



Saproxylic beetles in Swedish boreal production forests in relation to local and landscape factors

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Abstract

Boreal forests undergo rapid transformation from more or less intact states to even-aged production stands, due to the expanding clearcutting practice. Deepened knowledge on how species diversity and composition vary with local resource availability, such as dead wood, as well with remaining never clearcut forest (having long continuity = ‘continuity forest’) in the surrounding landscape, is essential for the formulation of conservation strategies. In each of six 15×15 km study areas in mid-boreal Sweden (12 000 km²) we sampled saproxylic beetles through sieving of bark from *Picea abies* logs in early stages of decay with bark still attached, within 5 production forests and 5 woodland key habitats (biodiversity hotspots, used as reference; ‘WKH’). A total number of 5147 individuals and 78 taxa were found. Beetle diversity related positively to the local factor of sieved bark area, while the share of continuity forest in the surroundings (5 km buffer; varying 5 – 29% among study stands) was less important, and even showed negative relationships. Species richness was higher in > 60 years old than 0–60 years old production forests but we did not detect a change with age in species composition. The production forests > 60 years old and WKH were similar regarding species richness and composition. WKH had more species of conservation concern than the production forests.

Keywords Bark-sieving · Clearcutting · Dead wood · Log · Norway spruce *Picea abies* · Species of conservation concern · Woodland key habitat (WKH)

Implications for conservation

An increase in local dead wood amount would benefit saproxylic beetles species richness in north European boreal production forests. Production forests > 60 years old may be of interest to species of conservation concern, although WKH seem considerably more important.

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Introduction

Many boreal forest landscapes have undergone strong anthropogenic transformation through clearcutting forestry resulting in a dramatic reduction in the area of intact forests, with subsequent risk of undermining biodiversity, ecological processes and the delivery of ecosystem services (Watson et al. 2018). Northern Europe is the boreal region with the longest and most intense forestry practices, in many parts with large-scale application of clearcutting since the mid-1900s, resulting in only small areas remaining with limited human impact (Potapov et al. 2017; Svensson et al. 2019). Along with the transformation of forests, the amount of dead wood has decreased drastically, as have many dead wood (saproxylic) species (Stokland et al. 2012; SLU Art-databanken 2020). In contrast, after natural disturbances, the volume of dead trees can exceed that of living trees, thus forming a large habitat resource for saproxylic species (Seibold and Thorn 2018).

Dead wood is an important habitat for numerous invertebrates, fungi and other taxonomic groups (Seibold and Thorn 2018) but despite much research during the last decades large uncertainty remains on the relative importance of different scales, a knowledge essential for the formulation of conservation strategies. Studies so far show varying results, restricting abilities for generalizations (Sverdrup-Thygeson et al. 2014; Kärvmö et al. 2021) with some studies pointing to large importance of the local scale (e.g. Lassauce et al. 2011) while others have identified positive landscape effects (e.g. Gibb et al. 2006a; Olsson et al. 2012 Häläinen et al. 2023) or lack of or varying effects (e.g. Ranius et al. 2015; Jacobsen et al. 2020). Saproxylic beetles are frequently used to assess status and dynamics of biodiversity in forests under human transformation, due to their high diversity, comparatively well-known taxonomy and possibility for detection (Grove 2002; Stokland et al. 2012). For instance, the number of obligate saproxylic beetles from the Nordic countries is estimated to about 1100 (Stokland et al. 2012).

A large interest in applied conservation research has resulted in a strong emphasis on the oldest and least anthropogenically affected forests (e.g. Kouki et al. 2012; Svensson et al. 2020), although clearcuts have attracted increased attention not the least regarding saproxylic beetles (e.g. Rubene et al. 2017; Johansson et al. 2020), and specific production forest stages like thinned stands have also been studied regarding these organisms (Stenbacka et al. 2010; Gran and Götmark 2021). Occurrence and dynamics of saproxylic beetles are driven by factors acting at different scales, from individual dead wood objects

to landscapes and above (Sverdrup-Thygeson et al. 2014). At the local scale, amount of dead wood is a strong driver (Seibold and Thorn 2018), and species communities also vary depending on microclimatic factors, e.g. how much light that reaches the logs or snags (Lindhe et al. 2005; Seibold et al. 2016). Many studies also point to a significance of landscape properties (e.g. Rubene et al. 2017; Ekström et al. 2021) although detailed studies with replicated landscapes are scarce (but see Olsson et al. 2012). Despite this knowledge-base, studies on species diversity and composition of various taxonomic groups of different ages of boreal, even-aged production forests are few (but see López-Bedoya et al. 2021). One evident knowledge gap is the possible importance of so far never clearcut forests, i.e. forests with long continuity (here called ‘continuity forest’) still remaining in the landscapes, to dead wood organisms.

Our main aim is to increase insights into drivers of saproxylic beetle diversity and community composition in landscapes dominated by even-aged, coniferous production forests but with still some continuity forest remaining. We investigate boreal landscapes in Sweden, since long transformed by industrial forestry but where some forests without clearcutting impact still occur (Svensson et al. 2019). Although some of these long-continuity forests have been set-aside as conservation areas most are production forests, managed through selective harvest, first through high-grading (removal of the largest trees) and later through repeated thinning. We specifically want to add knowledge on the relative role of local bark amount versus continuity forest in the landscape. To clearly link to nature conservation, we also include old spruce forests identified as biodiversity hotspots, ‘woodland key habitats’ (abbreviated WKH), mapped in a nation-wide survey (Timonen et al. 2010; Wester and Engström 2016), and we also target species of conservation concern. We survey beetles in logs of Norway spruce in an early stage of decomposition when the bark is still attached to the trunk, a substrate to which a large number of saproxylic beetles are associated (e.g. Djupström et al. 2008). Our assumptions are that:

- i. local amount of dead wood is a strong driver of species richness and composition.
- ii. amount of never clearcut, long-continuity forest (continuity forest) in the surrounding landscape is also a strong driver.
- iii. species richness is higher in old compared to young production forest and species composition differs between forest ages.

Methods

Sweden is an ideal study system for even-aged forests since clearcutting forestry has been predominant in all parts of the country since the middle of the last century, and consequently, even-aged stands < 60 years old form large parts of the landscapes. Most forests > 60 years old have never been clearcut although this harvest practice also occurred in some regions prior to the 1950–60s (Lundmark et al. 2013). Production forests comprise 86% of the productive forestland of 23 million ha, with the rest set aside for conservation, by the state (6%) or through retention actions mainly within certification commitments (8%) (SCB 2022). The minimum rotation time ranges between 45 and 100 years, increasing towards the north (Roberge and Fries 2020). Clearcuts are usually regenerated with either Norway spruce *Picea abies* (L.) H.Karst. or Scots pine *Pinus sylvestris* L., each comprising about 40% of the total wood volume in the country (Skogsdata 2020). The dead wood amount on average per hectare for boreal production forests increases with forest age from 3 m³ha⁻¹ for the age class 21–40 years to 16 m³ha⁻¹ for forests > 120 years according to the Swedish National Forest Inventory (Skogsdata 2020). For the

youngest age-class, 0–20 years, retention of dead wood has contributed to current levels of approximately 8 m³ha⁻¹ (Skogsdata 2020).

The study was conducted within the counties of Jämtland and Västernorrland, mid-boreal Sweden, covering approximately 12 000 km² (Fig. 1a, b). In order to capture as large as possible range in landscape proportion of continuity forest, we initially identified 6 15 × 15 km study areas varying in this respect (Fig. 1b). Within each study area we inventoried saproxylic beetles in spruce logs in production forests of different ages, and as a reference in WKH (Fig. 1c, d). A ‘landscape’ was defined as a circular 5 km buffer zone around each production forest stand and key habitat.

Selection of study areas

To identify study areas, we used a high-resolution mapping of remaining, not previously clearcut forests in boreal Sweden covering production forests as well as areas set aside for conservation (Ahlkrona et al. 2017a). The mapping is based on a semi-automatic change detection analysis of satellite images taken between 1973 and 2015, later updated with a visual detection of aerial photos from the

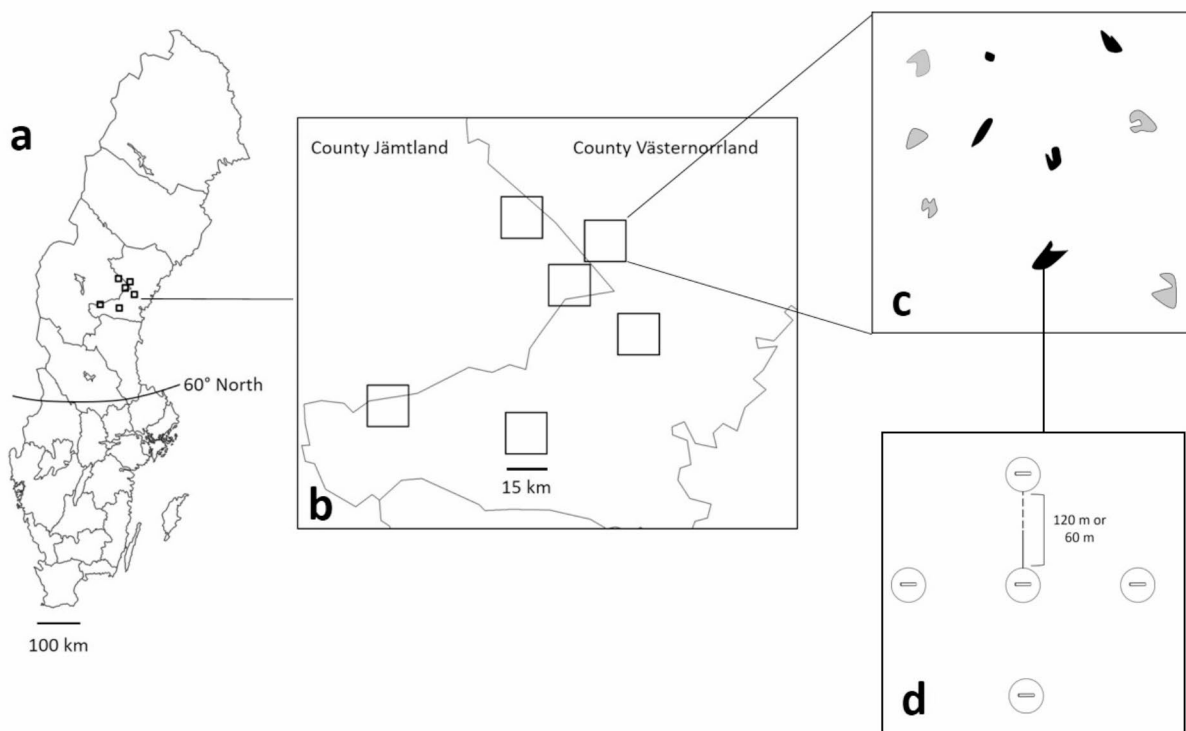


Fig. 1 Sampling design with the position of the six 15 × 15 km study areas (a) in mid-boreal Sweden within (b) the counties of Jämtland and Västernorrland, (c) one study area including five production forests (grey) and five WKH (black), and (d) five random circular plots in each production forest or WKH, with a radius of 30 m (area 2800 m²), with one sampled log in each for which 0.5 m² bark (if possible) was sampled

1950s and 1960s (Ahlkrona et al. 2017b, 2019). However, since clearcutting is an ongoing forest harvesting practice resulting in rapid landscape changes, we used landcover data including clearcuts from 2018 (Swedish Environmental Protection Agency 2019) to correct for changes since 2017. To further compensate for clearcuttings made between 2018 and 2019, we used data from the clearcutting database of the Swedish Forestry Agency. These never clearcut, long-continuity forests (continuity forests) correspond to the pCF category of Svensson et al. (2019). A continuity forest raster and a mask grid covering the entire forestland of the two counties was used, with a 10 m resolution. Based on searches of 15×15 km surroundings from each 10×10 m cell, we identified the 6 study areas with the largest range in landscape proportion of continuity forest, resulting in a variation between 4% and 25%. (Fig. 1b). All analyses were conducted in ArcMap 10.7.

Selection of production forests and WKH

Within each of the six 15×15 km study areas, we selected five production stands and five WKH based on the criteria that they should be spruce-dominated and be on mesic soil (to decrease the environmental variation and to focus on the most common soil type). (Fig. 1c). Production stands were identified from the stand-database of the forestry company SCA and from a free data source showing the approximate forest age (SLU 2010), followed by field inspection (July – September 2019). In each of the 15×15 km study areas, one stand in each of the age-classes 0–20, 21–40, 41–60, 61–80, 81 – >120 years was selected. This fine-scale division was made to enable detailed age-class analyses. WKH have in a large national survey been identified as especially valuable to biodiversity and are in the region dominated by old coniferous forest with high structural diversity (Wester and Engström 2016). From the WKH database of the Swedish Forestry Agency, we selected coniferous-dominated stands on mesic soil. All production forest stands in the oldest age-category (81 - >120 years) and all WKH were in the remote-sensing analysis identified as continuity forest.

Sampling of logs

We used an area-based sampling design with selection of a maximum of 5 logs in each forest stand, within an area of 1.4 ha. This was a deliberate strategy to reflect that availability of logs (and thus habitat available to saproxylic species) vary between forest ages (Skogsdata 2020), and with the expectation that <5 logs would be available in some of the youngest stands. One log of Norway spruce *Picea abies* was selected within each of five circular plots per stand with a radius of 30 m (2800 m²). For stands <1.4 ha in size,

the whole stand was searched (Fig. 1d). The first plot was positioned at the stand center, and the following four plots in directions N, E, S, W, at a distance of 120 m from the center point for stands >5 ha and at 60 m for stands <5 ha in size (Fig. 1d). In a few cases, the stand was so difficult to traverse that the first plot was a random point at the part of entry, with enough space for four additional plots. The first log found when searching clockwise from the center point in the plot was selected. Criteria for logs were (i) Norway spruce *P. abies*, (ii) decomposition category II and III according to Siitonen and Saristo (2000) implying early stages of decay before most of the bark has fallen off but excluding logs dead less than one year (with fresh phloem), (iii) diameter > 10 cm, (iv) mesic soil (the part > 10 cm in diameter), and v) > 10 m from stand edge towards a habitat clearly deviating from the stand structure (e.g. clearcut, lake). Sampling was performed in September 2019. Totally, 6 study areas, 30 WKH, 30 production forests and 242 logs (<5 logs were found in 22 of the stands) were included in the study.

Beetle sampling and identification

The sampling procedure was modified after Djupström et al. (2008). A piece of bark maximum 0.5 m² was collected from each sample log, its area was recorded, and was sieved for one minute through a metal wire net mesh. This method captures beetles that with certainty have colonized the bark, in contrast to flight traps which catch beetles during their dispersal phase (Djupström et al. 2008). Beetles were extracted by placing the finer fractions from the sieving under a lamp in Tullgren funnels (Southwood and Henderson 2000) at the same day as the collection of bark. The nomenclature followed the Swedish taxonomic database Dyntaxa (www.dyntaxa.se). Classification of red-listed species follows SLU ArtDatabanken (2020).

Statistical analysis

All statistical analyses were performed using the R software, version 4.4.0 (R Core Team 2024). To estimate how large proportion of the total species pool we captured, we constructed a species accumulation curve and extrapolated the curve to its asymptote (using the R package iNEXT, Hsieh et al. 2024).

To ensure statistical power, the age-classes were merged into 0–60 years old ('young production forest'; 18 stands), and > 60 years old ('old production forest'; 12 stands). For these two production forest age-classes and the WKH (in the following 'stand categories'), we first calculated (for each stand) the total number of sampled logs, total bark amounts, and the landscape proportion of continuity forest

within a 5 km buffer (all three later used as explanatory variables), as well species richness and the Shannon diversity index (both later used as response variables). We then tested the correlation between all these variables and their relation with stand category using Spearman rank correlations and Kruskal-Wallis tests with associated post-hoc test (for comparisons with stand category). After initial testing, we removed the number of logs from further analysis since it was strongly correlated with the total amount of sieved bark ($\rho=0.96$, $p<0.001$, Supplementary Materials Table A1).

To analyze species richness and the Shannon diversity index in relation to the remaining explanatory variables mentioned above, we built generalized linear mixed effect models (GLMMs) using the *glmmTMB* package (Brooks et al. 2017), with study area identity (6 study areas) as random effect. For species richness, we used poisson distributions and for the Shannon diversity index we used a normal distribution. For bark amounts we also tested the squared term as we expect an asymptotic relationship with increasing bark amounts. Models were built based on AIC, and the final (best) model was the one with the lowest AIC. To test if the species richness of all stand categories was explained by the landscape proportion of continuity forest within 5 km, we also fitted separate models for each stand category.

As a complement to the analysis of all species jointly we also tested species richness of a sub-group of species of conservation concern comprising red-listed species (SLU Art-Databanken 2020) and indicator species of forests with high conservation value (Nitare 2019): *Agathidium nigrinum*, *Atomaria alpina*, *Atomaria subangulata*, *Cis dentatus*, *Corticaria lapponica*, *Ernobius explanatus*, *Euedectus giraudi*, *Hylurgops glabratus*, *Olisthaerus substriatus*, *Orchesia fasciata*, *Peltis ferruginea* and *Zilora ferruginea*.

To describe the general beetle species composition, we performed a nonmetric multidimensional scaling (NMDS) analysis on the total number of individuals in each stand. The NMDS was performed with the R package *vegan* (Oksanen et al. 2022) using the Bray–Curtis dissimilarity index. We had to use three dimensions to reduce the stress value to acceptable levels (<0.2 , McCune and Grace 2002). We only included species that were present in at least eight stands (14 in total) to improve model convergence. Significant relationships between species composition and explanatory variables (stand category, amount of continuity forest in the surrounding landscape, and bark amount) were assessed with Permutational Multivariate Analysis of Variance (function *adonis2* in *vegan*; Oksanen et al. 2022).

To compare beetle dissimilarity among stands (β -diversity) between stand categories we used the Bray-Curtis similarity indices obtained with the *betapart* package in R (Beselga and Orme 2020). The distributions within

each category were then compared using ANOVA and pairwise differences were assessed with Tukeys HSD (post hoc) test.

To assess how dominant species were associated with stand categories, the amount of continuity forest in the surrounding landscape, and the amount of bark sieved we used non-parametric tests (Kruskal-Wallis for stand category and Spearman rank correlations for continuity forest and amount of bark). We used the total number of individuals and tested all species occurring in at least eight stands (14 species in total).

Results

General characterization

In total we recorded 5147 saproxylic beetles distributed among 78 species. The total number of logs sampled was 50 for young production stands, 54 for old production stands, and 138 for WKH, and the corresponding numbers for total bark amounts were: 22.1 m², 26.7 m², and 68.3 m². The number of sampled logs and amount of sieved bark increased with stand age (Supplementary Materials Fig. A1). The rarefaction analysis indicated that about 62% of the total species pool was captured in our sample (Supplementary Materials Fig. A2). The most common species was the bark beetle *Crypturgus hispidulus* with 3038 individuals (59.0% of the total number), followed by *Leptusa pulchella* (440, 8.5%), *Polygraphus punctifrons* (373, 7.2%), *Dryocoetes autographus* (310, 6.0%), and *Rhizophagus dispar* (220, 4.3%) (Supplementary Materials Table A2). These five species, hence, comprised almost 85% of all species records, while most species had very few individuals with a median of 3.

Species diversity

The number of species per stand ranged between 0 and 17 (mean = 8.6, SE = 0.52), and the number of individuals ranged between 0 and 381 (mean = 91.9, SE = 12.2). Only 7 individuals of species of conservation concern were found in production forests (one in young and 6 in old), while 47 were found in WKH. The average number of species of conservation concern per stand was 1.57 (11 species in total) for WKH, 0.5 (3 species in total) for old production forest and 0.06 (1 species in total) for young production forest. The number of logs found in a stand and the total amount of sieved bark were clearly lower in young production forests compared to old production forests and WKH (Supplementary Materials Table A1). The proportion of continuity forest within 5 km did not differ between stand categories

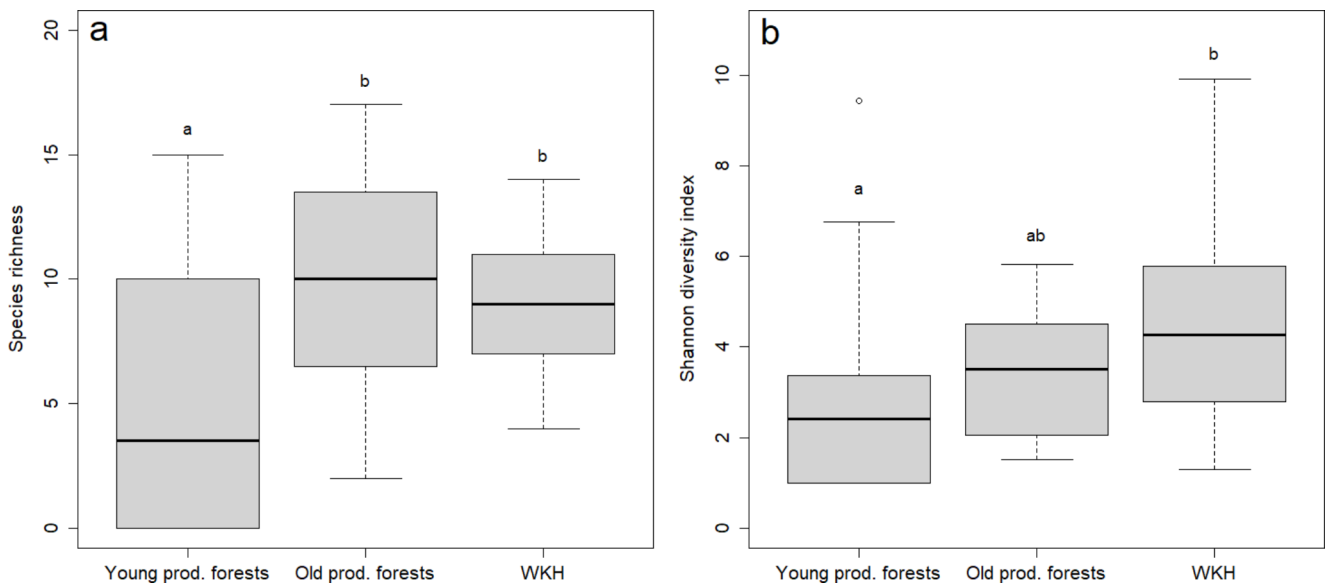


Fig. 2 The distribution of **a**) the species richness (total number of beetle species per stand, α -diversity) and **b**) the Shannon diversity index for each stand category. Letters (**a** or **b**) above each boxplot indicate significant differences among stand categories based on Dunn's post hoc test (the same letter signifies non-significant differences). Horizontal black line shows the median for each stand category

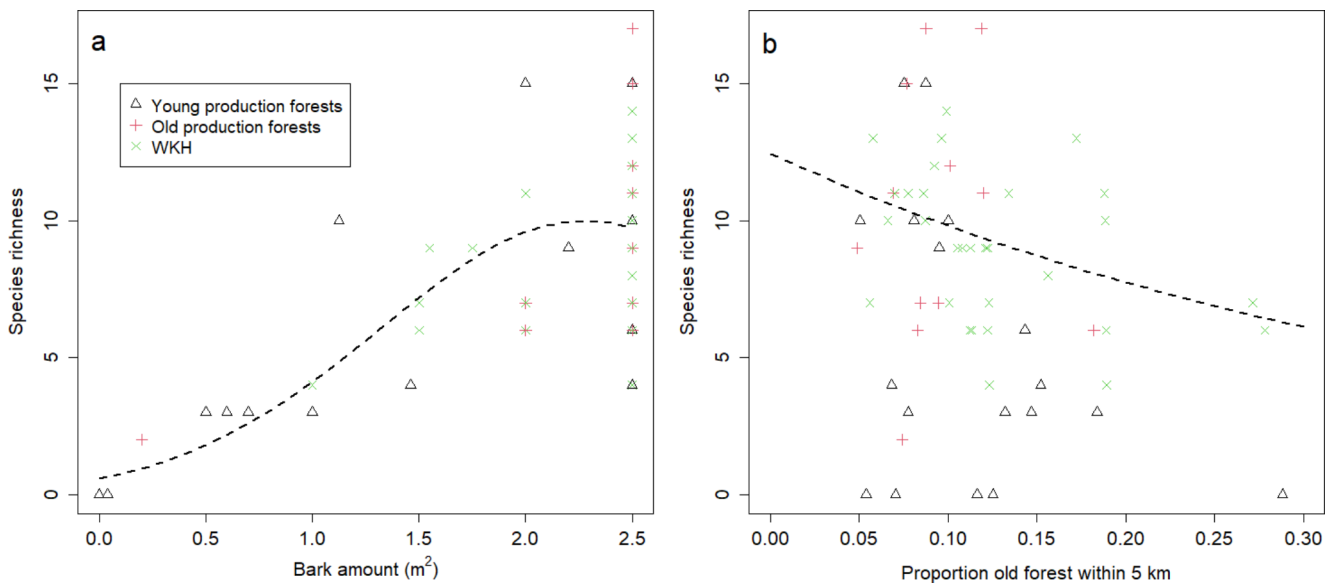


Fig. 3 Species richness (total number of beetle species per stand) in relation to **a**) the amount of sieved bark per sample stand, and **b**) the proportion continuity forest within 5 km from the focal stand ("andscape") in young production forests (0–60 years, $n = 18$), old production forests (> 61 years, $n = 12$), and for WKH ($n = 30$). Broken lines signify model predictions for each of the two explanatory variables when the other variable was kept constant at its mean value

(Supplementary Materials Table A1) and was not correlated to any of the other explanatory variables ($p > 0.5$). Species richness and the Shannon diversity index correlated significantly to both the number of logs, bark amounts, and were clearly lower in young production forests while there were no differences between the old production forests and the WKH (Supplementary Materials Table A1, Fig. 2). For species of conservation concern the number of species was significantly higher in the reference forests (WKH) compared

to both young ($p < 0.001$) and old ($p = 0.025$) production forests, while the latter two did not differ significantly.

According to the GLMMs total species richness increased with increasing bark amounts (where the negative squared term gives an asymptotic relationship, Fig. 3), while it decreased with increasing proportion of continuity forest within 5 km (Table 1; Fig. 3), although this relationship was weaker. When tested separately, only the young production forests showed a significant negative relationship with

Table 1 Parameter estimates (SE) for the generalized linear mixed effect models (GLMM) of total species richness, the Shannon diversity index, and the richness of species of conservation concern species, and the change in AIC (Δ AIC) when removing the variable from the final (best) model

	Total species richness		Shannon diversity index		Richness of species of conservation concern	
	Estimate (SE)	Δ AIC	Estimate (SE)	Δ AIC	Estimate (SE)	Δ AIC
Intercept	1.87 (0.07)		3.77 (0.25)		-3.01 (1.01)	
Bark amount	2.08 (0.42)	30.7	0.95 (0.26)	10.7		
Bark amount ²	-1.31 (0.35)	14.2				
Proportion continuity forests within 5 km buffer (landscape)	-0.12 (0.05)	3.9			-0.43 (0.25)	1.1
Stand category ^a						
-Old production forest					1.40 (1.15)	24.3
-WKH					3.03 (1.02)	

^a Stand category has two parameter estimates as the categories 'old production forests' and 'WKH' are compared to the reference category 'young production forests'

proportion of continuity forest within 5 km ($p < 0.001$), even if there was a tendency also for WKH ($p = 0.07$). The Shannon diversity index increased with bark amount (Table 1). When bark amount was a significant predictor in the model, stand category was unimportant to total species richness as well as Shannon diversity index. In contrast, the richness of species of conservation concern was mainly explained by stand category (Table 1), where WKH clearly had more species of conservation concern than production forests (regardless of age). Species of conservation concern, however, showed a tendency to decrease with the proportion of continuity forest within 5 km, but the change in AIC, when this variable was included in the model, indicated a weak relationship (Table 1).

Species composition, stand similarities and species abundances

The species composition was explained by the amount of bark ($R^2 = 0.11$, $F = 6.27$, $p = 0.001$; Fig. 4) while stand category and the proportion of continuity forest within 5 km were insignificant ($R^2 = 0.03$, $F = 0.90$, $p = 0.52$, and $R^2 = 0.01$, $F = 0.42$, $p = 0.89$, respectively). Also, when stand category was analyzed separately it remained insignificant ($R^2 = 0.04$, $F = 1.04$, $p = 0.38$).

The stand dissimilarity in species composition was significantly larger among young production stands compared to the old production forests ($p = 0.029$), while there was no difference compared to WKH (Fig. 5). There was no significant difference between the latter two.

The abundances of eight species were positively correlated with the amount of bark (Table 2) and one species *Cis punctulatus* showed a negative correlation with the proportion continuity forest within 5 km. Four species were affected by stand category, with three most common in old production forests (*Cis punctulatus*, *Crypturgus hispidulus*,

and *Leptusa pulchella*) and one in WKH (*Dropephylla liniaris*).

Discussion

Local amount of bark was the strongest driver of the saproxylic beetle diversity, and contrary to our expectations, landscape amount of continuity forest was considerably less important and even showed a negative, although weak, relationship with species richness. In line with one of our expected outcomes, species richness was higher in old than young production forests but on the other hand, species composition did not vary with age or between production forests and WKH. WKH hosted more species of conservation concern than old production forest.

Local and landscape factors

Earlier studies including the landscape scale point to variable outcomes regarding the relative role of local and landscape factors (Sverdrup-Thygeson et al. 2014). We suggest three possible explanations for this variation in results among studies. First, mapping of old forest is based on different data sources such as snapshot satellite images, forest-company and authority maps or a combination of remote sensing and forest inventory data. One advantage with our study is that we used a new dataset with high-resolution, temporal analysis of aerial photographs covering > 50 years, identifying forests that likely have never been clearcut, with considerable old-growth legacies, i.e. such that we named 'continuity forests' (Svensson et al. 2019). Second, different trapping methods such as flight traps, eclector traps, and as in our study sieving of bark, vary greatly in their effectiveness to capture saproxylic species (e.g. Martikainen and Kouki 2003). There are pros and cons with respective method with bark sieving and eclector traps capturing saproxylic species

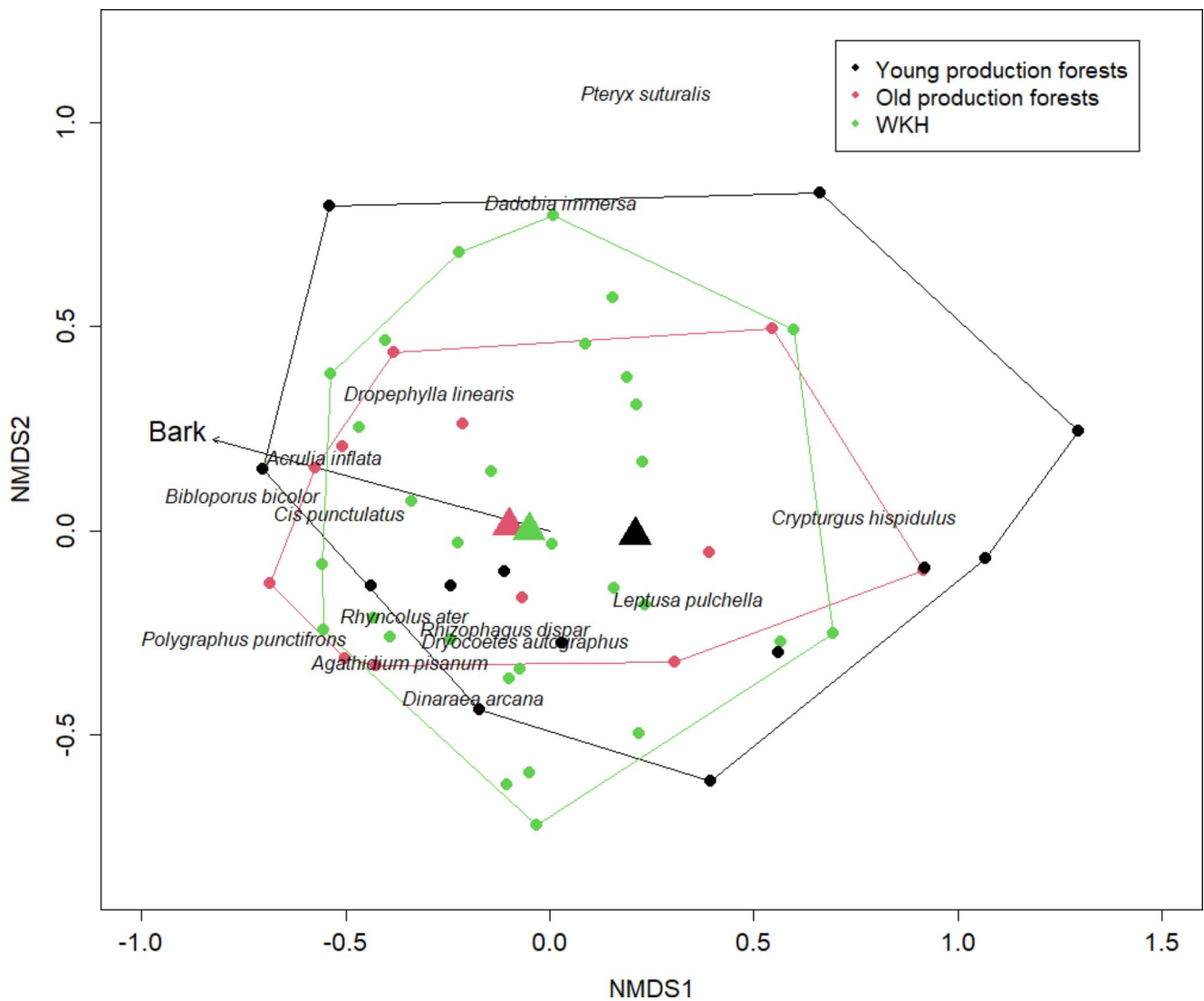


Fig. 4 The species composition of saproxylic beetles (occurring in at least eight stands) in young production forests (black dots), old production forests (red dots), and in WKH (green dots). The ordination was 3-dimensional to reach convergence (stress=0.18). However, for simplicity only the 2D-plots (of axes 1 and 2) are shown here. The polygons show the outer limits of each stand category and the triangles the corresponding centroids

from a specific piece of wood, while the local species pool of saproxylics as well as non-saproxylics are captured with window traps. Evaluations point to bark sieving having higher shares of saproxylic species than eclector traps while eclector traps have the advantage of capturing species also inside the wood (Alinvi et al. 2007). Third, species richness and composition vary with decay stage, as shown by Jonsell et al. (2019) that in a time-series only found an effect of surrounding forest on saproxylic beetles in dead wood in late stages of decomposition. Since we used only slightly decayed spruce logs, we may have missed important variation. Further, our landscape proportion of continuity forests within 5 km ranged between 5% and 29% which might be too narrow to capture effects. Unfortunately, in

northern Europe, the boreal region with the longest history of clearcutting globally, continuity forests are today very uncommon, and thus higher proportions are difficult to find. Taken together, the current evidence-base seems too weak to enable general conclusions regarding landscape effects.

Forest age

The finding that young production forests (<60 years old) had lower total species richness than old forest (>60 years old) agrees with Stenbacka et al. (2010); one of few other studies including the full range of boreal production forest ages. As they did, we interpret this to be linked to habitat availability, in our case to the lower amount of logs and

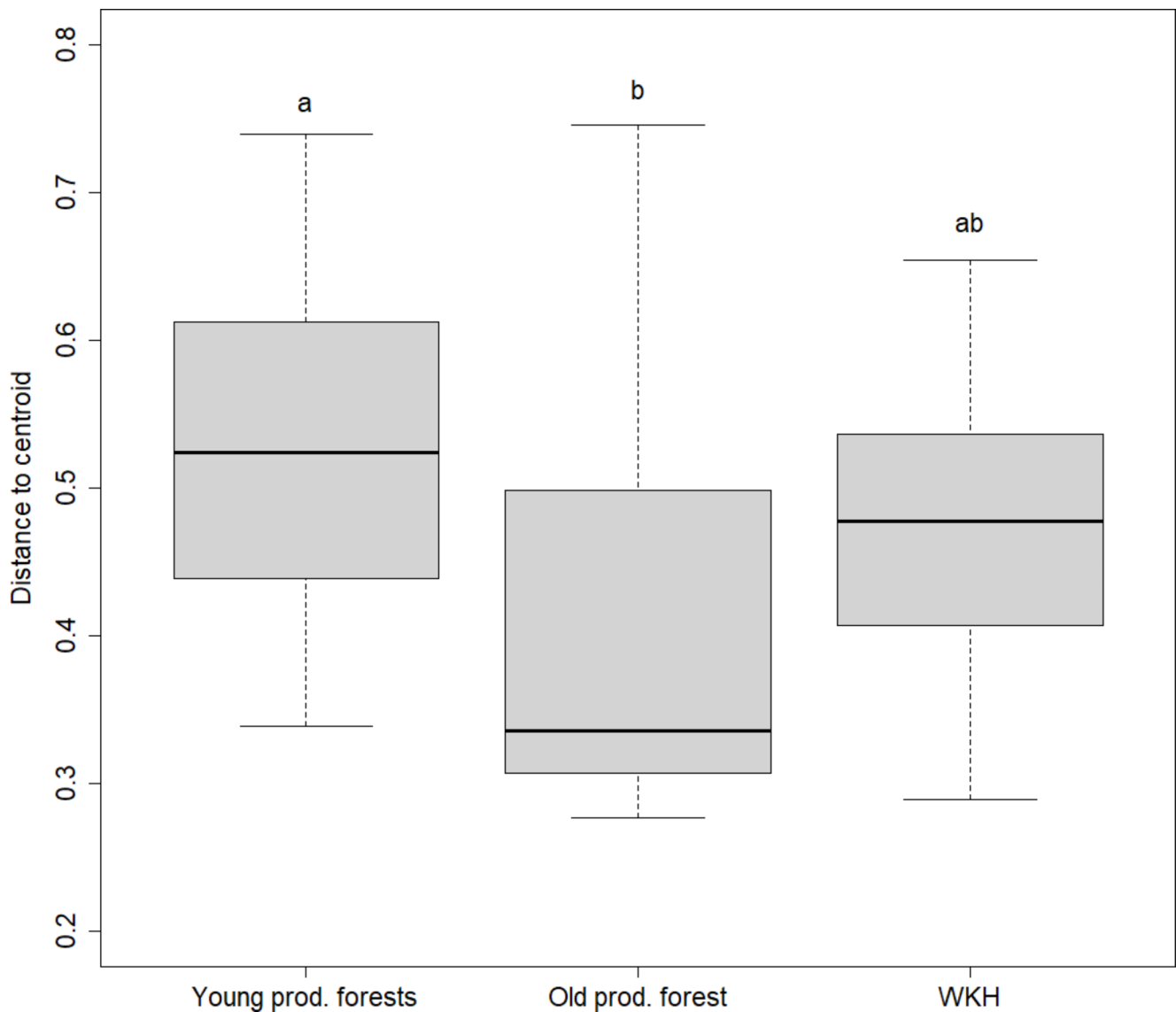


Fig. 5 The dissimilarity between stands (β -diversity) within each stand category. Letters (a and b) above each boxplot indicate significant differences among stand categories based on Tukey's post hoc test. Distance to centroid (the distance between each stand and the group centers based on principal coordinates) gives a measure of variation in species composition for each group, where larger values signify larger variation

bark in the young production forests. The sampling that we applied was designed to capture logs and bark in relation to their density, and we expected (and found) lower density in younger stands. Had we used a design with sampling of the same number of logs over areas varying in size (larger areas searched in low-density stands), the number of saproxylic beetles in the youngest age stages would have been overestimated. The low amount of dead wood and the increase with forest age is typical for clearcutting forestry in north Europe while it may be different in other regions, such as Central Europe where young coniferous stands can host a high richness of saproxylic beetles (Zumr et al. 2022). Also in some cases, such as following extensive tree die-back caused by bark beetle outbreaks, the situation may be different with

very high amounts of dead wood and a rich saproxylic fauna (e.g. Vrba et al. 2024), although absence of salvage logging then is a condition (Thorn et al. 2018). The lack of effect of forest age on species composition in our study was surprising since such could be expected from the change in environmental conditions during forest succession. For instance, light is a strong determinant of saproxylic species composition, with more species in open conditions (Lindhe et al. 2005; Seibold et al. 2016; Lettenmaier et al. 2022) and thus, a specific species composition could be expected in the young, comparatively open forests with a higher light availability compared to closed forest (Chen et al. 1993). Several studies that compare clearcuts to old forests (excluding intermediate age-classes) also point to clearcuts having a

Table 2 Tests of the relation between individual species abundance (of species occurring in at least eight stands) and the explanatory variables bark amounts, proportion of continuity forest (spearman rank correlations with correlation coefficient ρ and associated p -value), and stand category (Kruskal-Wallis test with χ^2 test statistic and associated p -value). Significant p -values are in written in bold

	Bark amount		Proportion continuity forest within 5 km		Stand category	
	p	p -value	p	p -value	χ^2	p -value
<i>Acrulia inflata</i>	0.353	0.008	-0.071	0.589	1.741	0.419
<i>Agathidium pisanum</i>	0.271	0.044	-0.139	0.289	3.266	0.195
<i>Bibloporus bicolor</i>	0.264	0.049	-0.225	0.084	1.382	0.501
<i>Cis punctulatus</i>	0.404	0.002	-0.303	0.019	8.059	0.018^a
<i>Crypturgus hispidulus</i>	0.429	0.001	-0.100	0.448	9.106	0.011^a
<i>Dadobia immersa</i>	0.049	0.719	-0.158	0.229	1.842	0.398
<i>Dinaraea arcana</i>	0.204	0.132	0.029	0.827	3.484	0.175
<i>Dropephylla linearis</i>	0.315	0.018	-0.106	0.418	6.829	0.033^b
<i>Dryocoetes autographus</i>	0.230	0.089	0.044	0.729	1.801	0.406
<i>Leptusa pulchella</i>	0.476	<0.001	-0.078	0.553	6.945	0.031^a
<i>Polygraphus punctifrons</i>	0.116	0.394	-0.042	0.749	3.363	0.186
<i>Pteryx suturalis</i>	0.175	0.198	-0.185	0.156	0.632	0.729
<i>Rhizophagus dispar</i>	0.368	0.005	-0.178	0.173	2.941	0.230
<i>Rhyncolus ater</i>	0.092	0.498	0.024	0.857	0.287	0.866

^a Most abundant in old production forests, ^b Most abundant in WKH

different saproxylic beetle composition than forests mature to be harvested (e.g. Gibb et al. 2006b; Johansson et al. 2007; Jacobsen et al. 2020). The compositional similarity between young production forests, old production forests and WKH point to common, generalist species strongly driving species composition. The fact that five species comprised almost 90% of all captured individuals, and with a strong dominance of the bark beetle the *Crypturgus hispidulus*, indicate that a few species have a decisive influence on the diversity patterns.

The higher variation in species composition in the <60 year old than >60 year old stands (beta diversity) still point to the younger age-class having larger environmental variation. This is not surprising since this younger age-class comprises recently harvested, open, treeless areas as well as regenerating forests. Our data did not allow analyses with a finer age-class resolution but such a division will be essential for further studies. For the future, ideally, the youngest, open age-classes (about 0–30 years old) should be separated due to its deviating microclimatic conditions.

Production forests, WKH and species of conservation concern

Our reference stands, WKH, did not differ from the >60 year old production forests regarding species diversity and composition of saproxylic beetles. This is surprising since WKH were mapped using structural and species indicators in a nation-wide inventory to identify hotspots for biodiversity (Wester and Engström 2016). Nevertheless, in boreal Sweden, Hjältén et al. (2012) also failed to detect compositional differences for saproxylic beetles between old, managed forests and protected areas, and explained this with

many old stands never been clearcut in the past and thus having long tree continuity. In contrast to saproxylic species as a group, species of conservation concern were in our data-set significantly more common in WKH than in production forests. This result should be interpreted with some caution, due to the low total number of individuals; 54 for production forests and key habitats together, with almost 90% found in WKH. Still the rarefaction curve revealed that we had sampled a comparatively large proportion of the total species pool (Supplementary Materials Fig. A2). Both WKH and production forests >80 years old (comprising half of the stands in our age-category >60 years old) were in the remote sensing analysis found to be continuity (never clearcut), possibly indicating that they might be overall similar also regarding uncommon species, as has been found by Hjältén et al. (2012). Although the continuity forests have been selectively harvested at several occasions and also thinned, they have had a continuous tree-cover, and thus have a widely different background compared with stands emerging from clearcutting, although they may look surprisingly structurally similar. In the future, it will be important to, through a larger sample size, divide the age-class >60 years old further, and compare production forests >80 years old and WKH, especially regarding their content of species of conservation concern. This is especially urgent since there has been an intense debate on how much production forests, especially in the western part of boreal Sweden, qualify as WKH (Bjärstig et al. 2019; Hallberg-Sramek et al. 2020). Further, the so far never clearcut forests will soon disappear, if they are not protected (Ahlström et al. 2022). To fully evaluate the diversity patterns of saproxylic beetles, extended studies including a wider range of decay stages are

also needed (Martikainen and Kouki 2003; see also Burner et al. 2022).

Conclusions

In agreement with many other studies, we show that dead wood availability at local level is a strong driver of saproxylic beetle richness and composition in forests (e.g. Lassaue et al. 2011; Seibold and Thorn 2018). The conservation implication is that an increase in dead wood in production forests would benefit the saproxylic beetle fauna. Unexpectedly, we found a negative, although weak, relationship between amount of continuity forests and species richness of saproxylic beetles, indicating so far little known and unexplored mechanisms for patterns and dynamics of saproxylic species. More studies at the landscape scale are needed to understand interactions between production forests and the small proportion continuity forests remaining in the since long heavily transformed boreal forests of north Europe. Such knowledge is also relevant for other parts of the boreal region with expanding industrial forestry where strategies for maintenance of remnant old forests will be an important issue. For conservation, deeper analyses of the oldest, never clearcut production forests is also essential, including comparisons with the mapped biodiversity hotspots (WKH).

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Author contributions LG initiated the study, coordinated the beetle sampling, and wrote substantial parts of the manuscript. JA performed the remote sensing analyses, was responsible for the selection of study sites incl. field visits, and wrote parts of the manuscript. MattJ took part in the initiation of the study and in the interpretation of results. MJ, TL, JS, JW contributed to the interpretation of results. VJ took part in the initiation of the study, performed the statistical analyses, contributed to the interpretation of results, and wrote important parts of the manuscript. All authors contributed to the study design and examined the manuscript critically.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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