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From clear-cuts to nature reserves: saproxylic beetle diversity and deadwood availability in Norway spruce (*Picea abies* L.) stands in southern Sweden

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Abstract

Key message Norway spruce (*Picea abies* L.)-dominated production forests in southern Sweden had a significantly lower amount of deadwood and saproxylic beetle diversity compared to similar nature reserves, especially with regard to red-listed species. The species composition of beetles in reserves also differed from all young production forests. Enhanced conservation measures are essential to maintain biodiversity in production forests.

Context Forests are the most important biomes globally for biodiversity, and a high diversity in structures is important for species richness. In Sweden, 87% of the forest area is used for wood supply, which may affect forest structures and biodiversity.

Aims The aim of this study was to quantify the differences in the amount of deadwood and the saproxylic beetle diversity between typical *Picea abies* L. production forest stands of different ages and natural or near-natural forests.

Methods In the current study, we sampled saproxylic beetles and amount of deadwood in stands of spruce forests in southern Sweden that represent four different parts of the forestry cycle, and compare this with nearby, recently protected spruce dominated nature reserves. In addition, we also sampled five old forest reserves in the region.

Results The amount of deadwood was significantly higher in reserves than in production forests. In total, 478 saproxylic beetle species were caught and identified (in total 71,000 individuals). Overall, the highest species numbers were found in new and old reserves and 65–85-year-old production forests, while the lowest number was found in production forests of 15–25 and 35–45 years. The odds of finding nature value indicator species and red-listed species were significantly lower in all production forest types except 65–85-year-old ones compared to new nature reserves. This could be because clear-cutting practices did not become the main method for timber extraction until the early 1950s, meaning that some of the 60–85-year-old stands may never have been subjected to clear-cutting practices. However, old nature reserves had a clearly different composition regarding obligate saproxylic species, nature value indicators, and red-listed species compared to all production forest types.

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Conclusions The results bear relevance to the Swedish Forestry Act established in 1993, stating that the environmental goal and the goal of high wood production is equally important, since our forest types cover the period before and after. However, our results show that the 15–25-year-old forests are as species poor as the 35–45-year-old ones indicating that there was a lack of biologically important structures also after the change in policy.

Keywords Saproxylic beetles, Deadwood, Forestry, Nature reserves, Conservation, Fennoscandia

1 Introduction

Forests cover 31% of Earth's total land area (FAO &UNEP 2020) and are the most important biomes globally for biodiversity (Pan et al. 2013). A high biodiversity is crucial for functional forest ecosystems that can provide humanity with ecosystem services like e.g. food, wood, water supply and purification, carbon sequestration, medicine, and recreation (Orsi et al. 2020; Maier et al. 2021). Forest biodiversity is in turn linked to factors increasing structural complexity like age distribution, tree species diversity, dead and dying trees, and canopy openness (Hill et al. 2019). Globally, almost a third of the world's forests are managed primarily for production (FAO & UNEP 2020). In Europe, 75% of the forest area is used for wood supply (Forest Europe 2020) compared to 87% in Sweden (SCB 2019). Studies have shown that long periods of intensive forest management have created production forests structurally different from old growth forest (Esseen et al. 1997; Axelsson 2001). The use of forests in southern Sweden has a long and diverse history. Large areas of forest were historically used for grazing of livestock (Segerström and Emanuelsson 2002). In addition to that, especially the iron industry used large quantities of charcoal and wood. Both selective cutting and clear-cutting were used in the forests during this period (Axelsson and Angelstam 2011). After a long history of diverse forestry methods and forest uses, it was not until the 1950 s that Sweden began focusing on clear-cutting as the main forestry method (Kuuluvainen et al. 2012). A large proportion of the production forest thus consists of even-aged stands, with lower volumes of deadwood and less diverse structural elements compared to old growth forests (Siitonen 2001).

A high diversity in forest structures is probably the reason species richness is often higher in unmanaged forests compared to production forests (Paillet et al. 2010). One of the most important factors for biodiversity in forests is deadwood (Esseen et al. 1997; Grove 2002). Approximately 7500 forest species in Fennoscandia are saproxylic, i.e. dependent on deadwood, wood-inhabiting fungi, or on other saproxylic species during some part of their life cycle (Speight 1989; Stokland et al. 2012). Bauhus et al. (2018) estimates that 20–40% of all forest species are saproxylic and a recent study indicate even higher numbers, between 50 and 70%, within the three taxa Coleoptera, Arachnida, and Heteroptera (Graf et al. 2022). Several taxonomic groups have been used to compare biodiversity between production forests and old-growth forest including lichens (Nascimbene et al. 2013; Gustafsson et al 2025), fungi (Tomao et al. 2020), vascular plants (Widenfalk and Weslien 2009), bryophytes (Boudreault et al. 2018), and insects (Schowalter 2017). Saproxylic beetles compose a significant part of the boreal forest biodiversity and play a key role in forest dynamics since they contribute to decomposition of wood, nutrient cycling, and soil fertility (Grove 2002; Gutowski et al. 2005; McGeoch et al. 2007; Hardersen & Zapponi 2018), making them a suitable group for comparing species composition and diversity between forests.

The biodiversity of forests is a major part of the EU's biodiversity strategy for 2030. One part of the strategy is to develop closer-to-nature-forestry (Larsen et al. 2022). This management aims to improve diversity of tree species and structures including deadwood that is characteristics of natural forests (Larsen 2022). In the light of this, it is important to estimate the diversity in production forests to evaluate if forestry is in line with targets set. Swedish forestry has been taking steps to increase the diversity in production forests with several information campaigns about the importance of biodiversity in the early 1990s. They targeted forest owners and forestry officials after a period with many debates and conflicts over large-scale clear-cuts during the 1970s and 1980s (Simonsson et al. 2015).

With almost 90% of the forest area under management, it is important to understand how the composition and diversity of species differ between production stands of different ages and near-natural forests. In a meta-analysis of biodiversity differences between managed and unmanaged forests studies, comparisons were excluded between old growth forests and young production forests (Paillet et al. 2010). However, to understand the overall impact of forestry on biodiversity, it is important to also include younger production forests. Including typical younger forest stands established before and after the 1990 s also gives an opportunity to detect effects of the more environmentally friendly forestry practices that started in the 1990 s in Sweden (Simonsson et al. 2015). These practices included retention of forest elements during clear-cutting such as standing and downed dead trees, tree groups, and single trees of particular ecological value and small areas with valuable habitats. The effect of these management practices, where also production forest stands play a crucial role in conservation of biodiversity in forest landscapes, is largely untested (McGeoch et al. 2007).

The overall aim of this study was to compare habitat availability and species diversity between typical production forests of different ages and natural or near-natural reserves. Given that stand age and management history are intrinsically linked in Swedish production forestry, our design does not allow separation of age effects from management effects. However, it reflects the reality of Swedish forest landscapes where these factors are coupled, making our results directly applicable to current forest management decisions. We hypothesized that nature reserves would have higher diversity of (i) types of deadwood, (ii) saproxylic beetle species, (iii) red-listed species and nature value indicators, and that (iv) nature reserves would have larger volumes of deadwood and that (v) the composition of species will be different between the production forest stands and the nature reserves.

2 Material and methods

2.1 Study sites

A total of 30 forest stands were sampled in six sampling clusters. Six recently created (established between 2007 and 2017) nature reserves (NR) with *Picea abies* (L.)-dominated forests were sampled and within a 3-km radius of each reserve, four typical production stands of *P. abies* were sampled, one from each of the four age classes: 1–6 years (clear-cut), 15–25 years (young stands), 35–45 years (intermediate aged stands), and 65–85 years (mature stands) (Fig. 1). The 65–85-year-old stands in our study may have a history as uneven-aged forests while the other younger stands of production forests have been established after clear-cutting. All production stands are embedded in a matrix of similar production stands of different ages.

In addition, five long-established (between 1923 and 1945) nature reserves with *P. abies* dominated forest in the county were also sampled, resulting in a total of 35 stands sampled (Fig. 1).

2.2 Sampling design

Within each stand, beetles were sampled with five window traps (30×60 cm), hung 1.5 m above the ground. Each trap consisted of a transparent plexiglass sheet with a liquid-filled container underneath filled with a mix of water, propylene glycol, methylated spirits (to deter animal consumption), and detergent (to reduced surface tension).

Each trap was placed in spots where the habitat was representative for the specific stand and at least 25 m from the border of the stand, or other uncharacteristic habitat. Shrubs and twigs were removed from the

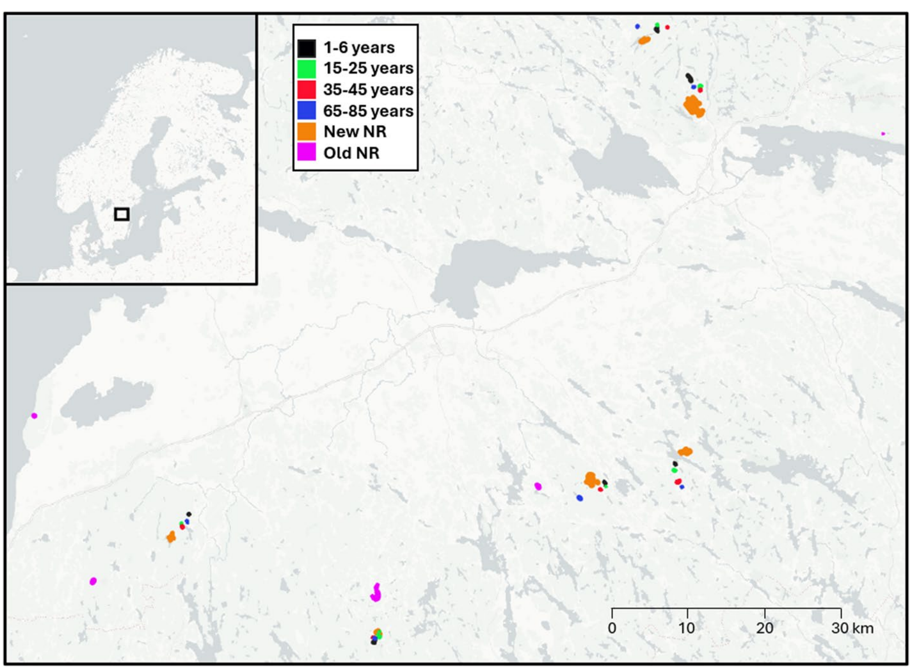

Fig. 1 Locations of the eleven study areas in Sweden, consisting of six sampling clusters with four production stands of different age and a newly established reserve within 3 km from each other and five single old reserves

immediate surrounding (4 m in diameter and 1.5 m in height) of the traps to make trap surroundings as similar as possible and with good flight conditions for beetles.

Traps were installed between 1 and 6 May 2020, emptied on two occasions (8–12 June and 13–18 July), at which point they were removed.

2.3 Species data

All beetles from the samples were sorted out and identified, the majority to the species level, but in some cases to the genus level. The saproxylic beetle species were assigned to three different classifications:

(i) Saproxylic species were classified into obligate saproxylic species, i.e. species that are exclusively dependent on deadwood or wood-inhabiting fungi or facultative saproxylic species, i.e. species that can complete some life stages on dead wood but are not strictly dependent on it;
(ii) Nature value indicator species, that we defined as species that at least at one point in time appeared on the Swedish red list;
(iii) Red-listed species, according to the current Swedish red-list (SLU Artdatabanken 2020).

2.4 Sampling of deadwood and diversity of deadwood

Eight 50 × 25 m sample plots (1 ha in total) were placed randomly within each stand. In each sampling plot all standing and lying deadwood objects > 10 cm in diameter and more than 1 m in length were recorded following Wijk (2016; 2017; 2019). For each object, diameter, tree species, height/length, and decay stage were recorded. The decay stage of the deadwood was recorded in five stages from fresh deadwood to strongly decayed deadwood (Swedish National Forest Inventory 2021).

The diameter was measured at 1.30 m, i.e. the diameter at breast height (dbh).

If standing deadwood was under 1.30 m but at least 0.50 m high with a diameter at the top of at least 10 cm, it was classified as a stump. The diameter of the stump was measured as close to the upper edge as possible, and the height was rounded up to 1 m if it was under 1 m.

A deadwood diversity index was calculated for each forest stand based on the number of unique combinations of deadwood characteristics. After excluding entries with unidentified substrate species, deadwood pieces were classified into three diameter size classes (0–20, 21–40, and > 40 cm) and two position types: standing deadwood (snags and stumps) and logs (fallen pieces). For logs, diversity was quantified as the number of unique combinations of diameter size class, decay stage, and tree species, while for standing deadwood, only diameter size class and tree species were considered. The total diversity score for each stand was the sum of log and standing deadwood diversity counts, providing a composite measure of both structural and compositional complexity of the deadwood assemblage.

2.5 Statistical analyses

To test the differences in deadwood amount between the six forest types, we used a generalized linear model (glm) with a normal distribution. The response variable (total amount of deadwood) was log-transformed and analysed in relation to forest type. Pair-wise comparisons between the six forest types were based on contrasts (function "glht" in R package "multcomp", Bretz et al. 2010).

To test the differences in deadwood diversity between the six forest types, we used a generalized linear model (glm) with a Poisson distribution. Pair-wise comparisons between the six forest types were based on contrasts (function "glht" in R package "multcomp", Bretz et al. 2010).

For the beetle data, we calculated the mean number of beetle species and mean number of individuals for the different forest types. Excluding data from the old reserves (as they are not located within the clusters of the production stands and the new reserves), we then calculated the ratio between the production stand and its corresponding nearby new nature reserve. These ratios were either expressed as response ratios (lnRR), or odds ratios (lnOR), with $CI_{95\%}$ and compared the phases in the forestry cycle with recent nature reserves, after adjusting for spatial structure in data.

Finally, we used principal component analysis (PCA) to describe how composition of saproxylic beetle species differed between different forest types. In addition, we conducted partial redundancy analysis (pRDA), using *Forest type*, *Deadwood volume*, and *Deadwood diversity* as explanatory variables and *Sampling cluster* as a covariable, excluding the old nature reserves. The three explanatory variables were tested separately but always together with *Sampling cluster*. We analysed the amount of compositional variation that could be explained by forest type, deadwood volume, and deadwood diversity (tested in permutation tests with 9999 permutations). As the forest type 1–6 years old had a distinct species community, analyses were done both with and without them to exclude that the differences were not only due to that. In both PCA and pRDA species, data was $\ln(x + 1)$-transformed.

3 Results

3.1 Species richness of saproxylic beetles and deadwood amount

A total of 70,948 beetle individuals of 478 saproxylic species were caught, out of which 329 species were obligate

Table 1 Outcome from pRDA (partial Redundancy Analysis) on different subsets of species data and effects of forest type, deadwood volume, and deadwood diversity. As the forest type 1–6 years had a distinct species community, analyses were done both with and without them. Data from old nature reserves were excluded, and spatial dependency in data accounted for by using "Sampling cluster" as covariable. NVI = nature value indicators, RL = Red listed species

		With 1–6		Without 1–6	
Species subset	Explanatory variable	Explained variance (%)	*P*-value	Explained variance (%)	*P*-value
ALL	DW diversity	8.7	0.0382	17.62	0.0014
ALL	DW volume	11.02	0.0164	21.63	0.0001
ALL	TYPE	56.79	0.0001	42.35	0.0001
Obligate	DW diversity	11.59	0.0024	14.36	0.0014
Obligate	DW volume	14.7	0.0002	17.29	0.0001
Obligate	TYPE	46.62	0.0001	35.76	0.0001
NVI	DW diversity	9.1	0.0023	13.07	0.001
NVI	DW volume	12.7	0.0001	17.26	0.0001
NVI	TYPE	29.19	0.0001	28.45	0.0002
RL	DW diversity	13.36	0.0036	21.38	0.0004
RL	DW volume	21.26	0.0001	29.65	0.0001
RL	TYPE	37.51	0.0001	39.42	0.0001

and 138 facultative (Table 1). Out of these, 24 were red-listed, and 75 were classified as nature value indicators. The number of species varied between 78 and 202 per stand and the number of individuals between 568 and 3757. The most common saproxylic species were *Quedius mesomelinus* (Marsh.) with 17,290 individuals, *Anaspis rufilabris* (Gyll.) (11,864) and *Dasytes plumbeus* (Müll.) (6727). A total of 117 species were found only in the nature reserves combining new and old reserves (in total 55 traps), whereas 56 species were unique for the production forest stands, combining 1–6-, 15–25-, 35–45-, and 65–85-year-old stands (in total 120 traps). Looking at individual forest types, new reserves had the largest number of unique species (42) followed by 1–6-year-old stands (27) and old reserves (14). The lowest number of unique species was found in 65–85-year-old stands (0), 15–25 years old (3) and 35–45 years old (7).

There was significantly more deadwood in the two types of nature reserves than in all of the production forest types (Fig. 2a). The lowest amount was found in

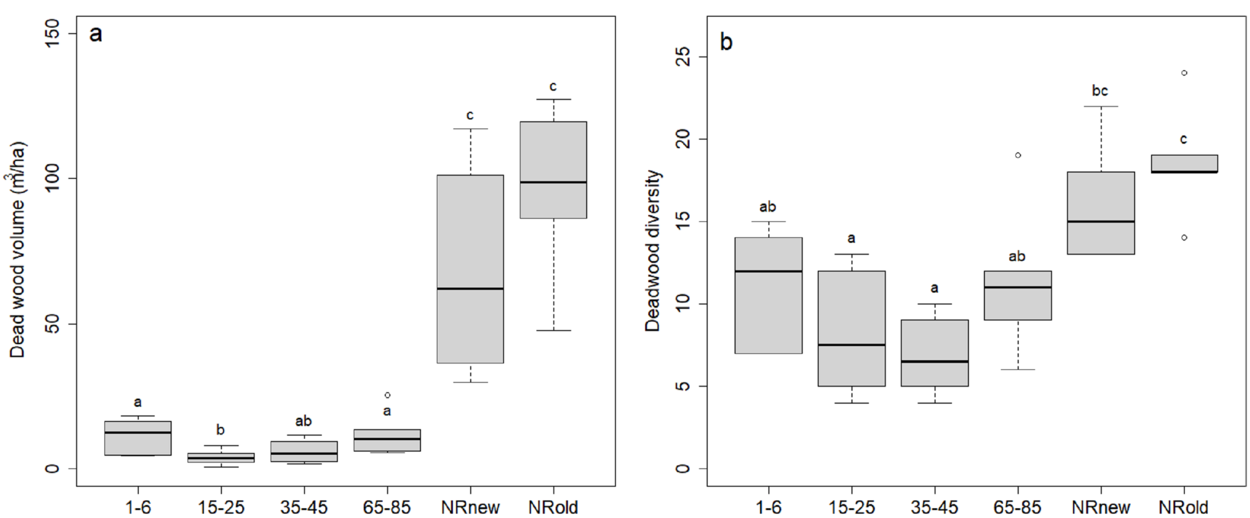

Fig. 2 **a** Mean volume of deadwood in managed forest stands of different age compared with newly established (NRnew) and old forest nature reserves (NRold), **b** mean deadwood diversity based on tree species, diameter and decay stage. Each boxplot displays the median (center line), first and third quartiles, range within 1.5 × IQR (whiskers), and outliers for each group. Different letters indicate statistical differences in deadwood volume between forest types based on pairwise comparisons

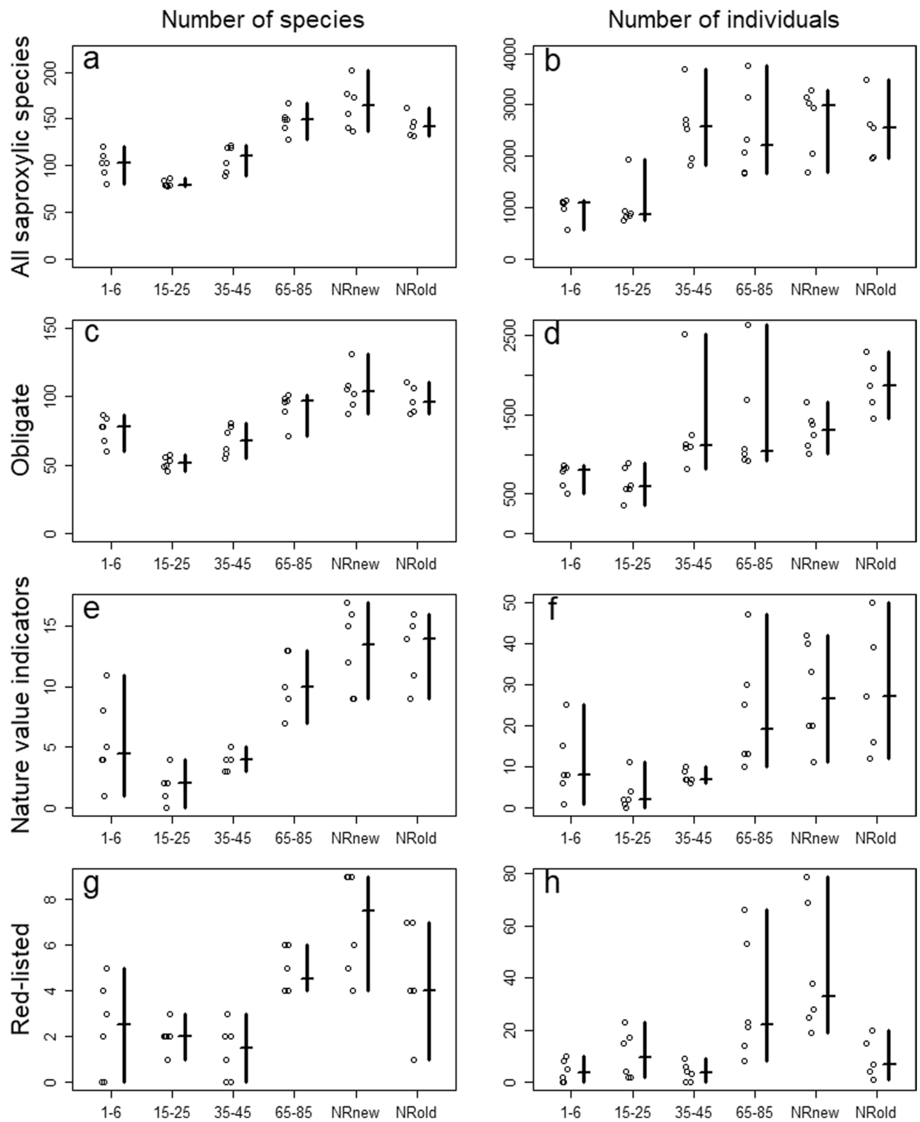

Fig. 3 Mean number and range of species and number of individuals for production forest stands of different age categories and newly established (NRnew) and old forest nature reserves (NRold)

production forests of 15–25 years. The deadwood diversity showed slightly different patterns with decreasing diversity from 1–6-year-old stands to the lowest in 35–45-year-old stands and with the highest diversity in old reserves (Fig. 2b).

3.2 Differences in species richness between production forests and reserves

Overall, for all species groups, the highest number of species was found in new and old reserves and 65–85-year-old stands, while the lowest number was found in 15–25- and 35–45-year-old stands (Fig. 3a). The total number of species was twice as high in the new reserves compared to 15–25-year-old stands. The highest number of nature value indicators was found in new and old nature reserves while the lowest number were found in production forests 15–25 and 35–45 years old. The 1–6-year-old stands showed a high variation in number of nature value indicator species and red-listed species with some clear-cuts matching the nature reserves in species number (Fig. 3e, g). The number of individuals partly shows different patterns. The total number of individuals for all species and for obligate species was lower for 1–6- and 15–25-year-old stands compared to older forest types. For nature value indicator species 65–85-year-old stands, NRnew and

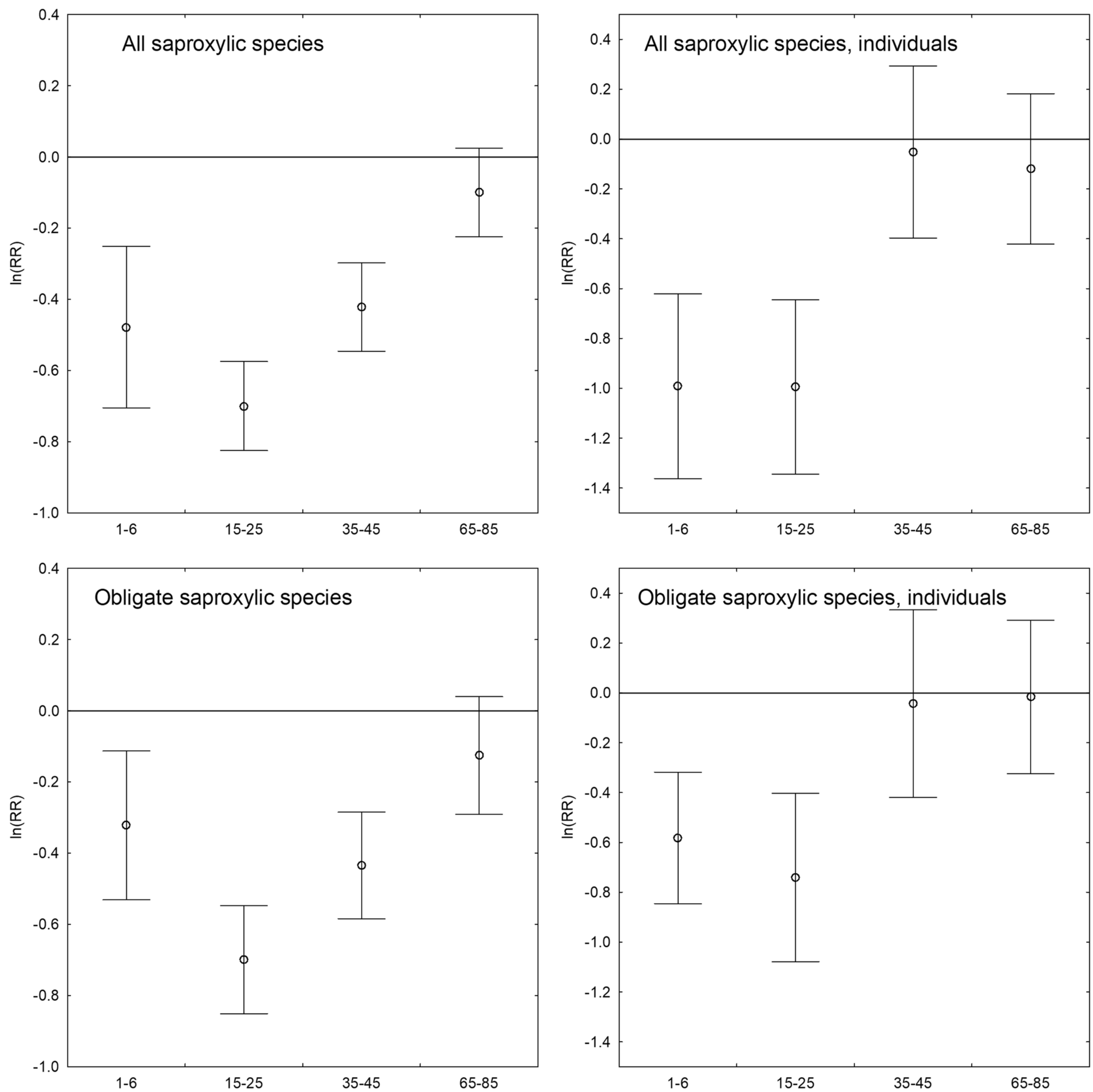

Fig. 4 Response ratios of mean species richness contrasting the four production forest types of different age categories with their corresponding new nature reserve (zero line). Values are ln(RR) with CI95%. CI overlapping the zero line means that there is no significant difference compared to NRnew

NRold showed a higher number of individuals, especially in comparison to 15–25 and 35–45, while there was a larger variation among the 1–6-year-old stands. Number of individuals of red-listed species was highest for 65–85-year-old stands and NRnew compared to the other forest types.

The results of the response ratios (lnRR) comparing the new nature reserves with its corresponding production stands in each sampling cluster, showed that there were significantly more species in the reserves than the three youngest forest types (Fig. 4). However, there was no significant difference in numbers of species between reserves and 65–85-year-old stands.

With regard to the number of individuals, there were significantly fewer individuals in the two youngest forest types compared to the reserves and no significant difference between the two oldest forest types (Fig. 4).

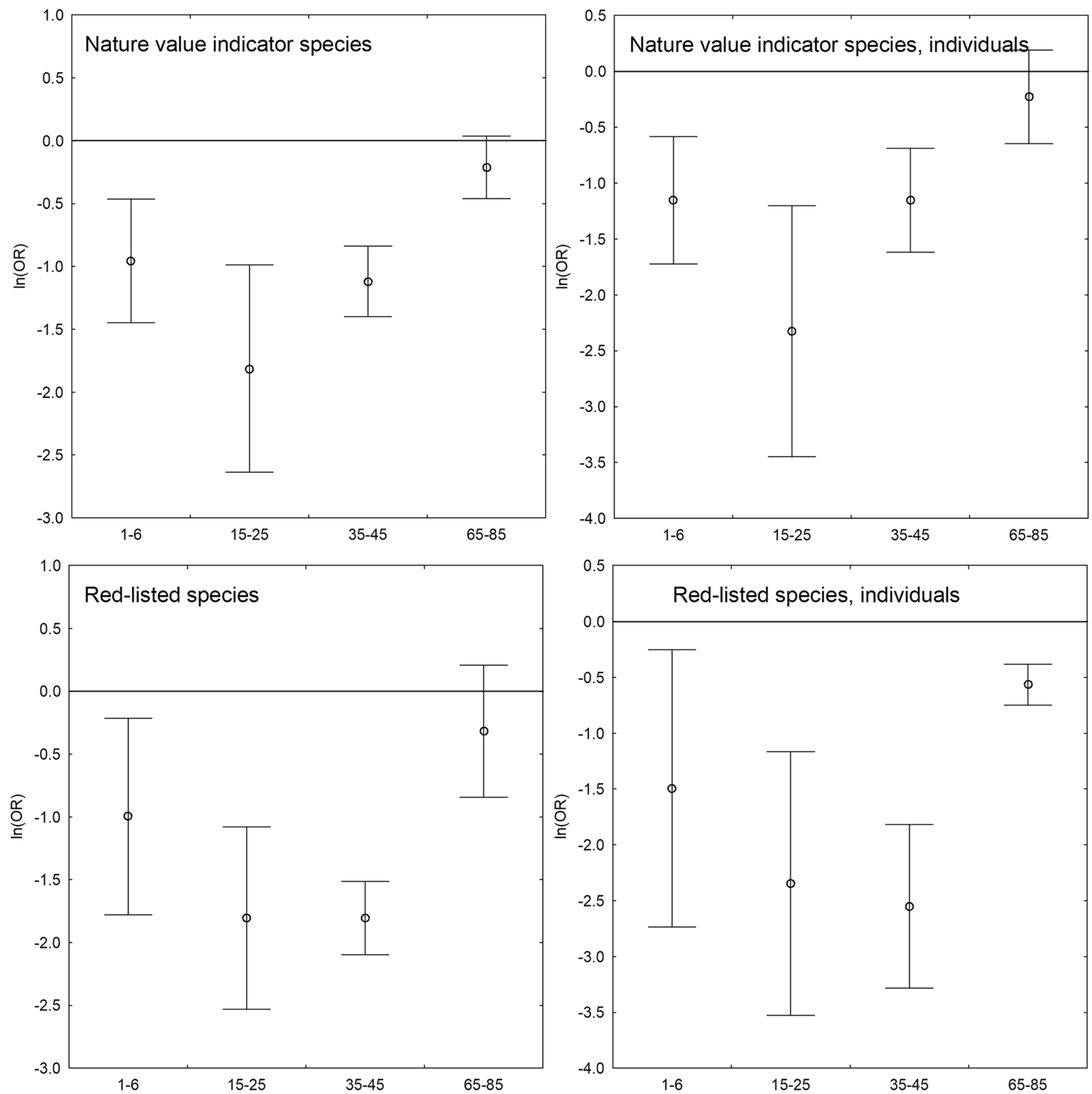

Fig. 5 Ratios for the odds of finding nature value indicator species, and red-listed species. The odds ratio contrast the four production forest types of different age categories with their corresponding new nature reserve (zero line). Values are ln(OR) with CI95%. CI overlapping the zero line means that there is no significant difference compared to NRnew

The odds of finding nature value indicator species, and red-listed species were significantly lower in 1–6-, 15–25-, and 35–45-year-old stands compared to new nature reserves (Fig. 5). There were no significant differences in the odds of finding nature value indicator species, and red-listed species in 65–85-year-old stands compared to new nature reserves except for number of red-listed individuals.

3.3 Differences in species composition between production forests and reserves

The 1–6-year-old stands had a distinctly different composition of saproxylic beetle species than other forest types, both for all species and obligate species (Fig. 6). Old nature reserves on the other hand show a clearly different composition with regard to obligate species, nature value indicators and red-listed species. The stands 15–25 and 35–45 years old were similar for all species groups.

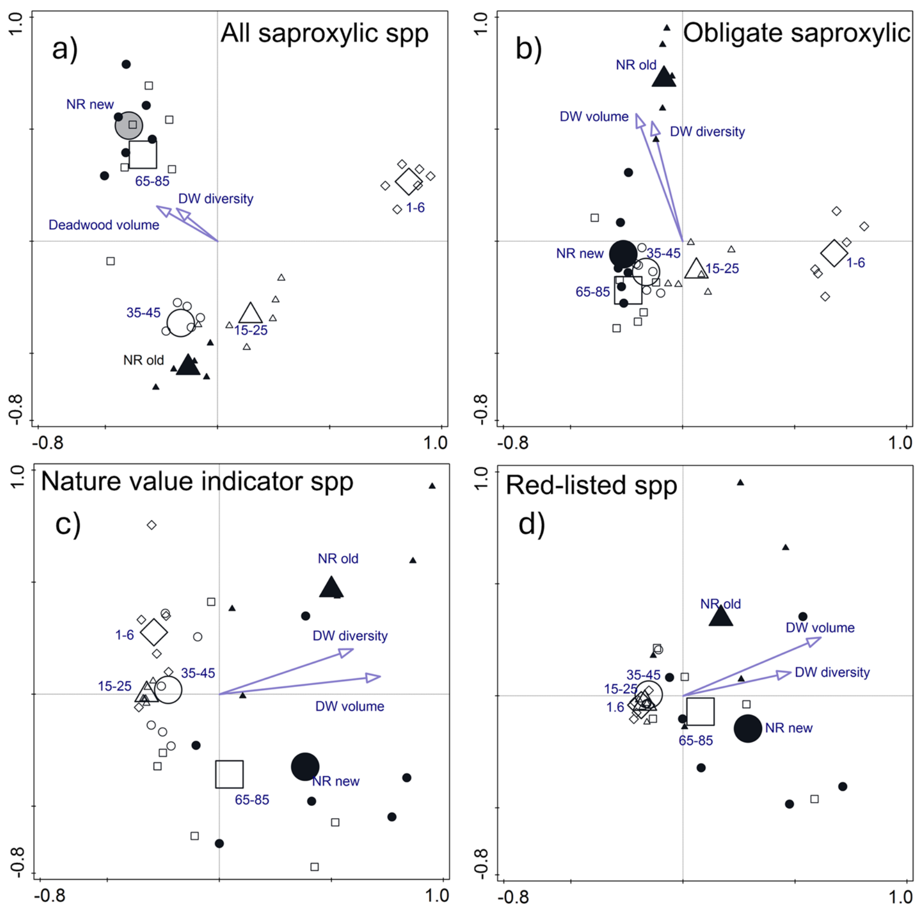

Fig. 6 PCA (principal component analysis) including two environmental variables of **a** all saproxylic species (eigenvalues of PC1 and PC2 were 0.3064 and 0.1043, respectively), **b** obligate saproxylic species (0.2778; 0.0855), **c** nature value indicator species (0.2028; 0.1021), and **d** red-listed species (0.3876; 0.1295). The large symbols show the centroid of the group of a certain forest type

Species composition in production forests 65–85 years old had overall some similarities with composition of new nature reserve, especially for all species and obligate species, less so for nature value indicators and red-listed species (Fig. 6).

When tested statistically, all compositional differences were highly significant, also when excluding stands 1–6 years old (Appendix). The pRDAs showed that forest type explained the majority of the variation, followed by deadwood volume and diversity of deadwood.

4 Discussion

Overall, our results confirmed our main hypothesis that spruce-dominated forests in reserves have a significantly higher species richness of saproxylic beetles than young spruce dominated production forests. The pattern of high diversity in the reserves was especially pronounced when comparing nature value indicators and red-listed species. There were on average 6 times more nature value indicators and 3.5 times more red-listed species in the new nature reserves compared to 15–45-year-old production forests. The majority of studies of saproxylic beetles in boreal forests have shown similar results, a lower diversity in production forests compared to unmanaged old growth forests (Martikainen et al. 2000; Stenbacka et al. 2010; Jacobsen et al. 2020; Burner et al. 2021, Gustafsson et al. 2024, but see Gran 2022). This has important conservation implications since production forests below 60 years now dominate the forest landscape in Sweden (Fig. 7), and 89% of the productive forest area are designated to forestry (SCB 2019). However, some older production forests of 60–85 years matched the diversity of reserves, showing that forest management history may be an important factor to take into consideration (Joelsson et al. 2017; 2018).

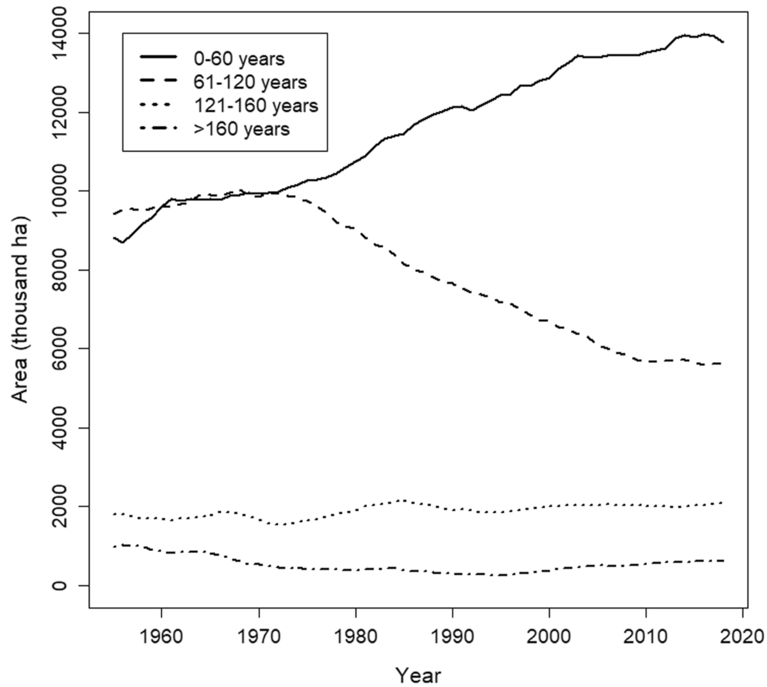

Fig. 7 Changes in area of productive forests in different ages across Sweden between 1955 and 2018. Data from the Swedish National Forestry Survey (Swedish University of Agricultural Sciences 2024)

The reasons for the lower richness in young production forests as shown in this study has been attributed both to low amounts and diversity of deadwood (Similä et al. 2003; Stenbacka et al. 2010; Seibold et al. 2016). The amount of deadwood was lowest in 15–25- and 35–45-year-old stands with on average 3.8 and 5.9 m^3/ha, respectively, which is in line with an average of 5 m^3/ha for forests stand 0–50 years based on data from the Swedish National Forest Inventory (Jonsson et al. 2016). A review of deadwood threshold data from European forests showed critical volumes of 20–30 m^3/ha for occurrence of deadwood dependent organisms in boreal coniferous forests (Müller & Bütler 2010). The existence of these critical thresholds is likely due to metapopulation dynamics; in areas with too low amounts of deadwood, extinction rates exceed colonization rates on substrates (Harrison 1991). The absence of many nature value indicator species in production forests in this study is in line with this, as these species generally have higher thresholds than common species (Müller & Butler 2010; Ylisirniö et al. 2016) or are specialized on substrates uncommon in managed forests (Parisi et al. 2020). Nilsson (1997) showed that *Bolitophagus reticulatus* (L.), feeding on *Fomes fomentarius* (L.) Fr. on dead birches, was absent from 75% of sites with 1–3 fruiting bodies, but present in all sites with over 25. Another example is the beetle *Peltis grossa* (L.) which showed a clear increased density when the number of high-cut stumps on clearcuts exceeded 4.5/ha (Djupström et al. 2024). In a study comparing saproxylic beetles in production forests and so called ecoparks, areas that combine production and nature conservation with at least 50% of the area managed to increase conservation values, red-listed species were totally absent from the production stands (Ekström et al. 2021). It is important to look at old-growth specialists and red-listed species as overall species richness may obscure patterns of this group (Lelli et al. 2019; Gran and Götmark 2021). In general, our results also showed that reserves harboured many species only found in these areas, lacking from production forests stands.

The diversity of deadwood was generally lower in the production forests compared to the reserves in this study in accordance with our hypothesis. Diversity of deadwood has been shown to be a crucial factor for saproxylic organisms (Stokland et al. 2012; Seibold et al. 2018). This likely explains why communities in older reserves differ from those in younger ones, despite rather similar total deadwood amounts; older reserves have had more time to accumulate larger and more diverse deadwood. Deadwood diversity (e.g. different sizes and decay stages) is crucial for many saproxylic organisms, with studies showing it better predicts species richness than deadwood volume (Similä et al. 2003; Bouget et al. 2013). Large logs (> 20 cm) are particularly important, supporting more species of polyporous fungi, which are vital for saproxylic beetles (Junninen & Komonen 2011).

The hypothesis that species composition would be different between the production forest stands and the nature reserves was partly supported. The communities of beetles in new reserves were more similar to 65–85-year-old stands than to those in old reserves. Some of the 65–85-year-old production forests showed similar species richness and composition to the new reserves. The reason for this could be that clear-cutting practices did not become the main method for timber extraction until early in the 1950 s, which means that some of the 60–85 stands may never have been clear-cut. Instead, they may have been subjected to selective cutting or used as forest grazing areas by domestic livestock (Milberg et al 2019; 2021), both practices that produce uneven-aged forests, which have been shown to reduce the negative effects on forest management on saproxylic beetle diversity (Joelsson et al. 2017; 2018). The new reserves and some of the older production stands may therefore share a similar history of land use, as few forests in southern Sweden have remained entirely free from human impact in the past.

The species compositions in old and new reserves differed from all young production forests, with 1–6-year-old stands (clear-cuts) showing the most distinct compositions. Clear-cutting practices have a short history but many species in boreal forests are adapted to large-scale natural disturbances, like fires and storms, creating deadwood in sunny conditions (Similä et al. 2002; 2003). It was therefore not surprising that clear-cuts had a slightly higher total number of species, nature value indicators and red-listed species than production forests of 15–25 and 35–45 years. Clear-cuts provide similar conditions to these natural disturbances, with deadwood in sun-exposed positions, attracting many species (Milberg et al. 2021). Furthermore, in addition to some coarse deadwood, a large amount of fine woody debris is created during the clear-cutting, which contribute to these differences (Jonsell et al. 2007). Other studies also show that several species are found almost exclusively on clear-cuts, and that clear-cut assemblages clearly differ from other stand types (McGeoch et al. 2007; Stenbacka et al. 2010). However, as the clear-cuts age, and the deadwood resources decline and the forests become darker, the overall number of species decline, and in the 15–25-year-old stands the saproxylic fauna is poor. Studies of biodiversity patterns along forests succession in mixed mountain forests in Central Europe have shown similar results (Hilmers et al. 2018).

5 Conclusions

This study compared forest stands established before and after the 1993 revision of the Swedish Forestry Act, which mandates equal prioritization of environmental objectives and high wood production (Lindahl et al. 2017), comparing stands aged 35–45 and 15–25 years, respectively. The comparison shows that both are species-poor, likely due to low levels of deadwood, especially large-diameter deadwood. Although deadwood has increased since 1993, it remains insufficient for many saproxylic species, contributing to the high number of red-listed species in Sweden (Müller & Butler 2010; Eide et al. 2020).

Clear-cutting practices result in even-aged stands, where deadwood quickly decays and disappears, leading to a bottleneck in availability before increasing in older forests (Jonsson et al. 2016). Ranius et al. (2003) simulated the amount of deadwood under different management regimes according to the Forest Certification Standard and showed that the amount of deadwood, even under certification, will go through a bottleneck in young production forest. It will start to increase in older forests closer to harvest, especially if they were more than approximately 90 years old (Ranius et al. 2003). However, with new genetically improved plant material of spruce, with higher growth rate, the optimal harvest age for future forests is calculated to be 68 years in the middle of Sweden (Rosvall et al. 2016). This gives little time for deadwood, especially large diameter logs, to be produced before clear-felling, leaving little time for large-diameter deadwood to develop, negatively affecting species richness (Junninen & Komonen 2011).

Clear-cutting in Sweden has a relatively short history, making it difficult to assess its long-term effects on species diversity after repeated clear-cutting across landscapes. However, a study by Ekström et al. (2021) shows that saproxylic beetle diversity is more similar between ecoparks and production forests in northern Sweden, where exploitation history is shorter, than in the south. Given current retention rates (Gustafsson et al. 2012), it is doubtful that the Swedish forestry model can sustain diversity as intended. Increasing retention rates could improve conditions for saproxylic organisms, but alternative forestry methods, such as uneven-aged forest management, may be more effective in maintaining species assemblages similar to those in old-growth stands (Joelsson et al. 2017; Joelsson et al. 2018).

Appendix

Table 2 List of species caught in the study and their classification. Nature value indicator species are defined as species that at least at one point in time appeared on the Swedish red list. The Red List classifications are based on The Swedish Red List from 2020 (SLU Artdatabanken 2020). Saproxylic class consist of obligate saproxylic species (O), i.e. species that are exclusively dependent on deadwood or wood-inhabiting fungi and facultative saproxylic species (F), species that can complete some life stages on dead wood but are not strictly dependent on it. Nomenclature according to de Jong (2016)

Family	Species	Nature value indicators	Red list category	Saproxylic class	No. individuals
Anthribidae	Dissoleucas niveirostris (Fabricius, 1798)		LC	O	3
Anthribidae	Platystomos albinus (Linnaeus, 1758)		LC	O	9
Anthribidae	Anthribus nebulosus (Forster, 1770)		LC	O	115
Buprestidae	Buprestis rustica (Linnaeus, 1758)		LC	O	3
Buprestidae	Anthaxia similis (Saunders, 1871)		LC	O	1
Buprestidae	Anthaxia quadripunctata (Linnaeus, 1758)		LC	O	20
Buprestidae	Agrilus pratensis (Ratzeburg, 1837)		LC	O	1
Buprestidae	Agrilus betuleti (Ratzeburg, 1837)		LC	O	1
Buprestidae	Agrilus viridis (Linnaeus, 1758)		LC	O	2
Buprestidae	Agrilus suvorovi (Obenberger, 1935)		LC	O	1
Cantharidae	Malthinus biguttatus (Paykull, 1800)		LC	O	7
Cantharidae	Malthinus flaveolus (Panzer, 1789)		LC	O	1
Cantharidae	Malthinus frontalis (Marsham, 1802)		LC	O	4
Cantharidae	Malthodes flavoguttatus (Kiesen-wetter, 1852)		LC	O	5
Cantharidae	Malthodes fuscus (Waltl, 1838)		LC	O	5
Cantharidae	Malthodes guttifer (Kiesenwetter, 1852)		LC	O	12
Cantharidae	Malthodes marginatus (Latreille, 1806)		LC	O	2
Cantharidae	Malthodes spathifer (Kiesenwet-ter, 1852)		LC	O	6
Carabidae	Tachyta nana (Gyllenhal, 1810)		LC	O	1
Cerambycidae	Tragosoma depsarium (Linnaeus, 1767)	NV	VU	O	1
Cerambycidae	Arhopalus rusticus (Linnaeus, 1758)		LC	O	3
Cerambycidae	Asemum striatum (Linnaeus, 1758)		LC	O	2
Cerambycidae	Tetropium castaneum (Linnaeus, 1758)		LC	O	52
Cerambycidae	Tetropium fuscum (Fabricius, 1787)		LC	O	10
Cerambycidae	Rhagium mordax (DeGeer, 1775)		LC	O	319
Cerambycidae	Rhagium inquisitor (Linnaeus, 1758)		LC	O	61
Cerambycidae	Oxymirus cursor (Linnaeus, 1758)		LC	O	9
Cerambycidae	Pachyta lamed (Linnaeus, 1758)	NV	NT	O	2
Cerambycidae	Gaurotes virginea (Linnaeus, 1758)		LC	O	10
Cerambycidae	Cortodera femorata (Fabricius, 1787)		LC	O	12
Cerambycidae	Grammoptera ruficornis (Fabricius, 1781)		LC	O	13
Cerambycidae	Alosterna tabacicolor (DeGeer, 1775)		LC	O	32
Cerambycidae	Stictoleptura maculicornis (DeGeer, 1775)		LC	O	22
Cerambycidae	Stictoleptura rubra (Linnaeus, 1758)		LC	O	3

Family	Species	Nature value indicators	Red list category	Saproxylic class	No. individuals
Cerambycidae	Anastrangalia sanguinolenta (Linnaeus, 1761)		LC	O	68
Cerambycidae	Anastrangalia reyi (Heyden, 1889)		LC	O	3
Cerambycidae	Judolia sexmaculata (Linnaeus, 1758)		LC	O	41
Cerambycidae	Leptura quadrifasciata (Linnaeus, 1758)		LC	O	4
Cerambycidae	Stenurella melanura (Linnaeus, 1758)		LC	O	194
Cerambycidae	Necydalis major (Linnaeus, 1758)	NV	LC	O	1
Cerambycidae	Obrium brunneum (Fabricius, 1792)	NV	NT	O	1
Cerambycidae	Molorchus minor (Linnaeus, 1758)		LC	O	48
Cerambycidae	Phymatodes testaceus (Linnaeus, 1758)		LC	O	18
Cerambycidae	Poecilium alni (Linnaeus, 1767)	NV	LC	O	8
Cerambycidae	Xylotrechus rusticus (Linnaeus, 1758)		LC	O	4
Cerambycidae	Xylotrechus antilope (Schönherr, 1817)	NV	NT	O	6
Cerambycidae	Clytus arietis (Linnaeus, 1758)		LC	O	38
Cerambycidae	Plagionotus arcuatus (Linnaeus, 1758)		LC	O	5
Cerambycidae	Pogonocherus hispidulus (Piller & Mitterpacher, 1783)		LC	O	4
Cerambycidae	Pogonocherus fasciculatus (DeGeer, 1775)		LC	O	9
Cerambycidae	Saperda scalaris (Linnaeus, 1758)		LC	O	2
Cerambycidae	Stenostola dubia (Laicharting, 1784)		LC	O	1
Cerambycidae	Tetrops praeusta (Linnaeus, 1758)		LC	O	1
Cerylonidae	Cerylon fagi (Brisout de Barneville, 1867)		LC	O	16
Cerylonidae	Cerylon histeroides (Fabricius, 1792)		LC	O	38
Cerylonidae	Cerylon ferrugineum (Stephens, 1830)		LC	O	23
Cerylonidae	Cerylon deplanatum (Gyllenhal, 1827)	NV	NT	O	3
Ciidae	Cis jacquemartii (Mellié, 1849)		LC	O	34
Ciidae	Cis micans (Fabricius, 1792)		LC	O	21
Ciidae	Cis boleti (Scopoli, 1763)		LC	O	16
Ciidae	Cis rugulosus (Mellié, 1849)	NV	NT	O	1
Ciidae	Cis quadridens (Mellié, 1849)		LC	O	19
Ciidae	Cis punctulatus (Gyllenhal, 1827)		LC	O	14
Ciidae	Cis dentatus (Mellié, 1849)		LC	O	38
Ciidae	Ennearthron cornutum (Gyllenhal, 1827)		LC	O	64
Ciidae	Orthocis alni (Gyllenhal, 1827)		LC	O	6
Ciidae	Cis vestitus (Mellié, 1849)		LC	O	4
Ciidae	Cis festivus (Panzer, 1793)		LC	O	8
Ciidae	Sulcacis nitidus (Fabricius, 1792)		LC	O	7
Ciidae	Ropalodontus perforatus (Gyllenhal, 1813)		LC	O	9
Cleridae	Tillus elongatus (Linnaeus, 1758)	NV	LC	O	3
Cleridae	Thanasimus formicarius (Linnaeus, 1758)		LC	O	84
Cleridae	Thanasimus femoralis (Zetterstedt, 1828)		LC	O	2
Corylophidae	Orthoperus atomus (Gyllenhal, 1808)		LC	F	2

Family	Species	Nature value indicators	Red list category	Saproxylic class	No. individuals
Corylophidae	Orthoperus corticalis (Redtenbacher, 1849)		LC	O	3
Cryptophagidae	Henoticus serratus (Gyllenhal, 1808)		LC	F	3
Cryptophagidae	Pteryngium crenatum (Fabricius, 1792)	NV	LC	O	24
Cryptophagidae	Micrambe abietis (Paykull, 1798)		LC	F	247
Cryptophagidae	Cryptophagus acutangulus (Gyllenhal, 1827)		LC	F	87
Cryptophagidae	Cryptophagus badius (Sturm, 1845)		LC	O	112
Cryptophagidae	Cryptophagus populi (Paykull, 1800)	NV	LC	F	1
Cryptophagidae	Cryptophagus pubescens (Sturm, 1845)		LC	F	140
Cryptophagidae	Cryptophagus micaceus (Rey, 1889)	NV	LC	O	21
Cryptophagidae	Cryptophagus saginatus (Sturm, 1845)		LC	F	82
Cryptophagidae	Cryptophagus dentatus (Herbst, 1793)		LC	F	178
Cryptophagidae	Cryptophagus dorsalis (Sahlberg, 1819)		LC	F	91
Cryptophagidae	Cryptophagus distinguendus (Sturm, 1845)		LC	F	62
Cryptophagidae	Cryptophagus scanicus (Linnaeus, 1758)		LC	F	1075
Cryptophagidae	Cryptophagus denticulatus (Heer, 1841)		LC	F	82
Cryptophagidae	Atomaria morio (Kolenati, 1846)		LC	F	31
Cryptophagidae	Atomaria ornata (Heer, 1841)		LC	F	150
Cryptophagidae	Atomaria fuscata (Schönherr, 1808)		LC	F	42
Cryptophagidae	Atomaria subangulata (J. Sahlberg, 1898)	NV	LC	O	6
Cryptophagidae	Atomaria bella (Reitter, 1887)		LC	O	28
Cryptophagidae	Atomaria atrata (Reitter, 1875)		LC	F	22
Cucujidae	Dendrophagus crenatus (Paykull, 1799)	NV	LC	O	4
Curculionidae	Rhyncolus ater (Linnaeus, 1758)		LC	O	12
Curculionidae	Rhyncolus sculpturatus (Waltl, 1839)		LC	O	4
Curculionidae	Magdalis phlegmatica (Herbst, 1797)		LC	O	5
Curculionidae	Magdalis nitida (Gyllenhal, 1827)		LC	O	1
Curculionidae	Magdalis linearis (Gyllenhal, 1827)		LC	O	2
Curculionidae	Magdalis frontalis (Gyllenhal, 1827)		LC	O	1
Curculionidae	Magdalis violacea (Linnaeus, 1758)		LC	O	3
Curculionidae	Magdalis carbonaria (Linnaeus, 1758)		LC	O	2
Curculionidae	Magdalis barbicornis (Latreille, 1804)		LC	O	1
Curculionidae	Magdalis duplicata (Germar, 1819)		LC	O	2
Curculionidae	Magdalis ruficornis (Linnaeus, 1758)		LC	O	3
Curculionidae	Hylobius abietis (Linnaeus, 1758)		LC	O	54
Curculionidae	Hylobius pinastri (Gyllenhal, 1813)		LC	O	1
Curculionidae	Pissodes castaneus (DeGeer, 1775)		LC	O	13
Curculionidae	Pissodes pini (Linnaeus, 1758)		LC	O	6
Curculionidae	Pissodes gyllenhalii (Gyllenhal, 1827)		LC	O	1
Curculionidae	Pissodes harcyniae (Herbst, 1795)	NV	NT	O	3
Curculionidae	Pissodes piniphilus (Herbst, 1797)		LC	O	3

Family	Species	Nature value indicators	Red list category	Saproxylic class	No. individuals
Curculionidae	Hylurgops palliatus (Gyllenhal, 1813)		LC	O	42
Curculionidae	Hylastes brunneus (Erichson, 1836)		LC	O	166
Curculionidae	Hylastes cunicularius (Erichson, 1836)		LC	O	5573
Curculionidae	Hylastes attenuatus (Erichson, 1836)		LC	O	659
Curculionidae	Hylastes opacus (Erichson, 1836)		LC	O	30
Curculionidae	Hylesinus varius (Fabricius, 1775)		LC	O	1
Curculionidae	Xylechinus pilosus (Ratzeburg, 1837)		LC	O	6
Curculionidae	Tomicus minor (Hartig, 1834)		LC	O	3
Curculionidae	Tomicus piniperda (Linnaeus, 1758)		LC	O	6
Curculionidae	Dendroctonus micans (Kugelann, 1794)		LC	O	3
Curculionidae	Phloeotribus spinulosus (Rey, 1883)		LC	O	37
Curculionidae	Polygraphus subopacus (Thomson, 1871)		LC	O	2
Curculionidae	Polygraphus poligraphus (Linnaeus, 1758)		LC	O	9
Curculionidae	Scolytus laevis (Chapuis, 1869)		NE	O	1
Curculionidae	Pityogenes chalcographus (Linnaeus, 1761)		LC	O	141
Curculionidae	Pityogenes trepanatus (Nördlinger, 1848)		LC	O	1
Curculionidae	Pityogenes quadridens (Hartig, 1834)		LC	O	24
Curculionidae	Pityogenes bidentatus (Herbst, 1783)		LC	O	12
Curculionidae	Orthotomicus suturalis (Gyllenhal, 1827)		LC	O	13
Curculionidae	Ips typographus (Linnaeus, 1758)		LC	O	479
Curculionidae	Dryocoetes villosus (Fabricius, 1792)	NV	LC	O	13
Curculionidae	Dryocoetes autographus (Ratzeburg, 1837)		LC	O	451
Curculionidae	Crypturgus subcribrosus (Eggers, 1933)		LC	O	17
Curculionidae	Crypturgus cinereus (Herbst, 1794)		LC	O	7
Curculionidae	Crypturgus pusillus (Gyllenhal, 1813)		LC	O	4
Curculionidae	Crypturgus hispidulus (Thomson, 1870)		LC	O	97
Curculionidae	Trypodendron domesticum (Linnaeus, 1758)		LC	O	25
Curculionidae	Trypodendron lineatum (Olivier, 1795)		LC	O	194
Curculionidae	Trypodendron signatum (Fabricius, 1792)		LC	O	4
Curculionidae	Anisandrus dispar (Fabricius, 1792)		LC	O	159
Curculionidae	Xyleborus cryptographus (Ratzeburg, 1837)		LC	O	1
Curculionidae	Xyleborinus saxesenii (Ratzeburg, 1837)	NV	LC	O	3
Curculionidae	Cryphalus asperatus (Gyllenhal, 1813)		LC	O	38
Curculionidae	Cryphalus saltuarius (Weise, 1891)		LC	O	9
Curculionidae	Pityophthorus micrographus (Linnaeus, 1758)		LC	O	15
Dasytidae	Aplocnemus impressus (Marsham, 1802)	NV	LC	O	1

Family	Species	Nature value indicators	Red list category	Saproxylic class	No. individuals
Dasytidae	Aplocnemus nigricornis (Fabricius, 1792)		LC	O	27
Dasytidae	Dasytes obscurus (Gyllenhal, 1813)		LC	O	48
Dasytidae	Dasytes caeruleus (DeGeer, 1774)		LC	O	4
Dasytidae	Dasytes niger (Linnaeus, 1761)		LC	O	577
Dasytidae	Dasytes plumbeus (Müller, 1776)		LC	O	6727
Dasytidae	Dasytes fusculus (Illiger, 1801)		LC	O	1
Dermestidae	Dermestes murinus (Linnaeus, 1758)		LC	F	1
Dermestidae	Attagenus pellio (Linnaeus, 1758)		LC	F	2
Dermestidae	Megatoma undata (Linnaeus, 1758)		LC	F	272
Dermestidae	Ctesias serra (Fabricius, 1792)		LC	O	119
Elateridae	Danosoma fasciatum (Linnaeus, 1758)	NV	NT	O	1
Elateridae	Denticollis linearis (Linnaeus, 1758)		LC	O	46
Elateridae	Ampedus sanguineus (Linnaeus, 1758)		LC	O	12
Elateridae	Ampedus pomorum (Herbst, 1784)		LC	O	12
Elateridae	Ampedus balteatus (Linnaeus, 1758)		LC	O	194
Elateridae	Ampedus praeustus (Fabricius, 1792)	NV	NT	O	1
Elateridae	Ampedus tristis (Linnaeus, 1758)		LC	O	26
Elateridae	Ampedus nigrinus (Herbst, 1784)		LC	O	101
Elateridae	Melanotus villosus (Geoffroy, 1785)		LC	O	279
Elateridae	Melanotus castanipes (Paykull, 1800)		LC	O	146
Elateridae	Ectinus aterrimus (Linnaeus, 1761)		LC	F	1
Elateridae	Cardiophorus ruficollis (Linnaeus, 1758)		LC	O	192
Endomychidae	Mycetina cruciata (Schaller, 1783)	NV	LC	O	48
Endomychidae	Endomychus coccineus (Linnaeus, 1758)		LC	O	7
Erotylidae	Tritoma bipustulata (Fabricius, 1775)		LC	O	43
Erotylidae	Triplax aenea (Schaller, 1783)		LC	O	10
Erotylidae	Triplax russica (Linnaeus, 1758)		LC	O	38
Erotylidae	Triplax rufipes (Fabricius, 1781)	NV	NT	O	3
Erotylidae	Dacne bipustulata (Thunberg, 1781)		LC	O	111
Eucnemidae	Microrhagus pygmaeus (Fabricius, 1792)		LC	O	5
Eucnemidae	Hylis procerulus (Mannerheim, 1823)		LC	O	1
Eucnemidae	Hylis cariniceps (Reitter, 1902)	NV	LC	O	4
Eucnemidae	Hylis olexai (Palm, 1955)	NV	LC	O	7
Eucnemidae	Drapetes mordelloides (Host, 1789)	NV	VU	O	1
Histeridae	Sphaerites glabratus (Fabricius, 1792)		LC	F	90
Histeridae	Plegaderus caesus (Herbst, 1792)	NV	LC	O	1
Histeridae	Gnathoncus nannetensis (Marseul, 1862)		LC	F	34
Histeridae	Gnathoncus buyssoni (Auzat, 1917)		LC	F	11
Histeridae	Dendrophilus pygmaeus (Linnaeus, 1758)		LC	F	1
Histeridae	Paromalus flavicornis (Herbst, 1792)		LC	O	4
Histeridae	Paromalus parallelepipedus (Herbst, 1792)	NV	LC	O	8

Family	Species	Nature value indicators	Red list category	Saproxylic class	No. individuals
Histeridae	Platysoma angustatum (Hoffmann, 1803)		LC	O	1
Histeridae	Platysoma lineare (Erichson, 1834)	NV	NT	O	1
Laemophloeidae	Cryptolestes abietis (Wankowicz, 1865)		LC	O	5
Laemophloeidae	Leptophloeus alternans (Erichson, 1846)		LC	O	1
Laemophloeidae	Cryptolestes corticinus (Erichson, 1846)		LC	O	1
Latridiidae	Latridius hirtus (Gyllenhal, 1827)		LC	O	4
Latridiidae	Latridius consimilis (Mannerheim, 1844)		LC	F	26
Latridiidae	Latridius porcatus (Herbst, 1793)		LC	F	2
Latridiidae	Latridius minutus (Linnaeus, 1767)		LC	F	12
Latridiidae	Enicmus fungicola (Thomson, 1868)		LC	O	177
Latridiidae	Enicmus rugosus (Herbst, 1793)		LC	O	798
Latridiidae	Enicmus testaceus (Stephens, 1830)		LC	O	494
Latridiidae	Enicmus transversus (Olivier, 1790)		LC	F	18
Latridiidae	Dienerella vincenti (Johnson, 2007)		LC	F	1
Latridiidae	Stephostethus lardarius (DeGeer, 1775)		LC	F	6
Latridiidae	Stephostethus pandellei (Brisout de Barneville, 1863)		LC	F	370
Latridiidae	Stephostethus alternans (Mannerheim, 1844)		LC	O	4
Latridiidae	Stephostethus rugicollis (Olivier, 1790)		LC	F	29
Latridiidae	Thes bergrothi (Reitter, 1880)		LC	F	2
Latridiidae	Cartodere nodifer (Westwood, 1839)		LC	F	245
Latridiidae	Cartodere constricta (Gyllenhal, 1827)		LC	F	71
Latridiidae	Corticaria lapponica (Zetterstedt, 1838)	NV	LC	O	13
Latridiidae	Corticaria serrata (Paykull, 1798)		LC	F	76
Latridiidae	Corticaria longicornis (Herbst, 1793)		LC	F	52
Latridiidae	Corticaria interstitialis (Mannerheim, 1844)	NV	NT	F	14
Latridiidae	Corticaria rubripes (Mannerheim, 1844)		LC	F	109
Latridiidae	Corticaria longicollis (Gyllenhal, 1827)		LC	F	139
Latridiidae	Corticaria lateritia (Mannerheim, 1844)		LC	O	30
Latridiidae	Cortinicara gibbosa (Herbst, 1793)		LC	F	162
Latridiidae	Corticarina similata (Gyllenhal, 1827)		LC	F	89
Leiodidae	Ptenidium turgidum (Thomson, 1855)	NV	LC	O	1
Leiodidae	Anisotoma humeralis (Fabricius, 1792)		LC	O	245
Leiodidae	Anisotoma axillaris (Gyllenhal, 1810)		LC	O	121
Leiodidae	Anisotoma castanea (Herbst, 1792)		LC	O	166
Leiodidae	Anisotoma glabra (Fabricius, 1787)		LC	O	102
Leiodidae	Anisotoma orbicularis (Herbst, 1792)		LC	O	39
Leiodidae	Liodopria serricornis (Gyllenhal, 1813)	NV	NT	O	20

Family	Species	Nature value indicators	Red list category	Saproxylic class	No. individuals
Leiodidae	Amphicyllis globiformis (Sahlberg, 1833)	NV	NT	F	15
Leiodidae	Agathidium varians (Beck, 1817)		LC	F	16
Leiodidae	Agathidium mandibulare (Sturm, 1807)	NV	LC	F	1
Leiodidae	Agathidium rotundatum (Gyllenhal, 1827)		LC	F	1
Leiodidae	Agathidium confusum (Brisout de Barneville, 1863)		LC	F	12
Leiodidae	Agathidium nigrinum (Sturm, 1807)	NV	LC	F	11
Leiodidae	Agathidium nigripenne (Fabricius, 1792)		LC	F	74
Leiodidae	Agathidium seminulum (Linnaeus, 1758)		LC	F	26
Leiodidae	Agathidium laevigatum (Erichson, 1845)		LC	F	40
Leiodidae	Agathidium pisanum (Brisout de Barneville, 1872)		LC	O	4
Lucanidae	Platycerus caprea (DeGeer, 1774)	NV	LC	O	9
Lucanidae	Platycerus caraboides (Linnaeus, 1758)		LC	O	6
Lucanidae	Sinodendron cylindricum (Linnaeus, 1758)		LC	O	1
Lycidae	Dictyoptera aurora (Herbst, 1784)		LC	O	52
Lycidae	Pyropterus nigroruber (DeGeer, 1774)		LC	O	5
Lycidae	Lygistopterus sanguineus (Linnaeus, 1758)		LC	O	13
Lymexylidae	Elateroides dermestoides (Linnaeus, 1761)		LC	O	224
Malachiidae	Malachius bipustulatus (Linnaeus, 1758)		LC	O	3
Melandryidae	Tetratoma fungorum (Fabricius, 1790)	NV	LC	O	3
Melandryidae	Hallomenus binotatus (Quensel, 1790)		LC	O	26
Melandryidae	Hallomenus axillaris (Illiger, 1807)	NV	LC	O	6
Melandryidae	Orchesia micans (Panzer, 1794)		LC	O	1
Melandryidae	Orchesia fasciata (Illiger, 1798)	NV	NT	O	1
Melandryidae	Orchesia undulata (Kraatz, 1853)		LC	O	8
Melandryidae	Abdera flexuosa (Paykull, 1799)	NV	LC	O	1
Melandryidae	Wanachia triguttata (Gyllenhal, 1810)	NV	LC	O	2
Melandryidae	Phloiotrya rufipes (Gyllenhal, 1810)	NV	LC	O	1
Melandryidae	Xylita laevigata (Hellenius, 1786)		LC	O	21
Melandryidae	Serropalpus barbatus (Schaller, 1783)	NV	LC	O	13
Melandryidae	Zilora ferruginea (Paykull, 1798)	NV	NT	O	3
Monotomidae	Rhizophagus depressus (Fabricius, 1792)		LC	O	12
Monotomidae	Rhizophagus ferrugineus (Paykull, 1800)		LC	O	141
Monotomidae	Rhizophagus picipes (Olivier, 1790)	NV	NT	O	1
Monotomidae	Rhizophagus dispar (Paykull, 1800)		LC	F	35
Monotomidae	Rhizophagus bipustulatus (Fabricius, 1792)		LC	O	229
Monotomidae	Rhizophagus nitidulus (Fabricius, 1798)		LC	O	4
Monotomidae	Rhizophagus fenestralis (Linnaeus, 1758)		LC	O	118

Family	Species	Nature value indicators	Red list category	Saproxylic class	No. individuals
Monotomidae	Rhizophagus cribratus (Gyllenhal, 1827)	NV	LC	O	5
Mordellidae	Tomoxia bucephala (Costa, 1854)		LC	O	77
Mordellidae	Mordella aculeata (Linnaeus, 1758)		LC	F	136
Mordellidae	Mordella holomalaena (Apfelbeck, 1914)		LC	F	14
Mordellidae	Curtimorda maculosa (Naezen, 1794)		LC	O	4
Mordellidae	Mordellistena variegata (Fabricius, 1798)	NV	LC	O	9
Mordellidae	Mordellochroa abdominalis (Fabricius, 1775)		LC	O	23
Mycetophagidae	Litargus connexus (Geoffroy, 1785)		LC	O	98
Mycetophagidae	Mycetophagus quadripustulatus (Linnaeus, 1761)	NV	LC	O	14
Mycetophagidae	Mycetophagus piceus (Fabricius, 1777)	NV	LC	O	15
Mycetophagidae	Mycetophagus decempunctatus (Fabricius, 1801)	NV	NT	O	2
Mycetophagidae	Mycetophagus multipunctatus (Fabricius, 1792)		LC	O	8
Mycetophagidae	Mycetophagus fulvicollis (Fabricius, 1792)	NV	NT	O	2
Mycetophagidae	Mycetophagus populi (Fabricius, 1798)		LC	O	1
Nitidulidae	Carpophilus marginellus (Motschulsky, 1858)		LC	F	1
Nitidulidae	Epuraea melanocephala (Marsham, 1802)		LC	F	17
Nitidulidae	Epuraea guttata (Olivier, 1811)	NV	LC	O	21
Nitidulidae	Epuraea neglecta (Heer, 1841)		LC	O	8
Nitidulidae	Epuraea pallescens (Stephens, 1835)		LC	O	17
Nitidulidae	Epuraea laeviuscula (Gyllenhal, 1827)		LC	O	1
Nitidulidae	Epuraea angustula (Sturm, 1844)		LC	O	1
Nitidulidae	Epuraea boreella (Zetterstedt, 1828)		LC	O	5
Nitidulidae	Epuraea marseuli (Reitter, 1872)		LC	O	283
Nitidulidae	Epuraea pygmaea (Gyllenhal, 1808)		LC	O	396
Nitidulidae	Epuraea binotata (Reitter, 1872)		LC	F	1
Nitidulidae	Epuraea terminalis (Mannerheim, 1843)		LC	F	4
Nitidulidae	Epuraea biguttata (Thunberg, 1784)		LC	O	12
Nitidulidae	Epuraea unicolor (Olivier, 1790)		LC	F	343
Nitidulidae	Epuraea variegata (Herbst, 1793)		LC	F	4
Nitidulidae	Epuraea muehli (Reitter, 1908)		LC	O	1
Nitidulidae	Epuraea aestiva (Linnaeus, 1758)		LC	F	2
Nitidulidae	Epuraea melina (Erichson, 1843)		LC	F	61
Nitidulidae	Epuraea rufomarginata (Stephens, 1830)		LC	F	135
Nitidulidae	Soronia punctatissima (Illiger, 1807)		LC	O	22
Nitidulidae	Soronia grisea (Linnaeus, 1758)		LC	O	139
Nitidulidae	Ipidia binotata (Reitter, 1875)	NV	LC	O	18
Nitidulidae	Cychramus variegatus (Herbst, 1792)		LC	F	529
Nitidulidae	Cychramus luteus (Fabricius, 1787)		LC	F	1151
Nitidulidae	Cryptarcha strigata (Fabricius, 1787)		LC	O	11
Nitidulidae	Cryptarcha undata (Olivier, 1790)	NV	LC	O	2

Family	Species	Nature value indicators	Red list category	Saproxylic class	No. individuals
Nitidulidae	Glischrochilus quadriguttatus (Fabricius, 1777)	NV	LC	O	38
Nitidulidae	Glischrochilus hortensis (Geoffroy, 1785)		LC	F	1660
Nitidulidae	Glischrochilus quadripunctatus (Linnaeus, 1758)		LC	O	769
Nitidulidae	Pityophagus ferrugineus (Linnaeus, 1758)		LC	O	432
Nitidulidae	Glischrochilus quadrisignatus (Say, 1835)		LC	F	1
Oedemeridae	Chrysanthia viridissima (Linnaeus, 1758)		LC	O	229
Oedemeridae	Chrysanthia geniculata (W. L. E. Schmidt, 1846)		LC	O	25
Oedemeridae	Calopus serraticornis (Linnaeus, 1758)		LC	O	8
Peltidae	Peltis ferruginea (Linnaeus, 1758)		LC	O	45
Peltidae	Thymalus limbatus (Fabricius, 1787)		LC	O	14
Peltidae	Grynocharis oblonga (Linnaeus, 1758)	NV	LC	O	3
Ptinidae	Ptinus dubius (Sturm, 1837)		LC	O	8
Ptinidae	Ptinus rufipes (Olivier, 1790)		LC	O	1
Ptinidae	Ptinus fur (Linnaeus, 1758)		LC	F	48
Ptinidae	Ptinus subpillosus (Sturm, 1837)		LC	O	258
Ptinidae	Ptinomorphus imperialis (Linnaeus, 1767)		LC	O	5
Ptinidae	Dryophilus pusillus (Gyllenhal, 1808)		LC	O	51
Ptinidae	Ernobius mollis (Linnaeus, 1758)		LC	O	5
Ptinidae	Ernobius angusticollis (Ratzeburg, 1837)		LC	O	2
Ptinidae	Ernobius abietinus (Gyllenhal, 1808)		LC	F	14
Ptinidae	Ernobius abietis (Fabricius, 1792)		LC	F	35
Ptinidae	Anobium punctatum (DeGeer, 1774)		LC	O	1
Ptinidae	Cacotemnus thomsoni (Kraatz, 1881)	NV	LC	O	1
Ptinidae	Microbregma emarginata (Duftschmid, 1825)	NV	LC	O	10
Ptinidae	Hadrobregmus pertinax (Linnaeus, 1758)		LC	O	40
Ptinidae	Ptilinus pectinicornis (Linnaeus, 1758)		LC	O	1
Ptinidae	Ptilinus fuscus (Geoffroy, 1785)	NV	LC	O	3
Ptinidae	Xyletinus pectinatus (Fabricius, 1792)	NV	NT	O	1
Ptinidae	Stagetus borealis (Israelsson, 1971)	NV	NT	O	9
Ptinidae	Dorcatoma chrysomelina (Sturm, 1837)		LC	O	20
Ptinidae	Dorcatoma punctulata (Mulsant & Rey, 1864)	NV	LC	O	3
Ptinidae	Dorcatoma dresdensis (Herbst, 1792)		LC	O	52
Ptinidae	Dorcatoma robusta (Strand, 1938)	NV	LC	O	8
Pyrochroidae	Pyrochroa coccinea (Linnaeus, 1761)		LC	O	6
Pyrochroidae	Schizotus pectinicornis (Linnaeus, 1758)		LC	O	68
Pythidae	Pytho depressus (Linnaeus, 1767)		LC	O	1
Salpingidae	Rabocerus foveolatus (Ljungh, 1823)		LC	O	1

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Salpingidae	Sphaeriestes castaneus (Panzer, 1796)		LC	O	20
Salpingidae	Salpingus planirostris (Fabricius, 1787)		LC	O	32
Salpingidae	Salpingus ruficollis (Linnaeus, 1761)		LC	O	61
Scirtidae	Prionocyphon serricornis (Müller, 1821)	NV	LC	O	7
Scraptiidae	Anaspis frontalis (Linnaeus, 1758)		LC	O	715
Scraptiidae	Anaspis marginicollis (Lindberg, 1925)		LC	O	77
Scraptiidae	Anaspis thoracica (Linnaeus, 1758)		LC	O	419
Scraptiidae	Anaspis rufilabris (Gyllenhal, 1827)		LC	O	11,864
Scraptiidae	Anaspis flava (Linnaeus, 1758)		LC	O	410
Silvanidae	Silvanus bidentatus (Fabricius, 1792)	NV	NT	O	6
Silvanidae	Silvanoprus fagi (Guérin-Méneville, 1844)		LC	F	40
Sphindidae	Sphindus dubius (Gyllenhal, 1808)		LC	F	55
Staphylinidae	Nevraphes coronatus (J. Sahlberg, 1881)		LC	F	1
Staphylinidae	Stenichnus godarti (Latreille, 1806)		LC	O	17
Staphylinidae	Stenichnus bicolor (Denny, 1825)		LC	F	1
Staphylinidae	Microscydmus nanus (Schaum, 1841)	NV	LC	O	3
Staphylinidae	Gabrius splendidulus (Gravenhorst, 1802)		LC	F	99
Staphylinidae	Bisnius fimetarius (Gravenhorst, 1802)		LC	F	108
Staphylinidae	Philonthus politus (Linnaeus, 1758)		LC	F	84
Staphylinidae	Philonthus succicola (Thomson, 1860)		LC	F	6
Staphylinidae	Philonthus addendus (Sharp, 1867)		LC	F	7
Staphylinidae	Bisnius subuliformis (Gravenhorst, 1802)		LC	O	4
Staphylinidae	Quedius dilatatus (Fabricius, 1787)	NV	LC	F	3
Staphylinidae	Quedius mesomelinus (Marsham, 1802)		LC	F	17,290
Staphylinidae	Quedius maurus (Sahlberg, 1830)		LC	O	9
Staphylinidae	Quedius cruentus (Olivier, 1795)		LC	F	7
Staphylinidae	Quedius scitus (Gravenhorst, 1806)		LC	F	8
Staphylinidae	Quedius xanthopus (Erichson, 1839)		LC	F	521
Staphylinidae	Quedionuchus glaber (O. Müller, 1776)		LC	O	3
Staphylinidae	Nudobius lentus (Gravenhorst, 1806)		LC	O	8
Staphylinidae	Atrecus longiceps (Fauvel, 1900)		LC	O	7
Staphylinidae	Bibloporus bicolor (Denny, 1825)		LC	O	24
Staphylinidae	Euplectus piceus (Motschulsky, 1835)		LC	F	1
Staphylinidae	Euplectus karsteni (Reichenbach, 1816)		LC	F	4
Staphylinidae	Euplectus mutator (Fauvel, 1895)		LC	O	3
Staphylinidae	Tyrus mucronatus (Panzer, 1803)		LC	F	4
Staphylinidae	Proteinus brachypterus (Fabricius, 1792)		LC	F	4
Staphylinidae	Acrulia inflata (Gyllenhal, 1813)		LC	F	7
Staphylinidae	Phyllodrepa melanocephala (Fabricius, 1787)		LC	F	35
Staphylinidae	Phyllodrepa floralis (Paykull, 1789)		LC	F	6

Family	Species	Nature value indicators	Red list category	Saproxylic class	No. individuals
Staphylinidae	Dropephylla linearis (Zetterstedt, 1828)	NV	LC	O	4
Staphylinidae	Omalium rivulare (Paykull, 1789)		LC	F	97
Staphylinidae	Phloeostiba plana (Paykull, 1792)		LC	O	22
Staphylinidae	Phloeostiba lapponica (Zetterstedt, 1838)		LC	O	1
Staphylinidae	Phloeonomus sjobergi (Strand, 1937)		LC	O	2
Staphylinidae	Xylodromus depressus (Gravenhorst, 1802)		LC	F	1
Staphylinidae	Deliphrum tectum (Paykull, 1789)		LC	F	1
Staphylinidae	Scaphidium quadrimaculatum (Olivier, 1790)		LC	O	8
Staphylinidae	Scaphisoma agaricinum (Linnaeus, 1758)		LC	F	58
Staphylinidae	Scaphisoma inopinatum (Löbl, 1967)		LC	O	6
Staphylinidae	Scaphisoma boreale (Lundblad, 1952)		LC	O	31
Staphylinidae	Scaphisoma assimile (Erichson, 1845)		LC	O	3
Staphylinidae	Oxytelus laqueatus (Marsham, 1802)		LC	F	3
Staphylinidae	Carphacis striatus (Olivier, 1795)	NV	VU	O	70
Staphylinidae	Lordithon thoracicus (Fabricius, 1777)		LC	F	1
Staphylinidae	Lordithon exoletus (Erichson, 1839)		LC	F	2
Staphylinidae	Lordithon lunulatus (Linnaeus, 1761)		LC	F	295
Staphylinidae	Parabolitobius inclinans (Gravenhorst, 1806)		LC	F	1
Staphylinidae	Sepedophilus littoreus (Linnaeus, 1758)		LC	F	75
Staphylinidae	Sepedophilus bipunctatus (Gravenhorst, 1802)	NV	LC	F	1
Staphylinidae	Aleochara sparsa (Heer, 1839)		LC	F	40
Staphylinidae	Aleochara stichai (Likovský, 1965)		LC	F	12
Staphylinidae	Aleochara moerens (Gyllenhal, 1827)		LC	F	4
Staphylinidae	Oxypoda recondita (Kraatz, 1856)		LC	F	1
Staphylinidae	Oxypoda alternans (Gravenhorst, 1802)		LC	F	107
Staphylinidae	Dexiogyia forticornis (Fauvel, 1886)		LC	F	1
Staphylinidae	Haploglossa gentilis (Märkel, 1844)	NV	LC	F	4
Staphylinidae	Haploglossa villosula (Stephens, 1832)		LC	F	49
Staphylinidae	Haploglossa marginalis (Gravenhorst, 1806)		LC	F	3
Staphylinidae	Phloeopora testacea (Mannerheim, 1830)		LC	O	29
Staphylinidae	Phloeopora concolor (Kraatz, 1856)		LC	O	1
Staphylinidae	Dadobia immersa (Erichson, 1837)		LC	O	1
Staphylinidae	Atheta subtilis (Scriba, 1866)		LC	F	75
Staphylinidae	Atheta dadopora (Thomson, 1867)		LC	F	11
Staphylinidae	Atheta sodalis (Erichson, 1837)		LC	F	8
Staphylinidae	Atheta gagatina (Baudi di Selve, 1848)		LC	F	5
Staphylinidae	Atheta trinotata (Kraatz, 1856)		LC	F	1
Staphylinidae	Atheta laevana (Mulsant & Rey, 1852)		LC	F	3
Staphylinidae	Atheta pilicornis (Thomson, 1852)		LC	F	4

Family	Species	Nature value indicators	Red list category	Saproxylic class	No. individuals
Staphylinidae	Atheta crassicornis (Fabricius, 1792)		LC	F	464
Staphylinidae	Atheta euryptera (Stephens, 1832)		LC	F	1
Staphylinidae	Atheta vaga (Heer, 1839)		LC	F	267
Staphylinidae	Atheta harwoodi (Williams, 1930)		LC	F	4
Staphylinidae	Atheta picipes (Thomson, 1856)		LC	F	59
Staphylinidae	Dinaraea linearis (Gravenhorst, 1802)		LC	O	4
Staphylinidae	Thamiaraea cinnamomea (Gravenhorst, 1802)		LC	O	61
Staphylinidae	Thamiaraea hospita (Märkel, 1844)	NV	NT	O	16
Staphylinidae	Pella cognata (Märkel, 1842)		LC	F	3
Staphylinidae	Pella lugens (Gravenhorst, 1802)		LC	F	45
Staphylinidae	Pella laticollis (Märkel, 1842)		LC	F	97
Staphylinidae	Gyrophaena affinis (Sahlberg, 1834)		LC	F	2
Staphylinidae	Gyrophaena gentilis (Erichson, 1839)		LC	F	2
Staphylinidae	Gyrophaena poweri (Crotch, 1866)		LC	F	1
Staphylinidae	Gyrophaena manca (Erichson, 1839)		LC	O	1
Staphylinidae	Gyrophaena boleti (Linnaeus, 1758)		LC	O	1
Staphylinidae	Bolitochara pulchra (Gravenhorst, 1806)		LC	F	1
Staphylinidae	Leptusa pulchella (Mannerheim, 1830)		LC	O	1
Staphylinidae	Leptusa fumida (Erichson, 1839)		LC	O	11
Staphylinidae	Anomognathus cuspidatus (Erichson, 1839)		LC	O	3
Staphylinidae	Placusa complanata (Erichson, 1839)		LC	O	3
Staphylinidae	Placusa depressa (Mäklin, 1845)		LC	O	6
Staphylinidae	Placusa tachyporoides (Waltl, 1838)		LC	O	144
Staphylinidae	Placusa incompleta (Sjöberg, 1934)		LC	O	18
Staphylinidae	Placusa atrata (Mannerheim, 1830)		LC	O	3
Tenebrionidae	Bolitophagus reticulatus (Linnaeus, 1767)		LC	O	6
Tenebrionidae	Diaperis boleti (Linnaeus, 1758)		LC	O	1968
Tenebrionidae	Palorus depressus (Fabricius, 1790)		LC	F	1
Tenebrionidae	Pseudocistela ceramboides (Linnaeus, 1758)		LC	O	4
Tenebrionidae	Mycetochara flavipes (Fabricius, 1792)		LC	O	7
Tenebrionidae	Mycetochara axillaris (Paykull, 1799)	NV	LC	O	1
Throscidae	Aulonothroscus brevicollis (Bonvouloir, 1859)	NV	LC	F	6
Trogossitidae	Nemozoma elongatum (Linnaeus, 1761)		LC	O	1
Zopheridae	Synchita humeralis (Fabricius, 1792)		LC	O	2
Zopheridae	Bitoma crenata (Fabricius, 1775)		LC	O	5

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Code availability
The custom code generated during the current study are available from the corresponding author on reasonable request.

Authors' contributions
Karl-Olof Bergman: Conceptualization, Supervision, Writing—original draft, Writing—review and editing, Methodology. Rebecca Petersen: Investigation, Data curation, Writing—original draft. Victor Johansson: Formal Analysis, Data curation, Writing—review and editing. Lars Westerberg: Writing—review & editing, Methodology. Per Milberg: Data curation, Formal Analysis,

Writing—review & editing. Nicklas Jansson: Conceptualization, Supervision, Methodology, Project administration, Writing—review and editing.

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Data availability
The datasets generated during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval
The authors declare that they obtained the approval of the County Administrative Board of Östergötland for conducting the studies in Göstrings urskog NR, Åbobranterna NR, Stockmossen NR, Högboda NR, Hjälmstorpenäs NR, Rödgölen NR, Säby Västerskog NR, Storpissan NR, Lysings urskog NR, Ycke NR, and Marielund NR.

Consent to participate
Not applicable.

Consent for publication
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Conflicts of interest
The authors declare that they have no conflict of interest.

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