could predict the species composition of certain long tree continuity stands, indicating that stands that have not been clear-cut may host unique species with a lower tolerance to disruptions in tree continuity. Dead birch wood volume was another of the environmental variables that partly explained beetle community composition, highlighting the importance of dead wood diversity. Many beetle species have strong associations with a single tree genus or species (Jonsell 2007), such as oak (*Quercus* sp.), Norway spruce (Burner et al. 2021), or as highlighted here, birch (Rubene et al. 2014). In pine-dominated forests, as those investigated in this study, even a small amount of deciduous wood, like birch, appears sufficient to create a different beetle composition.

Species turnover was the major contributor to beta diversity for all stand types, demonstrating that beetle species assemblages are variable between forest stands of all types. The relatively low nestedness indicates that each stand contributes to the total beetle diversity. In fact, almost all stands hosted species that were unique and not found in any other stands. The relatively small sample size, especially for the young and old clear-cut stands ($n = 5$), can also contribute to the low nestedness. There were trends towards a higher beetle species turnover in stands with long tree continuity (Figure 8a) which, although not significant ($p = 0.4$), is in line with the patterns observed both in the Venn diagram (Figure 7) and the NMDS analysis (Figure 9). Species composition of stands with long tree continuity seem to be more variable than stands regenerated after clear-cutting, so that they collectively host more species than clear-cut stands, even though each individual stand may host about the same number of species. This is in accordance with results of Gran (2022), that found that even though the alpha diversity of saproxylic beetles did not differ between managed and unmanaged stands, the beta and gamma diversity indicated the value of unmanaged forests to conserve the entire saproxylic beetle fauna.

Species with a higher dispersal ability tend to have a higher turnover component of beta diversity, while species with a lower dispersal ability tend to have a higher nestedness component, as exemplified with sexually and vegetatively reproducing epiphytic lichens (Brunialti et al. 2020). The relatively high turnover component in the present study, indicate that forest-dwelling beetles in boreal forests in general are not dispersal limited. Rather, it may be other characteristics of forest with long tree continuity that are more important, such as the different microhabitats present on habitat trees or in dead wood, or the tree species present, that enable them to host diverse community assemblages. Beta diversity of forest-dwelling beetles may have to be considered both on a spatial scale (between stands and regions) and on a host scale (between different host tree species or characteristics), as both scales have been found to affect beta diversity (Rieker et al. 2022; Seibold et al. 2023).

4.5 Management Implications

In the United Nations Sustainable Development Goal 15, life on land, the world community has resolved to promote the implementation of sustainable forest

management, to reduce the degradation of natural habitats, and to halt the loss of biodiversity (UN Department of Economic and Social Affairs), and in the Swedish environmental objectives of sustainable forests the country has undertaken to work for a rich diversity of plant and animal life in its forest ecosystems (Swedish Environmental Protection Agency). In this light, the development of forest management strategies that can sustain a diverse community of forest-dwelling fauna is an urgent need.

My results suggest that preserving the few remaining forests with undisrupted tree continuity in the Swedish boreal forest landscape is important to preserve a high beetle abundance and maintain a high level of the ecosystem functions performed by saproxylic beetles. The preservation of a these stands within a managed forest landscape is important to preserve habitat for the widest range of beetle species, including species associated with deciduous trees such as birch. Uneven-aged forest management may be an alternative to create favorable conditions for saproxylic beetles similar to unmanaged long tree continuity stands (Hjältén et al. 2017; Joelsson et al. 2017, 2018).

Further, my study suggests that ensuring a continuous of input of a large amount of dead wood will be important to maintain a high abundance and diversity of saproxylic beetles. Only two of the study sites (10 %) in my study, both being long tree continuity stands, reached the identified minimum dead wood volume threshold of 20-30 m³/ha needed to sustain species richness and sensitive individual species in boreal coniferous forests (Müller & Bütler 2010). Increasing dead wood volume can be done by artificial creation of dead wood, leaving naturally dead trees, retaining living trees to enable them to reach senescence and die naturally, and prolonging rotation times (Ehnström 2001; Similä et al. 2003; Laaksonen et al. 2020). More crucial than dead wood amount alone is to ensure a high diversity of microhabitats on living and dead trees. This can be done by paying attention so that retention trees and artificially created dead wood represent a range of stem diameters, positions, species and characteristics (Similä et al. 2003; Hjältén et al. 2012; Häggglund & Hjältén 2018). My study indicates that the preservation of even small amounts of wood from deciduous trees, like birch, creates habitat for species that otherwise would not be present at a given site. More research is needed into which types of microhabitats on living and dead wood are most important for beetles.

Finally, my results also highlight that forests managed through clear-cut forestry that have now been allowed to grow old and develop a distinct beetle community of likely more shade-tolerant species. These distinct communities can be maintained by preserving existing clear-cut stands that have been left unmanaged after harvest and by increasing rotation times.

4.6 Conclusions

I was able to, at least partly, separate the effects of tree continuity and structural complexity on the abundance, diversity, and species composition of forest-dwelling

beetles. This was achieved by explicitly selecting sites with a wide range of structural complexity both for stands that have been clear-cut and stands with a long tree continuity. In summary, my study indicates that, on a landscape levels, forests with a long tree continuity can host a wider range of species of forest-dwelling beetles than forest where the tree continuity has been disrupted by clear-cutting, even though the species richness is similar on the stand level. These species are likely to include those with a limited dispersal ability or those associated with specific dead wood types, such as dead birch wood. Forest-dwelling beetles in general are, however, found not to be dispersal limited on the spatial scales considered in my study.

Further, my study suggests that, within a boreal landscape featuring a range of structural complexity, the presence of varied microhabitats on dead wood and living habitat trees plays a more important role in influencing beetle diversity than stand age for any one stand. However, I found indications of that beetle abundance, primarily of common species, is higher in stands with a longer, undisrupted tree continuity. The amount of dead wood may increase the abundance of saproxylic species. Additionally, my study indicates that forests managed through clear-cutting may exhibit a smaller abundance of beetles belonging to a reduced but distinct species assembly as they mature and grow denser.

To sustain an ample abundance of a diverse beetle community in the managed boreal forest landscape in northern Sweden, I suggest preserving the remaining forests with an undisrupted tree continuity, ensuring a sufficiently large and continuous input of a wide diversity of living or dead wood using natural or artificial methods, and paying attention to the potential of previously clear-cut forests left unmanaged to develop distinct beetle habitats.

References

- Ahlström, A., Canadell, J.G. & Metcalfe, D.B. (2022). Widespread Unquantified Conversion of Old Boreal Forests to Plantations. *Earth's Future*, 10 (11), e2022EF003221. <https://doi.org/10.1029/2022EF003221>
- Anderson, M.J. (2006). Distance-Based Tests for Homogeneity of Multivariate Dispersions. *Biometrics*, 62 (1), 245–253. <https://doi.org/10.1111/j.1541-0420.2005.00440.x>
- Anderson, M.J., Ellingsen, K.E. & McArdle, B.H. (2006). Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, 9 (6), 683–693. <https://doi.org/10.1111/j.1461-0248.2006.00926.x>
- Bartoń, K. (2023). *MuMIn: Multi-Model Inference*. Version 1.47.5. <https://CRAN.R-project.org/package=MuMIn>
- Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19 (1), 134–143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>
- Baselga, A., Orme, D., Villeger, S., Bortoli, J.D., Leprieur, F., Logez, M., Martinez-Santalla, S., Martin-Devasa, R., Gomez-Rodriguez, C. & Crujeiras, R.M. (2023) *betapart: Partitioning Beta Diversity into Turnover and Nestedness Components*. Version 1.6. <https://CRAN.R-project.org/package=betapart>
- Berg, Å., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M. & Weslien, J. (1994). Threatened Plant, Animal, and Fungus Species in Swedish Forests: Distribution and Habitat Associations. *Conservation Biology*, 8 (3), 718–731. <https://doi.org/10.1046/j.1523-1739.1994.08030718.x>
- Bouget, C., Larrieu, L. & Brin, A. (2014). Key features for saproxylic beetle diversity derived from rapid habitat assessment in temperate forests. *Ecological Indicators*, 36, 656–664. <https://doi.org/10.1016/j.ecolind.2013.09.031>
- Brandel, G. (1990). *Volume functions for individual trees* (in Swedish with English summary). (Report; 26)
- Brandt, J.P., Flannigan, M.D., Maynard, D.G., Thompson, I.D. & Volney, W.J.A. (2013). An introduction to Canada's boreal zone: ecosystem processes, health,

sustainability, and environmental issues. *Environmental Reviews*, 21 (4), 207–226. <https://doi.org/10.1139/er-2013-0040>

Brin, A., Bouget, C., Brustel, H. & Jactel, H. (2011). Diameter of downed woody debris does matter for saproxylic beetle assemblages in temperate oak and pine forests. *Journal of Insect Conservation*, 15 (5), 653–669. <https://doi.org/10.1007/s10841-010-9364-5>

Brunialti, G., Giordani, P., Ravera, S. & Frati, L. (2020). The Reproductive Strategy as an Important Trait for the Distribution of Lower-Trunk Epiphytic Lichens in Old-Growth vs. Non-Old Growth Forests. *Forests*, 12 (1), 27. <https://doi.org/10.3390/f12010027>

Burner, R.C., Birkemoe, T., Stephan, J.G., Drag, L., Muller, J., Ovaskainen, O., Potterf, M., Skarpaas, O., Snäll, T. & Sverdrup-Thygeson, A. (2021). Choosy beetles: How host trees and southern boreal forest naturalness may determine dead wood beetle communities. *Forest Ecology and Management*, 487, 119023. <https://doi.org/10.1016/j.foreco.2021.119023>

Cáceres, M.D. & Legendre, P. (2009). Associations between species and groups of sites: indices and statistical inference. *Ecology*, 90, 3566–3574. <https://doi.org/10.1890/08-1823.1>

Cardoso, P., Barton, P.S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T., Fukushima, C.S., Gaigher, R., Habel, J.C., Hallmann, C.A., Hill, M.J., Hochkirch, A., Kwak, M.L., Mammola, S., Ari Noriega, J., Orfinger, A.B., Pedraza, F., Pryke, J.S., Roque, F.O., Settele, J., Simaika, J.P., Stork, N.E., Suhling, F., Vorster, C. & Samways, M.J. (2020). Scientists' warning to humanity on insect extinctions. *Biological Conservation*, 242, 108426. <https://doi.org/10.1016/j.biocon.2020.108426>

Cooper, N. (2022). *NCmisc: Miscellaneous Functions for Creating Adaptive Functions and Scripts*. Version 1.2.0. <https://CRAN.R-project.org/package=NCmisc>

Dice, L.R. (1945). Measures of the Amount of Ecologic Association Between Species. *Ecology*, 26 (3), 297–302. <https://doi.org/10.2307/1932409>

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D. & Lautenbach, S. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36 (1), 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>

Ehnström, B. (2001). Leaving Dead Wood for Insects in Boreal Forests - Suggestions for the Future. *Scandinavian Journal of Forest Research*, 16, 91–98. <https://doi.org/10.1080/028275801300090681>

Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A.Z. & Schepaschenko, D.G. (2015). Boreal forest health and global change. *Science*, 349 (6250), 819–822. <https://doi.org/10.1126/science.aaa9092>

Gibb, H., Pettersson, R.B., Hjältén, J., Hilszczański, J., Ball, J.P., Johansson, T., Atlegrim, O. & Danell, K. (2006). Conservation-oriented forestry and early successional saproxylic beetles: Responses of functional groups to manipulated dead wood substrates. *Biological Conservation*, 129 (4), 437–450. <https://doi.org/10.1016/j.biocon.2005.11.010>

Gimmel, M.L. & Ferro, M.L. (2018). General Overview of Saproxylic Coleoptera. I: Ulyshen, M.D. (red.) *Saproxylic Insects: Diversity, Ecology and Conservation*. Springer International Publishing. 51–128. https://doi.org/10.1007/978-3-319-75937-1_2

Gran, O. (2022). Lower alpha, higher beta, and similar gamma diversity of saproxylic beetles in unmanaged compared to managed Norway spruce stands. Singh, R. (red.) (Singh, R., red.) *PLOS ONE*, 17 (7), e0271092. <https://doi.org/10.1371/journal.pone.0271092>

Haeler, E., Bergamini, A., Blaser, S., Ginzler, C., Hindenlang, K., Keller, C., Kiebacher, T., Kormann, U.G., Scheidegger, C., Schmidt, R., Stillhard, J., Szallies, A., Pellissier, L. & Lachat, T. (2021). Saproxylic species are linked to the amount and isolation of dead wood across spatial scales in a beech forest. *Landscape Ecology*, 36 (1), 89–104. <https://doi.org/10.1007/s10980-020-01115-4>

Haila, Y. & Kouki, J. (1994). The phenomenon of biodiversity in conservation biology. *Annales Zoologici Fennici*, 31 (1), 5–18

Hannigan, S., Nendel, C. & Krull, M. (2023). Effects of temperature on the movement and feeding behaviour of the large lupine beetle, *Sitona gressorius*. *Journal of Pest Science*, 96 (1), 389–402. <https://doi.org/10.1007/s10340-022-01510-7>

Hansen, A.J., Spies, T.A., Swanson, F.J. & Ohmann, J.L. (1991). Conserving Biodiversity in Managed Forests. *BioScience*, 41 (6), 382–392. <https://doi.org/10.2307/1311745>

Hellberg, E., Josefsson, T. & Östlund, L. (2009). The transformation of a Norway spruce dominated landscape since pre-industrial times in northern Sweden: the influence of modern forest management on forest structure. *Silva Fennica*, 43 (5). <https://doi.org/10.14214/sf.173>

Herve, M. (2023). *RVAideMemoire: Testing and Plotting Procedures for Biostatistics*. Version 0.9-83-7. <https://CRAN.R-project.org/package=RVAideMemoire>

Hjältén, J., Joelsson, K., Gibb, H., Work, T., Löfroth, T. & Roberge, J.-M. (2017). Biodiversity benefits for saproxylic beetles with uneven-aged silviculture. *Forest*

Ecology and Management, 402, 37–50.
<https://doi.org/10.1016/j.foreco.2017.06.064>

Hjältén, J., Stenbacka, F., Pettersson, R.B., Gibb, H., Johansson, T., Danell, K., Ball, J.P. & Hilszczański, J. (2012). Micro and Macro-Habitat Associations in Saproxylic Beetles: Implications for Biodiversity Management. Bruun, H.H. (red.) (Bruun, H. H., red.) *PLoS ONE*, 7 (7), e41100. <https://doi.org/10.1371/journal.pone.0041100>

Hodgson, J.A., Moilanen, A., Wintle, B.A. & Thomas, C.D. (2011). Habitat area, quality and connectivity: striking the balance for efficient conservation. *Journal of Applied Ecology*, 48 (1), 148–152. <https://doi.org/10.1111/j.1365-2664.2010.01919.x>

Hurvich, C.M., Tsai, C.-L., 1989. Regression and time series model selection in small samples. *Biometrika* 76, 297–307. <https://doi.org/10.1093/biomet/76.2.297>.

Hutchinson, G.E. (1957). Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, 22 (0), 415–427. <https://doi.org/10.1101/SQB.1957.022.01.039>

Hägglund, R. & Hjältén, J. (2018). Substrate specific restoration promotes saproxylic beetle diversity in boreal forest set-asides. *Forest Ecology and Management*, 425, 45–58. <https://doi.org/10.1016/j.foreco.2018.05.019>

Hämäläinen, A., Strengbom, J. & Ranius, T. (2018). Conservation value of low-productivity forests measured as the amount and diversity of dead wood and saproxylic beetles. *Ecological Applications*, 28 (4), 1011–1019. <https://doi.org/10.1002/eap.1705>

Irmeler, U., Arp, H. & Nötzold, R. (2010). Species richness of saproxylic beetles in woodlands is affected by dispersion ability of species, age and stand size. *Journal of Insect Conservation*, 14 (3), 227–235. <https://doi.org/10.1007/s10841-009-9249-7>

Jacobsen, R.M., Burner, R.C., Olsen, S.L., Skarpaas, O. & Sverdrup-Thygeson, A. (2020). Near-natural forests harbor richer saproxylic beetle communities than those in intensively managed forests. *Forest Ecology and Management*, 466, 118124. <https://doi.org/10.1016/j.foreco.2020.118124>

Janssen, P., Cateau, E., Fuhr, M., Nusillard, B., Brustel, H. & Bouget, C. (2016). Are biodiversity patterns of saproxylic beetles shaped by habitat limitation or dispersal limitation? A case study in unfragmented montane forests. *Biodiversity and Conservation*, 25 (6), 1167–1185. <https://doi.org/10.1007/s10531-016-1116-8>

Joelsson, K., Hjältén, J. & Work, T. (2018). Uneven-aged silviculture can enhance within stand heterogeneity and beetle diversity. *Journal of Environmental Management*, 205, 1–8. <https://doi.org/10.1016/j.jenvman.2017.09.054>

- Joelsson, K., Hjältén, J., Work, T., Gibb, H., Roberge, J.-M. & Löfroth, T. (2017). Uneven-aged silviculture can reduce negative effects of forest management on beetles. *Forest Ecology and Management*, 391, 436–445. <https://doi.org/10.1016/j.foreco.2017.02.006>
- Jonsell, M. (2007). Effects on biodiversity of forest fuel extraction, governed by processes working on a large scale. *Biomass and Bioenergy*, 31 (10), 726–732. <https://doi.org/10.1016/j.biombioe.2007.06.018>
- Jonsell, M., Weslien, J. & Ehnström, B. (1998). Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodiversity and Conservation*, 7 (6), 749–764. <https://doi.org/10.1023/A:1008888319031>
- Jost, L. (2006). *Entropy and diversity*. *Oikos*, 113 (2), 363–375. <https://doi.org/10.1111/j.2006.0030-1299.14714.x>
- Kassambara, A. (2023). *ggcorrplot: Visualization of a Correlation Matrix using "ggplot2"*. Version 0.1.4.1. <https://CRAN.R-project.org/package=ggcorrplot>
- Kindt, R. & Coe, R. (2005). *Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies*. World Agroforestry Centre (ICRAF). <http://www.worldagroforestry.org/output/tree-diversity-analysis>
- Koleff, P., Gaston, K.J. & Lennon, J.J. (2003). Measuring beta diversity for presence–absence data. *Journal of Animal Ecology*, 72 (3), 367–382. <https://doi.org/10.1046/j.1365-2656.2003.00710.x>
- Korhonen, L., Korhonen, K., Stenberg, P., Maltamo, M. & Rautiainen, M. (2007). Local models for forest canopy cover with beta regression. *Silva Fennica*, 41 (4). <https://doi.org/10.14214/sf.275>
- Kouki, J., Löfman, S., Martikainen, P., Rouvinen, S. & Uotila, A. (2001). Forest Fragmentation in Fennoscandia: Linking Habitat Requirements of Wood-associated Threatened Species to Landscape and Habitat Changes. *Scandinavian Journal of Forest Research*, 16 (sup003), 27–37. <https://doi.org/10.1080/028275801300090564>
- Kraut, A., Liira, J. & Lõhmus, A. (2016). Beyond a minimum substrate supply: Sustaining saproxylic beetles in semi-natural forest management. *Forest Ecology and Management*, 360, 9–19. <https://doi.org/10.1016/j.foreco.2015.10.016>
- Kyaschenko, J., Strengbom, J., Felton, A., Aakala, T., Staland, H. & Ranius, T. (2022). Increase in dead wood, large living trees and tree diversity, yet decrease in understory vegetation cover: The effect of three decades of biodiversity-oriented forest policy in Swedish forests. *Journal of Environmental Management*, 313, 114993. <https://doi.org/10.1016/j.jenvman.2022.114993>
- Laaksonen, M., Punttila, P. & Siitonen, J. (2020). Early-successional saproxylic beetles inhabiting a common host-tree type can be sensitive to the spatiotemporal

continuity of their substrate. *Biodiversity and Conservation*, 29 (9–10), 2883–2900. <https://doi.org/10.1007/s10531-020-02004-7>

Lachat, T. & Müller, J. (2018). Importance of Primary Forests for the Conservation of Saproxylic Insects. I: Ulyshen, M.D. (red.) *Saproxylic Insects: Diversity, Ecology and Conservation*. Springer International Publishing. 581–605. https://doi.org/10.1007/978-3-319-75937-1_17

Larrieu, L., Paillet, Y., Winter, S., Büttler, R., Kraus, D., Krumm, F., Lachat, T., Michel, A.K., Regnery, B. & Vandekerckhove, K. (2018). Tree related microhabitats in temperate and Mediterranean European forests: A hierarchical typology for inventory standardization. *Ecological Indicators*, 84, 194–207. <https://doi.org/10.1016/j.ecolind.2017.08.051>

Lassau, S.A., Hochuli, D.F., Cassis, G. & Reid, C.A.M. (2005). Effects of habitat complexity on forest beetle diversity: do functional groups respond consistently? *Diversity and Distributions*, 11 (1), 73–82. <https://doi.org/10.1111/j.1366-9516.2005.00124.x>

Lassaue, A., Paillet, Y., Jactel, H. & Bouget, C. (2011). Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecological Indicators*, 11 (5), 1027–1039. <https://doi.org/10.1016/j.ecolind.2011.02.004>

Lawrence, J.F. & Newton, A. (1995). Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names), Biology, Phylogeny, and Classification of Coleoptera. In: *Papers Celebrating the 80th Birthday of Roy A. Crowson*. 779–1092.

Lennon, J.J., Koleff, P., Greenwood, J.J.D. & Gaston, K.J. (2001). The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology*, 70 (6), 966–979. <https://doi.org/10.1046/j.0021-8790.2001.00563.x>

Linder, P. & Östlund, L. (1992). Förändringar i norra Sveriges skogar 1870-1991. *Svensk botanisk tidsskrift*, 86, 199–215

Linder, P. & Östlund, L. (1998). Structural changes in three mid-boreal Swedish forest landscapes, 1885–1996. *Biological Conservation*, 85 (1–2), 9–19. [https://doi.org/10.1016/S0006-3207\(97\)00168-7](https://doi.org/10.1016/S0006-3207(97)00168-7)

Lindhe, A. & Lindelöw, Å. (2004). Cut high stumps of spruce, birch, aspen and oak as breeding substrates for saproxylic beetles. *Forest Ecology and Management*, 203 (1–3), 1–20. <https://doi.org/10.1016/j.foreco.2004.07.047>

Lindhe, A., Lindelöw, Å. & Åsenblad, N. (2005). Saproxylic Beetles in Standing Dead Wood Density in Relation to Substrate Sun-exposure and Diameter. *Biodiversity and Conservation*, 14 (12), 3033–3053. <https://doi.org/10.1007/s10531-004-0314-y>

- Long, J.A. (2022). *jtools: Analysis and Presentation of Social Scientific Data*. Version 2.2.0. <https://cran.r-project.org/package=jtools>
- Lüdecke, D. (2023). *sjPlot: Data Visualization for Statistics in Social Science*. Version 2.8.15. <https://CRAN.R-project.org/package=sjPlot>
- Mac Arthur, R.H. & Wilson, E.O. (1967). *The Theory of Island Biogeography*. Princeton University Press. <http://www.jstor.org/stable/j.ctt19cc1t2>
- Martikainen, P., Siitonen, J., Punttila, P., Kaila, L. & Rauh, J. (2000). Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. *Biological Conservation*, 94 (2), 199–209. [https://doi.org/10.1016/S0006-3207\(99\)00175-5](https://doi.org/10.1016/S0006-3207(99)00175-5)
- Mery, G., Katila, P., Galloway, G., Alfaro, R.I., Kanninen, M., Lobovikov, M. & Varjo, J. (ed.) (2010). *Forests and society: responding to global drivers of change*. International Union of Forest Research Organizations. (IUFRO world series; v. 25)
- Müller, J. & Büttler, R. (2010). A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. *European Journal of Forest Research*, 129 (6), 981–992. <https://doi.org/10.1007/s10342-010-0400-5>
- Müller, J., Thorn, S., Baier, R., Sagheb-Talebi, K., Hassan V, B., Seibold, S., Ulyshen, M.D. & Gossner, M.M. (2016). Protecting the Forests While Allowing Removal of Damaged Trees may Imperil Saproxyllic Insect Biodiversity in the Hyrcanian Beech Forests of Iran: Protecting the forests. *Conservation Letters*, 9 (2), 106–113. <https://doi.org/10.1111/conl.12187>
- Müller, K. & Wickham, H. (2023). *tibble: Simple Data Frames*. Version 3.2.1. <https://CRAN.R-project.org/package=tibble>
- Nilsson, S.G. (1997). Forests in the Temperate–boreal Transition—Natural and Man-made Features. *Ecological Bulletins*, 1997 (46), 61–71. https://doi.org/10.1007/978-1-4615-3524-9_10
- Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O’Hara, R.B., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., Caceres, M.D., Durand, S., Evangelista, H.B.A., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M.O., Lahti, L., McGlenn, D., Ouellette, M.-H., Cunha, E.R., Smith, T., Stier, A., Braak, C.J.F.T. & Weedon, J. (2022). *vegan: Community Ecology Package*. Version 2.6-4. <https://CRAN.R-project.org/package=vegan>
- Olsson, J., Johansson, T., Jonsson, B.G., Hjältén, J., Edman, M. & Ericson, L. (2012). Landscape and substrate properties affect species richness and community composition of saproxyllic beetles. *Forest Ecology and Management*, 286, 108–120. <https://doi.org/10.1016/j.foreco.2012.08.033>
- Pedersen, T.L. (2023). *patchwork: The Composer of Plots*. Version 1.1.3. <https://CRAN.R-project.org/package=patchwork>

- Pilskog, H.E., Birkemoe, T., Evju, M. & Sverdrup-Thygeson, A. (2020). Species composition of beetles grouped by host association in hollow oaks reveals management-relevant patterns. *Journal of Insect Conservation*, 24 (1), 65–86. <https://doi.org/10.1007/s10841-019-00210-5>
- Pulliam, H.R. (2000). On the relationship between niche and distribution. *Ecology Letters*, 3 (4), 349–361. <https://doi.org/10.1046/j.1461-0248.2000.00143.x>
- R Core Team (2023). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. R version 4.3.1 (2023-06-16) -- "Beagle Scouts". <https://www.R-project.org/>
- Ranius, T., Niklasson, M. & Berg, N. (2009). Development of tree hollows in pedunculate oak (*Quercus robur*). *Forest Ecology and Management*, 257 (1), 303–310. <https://doi.org/10.1016/j.foreco.2008.09.007>
- Rieker, D., Krah, F.-S., Gossner, M.M., Uhl, B., Ambarli, D., Baber, K., Buscot, F., Hofrichter, M., Hoppe, B., Kahl, T., Kellner, H., Moll, J., Purahong, W., Seibold, S., Weisser, W.W. & Bässler, C. (2022). Disentangling the importance of space and host tree for the beta-diversity of beetles, fungi, and bacteria: Lessons from a large dead-wood experiment. *Biological Conservation*, 268, 109521. <https://doi.org/10.1016/j.biocon.2022.109521>
- Rubene, D., Wikars, L.-O. & Ranius, T. (2014). Importance of high quality early-successional habitats in managed forest landscapes to rare beetle species. *Biodiversity and Conservation*, 23 (2), 449–466. <https://doi.org/10.1007/s10531-013-0612-3>
- Runnel, K., Stephan, J.G., Jonsell, M., Kutser, K., Lõhmus, A., Strengbom, J., Tamm, H. & Ranius, T. (2021). Do different growth rates of trees cause distinct habitat qualities for saproxylic assemblages? *Oecologia*, 197 (3), 807–816. <https://doi.org/10.1007/s00442-021-05061-z>
- Sánchez-Bayo, F. & Wyckhuys, K.A.G. (2019). Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation*, 232, 8–27. <https://doi.org/10.1016/j.biocon.2019.01.020>
- Schiegg, K. (2000a). Are There Saproxylic Beetle Species Characteristic of High Dead Wood Connectivity? *Ecography*, 23 (5), 579–587
- Schiegg, K. (2000b). Effects of dead wood volume and connectivity on saproxylic insect species diversity. *Écoscience*, 7 (3), 290–298. <https://doi.org/10.1080/11956860.2000.11682598>
- Sebek, P., Vodka, S., Bogusch, P., Pech, P., Tropek, R., Weiss, M., Zimova, K. & Cizek, L. (2016). Open-grown trees as key habitats for arthropods in temperate woodlands: The diversity, composition, and conservation value of associated communities. *Forest Ecology and Management*, 380, 172–181. <https://doi.org/10.1016/j.foreco.2016.08.052>

Seibold, S., Bässler, C., Brandl, R., Fahrig, L., Förster, B., Heurich, M., Hothorn, T., Scheipl, F., Thorn, S. & Müller, J. (2017). An experimental test of the habitat-amount hypothesis for saproxylic beetles in a forested region. *Ecology*, 98 (6), 1613–1622. <https://doi.org/10.1002/ecy.1819>

Seibold, S. & Thorn, S. (2018). The Importance of Dead-Wood Amount for Saproxylic Insects and How It Interacts with Dead-Wood Diversity and Other Habitat Factors. I: Ulyshen, M.D. (red.) *Saproxylic Insects: Diversity, Ecology and Conservation*. Springer International Publishing. 607–637. https://doi.org/10.1007/978-3-319-75937-1_18

Seibold, S., Weisser, W.W., Ambarlı, D., Gossner, M.M., Mori, A.S., Cadotte, M.W., Haggé, J., Bässler, C. & Thorn, S. (2023). Drivers of community assembly change during succession in wood-decomposing beetle communities. *Journal of Animal Ecology*, 92 (5), 965–978. <https://doi.org/10.1111/1365-2656.13843>

Shannon, C.E., 1948. A Mathematical Theory of Communication. *The Bell System Technical Journal* 27, 379–423, 623–656.

Siitonen, J. (2001). Forest Management, Coarse Woody Debris and Saproxylic Organisms: Fennoscandian Boreal Forests as an Example. *Ecological Bulletins*, (49), 11–41

Siitonen, J., Martikainen, P., Punttila, P. & Rauh, J. (2000). Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. *Forest Ecology and Management*, 128 (3), 211–225. [https://doi.org/10.1016/S0378-1127\(99\)00148-6](https://doi.org/10.1016/S0378-1127(99)00148-6)

Siitonen, J. & Saaristo, L. (2000). Habitat requirements and conservation of *Pytho kolwensis*, a beetle species of old-growth boreal forest. *Biological Conservation*, 94 (2), 211–220. [https://doi.org/10.1016/S0006-3207\(99\)00174-3](https://doi.org/10.1016/S0006-3207(99)00174-3)

Similä, M., Kouki, J. & Martikainen, P. (2003). Saproxylic beetles in managed and seminatural Scots pine forests: quality of dead wood matters. *Forest Ecology and Management*, 174 (1–3), 365–381. [https://doi.org/10.1016/S0378-1127\(02\)00061-0](https://doi.org/10.1016/S0378-1127(02)00061-0)

Simpson, G.G. (1943). Mammals and the nature of continents. *American Journal of Science*, 241 (1), 1–31. <https://doi.org/10.2475/ajs.241.1.1>

Sippola, A., Siitonen, J. & Kallio, R. (1998). Amount and quality of coarse woody debris in natural and managed coniferous forests near the timberline in Finnish Lapland. *Scandinavian Journal of Forest Research*, 13 (1–4), 204–214. <https://doi.org/10.1080/02827589809382978>

SLU Artatabanken (2020). *Rödlistade arter i Sverige 2020 [Red-listed species in Sweden 2020] SLU Artatabanken* (in Swedish with English abstract) <https://www.artatabanken.se/globalassets/ew/subw/artd/6-publikationer/31.-rodlista-2020/rodlista-2020.pdf>

SLU Artdatabanken (2024). *Artfakta*. <https://artfakta.se>. (in Swedish).

Speight, M.C.D. (1989). *Saproxylic invertebrates and their conservation*. Council of Europe. (Nature and environment series; 42)

Statistics Sweden (2023). Land Use in Sweden 2020. 2023 (1). <https://www.scb.se/publikation/48948>

Stenbacka, F., Hjältén, J., Hilszczański, J., Dysenius, M., 2010. Saproxylic and non-saproxylic beetle assemblages in boreal spruce forests of different age and forestry intensity. *Ecological Applications* 20 (8), 2310–2321.

Stier, A.C., Geange, S.W., Hanson, K.M. & Bolker, B.M. (2013). Predator density and timing of arrival affect reef fish community assembly. *Ecology*, 94 (5), 1057–1068. <https://doi.org/10.1890/11-1983.1>

Sutherland, W.J., Freckleton, R.P., Godfray, H.C.J., Beissinger, S.R., Benton, T., Cameron, D.D., Carmel, Y., Coomes, D.A., Coulson, T., Emmerson, M.C., Hails, R.S., Hays, G.C., Hodgson, D.J., Hutchings, M.J., Johnson, D., Jones, J.P.G., Keeling, M.J., Kokko, H., Kunin, W.E., Lambin, X., Lewis, O.T., Malhi, Y., Mieszkowska, N., Milner-Gulland, E.J., Norris, K., Phillimore, A.B., Purves, D.W., Reid, J.M., Reuman, D.C., Thompson, K., Travis, J.M.J., Turnbull, L.A., Wardle, D.A. & Wiegand, T. (2013). Identification of 100 fundamental ecological questions. Gibson, D. (ed.) (*Journal of Ecology*, 101 (1), 58–67. <https://doi.org/10.1111/1365-2745.12025>

Sveaskog. *Stormen Hans drabbade Sveaskog hårt* [The storm Hans severely affected Sveaskog]. (In Swedish) <https://www.sveaskog.se/press-och-media/stormen-hans-drabbade-sveaskog-hart/> [2024-01-18].

Sverdrup-Thygeson, A., Gustafsson, L. & Kouki, J. (2014). Spatial and temporal scales relevant for conservation of dead-wood associated species: current status and perspectives. *Biodiversity and Conservation*, 23 (3), 513–535. <https://doi.org/10.1007/s10531-014-0628-3>

Swedish Environmental Protection Agency. *Swedish environmental objectives*. <https://www.naturvardsverket.se/en/om-miljoarbetet/swedish-environmental-objectives/> [2024-01-29]

Swedish Forest Agency <https://www.skogsstyrelsen.se/en/> [2024-01-18]

Swedish Forest Agency (2020). *Levande träd och buskar med naturvärden. Målbilder för god miljöhänsyn* [Living trees and shrubs with natural values. Guide for how to select habitat trees good environmental concern] (in Swedish). <https://www.skogsstyrelsen.se/globalassets/mer-om-skog/malbilder-for-god-miljohansyn/malbilder-trad-och-buskar-med-naturvarden-samt-dod-ved/levande-buskar-och-trad-med-naturvarden--exempel-2020.pdf>

Swedish Meteorological and Hydrological Institute (SMHI). *Maps of normal meteorological variables 1991-2020* (in Swedish). <http://www.smhi.se/data/meteorologi/kartor> [2023-10-13]

Swedish National Forest Inventory. *Fältinstruktion 2023 - Riksinventeringen av skog [Field instruction 2023 - National inventory of forest]* (2023) . <https://www.slu.se/en/Collaborative-Centres-and-Projects/the-swedish-national-forest-inventory/>

Sørensen, T. (1948). A Method of Establishing Groups of Equal Amplitude in Plant Sociology Based on Similarity of Species Content and its Application to Analyses of the Vegetation on Danish Commons. *Det Kongelige Danske Videnskabernes Selskab Biologiske Skrifter*, 5 (4)

Thorn, S., Seibold, S., Leverkus, A.B., Michler, T., Müller, J., Noss, R.F., Stork, N., Vogel, S. & Lindenmayer, D.B. (2020). The living dead: acknowledging life after tree death to stop forest degradation. *Frontiers in Ecology and the Environment*, 18 (9), 505–512. <https://doi.org/10.1002/fee.2252>

Timonen, J., Siitonen, J., Gustafsson, L., Kotiaho, J.S., Stokland, J.N., Sverdrup-Thygeson, A. & Mönkkönen, M. (2010). Woodland key habitats in northern Europe: concepts, inventory and protection. *Scandinavian Journal of Forest Research*, 25 (4), 309–324. <https://doi.org/10.1080/02827581.2010.497160>

UN Department of Economic and Social Affairs. *Goal 15 | Department of Economic and Social Affairs*. <https://sdgs.un.org/goals/goal15> [2024-01-29]

Van Wagner, C.E. (1982). *Practical Aspects of the Line Intersect Method*. Petawawa National Forestry Institute.

Van Wagner, C.E. & Wilson, A.L. (1976). Diameter Measurement in the Line Intersect Method. *Forest Science*, 22 (2), 230–232

Vanha-Majamaa, I., Lilja, S., Ryömä, R., Kotiaho, J.S., Laaka-Lindberg, S., Lindberg, H., Puttonen, P., Tamminen, P., Toivanen, T. & Kuuluvainen, T. (2007). Rehabilitating boreal forest structure and species composition in Finland through logging, dead wood creation and fire: The EVO experiment. *Forest Ecology and Management*, 250 (1–2), 77–88. <https://doi.org/10.1016/j.foreco.2007.03.012>

Villéger, S., Grenouillet, G. & Brosse, S. (2013). Decomposing functional β -diversity reveals that low functional β -diversity is driven by low functional turnover in European fish assemblages: Decomposing functional β -diversity. *Global Ecology and Biogeography*, 22 (6), 671–681. <https://doi.org/10.1111/geb.12021>

Wagner, D.L., 2020. Insect Declines in the Anthropocene. *Annu. Rev. Entomol.* 65, 457–480. <https://doi.org/10.1146/annurev-ento-011019-025151>

- Weslien, J., Djupström, L.B., Schroeder, M. & Widenfalk, O. (2011). Long-term priority effects among insects and fungi colonizing decaying wood: Species interactions during wood decay. *Journal of Animal Ecology*, 80 (6), 1155–1162. <https://doi.org/10.1111/j.1365-2656.2011.01860.x>
- Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30, 279–338.
- Wickham, H. (2007). Reshaping Data with the reshape Package. *Journal of Statistical Software*, 21 (12), 1–20
- Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. <https://ggplot2.tidyverse.org>
- Wickham, H. (2022). *stringr: Simple, Consistent Wrappers for Common String Operations*. Version 1.5.0. <https://CRAN.R-project.org/package=stringr>
- Wickham, H., François, R., Henry, L., Müller, K. & Vaughan, D. (2023a). *dplyr: A Grammar of Data Manipulation*. Version 1.1.3. <https://CRAN.R-project.org/package=dplyr>
- Wickham, H., Vaughan, D. & Girlich, M. (2023b). *tidyr: Tidy Messy Data*. Version 1.3.0. <https://CRAN.R-project.org/package=tidyr>
- Wikars, L.-O., Sahlin, E. & Ranius, T. (2005). A comparison of three methods to estimate species richness of saproxylic beetles (Coleoptera) in logs and high stumps of Norway spruce. *The Canadian Entomologist*, 137 (3), 304–324. <https://doi.org/10.4039/n04-104>
- Yan, L. (2023). *ggvenn: Draw Venn Diagram by "ggplot2"*. Version 0.1.10. <https://CRAN.R-project.org/package=ggvenn>
- Økland, B., Bakke, A., Hågvar, S. & Kvamme, T. (1996). What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. *Biodiversity and Conservation*, 5 (1), 75–100. <https://doi.org/10.1007/BF00056293>
- Östlund, L., Zackrisson, O. & Axelsson, A.-L. (1997). The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Canadian Journal of Forest Research*, 27 (8), 1198–1206. <https://doi.org/10.1139/x97-070>

Popular science summary

Biodiversity, the variety of all the different organisms living in a given area, plays a crucial role in maintaining healthy ecosystems. To be able to conserve ecosystems we need to understand the processes that maintain a high biodiversity. This study delves into the biodiversity of beetles residing in pine forests in northern Sweden. Beetles contribute to nutrient recycling by decomposing dead material, and they serve as an important food source for other animals.

Two key factors influencing beetle diversity are habitat limitation and dispersal limitation. Habitat limitation is determined by the availability and diversity of structures and substrates, such as dead wood, that many forest-dwelling beetles rely on. Dispersal limitation means that beetles will not colonize new areas if suitable habitats are too far apart.

In Sweden, much of the forest is managed using clear-cut forestry in which entire sections of forests are harvested at once. It is known that clear-cut forestry can be harmful for the diversity of beetles. It is, however, unclear to what extent this is because the regular removal of trees, disrupting the tree continuity, causes dispersal limitation or because the new forests emerging after harvest are missing essential structures, causing habitat limitation.

In this study, beetles were trapped in twenty different forests, half of which had been clear-cut and half of which had not. The beetles were then studied to identify which species they belonged to. The amount and variation of dead wood and so-called habitat trees (old or large trees with special structures) was measured in the same forests. By selecting sites with varying levels of availability and variety of dead wood and habitat trees, the study aimed to distinguish between the effects of disrupting tree continuity and losing habitat structures.

The findings revealed that for an individual forest a high amount and variation of habitats on living or dead wood was more important for beetle diversity than if or how long ago the forest was harvested. But collectively, forests that had not been clear-cut exhibited a broader range of species than those that had been clear-cut. The species present only in forests that have not been clear-cut could for example require specific types of habitats that are more common in forests that have not been clear-cut. Clear-cut forests that now had been allowed to grow older and denser had fewer beetles, but had a distinct beetle community.

To be able to sustain a diverse beetle community in the managed forests in northern Sweden, the study suggests that the forests that have not been clear-cut should be preserved and that a sufficiently large and consistent input of dead wood should be maintained.

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Appendix 1 – Supplementary information

Table S1. Equations used to calculate dead wood volume. DBH, diameter at breast height (130 cm).

Equation	Usage	Explanation	Reference	Notes
$V = \frac{k}{L} \sum d^2$	Lying dead wood	V , volume in m ³ /ha; k , constant 1.234; L , length of the transect in meters; d , diameter in cm of each wood piece where it intersects with the line transect	(Van Wagner 1982)	For simplicity dead wood pieces were assumed to be horizontal; the tilt of dead wood pieces was during the survey observed to be negligible in most cases. Ground slope was also not considered and should only have a minor impact on the dead wood calculations.
$V = 10^{-1.20914} \times d^{1.94740} \times (d + 20.0)^{-0.05947} \times h^{1.40958} \times (h - 1.3)^{-0.45810}$	Standing dead pine (height ≥ 4 m)	V , volume in dm ³ ; d , DBH in cm; h , height in meters	(Brandel 1990)	Gives the volume above the stump and hence slightly underestimates the wood volume. The volume was added for each stand and divided by

$$V = 10^{-0.79783} \times d^{2.07157} \times (d + 20.0)^{-0.73882} \times h^{3.16332} \times (h - 1.3)^{-1.82622}$$

$$V = 10^{-0.84627} \times d^{2.23818} \times (d + 20.0)^{-1.06930} \times h^{6.02015} \times (h - 1.3)^{-4.51472}$$

$$V = h\pi \frac{d^2}{2}$$

				the area of the band transects (0.225 hectare) to get the estimated volume for each stand in m ³ /ha.
Standing dead spruce (height ≥ 4 m)	V , volume in dm ³ ; d , DBH in cm; h , height in meters	(Brandel 1990)	See above.	
Standing dead birch and goat willow (height ≥ 6 m)	V , volume in dm ³ ; d , DBH in cm; h , height in meters	(Brandel 1990)	See above.	
Standing dead wood below the heights indicated above, stumps	V , volume in dm ³ ; h , height in dm; d , diameter in dm	Volume of a cylinder	Diameter: for standing dead wood, DBH; for stumps, average diameter. The volume was added for each stand and divided by the area of the band transects (0.225 hectare) to get the estimated volume for each stand in m ³ /ha.	

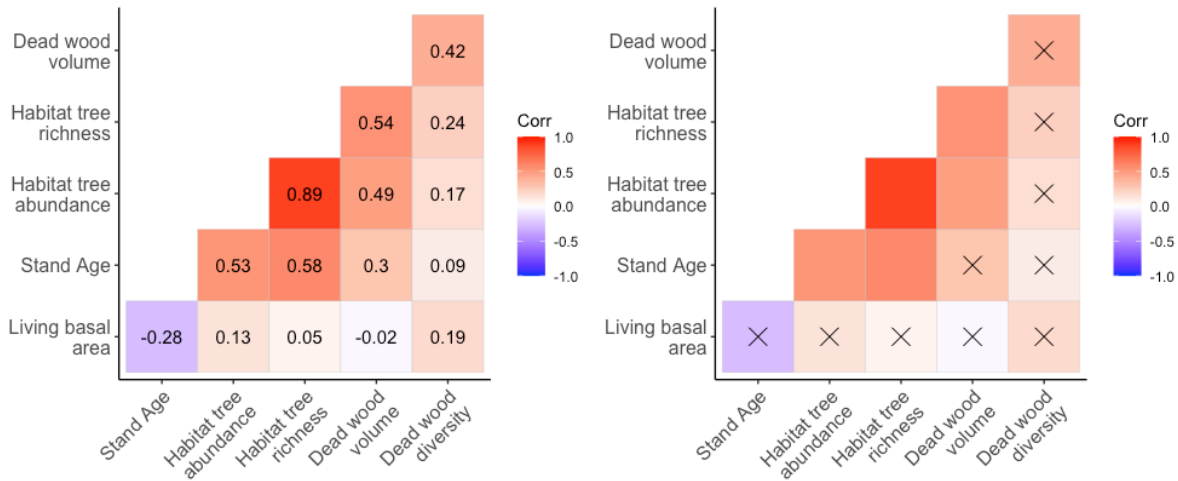


Figure S1. Correlation matrices of stand age and structural complexity variables used in multiple linear regression models. Left panel shows the Pearson correlation coefficient (r) and the right panel crosses out the correlations that are **not** statistically significant at $\alpha = 0.05$.

Table S2. Identified multiple linear regression models of abundance, richness, and diversity of beetles collected using flight intercept traps in boreal pine forests in northern Sweden. S.E., standard error; d.f., degrees of freedom; AICc, Akaike information criterion adjusted for small sample sizes. Models marked in red have the lowest AICc. Those models are together with the models marked in blue, which are within two AICc units of the models with the lowest AICc, included in the results. AICc cannot be compared between models with different sample size, AICc is compared independently in such cases. Letters in parentheses (a-h) indicate between which models AICc was compared.

Dependent variable	Predictors	Estimate	S.E.	p	d.f.	AICc
Beetle abundance (a)	Intercept	548.289	107.219	7.26e-05	18	244.7146
	Basal area	-11.210	4.928	0.0354		
Beetle abundance (a)	Intercept	191.4141	59.9247	0.00503	18	245.3389
	Stand age	1.0608	0.5022	0.04889		
Beetle abundance (b)	Intercept	286.5124	109.1639	0.02000	14	216.8992
	Habitat tree abundance	38.9426	11.4467	0.00429		
	Basal area	-0.3720	5.0851	0.94271		
	Habitat tree abundance: Basal area	-1.6259	0.5135	0.00686		
Beetle abundance (b)	Intercept	299.613	111.873	0.01801	14	217.8287
	Habitat tree richness	92.101	30.755	0.00965		
	Basal area	-1.148	5.229	0.82945		

	Habitat tree richness: Basal area	-3.750	1.429	0.02004		
Beetle abundance (b)	Intercept	354.002	128.596	0.0148	15	220.4547
	Dead wood diversity	100.748	50.157	<u>0.0629</u>		
	Basal area	-11.629	5.114	0.0381		
Beetle abundance (b)	Intercept	468.378	107.991	0.000586	15	221.1026
	Habitat tree richness	12.966	7.072	<u>0.086643</u>		
	Basal area	-9.176	5.003	<u>0.086528</u>		
Beetle abundance (b)	Intercept	333.5352	82.8999	0.00126	14	223.7362
	Stand age	-0.5552	0.8722	0.53465		
	Habitat tree richness	-37.2518	25.8671	0.17182		
	Stand age: Habitat tree richness	0.3838	0.2112	<u>0.09058</u>		
Beetle richness (c)	Intercept	40.53000	10.70165	0.0020	14	133.2909
	Habitat tree abundance	3.00785	1.12215	0.0179		
	Basal area	-0.13574	0.49851	0.7894		
	Habitat tree abundance: Basal area	-0.11555	0.05034	0.0377		
Beetle richness (c)	Intercept	38.608	3.192	1.83e-09	16	134.8495
	Habitat tree richness	1.345	0.684	<u>0.0669</u>		
Beetle richness (c)	Intercept	39.0163	3.0747	9.12e-10	16	134.9855
	Habitat tree abundance	0.4216	0.2188	<u>0.0719</u>		
Beetle richness (c)	Intercept	52.95060	7.34881	4.53e-06	14	136.5048
	Habitat tree richness	-2.91600	2.29303	0.2242		
	Stand age	-0.16216	0.07732	<u>0.0546</u>		
	Habitat tree richness: Stand age	0.03990	0.01872	<u>0.0512</u>		
Beetle diversity (d)	Intercept	28.95033	3.60789	2.35e-07	18	132.9402

Beetle diversity (e)	Stand age	-0.06042	0.03024	<u>0.061</u>		
	Intercept	20.92011	3.87387	7.36e-05	15	114.7117
Beetle diversity (e)	Stand age	-0.05034	0.02501	<u>0.0624</u>		
	Dead wood diversity	0.66174	0.29608	0.0411		
	Intercept	27.13163	3.14487	3.36e-07	15	115.4139
Beetle diversity (e)	Stand age	-0.08236	0.03119	0.0185		
	Habitat tree richness	0.94731	0.46060	<u>0.0575</u>		
Beetle diversity (e)	Intercept	15.6652	3.1232	0.000127	16	115.6531
	Dead wood diversity	0.6061	0.3217	<u>0.077857</u>		
Beetle diversity (e)	Intercept	26.95523	3.18817	4.33e-07	15	115.9990
	Stand age	-0.07613	0.03053	0.0248		
	Habitat tree abundance	0.27316	0.14367	<u>0.0766</u>		
Beetle diversity (e)	Intercept	8.78262	4.84345	<u>0.0913</u>	14	119.0885
	Dead wood diversity	1.28507	0.52747	0.0288		
	Dead wood volume	0.87253	0.47918	<u>0.0901</u>		
	Dead wood diversity: Dead wood volume	-0.07737	0.04299	<u>0.0935</u>		
Beetle diversity (e)	Intercept	10.6034	4.1849	0.0239	14	119.3028
	Dead wood diversity	1.2389	0.4862	0.0232		
	Habitat tree richness	1.6921	1.0058	0.1147		
	Dead wood diversity: Habitat tree richness	-0.1916	0.1087	<u>0.0997</u>		
Saproxylic beetle abundance (f)	Intercept	69.7446	38.7576	<u>0.0887</u>	18	227.9085
	Stand age	0.8637	0.3248	0.0160		
Saproxylic beetle abundance (f)	Intercept	323.851	73.915	0.00036	18	229.8360
	Basal area	-7.417	3.397	0.04250		
Saproxylic beetle abundance (g)	Intercept	140.888	23.417	1.8e-05	16	207.7899
	Dead wood volume	2.852	1.492	<u>0.074</u>		

Saproxylic beetle diversity (h)	Intercept	17.74861	2.70948	3.72e-06	18	121.4856
	Stand age	-0.04230	0.02271	<u>0.0789</u>		
Saproxylic beetle diversity (i)	Intercept	16.96102	2.55352	7.85e-06	15	107.9152
	Stand age	-0.06213	0.02532	0.0268		
	Habitat tree richness	0.70549	0.37399	<u>0.0788</u>		

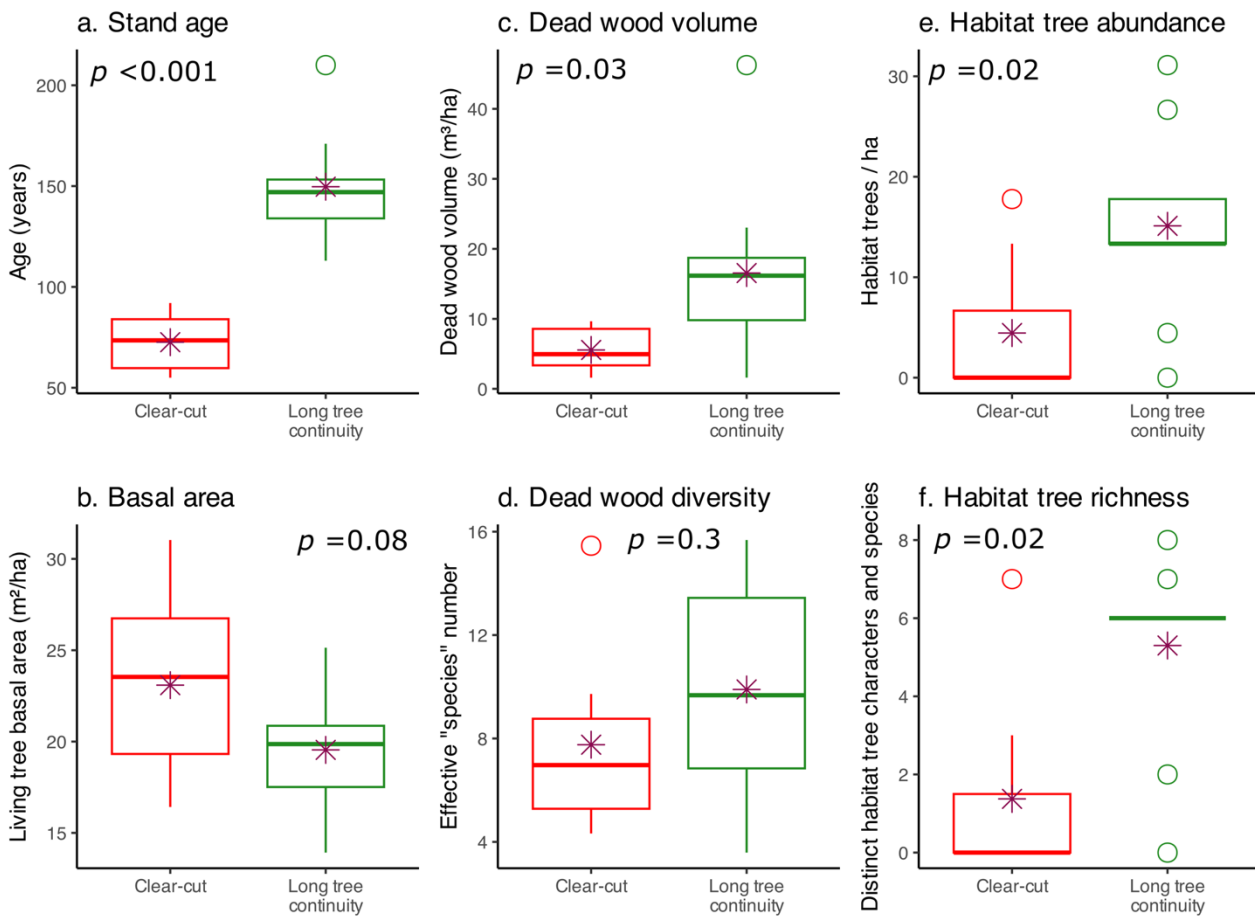


Figure S2. Stand age and forest structural complexity variables in forest stands with long tree continuity and forest stands that have been clear-cut. The asterisk indicates the mean. The p-values from the t-tests are indicated. Dead wood survey was not possible in two of the clear-cut stands due to wind damage.

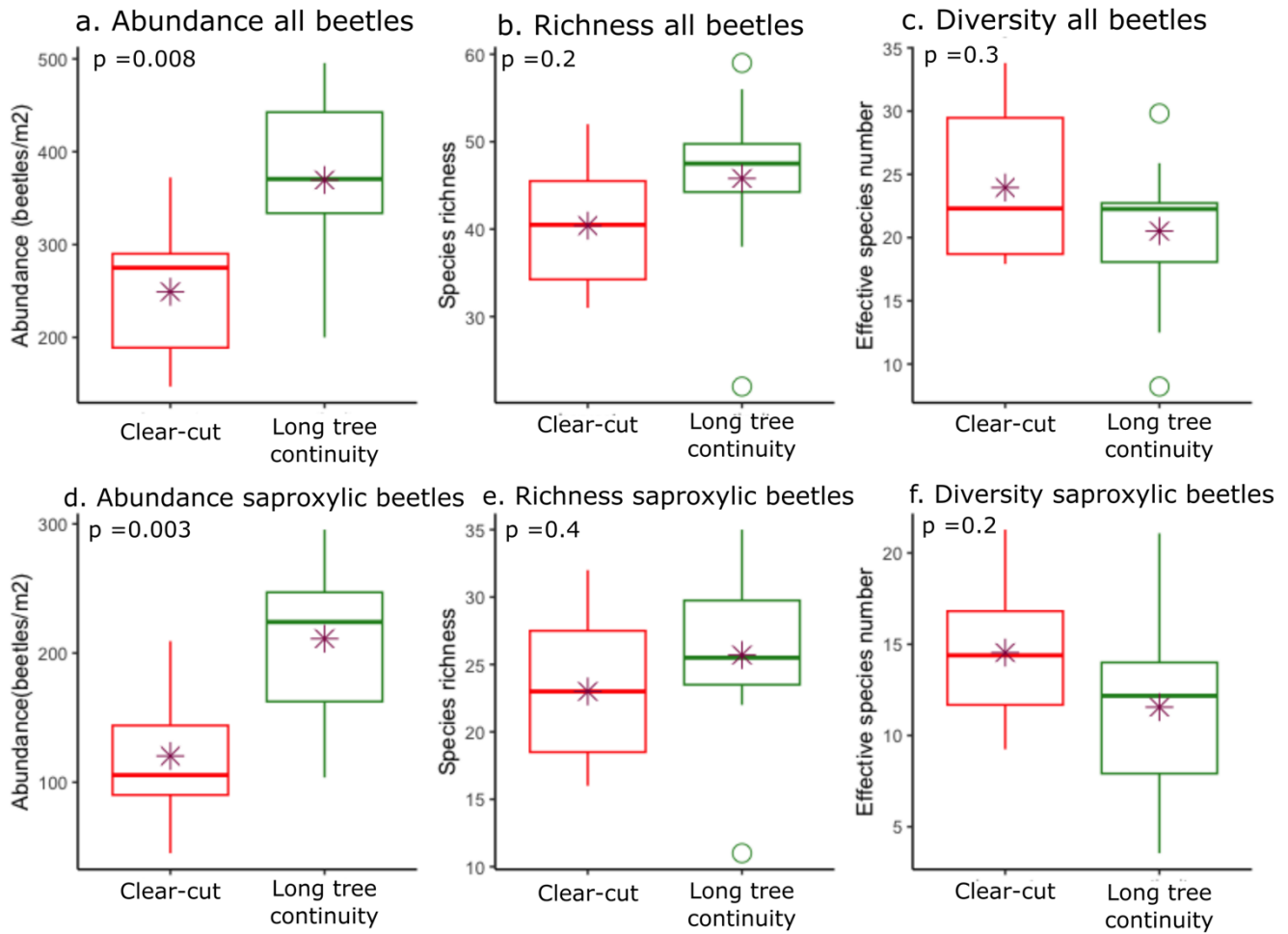
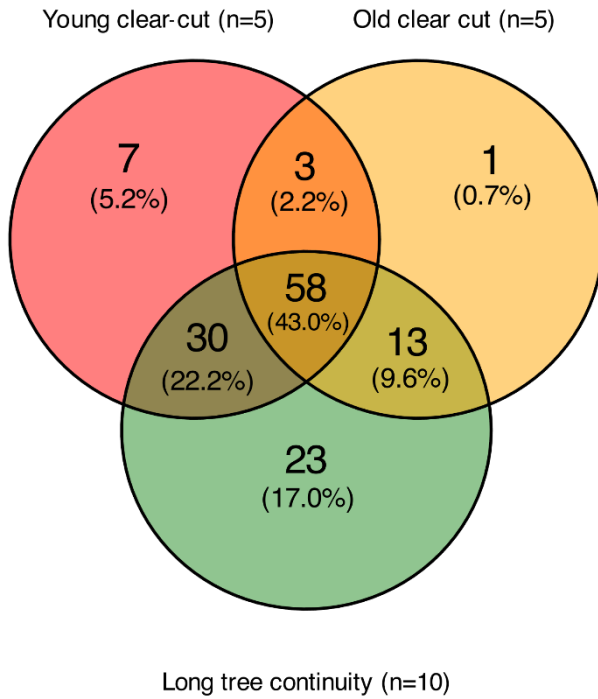


Figure S3. Abundance per catch effort (per m² of trap window), richness and diversity of beetles in forest stands with long tree continuity and forest stands that have been clear-cut. The asterisk indicates the mean. The p-values from the t-tests are indicated.

a. All beetle species (without singletons)



b. Saproxylic beetle species (singletons removed)

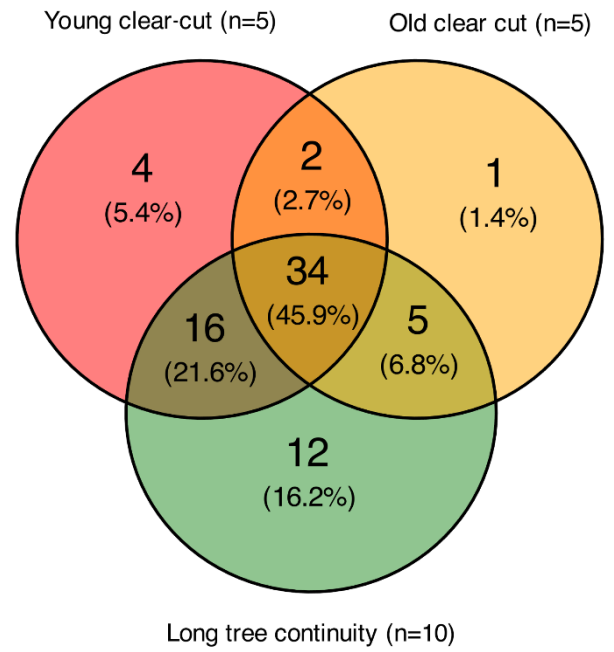


Figure S4. Venn diagrams showing the occurrence of beetle species in forest stands with long tree continuity (mean 150 years) and forest stands that have been clear-cut. The clear-cut stands are divided into young (mean 61 years) and old clear-cuts (mean 78 years). Species only present once in the data set (singletons) have been removed.

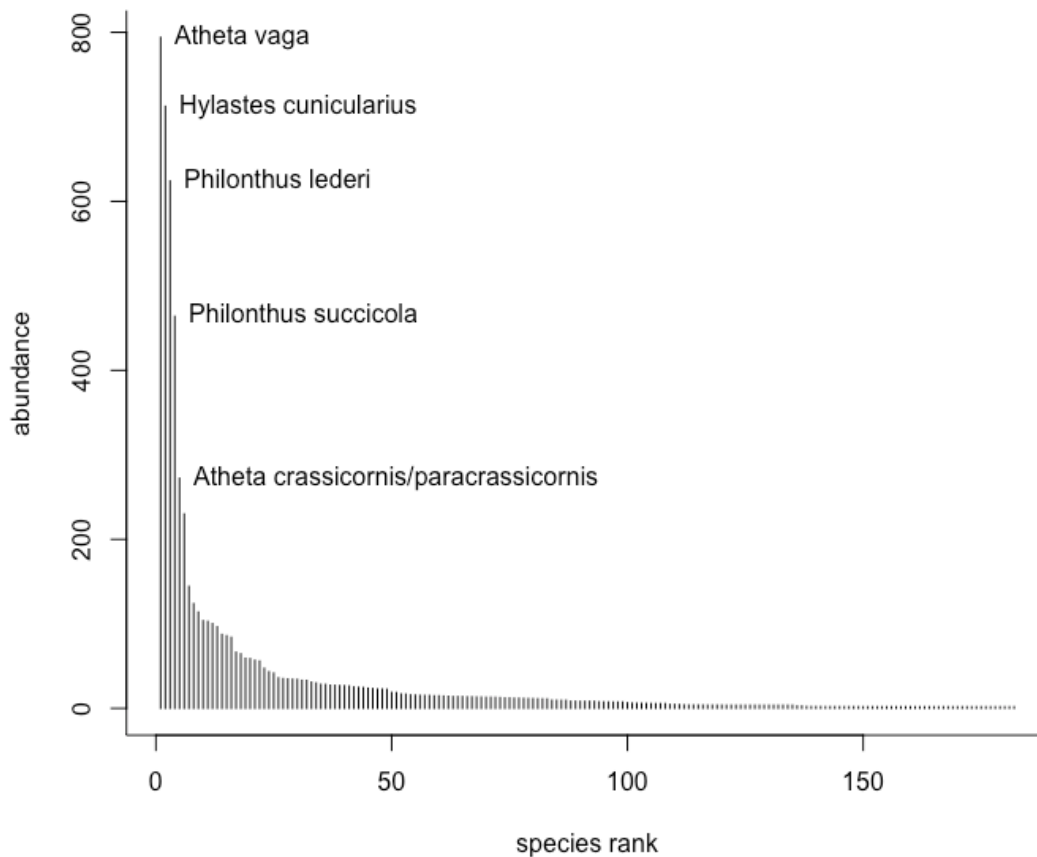


Figure S5. Rank abundance curve of all beetle species collected across all sites. The species names of the five most abundant species are shown. Abundance per catch effort (per m² of trap window).

Table S3. Test results from *t*-tests and analyses of variance (ANOVA) of beta diversity and the turnover and nestedness components. All beetle species and saproxylic beetle species are tested separately. CC, clear-cut; YCC, young clear-cut; OCC, old clear-cut; LTC, long tree continuity.

Turnover all beetle species					
t-test (CC vs LTC)	Degrees of freedom	Mean CC	Mean LTC	t-value	<i>p</i>
	17.709	0.3441355	0.3620991	0.6426	0.5287
ANOVA (YCC vs OCC vs LTC)					
	Degrees of freedom	Sum of Squares	Mean Square	F-value	<i>p</i>
Stand types	2	0.011496	0.0057478	1.165	0.3356
Residuals	17	0.083876	0.0049339		
Nestedness all beetle species					
t-test (CC vs LTC)	Degrees of freedom	Mean CC	Mean LTC	t-value	<i>p</i>
	12.999	0.04217057	0.04109769	0.057262	0.9552

ANOVA (YCC vs OCC vs LTC)	Degrees of freedom	Sum of Squares	Mean Square	F-value	<i>p</i>
Groups	2	0.000401	0.00020049	0.1002	0.9052
Residuals	17	0.034013	0.00200074		
Total beta diversity all beetle species					
t-test (CC vs LTC)	Degrees of freedom	Mean CC	Mean LTC	t-value	<i>p</i>
	13.172	0.3835307	0.4053422	0.63036	0.5392
ANOVA (YCC vs OCC vs LTC)	Degrees of freedom	Sum of Squares	Mean Square	F-value	<i>p</i>
Groups	2	0.01557	0.0077850	1.1402	0.343
Residuals	17	0.11607	0.0068277		
Turnover saproxylic beetle species					
t-test (CC vs LTC)	Degrees of freedom	Mean CC	Mean LTC	t-value	<i>p</i>
	17.151	0.3604069	0.3475838	0.3365	0.7406
ANOVA (YCC vs OCC vs LTC)	Degrees of freedom	Sum of Squares	Mean Square	F-value	<i>p</i>
Groups	2	0.00545	0.0027250	0.3628	0.701
Residuals	17	0.12768	0.0075109		
Nestedness saproxylic beetle species					
t-test (CC vs LTC)	Degrees of freedom	Mean CC	Mean LTC	t-value	<i>p</i>
	15.852	0.05484996	0.05091673	0.21491	0.8326
ANOVA (YCC vs OCC vs LTC)	Degrees of freedom	Sum of Squares	Mean Square	F-value	<i>p</i>
Groups	2	0.0004597	0.00022987	0.1347	0.8749
Residuals	17	0.0290074	0.00170632		
Total beta diversity saproxylic beetle species					
t-test (CC vs LTC)	Degrees of freedom	Mean CC	Mean LTC	t-value	<i>p</i>
	16.788	0.4108242	0.3952141	0.36203	0.7218
ANOVA (YCC vs OCC vs LTC)	Degrees of freedom	Sum of Squares	Mean Square	F-value	<i>p</i>
Groups	2	0.006837	0.0034186	0.3196	0.7307
Residuals	17	0.181850	0.0106971		

Table S4. Environmental vectors from the NMDS analysis. The analysis of all beetle species and saproxylic species was done separately.

All beetle species				
Environmental variable	NMDS1	NMDS2	r ²	p
Dead wood volume	0.87148	-0.49042	0.0634	0.620
Habitat tree abundance	0.10278	-0.99470	0.0560	0.683
Stand age	0.79749	-0.60334	0.2686	<u>0.076</u>
Basal area	-0.99997	0.00835	0.3737	0.030
Habitat tree richness	0.24354	-0.96989	0.1438	0.310
Standing dead wood volume	0.84913	-0.52818	0.0578	0.655
Lying dead wood volume	0.85139	-0.52453	0.0491	0.685
Stump volume	0.03417	0.99942	0.0477	0.714
Dead wood volume with signs of fire	-0.58120	0.81376	0.1489	0.281
Dead pine wood volume	0.99945	-0.03325	0.0598	0.646
Dead spruce volume	0.77062	-0.63730	0.1743	0.247
Dead birch wood volume	-0.09874	-0.99511	0.2914	<u>0.061</u>
Dead wood volume with decay class 1	0.85253	-0.52267	0.0379	0.753
Dead wood volume with decay class 2	0.61865	-0.78566	0.1494	0.298
Dead wood volume with decay class 3	0.93173	-0.36315	0.0454	0.707
Dead wood volume with decay class 4	0.05853	0.99829	0.0664	0.567
Dead wood diversity	-0.26626	-0.96390	0.0949	0.483
Saproxylic beetle species				
Environmental variable	NMDS1	NMDS2	r ²	p
Dead wood volume	0.82600	-0.56367	0.1123	0.398
Habitat tree abundance	-0.22979	-0.97324	0.0955	0.458
Stand age	0.52601	-0.85048	0.2145	0.168
Basal area	-0.99644	0.08428	0.4147	0.023
Habitat tree richness	-0.22201	-0.97504	0.1562	0.258
Standing dead wood volume	0.89383	-0.44841	0.0907	0.477

Lying dead wood volume	0.77968	-0.62617	0.0882	0.480
Stump volume	0.98287	-0.18432	0.0025	0.983
Dead wood volume with signs of fire	-0.45866	0.88861	0.0986	0.462
Dead pine wood volume	0.98697	-0.16089	0.0926	0.481
Dead spruce volume	0.55632	-0.83097	0.0720	0.571
Dead birch wood volume	-0.10200	-0.99478	0.3360	<u>0.051</u>
Dead wood volume with decay class 1	0.88788	-0.46007	0.0676	0.576
Dead wood volume with decay class 2	0.42084	-0.90713	0.1758	0.233
Dead wood volume with decay class 3	0.89088	-0.45424	0.1063	0.427
Dead wood volume with decay class 4	0.47003	0.88265	0.0344	0.769
Dead wood diversity	-0.26951	-0.96300	0.0989	0.455

Table S5. Indicator species from the NMDS analysis. Only statistically significant species ($p < 0.05$) are shown. The analysis of all beetle species and saproxylic species was done separately.

All beetle species

Young clear-cut (mean 61 years)		
Species	Test statistic	p
<i>Anisotoma humeralis</i>	0.845	0.015
<i>Sphaerites glabratus</i>	0.775	0.030
<i>Cis comptus</i>	0.725	0.030
Old clear-cut (mean 78 years)		
Species	Test statistic	p
<i>Anthonomus phyllocola</i>	0.803	0.025
<i>Gnathoncus buyssoni</i>	0.796	0.010
<i>Rhizophagus fenestralis</i>	0.776	0.030
<i>Melanotus castanipes</i>	0.676	0.035
Long tree continuity (mean 150 years)		
Species	Test statistic	p
<i>Rhagonycha atra</i>	0.791	0.025
<i>Anaspis arctica</i>	0.790	0.045
Young + old clear-cut		
Species	Test statistic	p

<i>Protaetia cuprea</i>	0.92	0.005
<i>Athous subfuscus</i>	0.84	0.030
Young clear-cut + long tree continuity		
Species	Test statistic	p
<i>Hylastes cunicularius</i>	0.943	0.050
<i>Malthodes sp.</i>	0.922	0.015
<i>Gabrius expectatus</i>	0.872	0.030
Saproxyllic beetle species		
Young clear-cut (mean 61 years)		
Species	Test statistic	p
<i>Anisotoma humeralis</i>	0.845	0.010
<i>Malthodes sp.</i>	0.836	0.045
<i>Cis comptus</i>	0.725	0.035
Old clear-cut (mean 78 years)		
Species	Test statistic	p
<i>Gnathoncus buyssoni</i>	0.796	0.005
<i>Rhizophagus fenestralis</i>	0.776	0.035
<i>Melanotus castanipes</i>	0.676	0.025
Long tree continuity (mean 150 years)		
Species	Test statistic	p
<i>Anaspis arctica</i>	0.79	0.045
Young clear-cut + long tree continuity		
Species	Test statistic	p
<i>Hylastes cunicularius</i>	0.943	0.025
<i>Gabrius expectatus</i>	0.872	0.050

Appendix 2 – Species list

Table S6. List of beetle species collected using flight intercept traps in boreal pine forests in northern Sweden. Species list as after the pooling and exclusion adjustments outlined in Materials and Methods. Species are in taxonomic order. Red-list status, ecological guild, and abundance in respective stand. YCC, young clear-cut (mean age 61 years, n = 5); OCC, (old clear-cut mean age 78 years, n = 5); LTC, long tree continuity (mean age 150 years, n = 10).

Family name [†]	Species name including author [†]	Red-list status [‡]	Ecological guild [§]	YCC1 ^a	YCC2 ^a	YCC3 ^e	YCC4 ^a	YCC ^a	OCC ^b	OCC2 ^b	OCC3 ^a	OCC4 ^b	OCC5 ^b	LTC1 ^e	LTC2 ^a	LTC3 ^a	LTC4 ^a	LTC5 ^c	LTC6 ^a	LTC7 ^a	LTC8 ^a	LTC9 ^d	LTC10 ^a
Carabidae	<i>Dromius agilis</i> (Fabricius, 1787)	LC	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Hydrophilidae	<i>Cercyon tristis</i> (Illiger, 1801)	LC	G	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphaeritidae	<i>Sphaerites glabratus</i> (Fabricius, 1792)	LC	G	0	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Histeridae	<i>Plegaderus vulneratus</i> (Panzer, 1797)	LC	S	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Gnathoncus buyssoni</i> Auzat, 1917	LC	S	2	0	0	0	0	1	4	0	5	3	0	0	0	0	2	1	0	0	0	0
	<i>Margarinotus striola</i> (Sahlberg, 1819)	LC	G	0	0	0	1	1	1	0	1	0	0	0	1	2	0	0	0	0	0	0	0
Ptiliidae	<i>Acrotichis</i> sp. Motschulsky, 1848	LC	G	0	0	0	0	0	0	0	0	2	0	0	0	1	1	0	0	1	0	0	0
Leiodidae	<i>Agathidium seminulum</i> (Linnaeus, 1758)	LC	S	0	1	0	0	0	1	0	0	0	1	0	2	1	0	0	0	0	0	1	0
	<i>Anisotoma axillaris</i> Gyllenhal, 1810	LC	S	4	0	5	5	4	0	0	2	0	2	2	0	0	2	6	1	3	5	0	0
	<i>Anisotoma castanea</i> (Herbst, 1792)	LC	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0

Silphidae
Staphylinidae

<i>Anisotoma glabra</i> (Kugelann, 1794)	LC	S	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	
<i>Anisotoma humeralis</i> (Fabricius, 1792)	LC	S	1	3	1	2	5	0	0	0	0	0	0	5	0	0	1	2	1	0	1	
<i>Catops alpinus</i> Gyllenhal, 1827	LC	G	0	1	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0	2	1	1
<i>Catops tristis</i> (Panzer, 1793)	LC	G	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Sciodrepoides alpestris</i> Jeannel, 1934	LC	G	0	1	0	1	0	0	0	2	0	0	0	0	0	1	0	0	1	0	0	0
<i>Sciodrepoides watsoni</i> (Spence, 1815)	LC	G	3	4	0	1	1	1	4	2	5	0	0	7	0	2	1	4	1	15	2	0
<i>Nicrophorus vespilloides</i> Herbst, 1783	LC	G	1	0	0	0	0	2	1	1	1	0	0	0	2	0	0	1	4	0	0	1
<i>Stenichnus godarti</i> (Latreille, 1806)	LC	S	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Anthophagus omalinus</i> Zetterstedt, 1828	LC	G	0	0	0	5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Olophrum fuscum</i> (Gravenhorst, 1806)	LC	G	2	3	0	0	0	0	0	0	0	0	0	5	0	0	3	8	0	2	0	0
<i>Omalius rivulare</i> (Paykull, 1789)	LC	G	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	1	0	0
<i>Omalius septentrionis</i> Thomson, 1857	LC	G	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0
<i>Omalius strigicolle</i> Wankowicz, 1869	LC	G	0	1	0	0	0	0	0	0	0	1	0	1	3	0	0	0	0	0	0	0
<i>Megarthus depressus</i> (Paykull, 1789)	LC	G	0	2	0	0	0	1	0	2	0	0	0	0	0	0	0	2	0	1	0	0
<i>Megarthus nitidulus</i> Kraatz, 1857	LC	G	0	3	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Euplectus</i> sp. Leach, 1817	-	?	0	0	0	1	1	0	0	2	0	0	1	0	0	1	0	0	0	0	0	0
<i>Bryoporus cernuus</i> (Gravenhorst, 1806)	LC	G	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Lordithon lunulatus</i> (Linnaeus, 1760)	LC	S	2	4	0	2	0	1	0	3	0	0	9	3	2	0	0	4	0	3	2	0
<i>Lordithon speciosus</i> (Erichson, 1839)	LC	S	0	1	0	0	0	1	0	2	1	0	0	9	10	1	0	7	1	10	1	0
<i>Mycetoporus piceolus</i> Rey, 1883	NA 2000- 2015	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Sepedophilus immaculatus</i> (Stephens, 1832)	LC	G	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
<i>Sepedophilus littoreus</i> (Linnaeus, 1758)	LC	S	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Tachinus basalis</i> * Erichson, 1839	DD 2000- 2005	G	0	2	0	1	0	3	0	1	3	0	0	1	0	0	0	0	3	1	0	0
<i>Tachinus laticollis</i> Gravenhorst, 1802	LC	G	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tachinus pallipes</i> (Gravenhorst, 1806)	LC	G	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0
<i>Aleochara moerens</i> Gyllenhal, 1827	LC	G	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	<i>Anomognathus cuspidatus</i> (Erichson, 1839)	LC	S	1	0	0	0	1	0	0	1	0	2	0	1	0	3	0	0	0	2	1	0
	<i>Atheta brunneipennis</i> (Thomson, 1852)	LC	?	0	0	1	2	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0
	<i>Atheta corvina</i> (Thomson, 1856)	LC	G	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
	<i>Atheta crassicornis</i> (Fabricius, 1793) / <i>Atheta paracrassicornis</i> Brundin, 1954	-	G	14	2	3	5	5	2	5	1	6	6	0	4	9	17	8	14	7	9	12	12
	<i>Atheta graminicola</i> (Gravenhorst, 1806)	LC	G	0	1	1	0	0	0	0	0	0	0	2	1	0	1	0	0	1	0	0	0
	<i>Atheta harwoodi</i> Williams, 1930	LC	G	0	0	0	0	0	0	1	0	0	0	4	0	0	0	0	0	0	2	0	0
	<i>Atheta intermedia</i> (Thomson, 1852)	LC	G	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	4
	<i>Atheta nesslingi</i> Bernhauer, 1928	LC	G	0	0	0	0	0	1	0	0	0	4	0	1	0	0	0	0	0	0	1	0
	<i>Atheta picipes</i> (Thomson, 1856)	LC	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
	<i>Atheta vaga</i> Heer, 1839	LC	S	10	24	16	15	50	3	13	14	7	4	39	42	24	18	12	21	14	55	11	4
	<i>Dinaraea aequata</i> (Erichson, 1837)	LC	S	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
	<i>Oxypoda alternans</i> (Gravenhorst, 1802)	LC	G	4	2	0	5	0	0	0	0	2	0	0	2	1	4	0	0	32	1	7	0
	<i>Oxypoda opaca</i> (Gravenhorst, 1802)	LC	G	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Scaphisoma agaricinum</i> (Linnaeus, 1758)	LC	S	1	0	0	0	0	0	1	0	1	2	0	0	0	0	0	2	0	0	0	0
	<i>Atrecus pilicornis</i> (Paykull, 1790)	LC	S	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
	<i>Bisnius puella</i> (Nordmann, 1837)	LC	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0
	<i>Gabrius expectatus</i> Smetana, 1952	LC	S	1	1	2	1	2	0	0	1	0	0	4	0	1	1	6	5	0	1	0	1
	<i>Philonthus lederi</i> Eppelsheim, 1893	LC	?	8	32	10	16	13	22	14	15	4	5	5	15	52	8	10	1	48	19	18	7
	<i>Philonthus succicola</i> Thomson, 1860	LC	G	4	27	2	24	5	8	32	14	3	4	2	11	37	3	9	3	18	9	13	14
	<i>Quedionuchus glaber</i> (O. Müller, 1776)	LC	S	0	2	0	1	0	0	0	0	0	0	0	2	1	0	1	1	1	1	1	0
	<i>Quedius mesomelinus</i> (Marsham, 1802)	LC	S	0	1	0	0	0	2	1	1	2	0	0	0	0	0	1	1	0	0	0	3
	<i>Quedius tenellus</i> (Gravenhorst, 1806)	LC	G	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
	<i>Xantholinus linearis</i> (Olivier, 1794)	LC	G	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Lucanidae	<i>Platycerus caprea</i> (De Geer, 1774)	NT 2000	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Scarabaeidae	<i>Acrossus depressus</i> (Kugelann, 1792)	LC	G	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
	<i>Acrossus rufipes</i> (Linnaeus, 1758)	LC	G	0	0	1	0	0	0	0	0	2	0	0	0	2	0	0	0	0	0	0	1
	<i>Agoliinus piceus</i> (Gyllenhal, 1808)	LC	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

	<i>Planolinoides borealis</i> (Gyllenhal, 1827)	LC	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1		
	<i>Protaetia cuprea</i> (Fabricius, 1775)	NE 2010	G	2	3	2	2	3	1	2	2	6	1	0	2	0	0	2	2	1	2	0	0
Scirtidae	<i>Contacyphon coarctatus</i> (Paykull, 1799)	LC	G	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	
	<i>Contacyphon padi</i> (Linnaeus, 1758)	LC	G	0	1	1	0	2	0	0	0	0	0	0	0	3	2	5	0	0	0	0	
	<i>Microcara testacea</i> (Linnaeus, 1767)	LC	G	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	
Throscidae	<i>Trixagus dermestoides</i> (Linnaeus, 1767)	LC	G	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Elateridae	<i>Athous subfuscus</i> (Müller, 1764)	LC	G	5	0	4	0	1	4	9	4	3	4	0	2	2	0	0	2	0	0	4	
	<i>Denticollis borealis</i> (Paykull, 1800)	NT 2000- 2020	S	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
	<i>Denticollis linearis</i> (Linnaeus, 1758)	LC	S	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	2	0	
	<i>Diacanthous undulatus</i> (De Geer, 1774)	NT 2000, 2010	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	
	<i>Eanus costalis</i> (Paykull, 1800)	LC	?	9	3	4	5	0	0	2	1	4	1	2	6	3	10	4	2	1	6	0	0
	<i>Liotrichus affinis</i> (Paykull, 1800)	LC	G	0	0	0	0	0	0	0	0	0	0	0	0	3	1	0	0	0	0	0	
	<i>Orithales serraticornis</i> (Paykull, 1800)	LC	G	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Paraphotistus impressus</i> (Fabricius, 1792)	LC	G	0	0	2	0	2	0	0	0	2	0	0	0	2	0	0	0	0	0	1	
	<i>Ampedus balteatus</i> (Linnaeus, 1758)	LC	S	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Ampedus nigrinus</i> (Herbst, 1784)	LC	S	6	1	0	1	1	1	0	2	2	1	3	1	0	4	0	2	3	2	0	0
	<i>Ampedus tristis</i> (Linnaeus, 1758)	LC	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	
	<i>Sericus brunneus</i> (Linnaeus, 1758)	LC	G	8	0	0	0	0	0	0	0	1	0	0	2	0	1	1	1	0	2	0	0
	<i>Melanotus castanipes</i> (Paykull, 1800)	LC	S	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	
Lycidae	<i>Dictyoptera aurora</i> (Herbst, 1784)	LC	S	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2	1	0	0	0
Cantharidae	<i>Cantharis obscura</i> Linnaeus, 1758	LC	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	
	<i>Podabrus alpinus</i> (Paykull, 1798)	LC	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
	<i>Podistra rufotestacea</i> (Letzner, 1845)	LC	G	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	1	0	0	
	<i>Podistra schoenherri</i> (Dejean, 1837)	LC	G	3	17	2	14	3	1	11	1	5	5	0	3	2	6	1	3	14	14	14	0
	<i>Rhagonycha atra</i> (Linnaeus, 1767)	LC	G	0	1	0	0	0	0	0	0	0	0	1	2	3	0	3	2	1	4	0	
	<i>Rhagonycha elongata</i> (Fallén, 1807)	LC	G	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	0	0	0	0	

	<i>Malthinus biguttatus</i> (Linnaeus, 1758)	LC	G	4	0	0	1	0	0	0	1	0	0	0	2	0	0	2	0	0	6	2	0
	<i>Malthinus flaveolus</i> (Herbst, 1786)	LC	S	0	0	0	0	1	0	0	0	0	3	0	0	0	0	0	0	1	0	0	0
	<i>Malthodes sp.</i> Kiesenwetter, 1852	-	G	14	4	3	3	10	1	0	0	0	0	0	6	3	4	3	1	2	16	5	0
Dermestidae	<i>Dermestes murinus</i> Linnaeus, 1758	LC	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Ptinidae	<i>Dorcatoma robusta</i> Strand, 1938	LC	S	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Lymexylidae	<i>Elateroides dermestoides</i> (Linnaeus, 1760)	LC	S	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Cleridae	<i>Thanasimus formicarius</i> (Linnaeus, 1758)	LC	S	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dasytidae	<i>Aplocnemus tarsalis</i> (Sahlberg, 1822)	LC	?	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
	<i>Dasytes plumbeus</i> (Müller, 1776)	LC	S	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
Nitidulidae	<i>Eपुरaea aestiva</i> (Linnaeus, 1758)	LC	G	0	0	0	0	0	0	0	0	0	0	0	0	4	0	4	0	0	0	0	0
	<i>Eपुरaea boreella</i> (Zetterstedt, 1828)	LC	S	0	0	0	0	2	0	0	2	0	2	2	3	1	3	0	0	0	2	0	0
	<i>Eपुरaea silacea</i> (Herbst, 1783)	LC	S	0	2	1	0	1	0	0	2	0	1	0	1	2	2	1	0	1	0	0	0
	<i>Eपुरaea unicolor</i> (Olivier, 1790)	LC	S	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Cychramus variegatus</i> (Herbst, 1792)	LC	S	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Nitidula bipunctata</i> (Linnaeus, 1758)	LC	G	1	0	0	0	0	0	0	0	0	1	1	0	1	3	2	0	3	0	0	0
	<i>Omosita depressa</i> (Linnaeus, 1758)	LC	G	0	3	0	0	0	1	0	2	2	0	0	0	1	1	1	0	0	1	0	1
	<i>Soronia grisea</i> (Linnaeus, 1758)	LC	S	0	0	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0
	<i>Soronia punctatissima</i> (Illiger, 1794)	LC	S	1	1	1	0	0	0	2	3	0	1	0	1	0	0	0	1	1	1	0	0
	<i>Thalycra fervida</i> (Olivier, 1790)	LC	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Glischrochilus hortensis</i> (Geoffroy, 1785)	LC	S	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Glischrochilus quadripunctatus</i> (Linnaeus, 1758)	LC	S	1	1	1	1	4	0	0	0	0	1	1	0	0	1	1	0	1	0	1	0
	<i>Pityophagus ferrugineus</i> (Linnaeus, 1760)	LC	S	0	0	1	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0
Monotomidae	<i>Rhizophagus dispar</i> (Paykull, 1800)	LC	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	<i>Rhizophagus fenestralis</i> (Linnaeus, 1758)	LC	S	0	0	0	0	1	1	3	3	0	2	0	0	1	0	1	0	0	1	0	1
	<i>Rhizophagus ferrugineus</i> (Paykull, 1800)	LC	S	2	0	3	1	0	0	4	1	0	0	0	4	4	1	2	1	2	2	1	0
Silvanidae	<i>Dendrophagus crenatus</i> (Paykull, 1799)	NT 2000	S	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
	<i>Silvanoprus fagi</i> (Guérin-Ménéville, 1844)	LC	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

Cucujidae	<i>Pediacus fuscus</i> Erichson, 1845	NT 2020	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Cryptophagidae	<i>Cryptophagus badius</i> Sturm, 1845	LC	S	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Cryptophagus lapponicus</i> Gyllenhal, 1827	LC	S	3	2	0	6	2	1	4	2	1	1	0	6	2	8	3	6	3	3	1	1
	<i>Cryptophagus scanicus</i> (Linnaeus, 1758)	LC	G	3	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
	<i>Atomaria sp.</i> Stephens, 1830	-	?	0	0	0	1	0	0	1	0	1	1	1	0	2	0	1	1	0	0	2	0
Erotylidae	<i>Dacne bipustulata</i> (Thunberg, 1781)	LC	S	0	1	1	0	1	0	0	0	0	0	1	0	0	0	1	0	2	0	0	0
	<i>Triplax aenea</i> (Schaller, 1783)	LC	S	0	0	0	2	1	0	0	2	0	0	1	0	0	0	1	0	1	3	1	1
	<i>Triplax russica</i> (Linnaeus, 1758)	LC	S	0	0	0	0	0	0	0	0	1	0	1	1	2	0	1	1	0	0	0	0
	<i>Triplax scutellaris</i> Charpentier, 1825	LC	S	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	3	0
Byturidae	<i>Byturus tomentosus</i> (De Geer, 1774)	LC	H	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Cerylonidae	<i>Cerylon ferrugineum</i> Stephens, 1830	LC	S	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
	<i>Cerylon histerooides</i> (Fabricius, 1792)	LC	S	0	1	0	0	0	2	6	0	1	0	0	1	0	0	3	0	0	0	3	0
Coccinellidae	<i>Nephus bisignatus*</i> (Boheman, 1850)	LC	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	0	0
	<i>Scymnus limbatus</i> Stephens, 1832	LC	G	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
	<i>Coccinella hieroglyphica</i> Linnaeus, 1758	LC	G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
	<i>Psyllobora vigintiduopunctata</i> (Linnaeus, 1758)	LC	G	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Latridiidae	<i>Enicmus rugosus</i> (Herbst, 1793)	LC	S	3	4	0	4	3	2	6	0	4	1	0	1	9	1	5	1	1	3	1	5
	<i>Latridius minutus</i> (Linnaeus, 1767)	LC	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
	<i>Stephostethus pandellei</i> (Brisout de Barneville, 1863)	LC	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
	<i>Corticaria gibbosa</i> (Herbst, 1793)	LC	G	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Mycetophagidae	<i>Mycetophagus multipunctatus</i> Fabricius, 1792	LC	S	0	1	1	1	0	0	0	1	0	0	0	2	0	2	3	0	0	6	0	0
Ciidae	<i>Cis bidentatus</i> (Olivier, 1790)	LC	S	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0
	<i>Cis boleti</i> (Scopoli, 1763)	LC	S	1	0	0	0	2	0	0	0	0	1	0	0	3	1	1	0	0	0	0	0
	<i>Cis comptus</i> Gyllenhal, 1827	LC	S	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
	<i>Cis micans</i> (Fabricius, 1792)	LC	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Orthocis alni</i> (Gyllenhal, 1813)	LC	S	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tetratomidae	<i>Tetratoma ancora</i> Fabricius, 1790	LC	S	2	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	

		NT 2000- 2010	S	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	
Melandryidae	<i>Hallomenus axillaris</i> (Illiger, 1807)		S	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	
	<i>Abdera affinis</i> (Paykull, 1799)	LC	S	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	
	<i>Orchesia micans</i> (Panzer, 1793)	LC	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
	<i>Xylita laevigata</i> (Hellenius, 1786)	LC	S	1	1	0	0	2	0	0	0	2	1	0	4	0	0	2	0	0	0	0	0
Mordellidae	<i>Curtimorda maculosa</i> (Naezen, 1794)	LC	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
	<i>Mordellistena humeralis</i> (Linnaeus, 1758)	NT 2010- 2020	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Pythidae	<i>Pytho depressus</i> (Linnaeus, 1767)	LC	S	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Pyrochroidae	<i>Schizotus pectinicornis</i> (Linnaeus, 1758)	LC	S	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Salpingidae	<i>Salpingus ruficollis</i> (Linnaeus, 1760)	LC	S	0	0	0	2	0	0	0	0	0	2	0	0	0	2	0	0	0	0	0	0
Scraptiidae	<i>Anaspis arctica</i> * Zetterstedt, 1828	LC	S	0	2	0	0	1	0	0	0	0	0	0	10	21	1	2	2	7	5	0	0
	<i>Anaspis frontalis</i> (Linnaeus, 1758)	LC	S	3	0	0	0	0	1	1	0	2	0	1	0	0	0	0	0	4	0	4	4
	<i>Anaspis marginicollis</i> Lindberg, 1925	LC	S	1	3	0	2	2	1	0	0	4	2	0	0	2	0	0	4	1	1	2	2
	<i>Anaspis rufilabris</i> (Gyllenhal, 1827)	LC	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Tenebrionidae	<i>Mycetochara flavipes</i> (Fabricius, 1792)	LC	S	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
	<i>Mycetochara obscura</i> (Zetterstedt, 1840)	NT 2000- 2010	S	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	1	0	0
Cerambycidae	<i>Rhagium inquisitor</i> (Linnaeus, 1758)	LC	S	0	0	0	0	1	0	1	1	0	0	0	0	1	1	1	0	0	0	2	0
	<i>Rhagium mordax</i> (De Geer, 1775)	LC	S	0	0	0	1	0	0	0	0	0	0	0	3	0	0	0	1	1	1	1	1
	<i>Molorchus minor</i> (Linnaeus, 1758)	LC	S	1	1	0	0	2	2	0	1	2	2	0	4	3	2	0	2	2	1	3	3
	<i>Pogonocherus decoratus</i> Fairmaire, 1855	LC	S	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	3	1	0	0	0
Chrysomelidae	<i>Crepidodera fulvicornis</i> (Fabricius, 1792)	LC	H	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
	<i>Lochmaea caprea</i> (Linnaeus, 1758)	LC	H	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
	<i>Cryptocephalus</i> sp. Müller, 1764	-	H	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Rhynchitidae	<i>Deporaus betulae</i> (Linnaeus, 1758)	LC	H	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Curculionidae	<i>Polydrusus tereticollis</i> (DeGeer, 1775)	LC	H	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Strophosoma capitatum</i> (De Geer, 1775)	LC	H	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0

<i>Anthonomus phyllocola</i> (Herbst, 1795)	LC	H	0	2	0	0	0	0	1	6	6	1	0	0	0	0	2	0	0	0	1	0	0
<i>Anthonomus rubi</i> (Herbst, 1795)	LC	H	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Tachyerges decoratus</i> (Germar, 1821)	LC	H	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Magdalis duplicata</i> Germar, 1819	LC	S	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
<i>Magdalis violacea</i> (Linnaeus, 1758)	LC	S	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hylobius abietis</i> (Linnaeus, 1758)	LC	S	0	2	4	1	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	1
<i>Pissodes gyllenhalii</i> (Sahlberg, 1834)	LC	S	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pissodes pini</i> (Linnaeus, 1758)	LC	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Crypturgus hispidulus</i> Thomson, 1870	LC	S	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Dryocoetes autographus</i> (Ratzeburg, 1837)	LC	S	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	3
<i>Hylastes cunicularius</i> Erichson, 1836	LC	S	3	14	25	3	5	1	0	0	2	7	0	19	22	3	48	93	12	4	73	17	
<i>Pityogenes bidentatus</i> (Herbst, 1783)	LC	S	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	0	0	0
<i>Pityogenes chalcographus</i> (Linnaeus, 1761)	LC	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Trypodendron lineatum</i> (Olivier, 1795)	LC	S	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0

* New record for the province of Pite Lappmark

† Taxonomic order as according to Biology, Phylogeny, and Classification of Coleoptera (Lawrence and Newton 1995) with names updated according to Artfakta (artfakta.se, SLU Artdatabanken 2024)

‡ LC, Least Concern; NT, Near Threatened; DD, Data Deficient; NA, Not Applicable. According to the Swedish red-list, updated every five years, most recently 2020 (SLU Artdatabanken 2020). When status departs from LC in any of the assessments from 2000-2020 the year(s) are indicated.

^ G, ground dwelling; H, herbivore; S, saproxylic; ?, not investigated/unclear. Guild division provided by Ass. Prof. Mats Jonsell (pers. com.).

Total area of window trap indicated as follows.

^a 0.54 m²

^b 0.51 m²

^c 0.48 m²

^d 0.45 m²

^e 0.36 m²

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