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Research article

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

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ABSTRACT

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

1. Introduction

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

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

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

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

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

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

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

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

2. Material and methods

2.1. Study areas and sampling design

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

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

2.2. Beetle sampling and classification

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

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

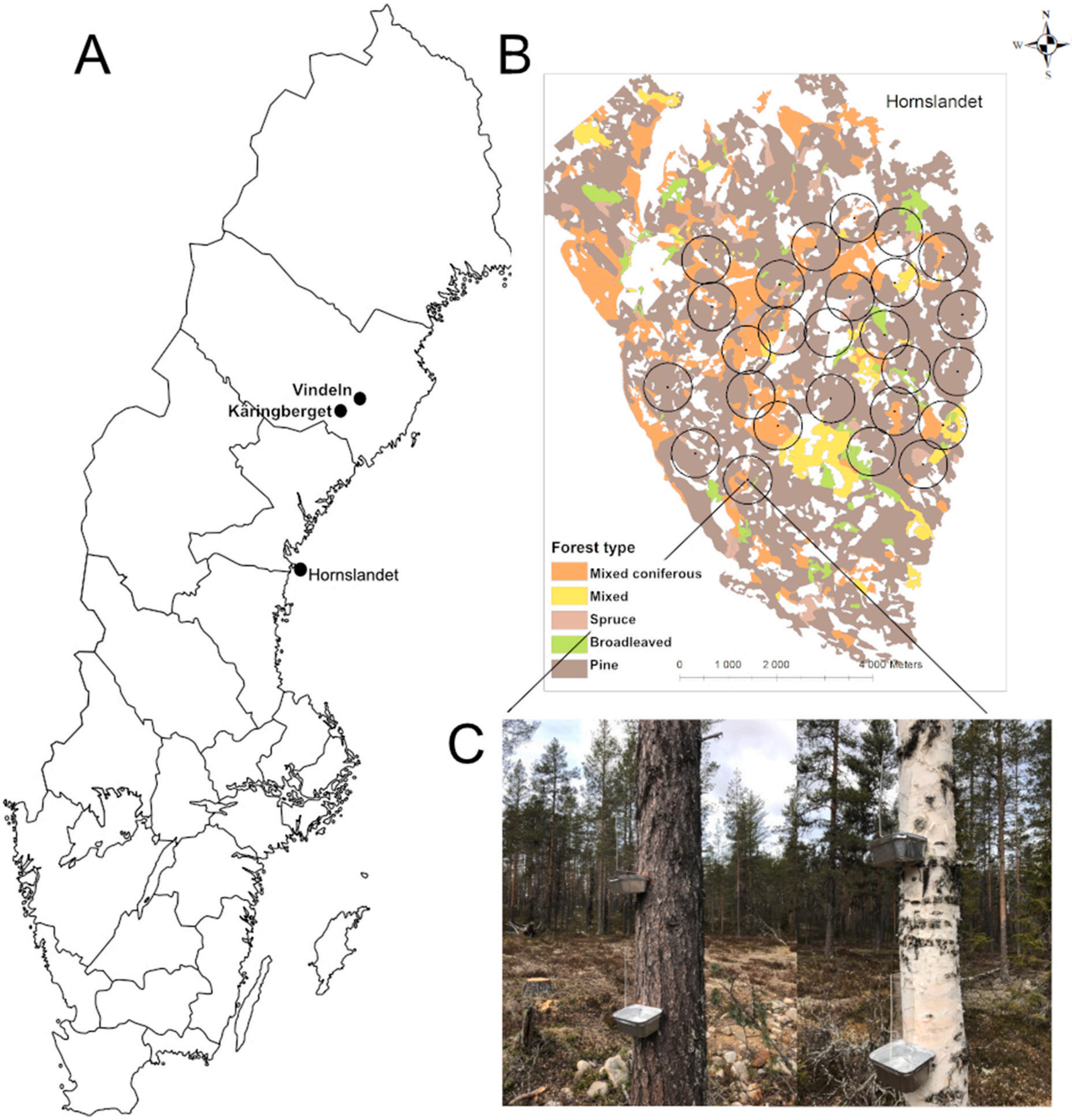

Fig. 1. A map of the locations of study landscapes in Sweden (A). An example of the placement of the plots in the landscapes (black dot), with 500 m radius buffer (B). Each plot contain one pair of high stumps of Scots pine and Silver birch, with two flight intercept traps per high stump (C).

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

2.3. Field measurements and environmental data collection

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

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

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

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

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

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

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

2.4. Statistical analyses

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

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

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

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

3. Results

3.1. Species diversity among functional guilds

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

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

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

3.2. Trait – environment interactions

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

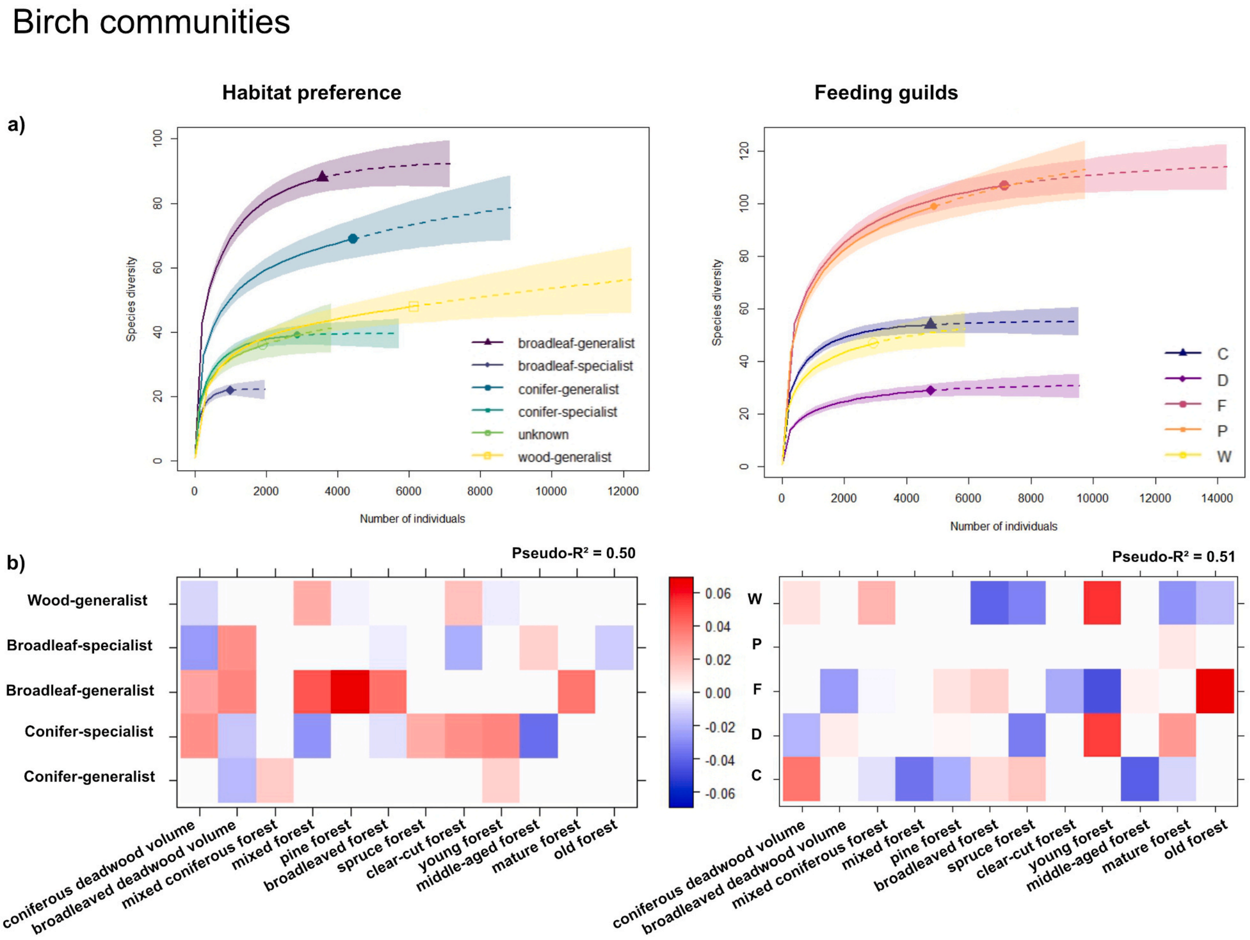

Fig. 2. Rarefaction curves for birch communities (a) with 95% confidence intervals (shaded areas) comparing the γ-diversity of ecological traits. Heat maps (b) of interaction coefficients for birch communities between traits (vertical axe) and environmental variables (horizontal axe) showing positive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

different trait groups.

3.2.1. *Trait responses to local deadwood amounts*

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

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

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

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

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

Among beetle communities sampled from pine stumps, conifer

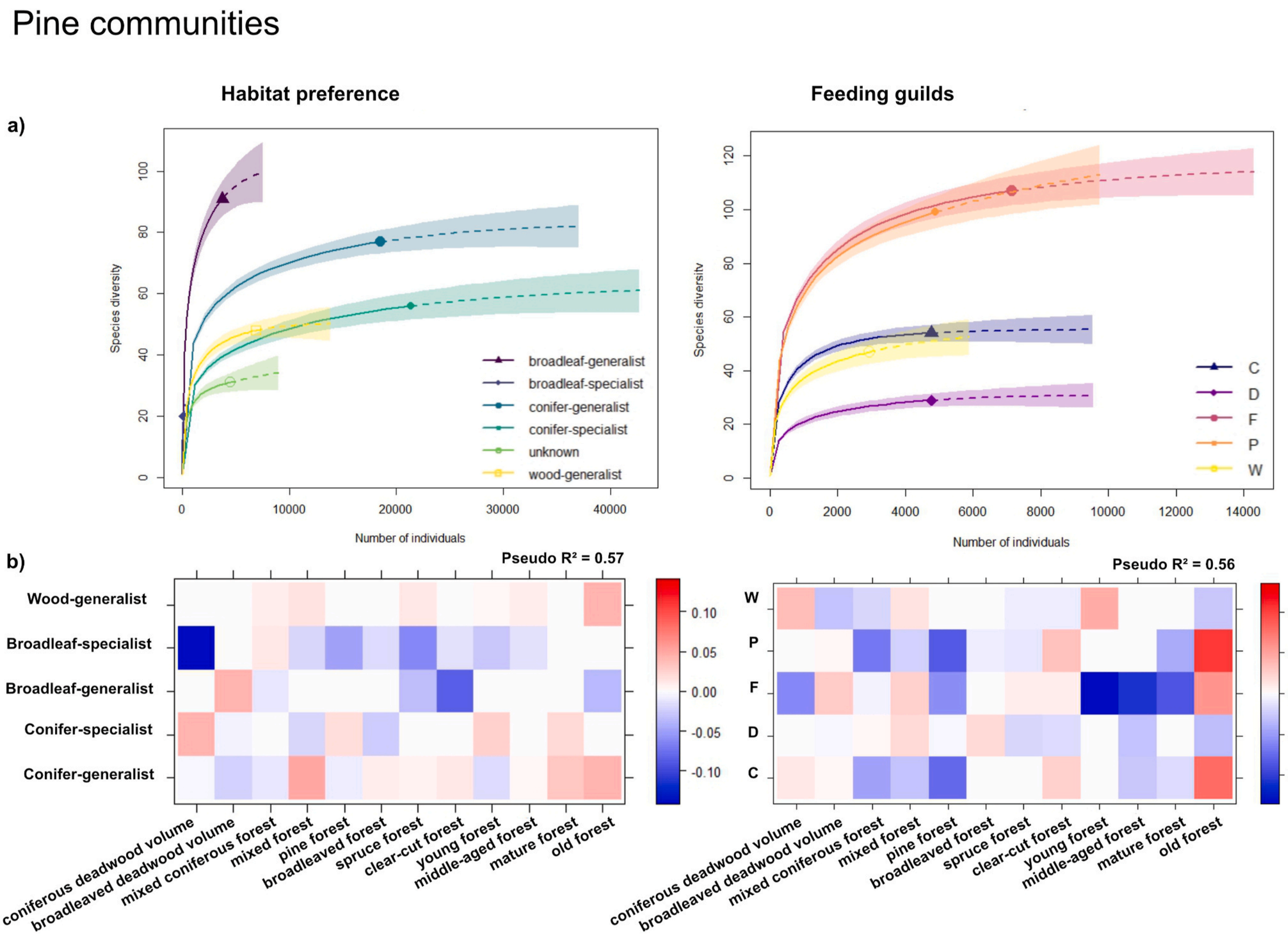

Fig. 3. Rarefaction curves for pine communities (a) with 95% confidence intervals (shaded areas) comparing the γ-diversity of ecological traits. Heat maps (b) of interaction coefficients for pine communities between traits (vertical axe) and environmental variables (horizontal axe) showing positive (red),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

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

4. Discussion

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

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

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

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

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

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

4.2. Importance of forest structures in the landscape

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

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

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

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

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

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

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

5. Conclusions

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

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

CRediT authorship contribution statement

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

Declaration of competing interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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

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