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RESEARCH ARTICLE

A decadal study reveals that restoration guided by an umbrella species does not reach target levels

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Abstract

1. Maintaining structural and functional elements of ecosystems are essential in order to preserve biodiversity and ecosystem function. As a means of guiding conservation work, the umbrella species concept was developed. In Sweden, one putative umbrella species, the white-backed woodpecker, has guided conservation and restoration of deciduous forests for two decades.
2. Here, we evaluate the decadal effects of restoration aimed at the white-backed woodpecker on biodiversity of saproxylic beetles. We compare stands that were restored 12 to 21 years ago to non-restored stands and historical white-backed woodpecker habitats acting as restoration target stands.
3. Restored stands contained higher deciduous deadwood volumes than non-restored stands but lower volumes than restoration target stands. The deadwood in restored stands was concentrated in later decay stages, whereas target stand deadwood was more evenly distributed across decay stages.
4. Restored stands had similar species richness and abundance of most groups of saproxylic beetles compared with non-restored stands while not reaching the levels of restoration target stands. Species assemblages differed among all stand types with restored stands supporting late decay stage and generalist species while target stands supported more deciduous associated and threatened species.
5. *Synthesis and applications*: We conclude that after one to two decades, restoration improve stand structure and benefit beetle diversity but that target levels are not yet reached. Thus, only partial restoration is achieved. Our results stress that for restoration to be successful both continuous and repeated restoration efforts are needed and that it is important to identify target levels of important habitat characteristics when assessing restoration outcome.

KEYWORDS
beetle, biodiversity, community ecology, conservation, deadwood, deciduous, focal species, forest

1 | INTRODUCTION

Maintaining biodiversity is essential to ensure stable and functional ecosystems (Díaz et al., 2013; Oliver et al., 2015). Human land use, including degradation and habitat loss (Betts et al., 2017; Newbold et al., 2015), has led to worldwide biodiversity declines (Jaureguiberry et al., 2022), which in turn calls for large-scale conservation and restoration (Aronson & Alexander, 2013; Benayas et al., 2009). The process of natural ecosystem recovery can be very slow, spanning decades or even centuries (Dobson et al., 1997). Thus, restoration is often needed (Gann et al., 2019) especially for rare or remnant habitat types and if source populations are lacking (Brederveld et al., 2011).

Internationally, forest restoration research is generally focussed on replanting or reseeding of severely degraded habitats. In boreal forests of Fennoscandia, restoration is focussed on restoring structural elements, for example, deadwood, in degraded forests. Common methods are to mimic natural processes such as fire and gap dynamics, so-called natural-disturbance-emulation (NDE) (Gauthier et al., 2009; Hjältén et al., 2023). However, for some habitats, NDE does not provide suitable habitats in short term. One example is natural regeneration of deciduous forest, which might take decades. To generate deciduous dominated stands and deciduous deadwood immediately, direct management of the tree species composition is needed.

Biodiversity conservation is often resource demanding why the development of cost-efficient methods is crucial. The umbrella species concept is based on the idea that conservation focussed on focal species with particularly high demands on habitat quality or size, will also benefit co-occurring species (Fleishman et al., 2000; Lambeck, 1997). When selected using appropriate criteria, umbrella species can be a useful concept in guiding restoration work (Branton & Richardson, 2014; Hurme et al., 2008; Roberge & Angelstam, 2004). Birds are widely used as umbrella species since many species have high demands on both habitat size and quality. In addition, many birds are charismatic, which increase engagement from the public and possibilities of funding (Branton & Richardson, 2011; Roberge et al., 2008; Smith & Sutton, 2008). The high demand of habitat quality and size makes the white-backed woodpecker (*Dendrocopos leucotos*) a putative umbrella species (Roberge et al., 2008). Once widespread throughout Sweden (Aulén, 1988), this critically endangered species has guided restoration of deciduous forest for two decades (Mild & Stighäll, 2005). The white-backed woodpecker demands deciduous forest with large amounts of deadwood, a habitat type almost lost from the Swedish landscape (Axelsson et al., 2002; de Jong, 2002).

Restoration aimed to provide food and nesting possibilities for the white-backed woodpecker, in total, spans tens of thousands of hectares in Sweden. The most commonly used method is to remove spruce in stands where deciduous trees are abundant and thus provide adequate levels of deciduous dominated forest rich in deadwood. A previous study found that restoration of habitat for the white-backed woodpecker supports many deciduous associated beetle species and species of conservation concern in short term, 2–12 years of postrestoration (Bell et al., 2015). However, our knowledge of the long-term effect of restoration for the white-backed woodpecker is limited and thus urgently needed.

Saproxylic beetles are highly represented among forest biodiversity, including species of conservation concern and provide the main food source for the white-backed woodpecker (Hjältén et al., 2023). In addition, saproxylic beetles respond quickly to change in their surrounding environment, making them an appropriate organism group to study in assessing ecological restoration effects on biodiversity.

Biodiversity patterns are scale-dependent (Chase et al., 2019) and a hierarchical approach is often used in biodiversity studies (Gran, 2022; Rubene et al., 2015) going from landscape (γ-diversity) to local (α-diversity) scale while also describing the variation of communities (β-diversity). For example, although α-diversity may be low in a certain habitat type, the overall γ-diversity may be great due to a greater among habitat variability (β-diversity) (Vellend, 2016). This hierarchical approach is thus useful to discern diversity patterns following, for example, ecological restoration.

With the umbrella species concept as a guiding framework, we aim to investigate the decadal effects of ecological restoration on forest stand structures and α-, β-, and γ-diversity of saproxylic beetles by re-visiting the restored stands in Bell et al. (2015), 12–21 years after restoration.

Even though a focal species is not currently inhabiting a site, it may still serve a high value for biodiversity and could thus under the wider umbrella species concept serve as a restoration target (Lõhmus et al., 2021). We therefore define deciduous forest habitat with recent occurrence of breeding white-backed woodpeckers as a restoration target habitat. We define stands that have potential for restoration but are non-restored as reference stands. With the forest landscapes of Sweden being highly degraded and fragmented, hindering dispersal and colonisation of many species, for example, (Edman et al., 2004) and with restoration typically resulting in novel ecosystems supporting different species and structures than, for example, target ecosystems (Aerts & Honnay, 2011), we predict only partial rather than full restoration (Gann et al., 2019). This study is unique as it addresses two major gaps in previous research; we investigate restoration in the context of both negative and positive reference stands and we evaluate decadal effects of restoration. We predict that:

1. Structures of importance to beetle diversity, such as canopy layering and deadwood, will continuously be generated in target stands, whereas restoration stands had a one-time pulse of created structures. Therefore, we expect that living trees in target stands will be distributed in a j-shape of mainly deciduous trees whereas restored stands will have a large proportion of coniferous trees in smaller diameter classes.
2. Deadwood volumes in restored stands will be greater than in non-restored stands but lower than in target stands and concentrated

in later decay stages since deadwood created from restoration was a one-time addition, whereas target stands will have a more even distribution of deadwood among decay stages as a result of continuous supply.

3. We expect the α-diversity of saproxylic beetles, including species of conservation concern, main prey species of the white-backed woodpecker and species preferring deciduous deadwood to be greater in restored than non-restored and similar to target stands. Due to high amounts of late decay deadwood in restored stands, we expect α-diversity of late decay stage species to be greater in restored than non-restored and target stands.
4. Given that that non-restored and restored stands have a management history, which usually results in homogenous stands, we expect overall saproxylic beetle β-diversity to be lower in these stands compared with target stands, which we expect to be more structurally heterogeneous. Responses may be trait-specific, with, for example, coniferous and deciduous specialists responding differently based on variation in forest structures.
5. We expect the overall γ-diversity to be greatest in target stands and restored stands to display intermediate γ-diversity between non-restored and target stands.

2 | MATERIALS AND METHODS

2.1 | Study area

This study was conducted in the central boreal zone in Värmland and Dalsland counties, Sweden (Ahti et al., 1968) between latitudes 59.1–59.9° N and longitudes 12.0–13.7° E (Figure S1). In total, 23 stands were included in the study: eight stands restored in 2000–2010, seven commercially managed mixed stands targeted for restoration that had not been restored and eight stands consisting of historical breeding habitat for the white-backed woodpecker, hereafter target stands, these stands hosted breeding white-backed woodpeckers up until 2005–2016. The target stands are considered to have the highest potential to host breeding pairs of the white-backed woodpecker in their respective region, and extensive restoration work has been done in the landscape surrounding these stands for more than 20 years. The average stand size was 11.4, 5.7 and 9 hectares for non-restored, restored and target stands, respectively. Prior to restoration, restored and non-restored stands were deemed similar regarding environmental variables based on stand data and field visits. Non-restored stands are production stands that have undergone conventional forest management, but where the proportion of deciduous trees is higher than average, making them suitable for restoration. In 2000–2010, spruce trees were removed from the restored stands. Some deciduous trees were girdled or made into high-stumps (Bell et al., 2015). The field studies conducted in protected areas had permission granted by the County Administration Board of Värmland [525-4458-2021]. The study did not require ethical approval.

2.2 | Environmental data

Tree species and diameter at breast height (DBH, 1.3 m) were recorded for all living trees higher than 1.3 m and >5 cm in DBH within a 10-m circular sample plot at the centre of each stand. Coarse woody debris (DBH >10 cm, length/height >1.3 m) was measured within one 25-m circular sample plot, at the centre of each stand. We divided all deadwood by type (logs and snags), tree species and decay stage following Gibb et al. (2005) for logs and Jung et al. (1999) for snags. Top and bottom diameter and length was measured for logs. For snags, we measured diameter in breast height and assessed height. Deadwood volumes for logs and snags up to 6-m height (as these snags were usually broken) were calculated as cylinders. For taller snags (>6 m), we used Brandel's (1990) southern Sweden volume functions for pine and spruce with birch being used for all deciduous tree species.

2.3 | Beetle sampling

Three IBL2, flight-intercept traps were strung between trees at breast height in a North, South-east, South-west pattern based on the centre of each stand, approximately 30–70 m from the stand centre. IBL2 traps are large (base 1 m, height 1 m, intercept area 0.3 m^3); semi-transparent flight-intercept traps shaped like downward facing triangles (Bell et al., 2015). All flying invertebrates were contained in bottles, filled to one-third with 70% propylene glycol and some detergent, at the bottom of the traps. The traps were equipped with water-diverging modules that prevent rainwater from entering and flooding the bottles. The traps were set out in the first week of June 2021 and collected in mid-October 2021. An expert taxonomist identified all saproxylic beetles to species level. We then categorised beetles based on their affiliation to deadwood, decay stage, tree species, their conservation status and if they were recorded as prey species for the white-backed woodpecker. This resulted in the following categories: (a) Saproxylics, (b) Saproxylic species of conservation concern, meaning that they have had the conservation status of NT or higher during the last three Swedish red lists (Gärdenfors, 2010; Swedish Species Information Centre, 2015, 2020), (c) WBW prey species, species pointed out as especially attractive as food for the white-backed woodpecker according to Aulén (1988), (d) Coniferous preferring, (e) Deciduous preferring, (f) Generalist, with no tree species preference, (g) Early, species occurring at early stages of deadwood decay, (h) Middle, middle decay species, (i) Late, late decay species and (j) decay stage generalists, with no known preferences of decay stage. The same species can occur in several groups. Classifications of ecological preferences were based on available literature (Hagge et al., 2019; Koch, 1992; Seibold et al., 2015) and personal communication with taxonomic experts; nomenclature following the Swedish Dyntaxa system (Dyntaxa, 2023).

2.4 | Statistical analysis

All analysis was performed in the statistical software program R vers. 4.0.2. (R Core Team, 2020). We used LM's to test for differences in forest structure variables. We tested the effect of stand type on α-diversity (species richness and abundance) of saproxylic beetles with LMM's on log-transformed beetle abundance data, between stand types, package lme4 (Bates et al., 2015) and GLMMs for richness with trap as a random effect and negative binomial or Poisson distribution; package GlmmTMB (Magnusson et al., 2017). As model diagnostics, we used residual plots and tested for overdispersion in the DHARMa package (Hartig & Hartig, 2017). We performed pairwise comparisons of the stand types with estimated marginal means in the package emmeans (Lenth et al., 2019). In case of missing traps, we produced a third 'dummy' trap based on the mean values of the two existing traps to get GLMM models to converge.

To calculate β-diversity, we performed BETADISPER on a Bray–Curtis distance matrix followed by an ANOVA to compare distances to the community centroid. For pairwise comparisons, we used permutest with 999 permutations. We investigated differences in species composition among stand types with PERMANOVA and visualised by NMDS with 999 permutations and Bray–Curtis dissimilarity measure, in the vegan package (Oksanen et al., 2007). In order to identify indicator species for the different stand types, we used the function multipatt with 999 permutations in the Indicspecies package (De Caceres et al., 2016). Finally, for γ-diversity analyses, we performed species accumulation curves using the iNEXT package with 95% confidence intervals (Hsieh et al., 2016).

3 | RESULTS

3.1 | Structures

Of the living trees, 56, 49 and 99 per cent were deciduous in restored stands, non-restored and target stands, respectively (Figure 1).

In restored stands, 60 per cent of trees smaller than 20 centimetres were coniferous. For non-restored stands, corresponding numbers were 48 per cent of trees smaller than 20 centimetres being coniferous and in target stands, 100 per cent of trees smaller than 20 centimetres being deciduous (Figure 1).

The deadwood volumes in restored stands was non-significantly lower than target stands ($p=0.15$) and near significantly greater than in non-restored stands ($p=0.075$) (Figure 1). Volumes of logs were similar between restored and target stands ($p=0.34$) but greater in restored and target than in non-restored stands ($p=0.024$). Coniferous deadwood volumes did not differ between stand types but volumes of deciduous deadwood was lower in restored compared with target stands ($p=0.03$) and greater in restored compared with non-restored ($p=0.006$). Restored stands were characterised by large proportions of deadwood logs in the later decay stages ($p=<0.001$), whereas logs in non-restored stands was more evenly spread among decay classes ($p=0.1494$) and for target stands, intermediate decay stages were greatest ($p=0.02$; Figure 1).

3.2 | Beetles

We caught 16,324 individuals and 322 species of saproxylic beetles with 58, 38 and 28 species unique for target, restored and non-restored stands, respectively, and 119 species occurred in all stand types (Figure S2).

3.2.1 | α-Diversity

We found greater α-diversity in terms of both species richness and abundance in target stands than the other stand types for saproxylic, conservation concern, white-backed woodpecker prey, deciduous and generalist species but lower α-diversity of coniferous species (Table S1, Figures 2 and 3). Restored stands displayed similar levels of α-diversity as non-restored stands for all saproxylic, white-backed woodpecker prey, deciduous and generalist species. Coniferous and early decay stage species was less abundant and species of conservation concern species was more abundant in restored compared with non-restored stands (Tables S1 and S2, Figures 2 and 3).

3.2.2 | β-Diversity

Assemblage composition differed significantly among all stand types for all beetle groups (Table S3, Figure 4). We found differences in β-diversity for species of conservation concern ($p=0.043$), WBW prey ($p=0.01$) and deciduous species ($p=0.001$; Table S3, Figure 4). Pairwise comparisons revealed a greater β-diversity in target stands compared with restored stands for species of conservation concern ($p=0.01$) and lower in target stands than in restored stands for WBW prey species ($p=0.02$; Figure 4). For deciduous species, β-diversity was highest in restored stands, followed by non-restored and target stands (Table S3, Figure 4). For late decay stage species, β-diversity was lower in target stands compared with non-restored and restored stands (Table S3, Figure 4). We also found less overlap among stand types for early decay stage species compared with species associated with mid and late decay stages (Figure 4).

Restored stands displayed seven indicator species of which five had no tree species association. Target stands had 23 indicator species of which 12 preferred deciduous trees and non-restored

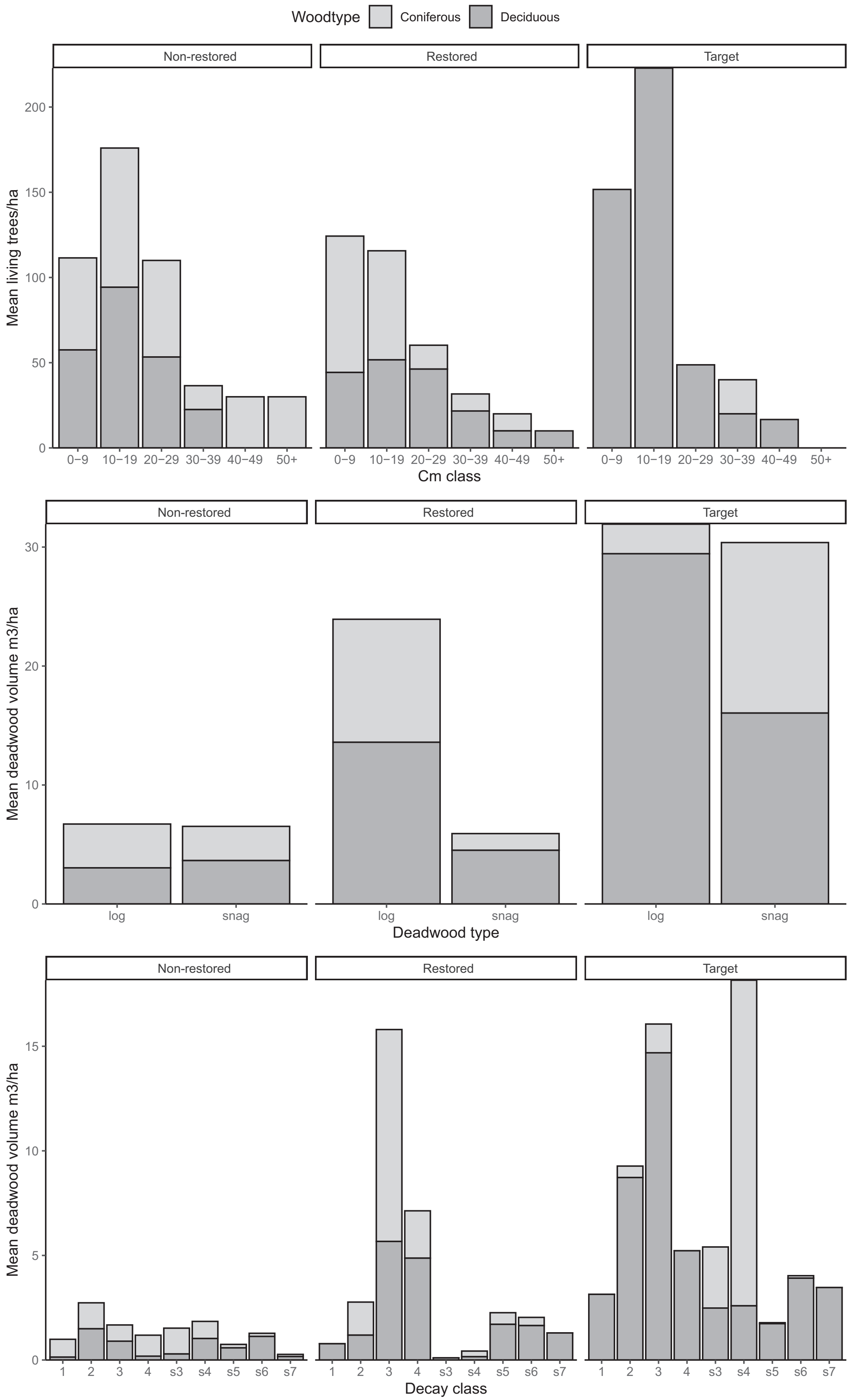


FIGURE 1 Mean values of environmental variables per stand type. Decay classes 1–4 (Gibb et al., 2005) are for logs and s3–s7 is for snags (Jung et al., 1999) with higher decay classes indicating higher decay.

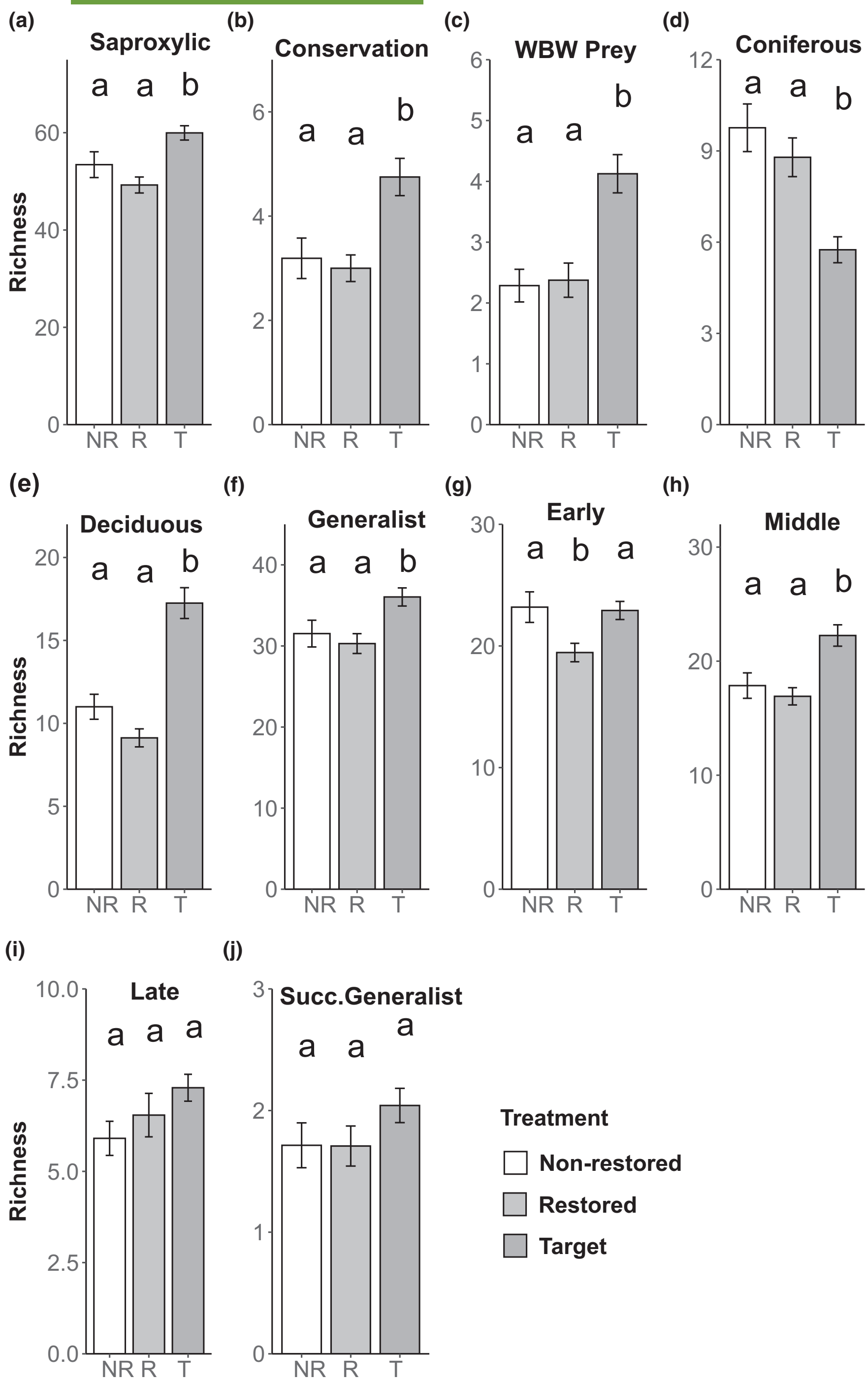


FIGURE 2 Mean ± SE species richness of saproxylic beetle groups in the different stand types. Unique letters indicate significant differences and shared letters indicate non-significance from emmeans results. (a) Saproxylic beetles, (b) species of conservation concern, (c) white-backed woodpecker prey species, (d) coniferous preferring species, (e) deciduous preferring species, (f) tree generalist species without tree species preference, (g) early decay stage species, (h) middle decay stage species, (i) late decay stage species, and (j) secay stage generalists.

stands 18 indicator species with nine preferring coniferous trees (Table S4).

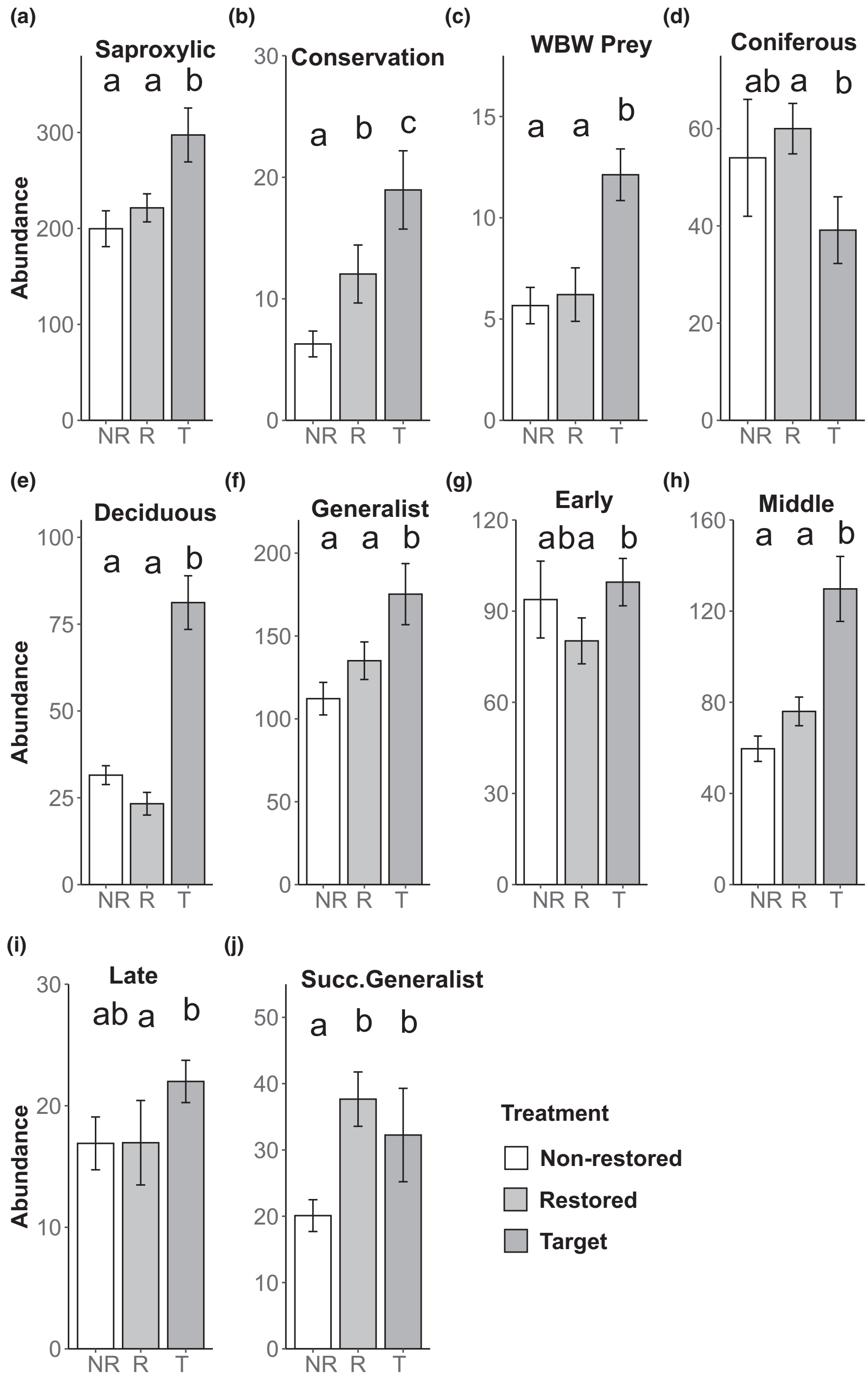
3.2.3 | γ-Diversity

Rarefaction curves displayed generally overlapping trajectories between stand types (Figure 5). Extrapolated trajectories show that the γ-diversity of saproxylic, conservation concern and deciduous species is greater in target than non-restored stands and that late decay stage γ-diversity is greater in restored than non-restored stands (Figure 5).

4 | DISCUSSION

Studies on deciduous forest restoration and its impact on saproxylic beetles or other taxa are rare in boreal Fennoscandia. In fact, most studies are conducted in coniferous forests, where the use of negative references are common, while positive references are sparse (e.g. Hägglund et al., 2020). We do acknowledge that the restoration target habitats in our study are not 'natural' per se. Given the purpose of the restoration studied, we still consider these recent breeding habitats for the white-backed woodpecker suitable target stands. We emphasise the importance

FIGURE 3 Mean ± SE species abundance of saproxylic beetle groups in the different stand types. Unique letters indicate significant differences and shared letters indicate non-significance from emmeans results. (a) Saproxylic beetles, (b) species of conservation concern, (c) white-backed woodpecker prey species, (d) coniferous preferring species, (e) deciduous preferring species, (f) tree generalist species without tree species preference, (g) early decay stage species, (h) middle decay stage species, (i) late decay stage species, and (j) decay stage generalists.



of using appropriate references when assessing restoration, as only using one of negative or positive references greatly limits the potential of assessment. Our study provides novel insights into decadal effects of deciduous forest restoration in a managed landscape dominated by conifer forest plantations. As one of very few studies, we compared restored stands in relation to both ends of a restoration gradient including non-restored stands and target habitats. We show that after 12–21 years, restoration impacts both stand structure and beetle diversity. However, the restored stands display lower deciduous deadwood volumes and α-diversity (measured as species richness and abundance) and different assemblage composition compared with the target stands. This means that restored stands now differ from both target and non-restored stands. Our results show that deciduous forest restoration guided by an umbrella species achieves partial restoration of local stand structure and beetle diversity after two decades, although the qualities of target stands are not reached.

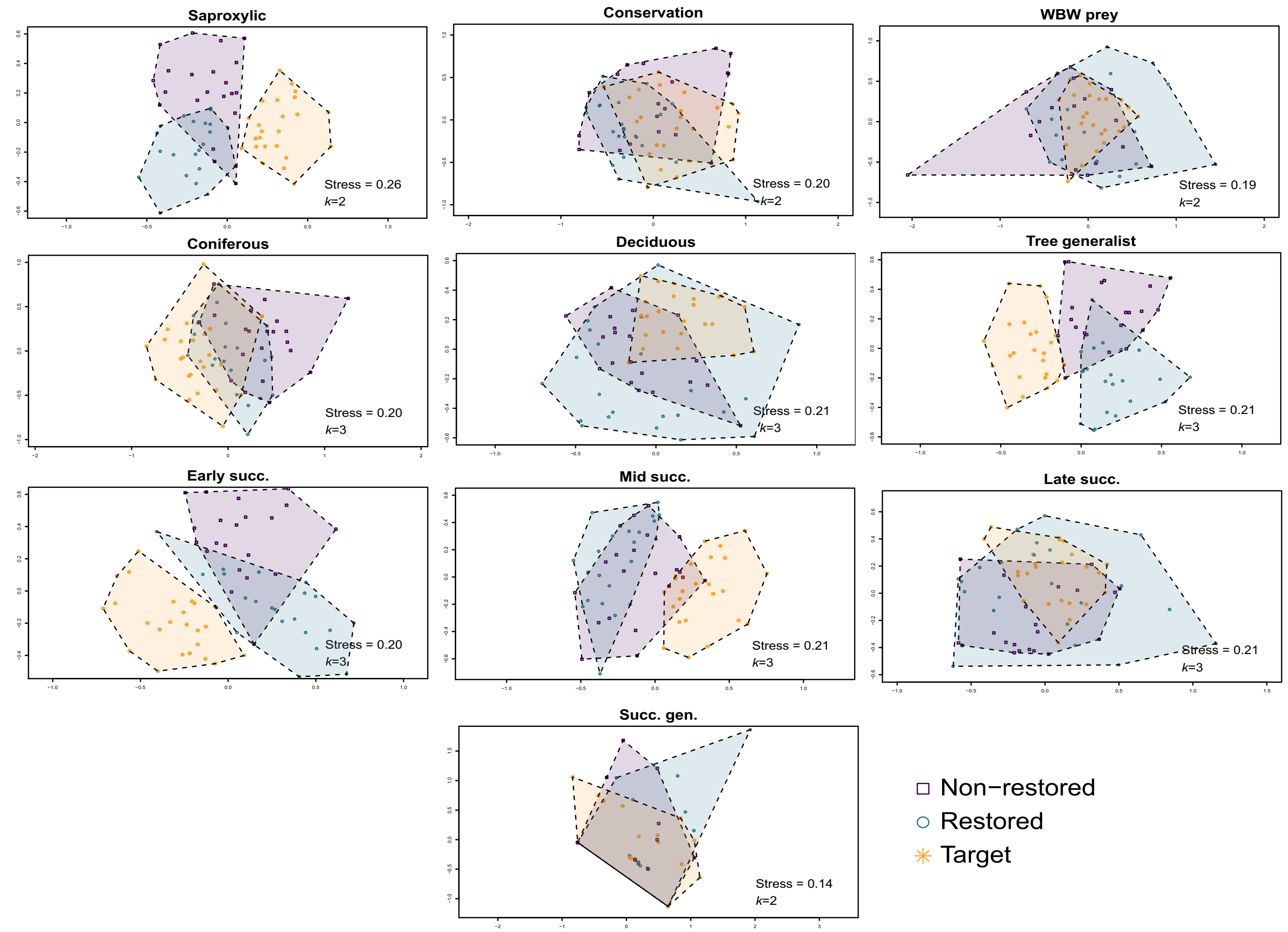


FIGURE 4 NMDS plot visualising differences in assemblage composition of saproxylic beetle groups in the different stand types.

4.1 | Structures

In line with Prediction 1, we found that forest structure differed between target stands and restored stands. Coniferous trees dominated tree regeneration in restored stands while deciduous trees dominated in target stands. This suggest that target stands will continue to be deciduous dominated without further interventions but that the restored stands will need repeated spruce removal. Hämäläinen et al. (2020) showed that spruce removal in white-backed woodpecker restoration could successfully benefit establishment of aspen but not birch saplings. In order to ensure successful establishment of deciduous seedlings, removing encroaching spruce and creating gaps large enough to increase light is needed (Götmark, 2007). Further measures such as site preparation and direct seeding of deciduous tree species might also be necessary (Castro et al., 2021). Tree size stratification is needed in order to ensure a future supply of deadwood in varying decay stages and tree species such as those found in target stands.

Aligning with Prediction 2, volumes of mainly deciduous deadwood in restored stands were greater than in non-restored stands but lower than in target stands. Deadwood in the restored stands was also allocated in the later decay stages while the target habitat had a more even spread among decay classes. The levels reached threshold levels of ~20–30 m^3/ha suggested in (Hekkala et al., 2023; Müller & Bütler, 2010) showing that the restorations have potential to benefit biodiversity. The deadwood created in our restoration stands consisted of fresh deadwood created at one occasion in even aged stands. This deadwood is now highly decayed and has fulfilled much of its initial purpose, at least for early decay stage saproxylic beetles. The structure of the initial forest stand determines the extent of how much deadwood can be created from living trees without depleting the future supply of deadwood or making the restored stand too sparse. These results implies an intermediate restoration effect, rather than complete restoration regarding tree species composition, layering and deadwood amount and quality.

4.2 | Beetles

We predicted the α-diversity of restored stands to be greater than non-restored and similar to target stands (Prediction 3). Instead, we found that both restored and non-restored stands displayed lower α-diversity than that of target stands and α-diversity of species

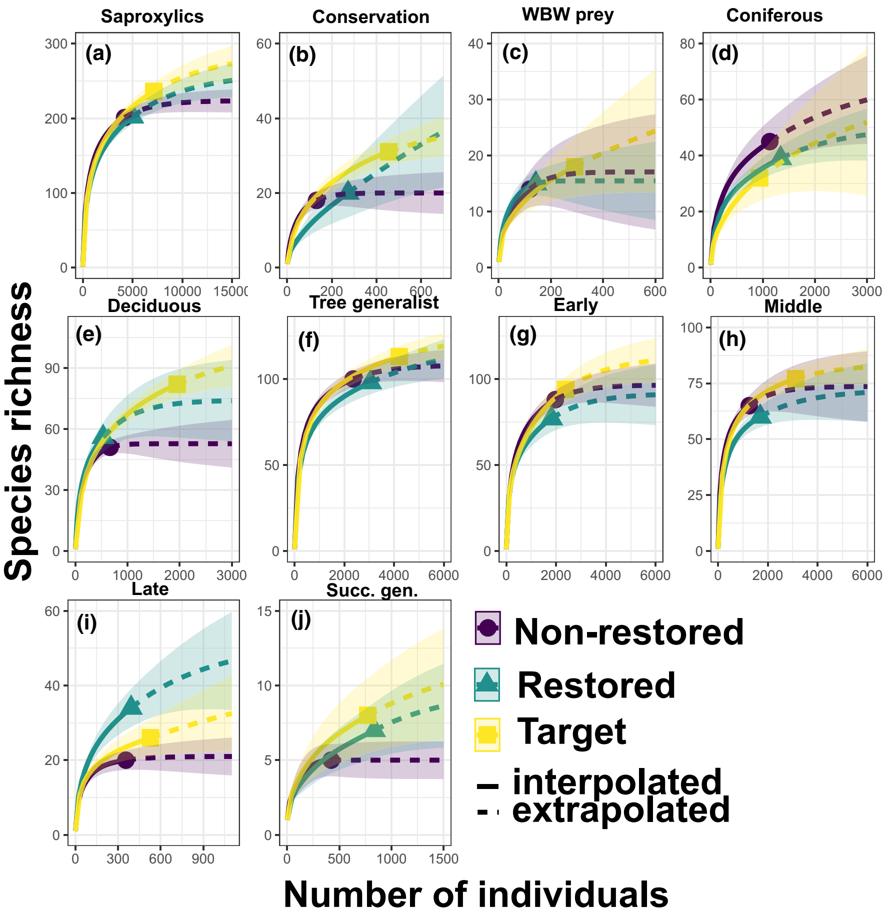


FIGURE 5 Rarefaction curves with 95% confidence intervals comparing γ-diversity of saproxylic beetle groups in the different stand types. (a) Saproxylic beetles, (b) species of conservation concern, (c) white-backed woodpecker prey species, (d) coniferous preferring species, (e) deciduous preferring species, (f) tree generalist species without tree species preference, (g) early decay stage species, (h) middle decay stage species, (i) late decay stage species, and (j) decay stage generalists.

associated with deadwood in late decay stages did not differ among stand types. After another 10 years, differences in species richness and abundance of deciduous associated and species of conservation concern between restored and non-restored stands, shown in Bell et al. (2015), could not be detected. Nor did restored stands reach levels of α-diversity similar to that of target stands. Fresh deadwood benefits many early decay stage beetle species causing an immediate increase in α-diversity at least in conifer dominated forest (Hägglund et al., 2020), an effect that may decrease to background levels as the deadwood decays (Jonsell et al., 2019). Target stands probably maintain higher levels of saproxylic beetle diversity due to the continuous supply of deadwood in various decay stages contrasting the one-time addition of deadwood in restored stands. Tree removal opens up the canopy and creates a warmer and drier microclimate, which may affect fungi negatively (Müller et al., 2010). As many deciduous-associated species are fungivores, this could explain the lack of difference in deciduous species between non-restored and restored stands.

We found partial support for our-fourth prediction that target stands would support greater β-diversity, but for species of conservation concern. For white-backed woodpecker prey species, deciduous and late decay stage species we found the opposite, with target stands displaying a lower β-diversity. This could be due to a variation in the baseline of forest structures in non-restored stands, a variation that is also realised after restoration through, for example, varying size and number of deciduous trees. In target stands, the overall quality may be high, resulting in higher species richness, whereas the variation between stands may not be as high, resulting in a comparatively lower β-diversity. For the overall saproxylic assemblage composition and the beetle sub-groups, we found distinct species assemblages in each stand type, with restored and non-restored stands more similar to each other than to target stands. We found relatively small overlaps among stand types for early decay stage species and more overlap for later decay stage species. This could be due to different colonisation patterns of deciduous and coniferous deadwood (Saint-Germain et al., 2007), where non-restored stands may favour early stage coniferous species, target stands mid and late deciduous species with an intermediate pattern in restored stands. This is further strengthened by the pattern we see in indicator species, with most coniferous specialists in non-restored stands being early decay stage specialists while deciduous specialists in target stands are represented among several decay stages with few indicator species overall in restored stands. However, assemblage composition in restored stands still differed from non-restored stands after more than 10 years, suggesting that restoration has managed to alter species composition into a new trajectory. The difference in stand structure and deadwood composition suggest however that the restored stands will not become more similar to the target stands with time. The majority of indicator species in target stands preferred deciduous deadwood, in non-restored stands indicator species were associated with coniferous deadwood while restored stands only had one deciduous indicator species. One of the strongest indicator species for target stands, *Sinodendron cylindricum*, is not only a deciduous specialist, but also considered an important prey species for the white-backed woodpecker, which further strengthens the position of these stands as restoration targets.

Although γ-diversity trajectories overlap between stands, extrapolation suggest greater γ-diversity in target compared to non-restored stands regarding saproxylics, conservation concern and deciduous species. However, predictions may be unreliable when extrapolated further than twice the reference sample (Chao et al., 2016). We did not find that restored stands had a greater α-diversity of late decay stage species as expected in Prediction 3; instead, we found this was the case for γ-diversity. This aligns well with structural elements as the majority of deadwood in restored stands belonged to later decay stages. Greater γ- and not α-diversity of late decay stage species indicates that only some restoration stands support these species. Once deadwood resources are depleted, late decay stage species may thus be lost, supporting the need for provisioning multiple decay stages in restored stands.

4.3 | Implications for restoration

We suggest that management strategies for restoration of habitat for the white-backed woodpecker need re-evaluation. In order to provide fresh deadwood to maintain high levels of saproxylic beetle diversity, restoration needs to be repeated every 10–20 years. Further action is also needed to ensure regeneration of deciduous trees and to prevent spruce encroachment (Hämäläinen et al., 2020). Since the initial number of large deciduous trees in stands subjected to restoration was low, repeated restoration may deplete the supply of large, old trees and the future supply of deadwood. We recommend restoration to be planned in adjacent stands in the landscape to make sure that stands are continuously restored every 10–20 years. Woodland key habitats and voluntary set-asides are usually small in size and fragmented in the forest landscape (Hof & Hjältén, 2018); hence, conventional forest management needs to contribute to the landscape supply of habitat for disturbance-dependent species including deciduous trees and deadwood (Tälle et al., 2023). Future supplies of deciduous trees should therefore be a priority across all stages of forest management, from regeneration of clear-cuts, promoting deciduous trees in pre-commercial and commercial thinning, to leaving deciduous trees as retention at final felling (Mild & Stighäll, 2005).

Previous research have shown that in order to maintain a rich beetle diversity, deadwood of varying species and decay stages in both shaded and sun-exposed conditions is needed (Hjältén et al., 2012; Seibold et al., 2016). Furthermore, planning for a continuous supply of snags in different decay stages is also important for cavity-nesting birds such as the white-backed woodpecker (Drapeau et al., 2009; Edworthy & Martin, 2013). For beetle assemblages associated with birch deadwood, the amount of deciduous deadwood within 100 m as well as the landscape-level amount of deciduous stands was important for providing rich assemblages (Johansson et al., 2017). To boost populations of deciduous-associated species in the landscape, it is likely important to complement spruce removal in deciduous rich stands with other disturbance emulating management such as prescribed burning and rewetting of wetlands.

We conclude that decades after restoration, restored stands do not produce more species or individuals than non-restored stands but support other species assemblages, mainly of generalist and late decay stage species, although dissimilar to target stands. More effort is thus needed to achieve restoration targets and the forest structure and tree species composition before restoration will surely determine restoration success. Additionally, future assessment of restoration success would also benefit from more precise host-use sampling of larvae and emerging adults such as wood dissection and rearing (Saint-Germain et al., 2006). Target stands are able to produce a continuous supply, whereas restoration manages to create a pulse but no continuous supply of deadwood. This suggests that several restoration stands are needed to fill the same function as a single target stand.

AUTHOR CONTRIBUTIONS

All authors (Albin Larsson Ekström, Joakim Hjältén and Therese Löfroth) were part of conceptualisation and planning of the study design. Albin Larsson Ekström was responsible for the collection of data and formal analysis and led the writing of the manuscript. All authors contributed to writing of the manuscript and have given their approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.c2fqz61gv (Larsson Ekström et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Map showing the location of the forest stands, sampling of environmental variables and an image of the IBL2-flight intercept traps used to sample invertebrates.

Figure S2. Venn-diagram displaying number of unique and shared species between stand types (percentage % of total species).

Table S1. GLMM and LMM results for Saproxylic (Sx), Conservation concern (Cons.), White-backed woodpecker prey (WBW), Coniferous (Con.), Deciduous (Dec.) and Generalist (Gen.) beetles. Non-restored stands (NR) is the intercept level.

Table S2. GLMM and LMM results for Early decay stage (Early), Middle decay stage (Middle), Late decay stage (Late) and Generalist (Gen.) beetles. Non-restored stands (C) is the intercept level. Significant results highlighted in bold.

Table S3. Result output from BETADISPER and Permutest given significance and PERMANOVA divided by beetle group.

Table S4. Indicator species for each stand type.

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