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Research article

# Translocating deadwood in ecological compensation benefits saproxylic beetles, but effects are dependent on substrate density

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ABSTRACT

Ecological compensation is increasingly used to offset habitat and biodiversity loss resulting from changes in land use, large infrastructure projects (e.g., roads and railroads) or industrial expansions (e.g., mines, harbours), but the effectiveness of specific compensation strategies remain largely untested. When old-growth forest ecosystems are impacted by such projects, designated compensation areas may also require additional restoration or habitat enrichment. For organisms that rely on habitats that require decades to develop, such as advanced decayed wood, restoration will require novel approaches. We tested whether translocation of deadwood of various decay stages and large dimensions enhance saproxylic beetle communities within compensation areas in a large boreal forest landscape in Sweden. Experimental plots (50 m in diameter) within the compensation zone were enriched with 0, 16, or 48 deadwood substrates. We collected beetles using flight intercept traps prior to translocation and again 1 and 4 years after translocation and compared species richness, abundance and assemblage composition across treatment and over time. We showed that translocation of relatively high densities of deadwood (48 substrates per plot) increased species richness of saproxylic beetles. Increased beetle richness could have occurred from direct transport of beetles in experimental substrates and/or through attraction of beetles to the translocated substrates. Our results indicate that translocation of deadwood can serve as an important tool in ecological compensation and restoration if sufficient amounts of deadwood are translocated. While promising, the long-term success of restoring saproxylic biodiversity through translocation of deadwood depends on whether translocated substrates continue to provide suitable habitat for beetles over time and whether benefits for biodiversity can be enhanced through targeted translocation of specific combinations of deadwood.

## 1. Introduction

Ecological restoration has emerged as an important strategy for mitigating human-caused biodiversity loss in boreal forests (Gustafsson et al., 2012; Halme et al., 2013) and throughout the world (UN Resolution 73/284, 2019). More recently, ecological compensation has become an important tool in restoration (Bull et al., 2013) to mitigate the adverse environmental impacts of large-scale land use, such as wind power parks and mining (Josefsson et al., 2021). In this context, compensation efforts are rooted in the 'no-net-loss' principle of biodiversity, aiming to offset any natural value losses resulting from human activities elsewhere (Bull et al., 2013; Gardner et al., 2013).

Successful compensation efforts in forested habitats may require rapid restoration of habitat elements that would normally develop over decades or centuries, such as large dead trees (>30 cm in diameter) or advanced decayed deadwood (Morris et al., 2006; Mäkinen et al., 2006; Stokland et al., 2012). These deadwood substrates provide important microhabitats and resources for diverse assemblages of wood-inhabiting organisms, including fungi, lichens, bryophytes, invertebrates and woodpeckers (Hekkala et al., 2023; Löfroth et al., 2023; Siitonen, 2001; Stokland et al., 2012). Practical strategies for deadwood enrichment can vary from small-scale actions such as artificial creation of high-stumps

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and dead trees (Komonen et al., 2014; Schroeder et al., 1999) up to large-scale emulation of natural disturbances, such as prescribed burning (e.g., Saint-Germain et al., 2004; Toivanen and Kotiaho, 2007; Hekkala et al., 2014; Heikkala et al., 2016; Hägglund and Hjältén, 2018). Several studies have shown that deadwood enrichment in managed forest increases the diversity and abundance of saproxylic beetles (Grove, 2002; Hjältén et al., 2023; Sandström et al., 2019).

Restored deadwood may not always support assemblages comparable to those found in deadwood deposited following natural disturbances or mortality. For example, fresh deadwood can increase saproxylic species richness, but the effects are limited to early successional species from the local species pool, including many cambivores (Andersson et al., 2015; Gibb et al., 2006; Hjältén et al., 2010; Lindhe et al., 2004; Sverdrup-Thygeson and Ims, 2002). Cambivores are adapted to respond immediately to supply of fresh deadwood and many species are specialized to a specific tree species. The adults use molecular cues including volatiles from the decaying wood and species specific pheromones to locate suitable substrate (Lieutier et al., 2004). The cambium is only suitable for one to three years after tree death so cambivore species richness and abundance are expected to increase directly after deadwood enrichment (Hjältén et al., 2012). Moreover, differences in insect assemblages among substrates are often attributed to interactions with decomposer fungi (Abrahamsson et al., 2008; Jonsell et al., 2005), forming complex interactions. Deadwood substrates generated through restoration often rely on local colonization by species and do not necessarily guarantee successful restoration if target species are unable to colonise the restored substrates (Hilderbrand et al., 2005; Palmer et al., 1997).

If densities of restored substrates are low, dispersal limitations or competition for these habitats may restrict colonization and reduce the success of restoration (Kouki et al., 2011). Interspecific competition for resources such as space, food, or microhabitats can result in competitive displacement or exclusion of species, while intraspecific competition does not necessarily reduce species richness in the same way, as individuals of the same species share similar ecological requirements and can employ density-dependent mechanisms to regulate population size (e.g., Brin and Bouget, 2018; Amarasekare, 2003). While colonization is more likely to occur in empty patches, certain species may still arrive at and interact with occupied patches, particularly in the case of facultative or competitive species. The role of prior occupants and priority effects (e.g., Fukami, 2015; Weslien et al., 2011) may further complicate these dynamics. While the density of some deadwood substrates can be modified operationally during the restoration effort, it is much more difficult to rapidly recreate substrates in advanced decomposition stages like old resin-impregnated kelo wood of coniferous tree species that is very resistant to decay (Larsson Ekström et al., 2023). Other substrates such as large, older trees are rare due to past forest management, e.g., through selective cuttings (Siitonen et al., 2000).

To enrich habitats with these older and slower forming deadwood substrates, restoration efforts may benefit from translocating existing colonized substrates into compensation areas. This approach of conservation translocations (‘the intentional human-mediated movement of species from one place to another with a primary objective of conservation benefits’ (IUCN/SSC, 2013; Seddon et al., 2014) has been applied to single species, including plants (e.g., Rout et al., 2009; Godefroid et al., 2011), lichens (e.g., Lidén et al., 2004; Smith, 2014), bryophytes (e.g., Merinero et al., 2020) and in recent projects invertebrate translocation, such as reestablishment of the Great Capricorn beetle (*Cerambyx cerdo*) in both Sweden and Poland (Drag and Cizek, 2015). Translocations of invertebrates through soil inoculation, where soil containing invertebrate communities is moved to restoration sites, highlights the potential for restoring ecosystems by translocating entire communities (“whole-of-community” rewilding (Contos et al., 2023, 2021)).

Recently, “whole-of-community” translocation of deadwood and associated species has gained attention as a novel approach to mitigate habitat and biodiversity loss (Tranberg et al., 2024). Translocating large pieces (i.e., logs) of both fresh and decayed deadwood presents logistical challenges related to collection, transport and deposition of substrates. While this approach is successful in increasing the volume and diversity of deadwood habitats, there remains a bias towards the translocation of less-decayed deadwood (Tranberg et al., 2024). Nevertheless, this approach could increase deadwood volumes at stand level to or above 20 $m^3$ $ha^{-1}$, which has been shown to serve as a level at which significantly more rare and red-listed forest species are found (Hekkala et al., 2023; Penttilä et al., 2004). Yet, it remains untested how effective different densities of deadwood translocations are in enriching saproxylic assemblages.

Here we assess the response of saproxylic beetles to translocation of deadwood from an impact to a compensation area in a conifer dominated boreal forest landscape with relatively low productivity in northern Sweden. The saproxylic beetle community in this area is quite species poor in an international perspective but more than 1300 saproxylic beetle species have been recorded in Sweden. Using flight intercept traps, we assessed the abundance, richness and assemblage composition of different feeding guilds of saproxylic beetles before, one and four years after, a large-scale translocation of fresh and decomposed, large diameter deadwood to experimental plots with different densities of translocated deadwood, 0, 16 or 48 substrates, with a length of 3–5 m and a mean volume of 0.292 $m^3$ (see Tranberg et al., 2024 for further information).

We predicted that:

1) Both abundance and species richness will increase for all feeding guilds of saproxylic beetles with increasing volumes of translocated deadwood, 2) Community composition will change as a direct response to deadwood enrichment via translocation, and the changes will be more pronounced in plots with higher densities of deadwood, and 3) The strongest species responses will be observed in cambivores, correlating with the large volumes of fresh deadwood translocated to the compensation area and their documented fast response to enrichment of fresh deadwood (e.g., Hjältén et al., 2012; Baber et al., 2016; Gossner et al., 2013, 2016; Komonen et al., 2014).

## 2. Material and methods

### 2.1. Study area

The experiment was conducted in northern Sweden, close to Gällivare (WGS84 67°8′11.3"N 20°40′0.4"E) within the northern boreal vegetation zone (Ahti et al., 1968). An expansion of the Aitik copper mine was expected to destroy an extensive forest area with high (376 ha) or very high (167 ha) conservation value (sensu the Swedish Standards Institute, 2014). The Swedish Land and Environmental Court of Appeal ruled to allow the exploitation but stated that ecological compensation areas must be set aside to compensate for the impact of the forest loss caused by the expansion.

Prior to the mine expansion, the impact area had high deadwood volumes (average of 21.1 $m^3$ $ha^{-1}$). The compensation area encompassed 397 ha including 192 ha of forests of high conservation value, but with moderate deadwood volumes (average of 9.3 $m^3$ $ha^{-1}$) and 205 ha of forests of low conservation value (113 ha) and non-productive land (Forsgren et al., 2016). Both impact and compensation areas had undergone previous forestry activities, primarily selective felling, but had not been managed in recent decades. The forests in the two areas were predominantly of conifer-dominated bilberry (*Vaccinium myrtillus* L.) type. Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) are the dominant species, with downy birch (*Betula pubescens* Ehrh.) and goat willow (*Salix caprea* L.) as subordinate tree species. In addition to the compensation area, one reference area was selected as background control to monitor interannual variation in saproxylic insects (Fig. 1; Table 1). The reference area is situated within Ätnarova Experimental Forest, a research area that covers 3500 ha, and is located

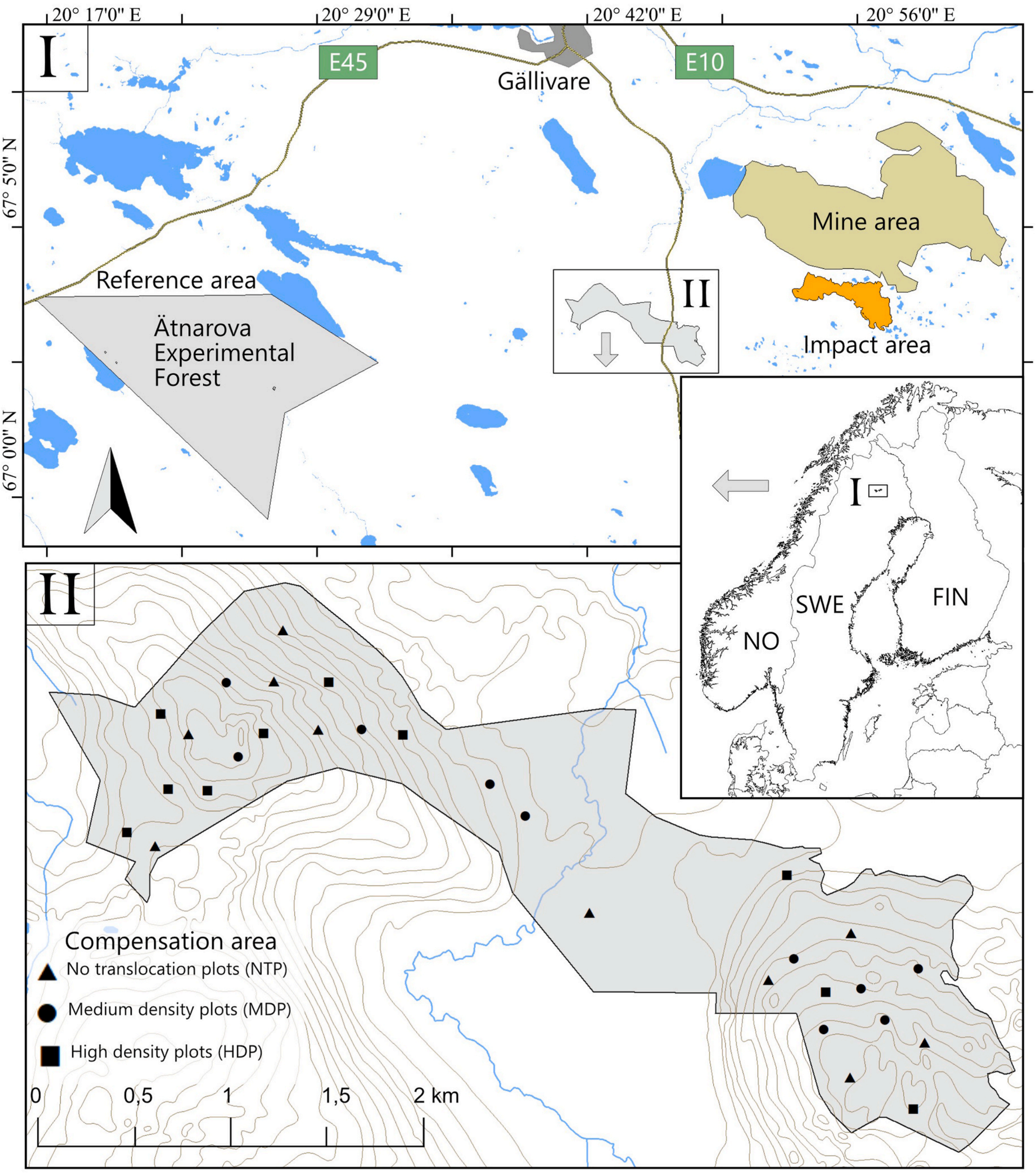

**Fig. 1.** Overview map of research area (subfigure I) in relation to Gällivare municipality, showing the mining area (light olive green), impact area (orange), compensation and reference areas (grey). Symbols in lower figure (subfigure II) indicate treatment plot type in the compensation area.

15 km west of the compensation area. The area borders Muddus National Park to the southwest and the forest types are dominated by old growth spruce and pine forests.

### 2.2. Experimental design

In early winter 2017, 637 deadwood substrates (3–5 m in length, mean volume 0.292 $m^3$ per substrate), consisting of both pine and spruce, were selected for translocation from the impact area to the compensation area (Table 1). We selected both standing (living nature value trees or standing dead trees “snags”) or lying substrates “logs” of advanced decay classes sensu Gibb et al. (2005): DC1 = bark intact or starting to loosen, >50 % bark remaining, wood hard; DC2<50 % bark remaining, surface of wood smooth, but beginning to soften, wood hard; DC3 = lacking bark, surface of wood soft, some crevices and some small pieces of wood lost or bigger wood fragments lost with a deformed surface. These deadwood substrates were further classified into eight quality classes according to tree species (pine/spruce) original position (snag/log) and decomposition stage (DC1-DC3), according to Tranberg et al. (2024).

The logs, along with associated saproxylic species of bryophytes, lichens, fungi and beetles living in and on the logs, were translocated from the impact area to the compensation area, situated 6 km west (Fig. 1). The methods used for translocating the deadwood followed a procedure which has more thoroughly been described in Lindroos et al. (2021) and Tranberg et al. (2024): (1) selection of substrates in impact area, (2) marking, transporting and storing of substrates, (3) transport to the compensation area, and (4) Deployment in the compensation area

**Table 1**
Site characteristics, tree species distribution of basal area for the three dominant tree species, deadwood volume (mean ± sd) for examined plots, addition by translocation and trees felled on site, number of plots within parenthesis. NTP; no translocation plots, MDP; medium-density plots and HDP; high-density plots and RA; Reference area.

| | Compensation area | | | Reference area |
|---|---|---|---|---|
| Elevation (m.a.s.l.) | 400–470 | | | 430–540 |
| Plot type/treatment | NTP (n = 10) | MDP (n = 10) | HDP (n = 10) | RA (n = 10) |
| Mean (±sd) basal area of living trees ($m^2$) | 23.5 ± 4.8 | 26.2 ± 4.6 | 26.0 ± 3.7 | 15.7 ± 3.4 |
| Tree species distribution (% of basal area) | | | | |
| *Pinus sylvestris* | 34 | 39 | 41 | 14 |
| *Picea abies* | 51 | 40 | 20 | 72 |
| *Betula* spp. | 14 | 21 | 39 | 13 |
| Deadwood volume before translocation ($m^3$ $ha^{-1}$) | 9.1 ± 3.9 | 10.6 ± 3.4 | 8.8 ± 2.8 | 29.3 ± 4.9 |
| Total number of translocated logs | 0 | 16 ± 1 | 48 ± 1 | 0 |
| Number of logs in DC1 | 0 | 8 ± 0.5 | 27 ± 0.5 | 0 |
| Trees felled on site (logs/plot) | 2 | 2 | 2 | 0 |
| Total translocated deadwood volume ($m^3$) to each plot (r = 25 m) | 0 | 6.0 ± 0.9 | 15.0 ± 1.0 | 0 |
| Translocated volume in DC1 | 0 | 3 ± 0.45 | 7.5 ± 0.5 | 0 |
| Deadwood volume after translocation ($m^3$ $ha^{-1}$) | 12.5 ± 1.9 | 15.4 ± 1.8 | 24.3 ± 2.0 | 29.3 ± 4.9 |

(Fig. 2). All translocated substrates were positioned as downed deadwood in the compensation area.

The compensation area includes 30 randomly selected experimental plots (50 m in diameter) separated by at least 150 m (mean Euclidian distance between all plots was 1866 m ± SD 1259 m). Ten plots were designated as controls (mean Euclidian distance to all plots 1818 m ± 1245 m), receiving no translocated logs (NTP = No Translocation Plots), 10 plots received 16 deadwood substrates, standardised so that each plot received two substrates of each of the eight deadwood quality classes described above (MDP = Medium-Density Plots) and 10 plots received 48 deadwood substrates, each plot received six substrates of each deadwood quality class (HDP = High-Density Plots) (Table 1). In all 30 experimental plots, one spruce and one pine tree were felled on site to serve as fresh substrate for future colonization of saproxylic organisms. Within the reference area, 10 circular plots (50 m diameter) were randomly distributed. No translocated deadwood items were added to the reference area.

## 2.3. *Beetle sampling*

Beetle sampling was conducted by placing two flight intercept traps (model IBL-2) within 10 m north and south of each plot centre. The trap is designed in the form of a triangular semi-transparent plastic intercept with an approximate area of 0.35 $m^2$. Each trap was equipped with a water removal funnel (allowing us to only collect the samples once per season) and a 600 ml collecting bottle. The collecting bottle was filled to approximately one-third of its capacity with a mixture of propylene glycol and water in a 50/50 ratio, with a small amount of detergent to remove the surface tension, following the approach outlined by Stenbacka et al. (2010). The traps were for each sampling year placed in field from the end of May/beginning of June (when most of the snow have melted and beetles start to get active in the area) until mid-September (onset of winter and beetles are not active any longer) the same year at which time the insect samples were collected. The sampling was conducted on three occasions: before translocation in 2017; the first season following translocation in 2018, and the fourth season following translocation in 2021 in both the compensation area and reference area. Nomenclature for the beetles follows the Swedish Dyntaxa system (Dyntaxa, 2023).

## 2.4. *Feeding guilds of beetles*

Following field sampling, samples were sorted and identified to the finest taxonomic level possible (species-level, but occasionally genus) by expert taxonomists. All species were categorized as saproxylic (both

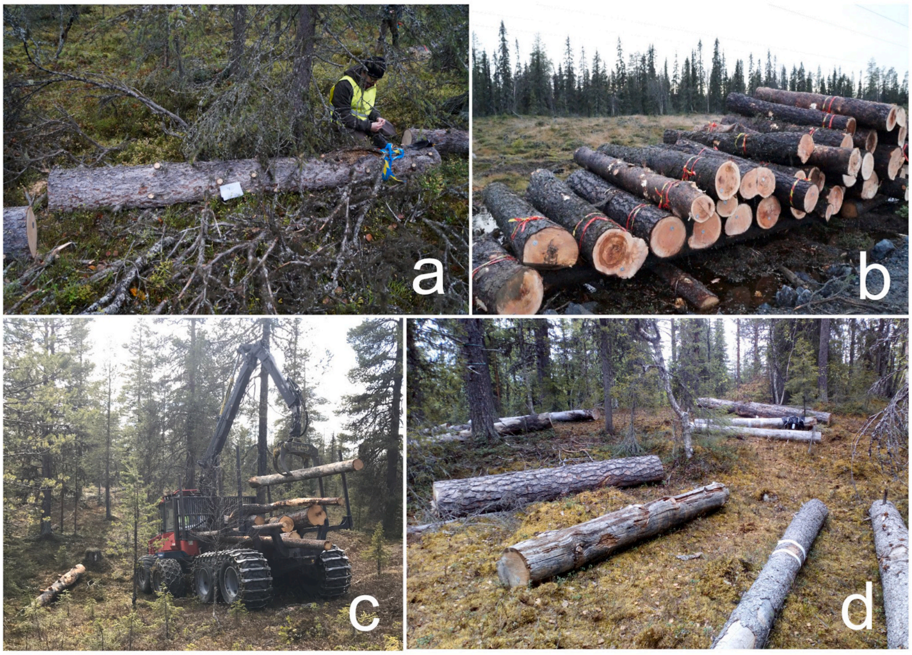

**Fig. 2.** Steps in the translocation process; a) selection of substrates, b) marking and storing of substrates, transport to the compensation area, c) forwarding to translocation plots, d) one of the HDPs (high density translocation plots) with 48 translocated substrates distributed to a 25 m radius sampling plot. Photo: Maria Nordlund (a–c) and Olov Tranberg (d).

facultative and obligate) or non-saproxylic, the latter were excluded from further analysis. Saproxylic species were further classified into feeding guilds (cambivores and woodborers were combined into one class) based on their nutritional ecology following Koch (1989a, 1989b, 1992), and expert opinions. In addition, species were classified as species of conservation concern when red-listed in any of the last three Swedish red lists (SLU Artdatabanken, 2020, 2015, 2010). A complete list of included species and classification can be found in Appendix 1. Based on recommendations from species taxonomists, *Zilora cfr elongata* was aggregated to findings of *Zilora ferruginea* and *Orthoperus cfr punctatus* was aggregated with *Orthoperus rogeri*. We excluded 34 specimens that were not possible to determine to species level from subsequent analyses; *Acrotrichis* sp. (29 specimens), *Atomaria* sp. (two specimens), *Epuraea* sp. (one specimen) and *Ptinella* sp. (two specimens).

### 2.5. Statistical analyses

To compare differences in species richness and abundance among the four treatments (NTP, MDP, HDP and RA) and three sampling years (2017, 2018 and 2021), we used generalized linear models (GLM) and the "glmmTMB" function from the "glmmTMB" package by Brooks et al. (2024) in R (R Core Team, 2021). We used a negative binominal distribution, with treatment, year, and their interaction, as fixed factors using log link function. The models were checked for overdispersion and residual plots were checked for outliers and model assumptions. Plot ID was initially included in model as a random factor, but it was later removed from both the GLM and PERMANOVA due to model convergence issues in PERMANOVA and overparameterization problems in GLM. For pairwise comparisons between treatments, we applied a post-hoc test with Tukey adjustment to account for multiple comparisons using the "emmeans" function from the "emmeans" R package by Lenth et al. (2023). We tested for spatial correlation by linear regressions for the species richness and abundance of saproxylic beetles in no translocation plots depending on the distance to the nearest translocation plot in R (R Core Team, 2021). We tested differences in gamma-diversity i.e., the total diversity across all plots within a treatment, with rarefaction curves produced with iNEXT (Hsieh et al., 2024; Chao et al., 2014).

To assess differences in species composition between treatments and years, we performed permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001) in PRIMER (PRIMER, 2007) with treatment, year, and their interaction as fixed factors, followed by post-hoc pairwise testing. We used a fourth root transformation of abundance data and used Bray-Curtis dissimilarity index as a community distance measure. To visualize assemblage composition we used non-metric multidimensional scaling (NMDS) applying the "metaMDS" function from the "vegan" package by Oksanen et al. (2020).

To determine which species contributed most to differences in the beetle assemblages, we performed similarity percentage analysis (SIMPER) in PRIMER (Anderson, 2001; Clarke, 1993), on fourth-root transformed data. SIMPER calculates the overall percentage contribution that each species makes to the average dissimilarity between two groups and lists the species in decreasing order of their importance in discriminating the two sets of samples (Clarke, 1993). The cut-off for the lists of species explaining differences was set to 50 % for all feeding guilds, except for species of conservation concern, where the limit was set to 90 %. Although SIMPER has been criticised for overweighting common species it is still an established method that is considered to accurately represent ecological community responses (Roberts, 2017; Warton et al., 2012). To identify species unique to different treatments, we conducted indicator species analysis (ISA) using the "multipatt" function from the "indicspecies" package (De Cáceres et al., 2022).

Nine traps were damaged in field and were excluded from the analysis, including two from NTPs, three from MDPs, three from HDPs, and one from reference area, distributed across all three sampling years. Since analyses were performed on trap level, both PERMANOVA and GLM are robust methods that can effectively accommodate variations in sample size.

## 3. Results

In total, we caught 31,147 individuals from 440 beetle species, of which 27,129 individuals (87 %) or 339 species (77 %) were saproxylic. Among the saproxylic beetles, the majority of species caught were fungivores (159 species, 16,523 individuals), followed by predators (129 species, 6908 individuals) and cambivores/woodborers (55 species, 4668 individuals). We collected a total of 49 species of conservation concern (1617 individuals) (28 species 2017, 36 species 2018 and 39 species 2021). Gamma diversity was higher in 2021 than in 2017 for saproxylic beetles. Gamma diversity did not differ among treatments but for cambivores and wood borers there was a trend with lower gamma diversity in the reference area in 2017 and 2021 and the opposite pattern in 2018 (Appendix 2). In 2018, species richness and abundance of saproxylic beetles in no translocation plots increased with distance to the nearest translocation plot (Appendix 3).

### 3.1. Species richness

There was a significant effect of treatment, year, and their interaction for the species richness of all saproxylics, all feeding guilds, and for species of conservation concern (not for year) (Table 3, Fig. 4). For the treatment within year interaction, prior to translocation of deadwood in 2017, overall species richness was higher in the medium-density plots than in the high-density plots and the reference area plots. In addition, species richness of species of conservation concern was also higher in medium-density plots than in high-density plots. (Fig. 3, Table 2).

Following the translocation in 2018, species richness of all saproxylics and the group cambivores + woodborers was higher in high-density plots than in no translocation plots. Additionally, species richness of all saproxylics, fungivores, predators and cambivores + woodborers was higher in medium- and high-density plots in comparison to the reference area. The richness of species of conservation concern was higher in medium-density plots than in the reference area. By 2021, species richness of all saproxylics was significantly higher in the high-density plots than in the no translocation plots. However, no significant differences were detected between high-density plots and the no translocation plots for other feeding guilds. The species richness of all saproxylics, fungivores and predators remained significantly higher in medium- and high-density plots compared to the reference area plots (Fig. 3, Table 2).

For the year within treatment interaction, in high-density plots, species richness increased from 2017 to 2021 for all beetle groups, except for cambivores + woodborers that remained unchanged. However, for fungivores, predators and species of conservation concern there was no significant difference between 2017 and 2018. In medium-density plots, species richness of all saproxylics and predators increased from 2017 to 2021. (Fig. 3, Table 2).

In contrast to the medium and high-density plots, overall species richness did not change in the no translocation plots nor the reference area plots between 2017 and 2021.However, species richness was significantly lower in 2018 than in 2017 in the reference plots for all saproxylics, fungivores, predators and cambivores + woodborers and for all saproxylics in the no translocation plots. Furthermore, species richness increased between 2018 and 2021 in most plot types for all saproxylics, predators (not no translocation plots), fungivores (not medium-density plots) and cambivores + woodborers (reference plots only) (Fig. 3, Table 2).

### 3.2. Abundance

For abundance (the number of observed beetle individuals), there was a significant effect of treatment, year and their interaction for all

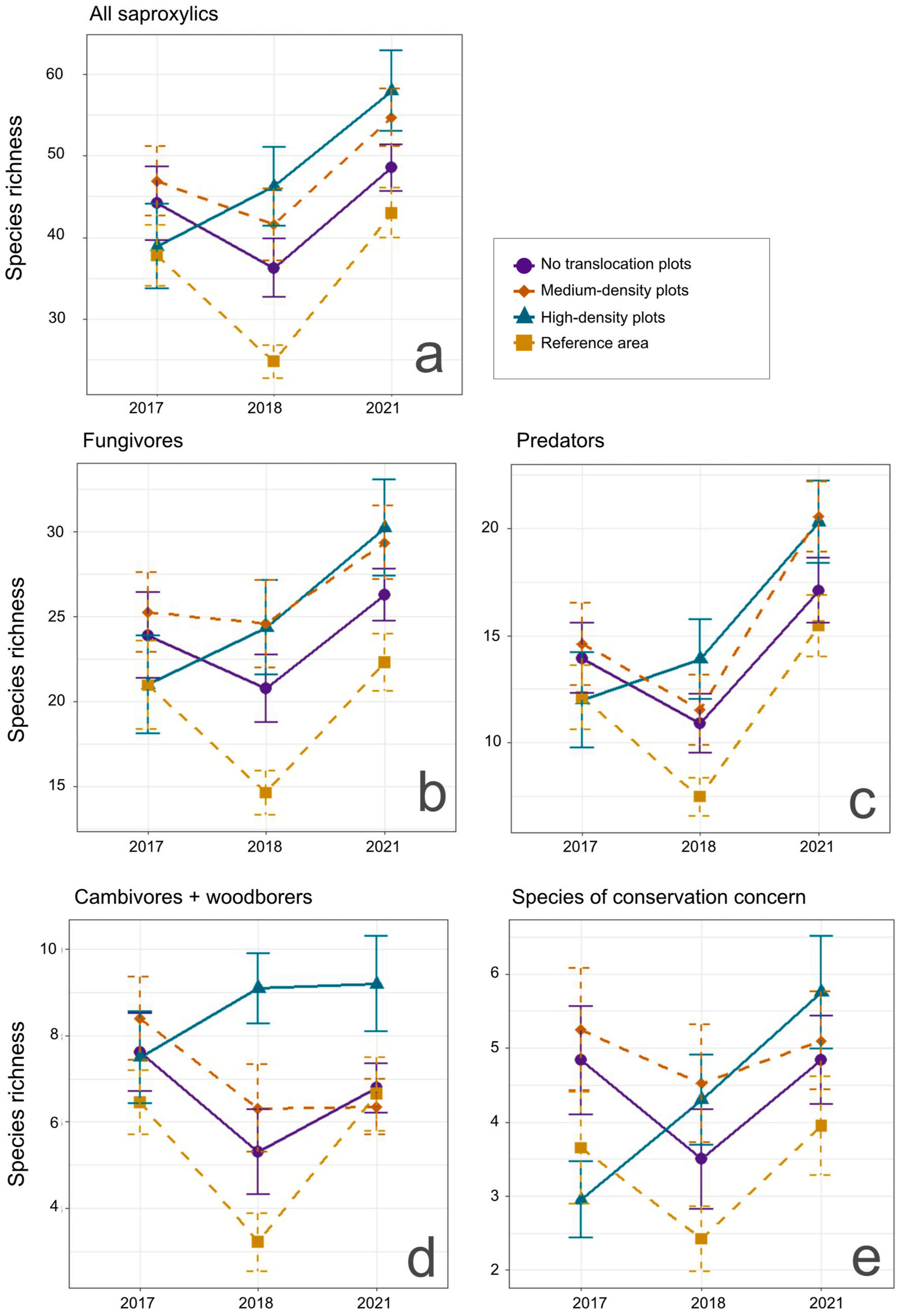

**Fig. 3.** Species richness (mean ± SE) of all saproxylic beetles and saproxylic beetles belonging to different feeding guilds over the sampling years: before translocation in 2017, one year after translocation in 2018, and four years after translocation in 2021. Treatments included an experimental control where no translocated deadwood was added, medium-density plots (addition of 16 substrates/plot), and high-density plots (addition of 48 substrates/plot) and the reference area. Note the varying y-axis scales.

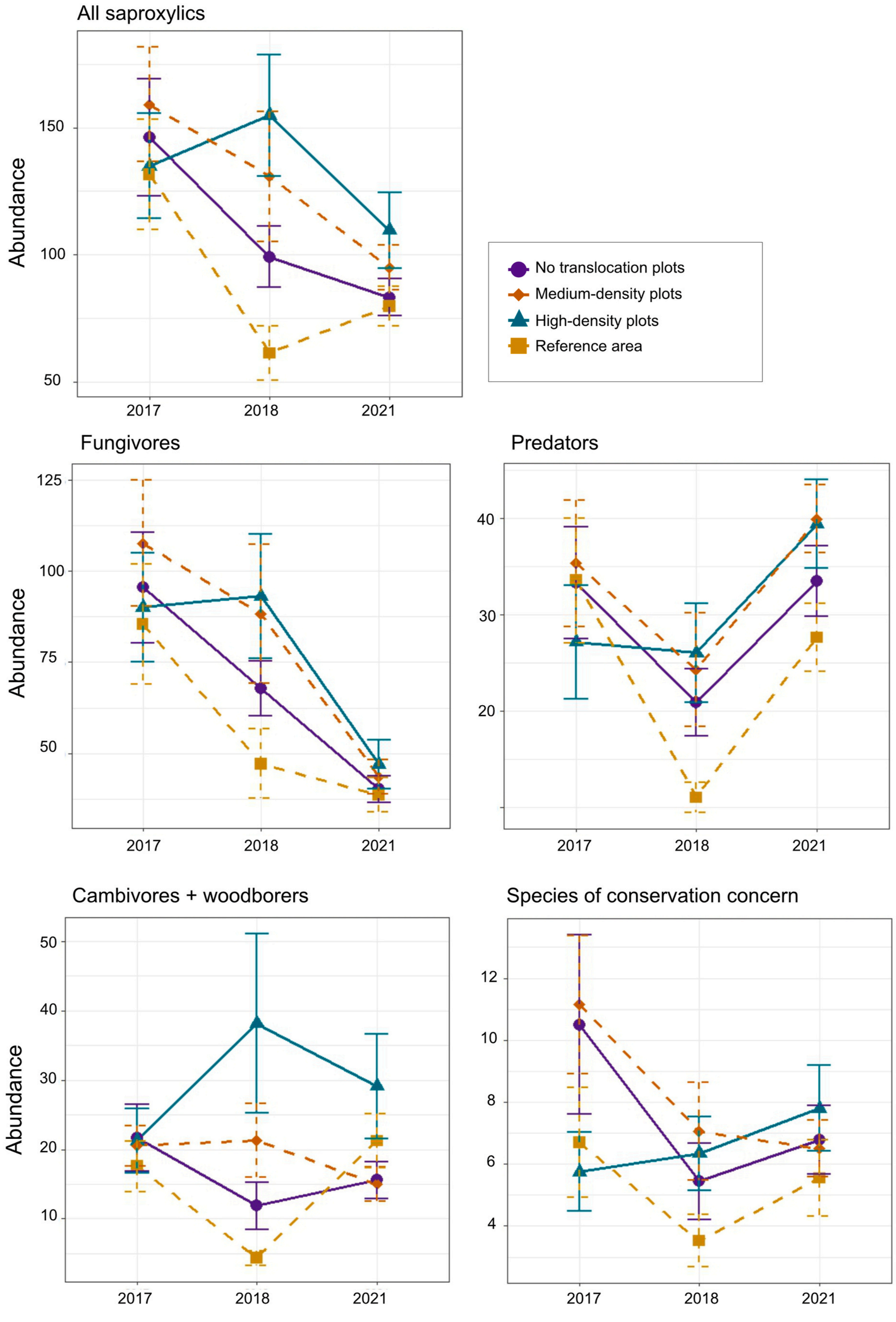

**Fig. 4.** Abundance (mean ± SE) of all saproxylic beetles and saproxylic species belonging to different feeding guilds over the sampling years: before translocation in 2017, one year after translocation in 2018, and four years after translocation in 2021. Treatments are no translocation plots (no deadwood addition), medium-density plots (addition of 16 substrates/plot), and high-density plots (addition of 48 substrates/plot) and the reference area. Note the varying y-axis scales.

**Table 2**
GLM results for species richness. Only significant results ($p < 0.05$) are presented for the pairwise Tukey posthoc comparisons.

| Feeding guild | Factor | $\chi^2$ | P | Pairwise Tukey-posthoc Treatment within Year | Pairwise Tukey-posthoc Year within Treatment |
|---|---|---|---|---|---|
| All saproxylics | | | | | |
| | Treatment | 149.531 | <0.001 | 2017: MDP > HDP**, MDP > RA*** | NTP: 2017 > 2018**, 2018 < 2021*** |
| | Year | 35.155 | <0.001 | 2018: NTP < HDP***, NTP > RA***, MDP > RA***, HDP > RA*** | MDP: 2017 < 2021*, 2018 < 2021*** |
| | Treatment x Year | 71.079 | <0.001 | 2021: NTP<HDP**, MDP>RA***, HDP > RA*** | HDP: 2017 < 2018*, 2017 < 2021***, 2018 < 2021*** |
| | | | | | RA: 2017 > 2018***, 2018 < 2021*** |
| Fungivores | | | | | |
| | Treatment | 74.518 | <0.001 | 2017: ns | NTP: 2018 < 2021* |
| | Year | 12.622 | 0.002 | 2018: NTP > RA***, MDP > RA***, HDP > RA*** | MDP: ns |
| | Treatment x Year | 29.380 | <0.001 | 2021: MDP > RA***, HDP > RA*** | HDP: 2017 < 2021***, 2018 < 2021* |
| | | | | | RA: 2017 > 2018***, 2018 < 2021*** |
| Predators | | | | | |
| | Treatment | 41.103 | <0.001 | 2017: ns | NTP: ns |
| | Year | 26.590 | <0.001 | 2018: NTP > RA***, MDP > RA***, HDP > RA*** | MDP: 2017 < 2021***, 2018 < 2021*** |
| | Treatment x Year | 25.064 | <0.001 | 2021: MDP > RA***, HDP > RA*** | HDP: 2017 < 2021***, 2018 < 2021*** |
| | | | | | RA: 2017 > 2018***, 2018 < 2021*** |
| Cambivores + Woodborers | | | | | |
| | Treatment | 49.0491 | <0.001 | 2017: ns | NTP: ns |
| | Year | 7.9874 | 0.018 | 2018: NTP < HDP***, MDP > RA***, HDP > RA*** | MDP: ns |
| | Treatment x Year | 32.9304 | <0.001 | 2021: ns | HDP: ns |
| | | | | | RA: 2017 > 2018***, 2018 < 2021*** |
| Species of conservation concern | | | | | |
| | Treatment | 19.8102 | <0.001 | 2017: MDP > HDP* | NTP: ns |
| | Year | 5.2005 | 0.074 | 2018: MDP > RA* | MDP: ns |
| | Treatment x Year | 17.9121 | 0.006 | 2021: ns | HDP: 2017 < 2021** |
| | | | | | RA: ns |

Whenever significant interactions were observed, we analysed each factor at every level of the other factor, e.g., 2018: NTP > RA means that the species richness was higher in No translocation plots 2018 compared to Reference plots 2018. NTP: No translocation plots, MDP: medium-density plots, HDP: high-density plots, RA: reference area. ns: no significance. Significance levels: * indicate a p-value ≤0.05, ** indicate a p-value ≤0.01, and *** indicate p-value ≤0.001. Model structure: count ~ treatment*year.

saproxylics, all feeding guilds and for species of conservation concern (Table 3, Fig. 4). For the treatment within year interaction, prior to the translocation of deadwood in 2017, abundance of all saproxylics, fungivores, predators or the group cambivores + woodborers did not differ between plot types. However, there were significantly more individuals of species of conservation concern in medium-density plots compared to high-density plots. One year post translocations in 2018, abundance of all saproxylic beetles and cambivores + woodborers was significantly higher in the high-density plots than the no translocation plots (Fig. 4, Table 3). Moreover, similarly as with species richness, the abundance of all saproxylics, fungivores, predators and cambivores + woodborers was significantly higher in the medium- and high-density plots than in the reference area plots in 2018 (Fig. 4, Table 3). Species of conservation concern did not show any significant response to the translocation treatments either in 2018 or 2021. All saproxylics, predators and cambivores + woodborers were also significantly more numerous in no translocation plots than in the reference area plots in 2018. By 2021, differences in abundance across treatments or between the compensation and reference areas abated for nearly all species groups. However, the abundance of cambivores + woodborers remained significantly higher in high-density plots than in medium-density plots (Fig. 4, Table 3).

For the year within treatment interaction, the abundance decreased significantly from 2017 to 2021 in no translocation, medium-density plots and reference area plots for all saproxylics, fungivores, predators (reference area plots only), cambivores + woodborers (reference area plots only) and species of conservation concern (no translocation plots only) (Fig. 4, Table 3).

### 3.3. *Assemblage composition*

Treatment, year and their interaction had a significant effect on assemblage composition of all saproxylics, all feeding guilds, and for species of conservation concern (Fig. 5, Table 4). The differences in assemblage composition for all saproxylic beetles and the feeding guilds were to a large extent attributed to significant variations between years, with 56–64 % of the variance explained by year and 18–26 % by treatment (Table 4). For the treatments within year interaction, in 2017, prior to translocation, no differences were found between treatment plots in the compensation area. However, the assemblage composition of all saproxylic beetles and all functional groups differed significantly between the reference area and the compensation area plots in all years, with the exception for species of conservation concern in 2021 (Table 4).

After translocation in 2018, the assemblages differed significantly between no translocation plots and both the medium- and high-density plots in the compensation area for of all saproxylics, fungivores, predators and cambivores + woodborers, but not for species of conservation concern. By 2021, assemblages differed between high-density plots and no translocation plots for all saproxylics, fungivores and cambivores + wood borers, but no significant differences were found between no translocation and medium-density plots (Fig. 5, Table 4 and Appendix 4).

For the year within treatment interaction, assemblage composition differed significantly across all years for all plot types and feeding guilds, except for species of conservation concern. For species of conservation concern, significant differences were observed across all years in high-density and reference plots, while in no translocation and medium-density plots, differences were only found between 2017 and 2018 (Fig. 5, Table 4, Appendix 4). The species that contributed most to

**Table 3**
Results of the GLMs for abundance of saproxylic beetles. Only significant results ($p < 0.05$) are presented for the pair-wise Tukey posthoc comparisons.

| Feeding guild | Factor | $\chi^2$ | P | Pairwise Tukey-posthoc Treatment within Year | Pairwise Tukey-posthoc Year within Treatment |
|---|---|---|---|---|---|
| All saproxylics | | | | | |
| | Treatment | 36.903 | <0.001 | 2017: ns | NTP: 2017 > 2021** |
| | Year | 17.594 | <0.001 | 2018: NTP<HDP*, NTP>RA*, MDP > RA***, HDP > RA*** | MDP: 2017 > 2021** |
| | Treatment x Year | 27.506 | <0.001 | 2021: ns | HDP: ns |
| | | | | | RA: 2017 > 2018***, 2017 > 2021* |
| Fungivores | | | | | |
| | Treatment | 19.226 | <0.001 | 2017: ns | NTP: 2017 > 2021***, 2018 > 2021*** |
| | Year | 33.278 | <0.001 | 2018: MDP > RA**, HDP > RA*** | MDP: 2017 > 2021***, 2018 > 2021** |
| | Treatment x Year | 12.758 | 0.047 | 2021: ns | HDP: 2017 > 2021**, 2018 > 2021** |
| | | | | | RA: 2017 > 2018***, 2017 > 2021*** |
| Predators | | | | | |
| | Treatment | 21.206 | <0.001 | 2017: ns | NTP: ns |
| | Year | 11.186 | 0.003 | 2018: NTP > RA*, MDP > RA***, HDP > RA*** | MDP: ns |
| | Treatment x Year | 22.848 | <0.001 | 2021: ns | HDP: ns |
| | | | | | RA: 2017 > 2018***, 2018 < 2021*** |
| Cambivores + Woodborers | | | | | |
| | Treatment | 61.381 | <0.001 | 2017: ns | NTP: ns |
| | Year | 8.700 | 0.013 | 2018: NTP < HDP***, NTP > RA***, MDP > RA***, HDP > RA*** | MDP: ns |
| | Treatment x Year | 72.01 | <0.001 | 2021: MDP < HDP* | HDP: ns |
| | | | | | RA: 2017 > 2018***, 2018 < 2021*** |
| Species of conservation concern | Treatment | 16.566 | <0.001 | 2017: MDP > HDP* | NTP: 2017 > 2018* |
| | Year | 11.615 | 0.003 | 2018: ns | MDP: ns |
| | Treatment x Year | 15.839 | 0.015 | 2021: ns | HDP: ns |
| | | | | | RA: ns |

Whenever significant interactions were observed, we analysed each factor at every level of the other factor, e.g., 2018: NTP > RA means that the abundance was higher in No translocation plots 2018 compared to Reference plots 2018. NTP: No translocation plots, MDP: medium-density plots, HDP: high-density plots, RA: reference area. ns: no significance. Significance levels: * indicate a p-value of less than 0.05, ** indicate a p-value of less than 0.01, and *** indicate p-value of less than 0.001. Model structure: count ~ treatment*year.

differences in species composition, as shown by the SIMPER analyses, generally contributed only around 1 % for all saproxylics and around 5 % for the feeding guilds, which means that many species collectively contributed to the observed differences in species composition between plot types and years. A list of the ten species that contributed the most to differences among treatments is found in Appendix 5. For all saproxylics, 61 species were significant in the indicator species analyses for either treatment or year (14 for 2017, 27 for 2018, and 20 for 2021). A notable number of indicator species were associated with the translocation treatments, with three species in medium-density plots, 15 species in high-density plots, and 15 species in both medium- and high-density plots. The reference area had 13 indicator species. A complete list of significant indicator species can be found in Appendix 6.

## 4. Discussion

Translocation of deadwood may be useful for restoring habitat elements and associated biodiversity that would otherwise take decades to develop (Tranberg et al., 2024). In our study, translocation of a large amount of deadwood resulted in at least a temporary increase in saproxylic beetle species richness four year after translocation. However, there were considerable between-year variation in beetle activity, resulting in a general decrease in overall beetle species richness the first year after translocation across all plot types except for the medium- and high-density plots, i.e., the plots receiving translocated deadwood. We also found that changes in richness and composition were related to the amount of deadwood translocated, i.e., the increase in beetle species richness and abundance was more pronounced in high-than in medium-density plots. The fact that species richness and abundance of saproxylic beetles in no translocation plots increased with distance to the nearest translocation plot indicate that translocated wood attracted beetles from a surrounding area larger than the closest distances between no translocation plots and translocation plots. Future studies will explore connectivity among plots and substrates in more detail. This suggests that the approach could be adapted and optimized based on the initial quality of the target area. To improve outcomes, translocations should aim to provide enough substrate to meet the threshold values in amount and quality needed to support viable populations of target species in the restored area.

### 4.1. Species richness and abundance

Our results provide two key indications supporting our predictions of increased species richness following deadwood translocation. Firstly, in both 2018 and 2021, we observed an increase in overall species richness within high-density (but not the medium-density) plots when compared to plots without translocated deadwood. Secondly, overall species richness increased from the pre-translocation season to the first season post-translocation in the high-density plots, and then again from the first season to the fourth season post-translocation in both the medium- and high-density plots but not in the no translocation plots. The similar gamma-diversity among treatments suggest that increases in species richness is mediated by increases in abundances.

This increase in overall species richness comprise an increase of approximately 10–15 species collected per plot corresponding to 15–25 % increase in species richness. As for the response of feeding guilds, fungivores and predators showed a significant increase in species richness in high- and medium-density plots (predators only) from 2017 to 2021. By contrast, species richness of cambivores + woodborers did not increase significantly from 2017 to 2021. The only indication of a

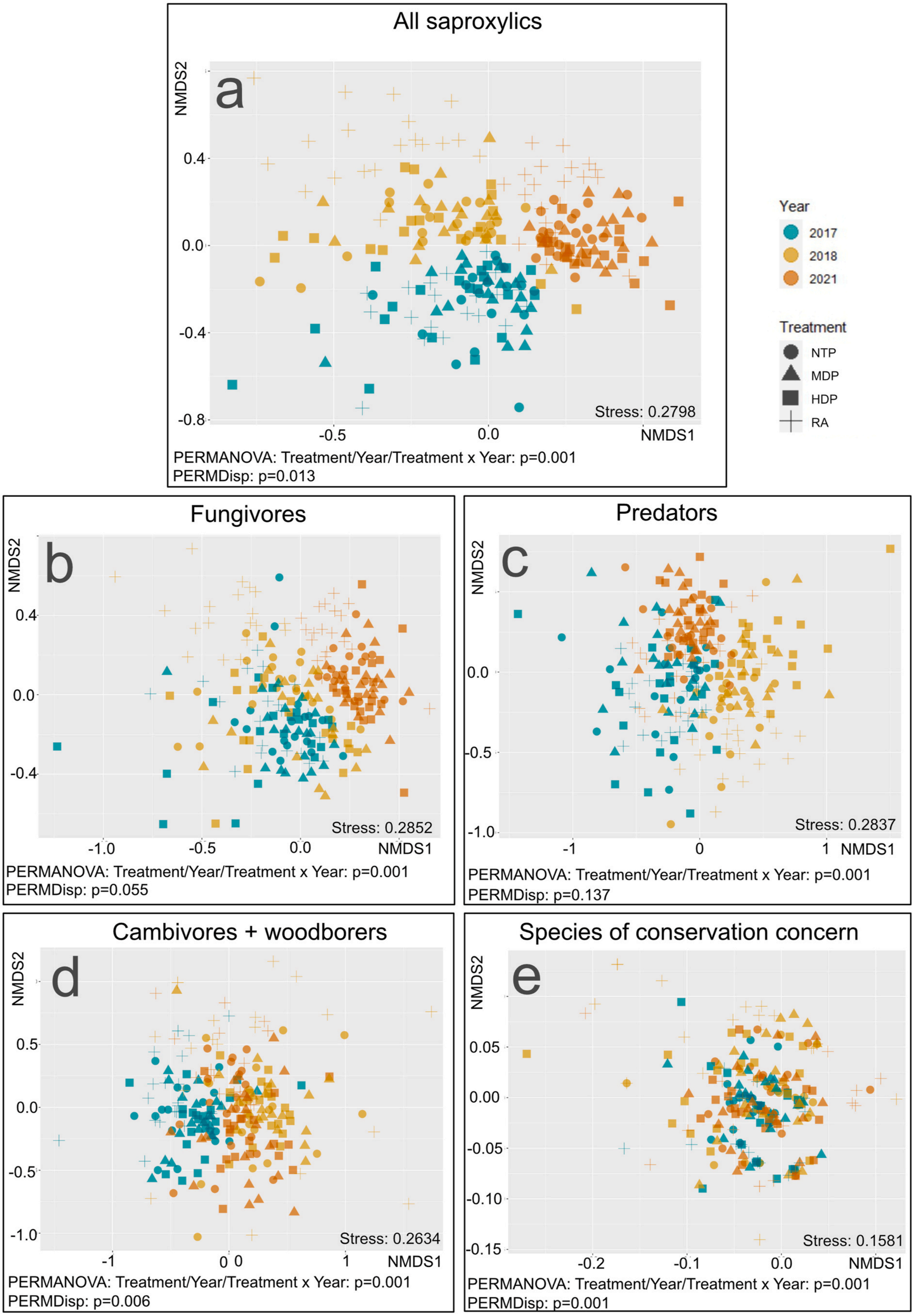

**Fig. 5.** NMDS ordination results for the community composition of saproxylic beetles at the trap level for the four studied treatment groups; no translocation plots (NTP), medium-density plots (MDP), high-density plots (HDP) and Reference Area (RA). The colors indicate the different sampling years.

**Table 4**
Result of PERMANOVA for assemblage composition of saproxylic beetles. Only significant results ($p < 0.05$) are presented for the pair-wise Tukey posthoc comparisons.

| Source | df | MS | SS | F | P | Pair-wise Tukey-posthoc Treatment within Year | Pair-wise Tukey-posthoc Year within Treatment |
|---|---|---|---|---|---|---|---|
| All saproxylics | | | | | | | |
| Treatment | 3 | 7924.7 | 23,774 | 5.26 | 0.001 | 2017: RA≠NTP***, MDP***, HDP*** | NTP: 2017≠2018***, 2017≠2021***, 2018≠2021*** |
| Year | 2 | 30,998 | 61,996 | 20.57 | 0.001 | 2018: RA≠NTP***, MDP***, HDP***; NTP≠MDP**, HDP***, ***; MDP≠HDP*, | MDP: 2017≠2018***, 2017≠2021***, 2018≠2021*** |
| Treatment x Year | 6 | 3225.5 | 19,353 | 2.14 | 0.001 | 2021: RA≠NTP***, MDP***, HDP*** | HDP: 2017≠2018***, 2017≠2021***, 2018≠2021***<br>RA: 2017≠2018***, 2017≠2021***, 2018≠2021*** |
| Fungivores | | | | | | | |
| Treatment | 3 | 7201.1 | 21,603 | 5.56 | 0.001 | 2017: RA≠NTP**, MDP**, HDP** | NTP: 2017≠2018***, 2017≠2021***, 2018≠2021*** |
| Year | 2 | 25,881 | 51,763 | 19.98 | 0.001 | 2018: RA≠NTP***, MDP***, HDP***; NTP≠MDP**, HDP** | MDP: 2017≠2018***, 2017≠2021***, 2018≠2021*** |
| Treatment x Year | 6 | 2683.6 | 16,101 | 2.07 | 0.001 | 2021: RA≠NTP***, MDP***, HDP*** NTP ≠HDP* | HDP: 2017≠2018***, 2017≠2021***, 2018≠2021***<br>RA: 2017≠2018***, 2017≠2021***, 2018≠2021*** |
| Predators | | | | | | | |
| Treatment | 3 | 6393.9 | 19,182 | 3.27 | 0.001 | 2017: RA≠NTP*, MDP**, HDP** | NTP: 2017≠2018***, 2017≠2021***, 2018≠2021*** |
| Year | 2 | 35,406 | 70,813 | 18.1 | 0.001 | 2018: NTP ≠MDP*, ≠HDP***, MDP ≠HDP*, RA**, HDP≠RA*** | MDP: 2017≠2018***, 2017≠2021***, 2018≠2021*** |
| Treatment x Year | 6 | 3350 | 20,100 | 1.71 | 0.001 | 2021: RA≠NTP***, MDP***, HDP*** | HDP: 2017≠2018***, 2017≠2021***, 2018≠2021***<br>RA: 2017≠2018***, 2017≠2021***, 2018≠2021*** |
| Cambivores + Woodborers | | | | | | | |
| Treatment | 3 | 11,300 | 33,900 | 6.50 | 0.001 | 2017: RA≠NTP***, MDP***, HDP*** | NTP: 2017≠2018***, 2017≠2021***, 2018≠2021*** |
| Year | 2 | 37,028 | 74,056 | 21.29 | 0.001 | 2018: NTP ≠MDP**, ≠ HDP ***, ≠RA*** MDP ≠ HDP *, ≠RA***, HDP ≠RA*** | MDP: 2017≠2018***, 2017≠2021***, 2018≠2021*** |
| Treatment x Year | 6 | 4022.6 | 24,135 | 2.31 | 0.001 | 2021: RA≠NTP***, MDP***, HDP***NTP ≠ HDP ***, MDP ≠ HDP **, | HDP: 2017≠2018***, 2017≠2021***, 2018≠2021***<br>RA: 2017≠2018***, 2017≠2021***, 2018≠2021*** |
| Species of conservation concern | | | | | | | |
| Treatment | 3 | 6238.1 | 18,714 | 2.71 | 0.001 | 2017: NTP ≠ HDP *, RA*, MDP ≠ HDP *,RA** | NTP: 2017≠2018* |
| Year | 2 | 15,955 | 31,911 | 6.95 | 0.001 | RA≠NTP***, MDP***, HDP*** | MDP: 2017≠2018* |
| Treatment x Year | 6 | 5469.3 | 32,816 | 2.38 | 0.001 | 2021: ns | HDP: 2017≠2018**, 2017≠2021*, 2018≠2021*<br>RA: 2017≠2018***, 2017≠2021*, 2018≠2021*** |

Only significant results ($p < 0.05$) are presented for the pair-wise Tukey posthoc comparisons. ≠ indicates a significant difference in assemblage composition. Whenever significant interactions were observed, we analysed each factor at every level of the other factor, e.g., 2018: NTP ≠ MDP means that the assemblage composition differed between the No translocation plots (NTP) and the medium-density plots (MDP). NTP: no translocation plots, MDP: medium-density plots, HDP: high-density plots, RA: reference area. ns: no significance. Significance levels: * indicate a p-value of less than 0.05, ** indicate a p-value of less than 0.01, and *** indicate p-value of less than 0.001.

positive response in cambivores + woodborers was a significantly higher species richness in high-density plots than in no translocation plots in 2018, indicative of an early response in cambivores. Thus, we found limited support for our predictions that addition of fresh deadwood would lead to increases in this functional group. Previous research on deadwood enrichment, which has mostly focused on fresh substrates of limited variety and quality have shown a strong positive response in cambivore species richness and abundance (e.g., Hjältén et al., 2012; Baber et al., 2016; Gossner et al., 2013, 2016; Komonen et al., 2014). However, in contrast to these studies we also translocated large amounts of deadwood on more advanced decay stages, in fact 50 % of the translocated deadwood belonged to more advanced decay stages (Tranberg et al., 2024). It is therefore logical that feeding guilds that utilize later decay stages, e.g., fungivores and predators showed a positive response to translocation and data from emergence traps on the translocated logs showed a higher emergence of fungivores and predators from deadwood in mid decay stages than in early decay stages (Tranberg, 2024).

Translocation of deadwood in advanced decay stages were expected to provide habitat for species associated with more uncommon substrates. These species generally occur in lower abundances and the chances to catch emerging individuals in flight intercept traps is thus also smaller (Hjältén et al., 2012; Stenbacka et al., 2010). In addition to simply adding fresh deadwood, we observed a significant presence of fungivores within the first year, which suggests that our method to some extent benefit species associated with various successional stages. Including a wide spectrum of deadwood substrates in translocations, not only provides more habitat, but also provides different substrate types, supporting a broader range of species in line with the habitat heterogeneity hypothesis by Whittaker (1972). This trend becomes increasingly clear when viewed in terms of species of conservation concern, as our results showed that their richness increased over time in high-density plots. Similar results have been shown in Komonen et al. (2014), where deadwood enrichment caused an increase in species richness of rare and red-listed species from the first post-treatment year to five years post-treatment.

As predicted, we found the strongest effect on species richness and abundances within the high-density plots, which could be explained by two mechanisms: 1) more species were translocated together with the deadwood in high-density plots, or 2) more species were attracted to the high-density plots from the surrounding landscape. Our study does not allow us to disentangle these two potential drivers behind the observed increase in species richness and abundance. Even so, data from emergence traps on the translocated logs (Tranberg, 2024) reveals that high numbers of cambivores emerged in 2018, mainly from early decay spruce logs. In our study, overall species richness continued to increase in both medium- and high-density plots between 2017 and 2021 while abundances did not change. This suggests that translocation resulted in a species enrichment but did not influence overall abundance. Thus, it is likely that the beetles caught in the flight intercept traps include a combination of species emerging from the translocated deadwood (e.g., cambivores) and species and individuals attracted from the surroundings (e.g., fungivores).

Within the feeding guilds, the pattern for species richness was similar but less pronounced with predators only showing a significant increase within translocation plots by 2021, suggesting a time lag in response to deadwood compared to their major prey species. This is consistent with previous studies where bark beetle predators have been shown to have similar habitat preferences as their prey (Johansson et al., 2007) and to increase later than bark beetles after deadwood enrichment (Heikkala et al., 2016; Hekkala et al., 2020; Hjältén et al., 2017; Hägglund and Hjältén, 2018; Kärvemo et al., 2017).

Contrary to our predictions, we did not find a general increase in beetle abundance in the translocation plots over the studied four years. Even so, in the first year following translocation, all saproxylic and cambivore + woodborer abundance was greater in high-density plots compared with plots with no translocation. This suggests that cambivores are attracted by volatile organic compounds (VOCs) released from fresh dead and dying trees (Tunset et al., 1993) and respond immediately to the deadwood enrichment. The increased abundance of cambivores after restoration and translocation aligns with our prediction that early successional species would respond immediately to deadwood enrichment, especially since around 50 percent of the translocated deadwood volume was in an early decay stages (Tranberg et al., 2024). In a study from the same plots (Tranberg, 2024) the proportion of predators more than doubled in emergence traps on the translocated logs in the second season (year 2019) after translocation, a trend evident across all substrates types except pine logs in mid decay classes. Taken collectively with our sampling from year 2021, this suggests that the initial attraction of cambivores to fresh deadwood may subsequently attract predators in the following years, contributing to the observed increase in predatory beetle species richness captured in our flight intercept traps and potentially influencing beetle community composition over time.

### *4.2. Assemblage composition*

Our prediction that assemblage composition would change as a response to translocation was partially supported. We found a difference in assemblages between no translocation and translocation plots for most feeding guilds in 2018, but this effect remained significant primarily for comparisons between no translocation and high-density plots in 2021 for all saproxylics and some feeding guilds, i.e., fungivores and cambivores/woodborers. This indicate a diminishing effect of translocation with time. However, more long-term studies are needed to confirm this pattern. Deadwood translocation generally interacted with year in shaping beetle assemblage composition, potentially reflecting both successional changes with time since translocation and deadwood decomposition (Seibold et al., 2023; Stokland et al., 2012), as well as inter-annual variations in weather (Müller et al., 2023).

The results of our study are not directly comparable to other deadwood enrichment studies, as they have only assessed enrichment using fresh wood. Further, enrichment of older deadwood in closed forests, as in our experiment, does not substantially alter canopy openness, unlike stand-replacing disturbances such as fires, which significantly increase deadwood volumes and alter canopy cover (Eriksson et al., 2013). Fire immediately induce turnover in beetle communities and increase species richness and abundance (Fredriksson et al., 2020; Johansson et al., 2007; Saint-Germain et al., 2004). However, our findings align more closely with studies involving deadwood enrichment through gap cuttings in mature to old forests (e.g., Hägglund et al., 2020; Hjältén et al., 2017) and suggest that local deadwood enrichment may not result in substantial assemblage turnover but can increase species richness and abundance, at least in the short term (Komonen et al., 2014).

Many species from various feeding guilds contributed modestly to the differences in assemblage compositions among different treatment types, as detailed in Appendix 5. This suggests that the observed shifts in assemblage compositions were not driven by significant changes in a few dominant species as in Komonen et al. (2014), but rather reflect a broader modification in assemblage composition.

Responses of rare and threatened species are by definition harder to detect due to their rarity (Martikainen and Kouki, 2003). However, the fact that we had higher numbers of indicator species in high-density plots than in medium-density plots or no translocation plots indicate that high-density plots have a higher probability to host intact species assemblages (i.e., most species can occur in most plots). This means that although the assemblage composition of species of conservation concern did not differ between medium- and high-density plots, the increased deadwood volumes likely supports larger populations of target species.

Species assemblages in the reference area were generally different from those in the compensation area and in general hosted fewer species and individuals. This is most likely due to differences in climatic conditions (e.g., altitude) as well as habitat conditions (e.g., tree species composition and mean basal area) between the two areas. The reference area has a continuity of deadwood, up to three times higher amounts than the compensation area before translocation and have a more open canopy with lower basal area. None of the translocation treatments reached the same amount of deadwood as the reference area on stand level. On the other hand, the translocated deadwood in the compensation area provided a diversity of deadwood concentrated in small plots, whereas the reference area contained more evenly distributed, more decayed whole trees. Thus, the differences between the reference and compensation areas can probably be attributed to their differences in deadwood volume, composition and continuity.

While this study demonstrates a 'proof-of-concept', several caveats must be considered. Firstly, significant heterogeneity in beetle composition was observed within the compensation area before translocation. For instance, plots designated for medium-density deadwood translocation initially had higher species richness than the high-density plots, potentially due to naturally occurring higher volumes of deadwood (Table 1). Conducting accurate and detailed baseline assessments of assemblages in proposed compensation areas is important before translocation, despite the additional costs, as this can help optimize the translocation strategies. Additionally, while altering habitat amount can boost species numbers and population sizes in the short term, long-term sustainability depends on habitat quality, continuity, connectivity, and landscape context (Djupström et al., 2024; Hanski, 1998; Lindman et al., 2020). Small, isolated populations are more vulnerable to extinction from stochastic events, predation, and competition than large populations that are not isolated (Hanski, 1998; Snäll et al., 2005), emphasizing the need for long-term monitoring. Therefore, if deadwood translocation is to be used as a compensation measure, it is essential to *ensure* that the resulting volumes and qualities in the compensation area meet or exceed the thresholds required by the target species or communities over the long term. One should also be aware that this study was conducted in a single boreal landscape, and additional studies in other landscapes and other forest types (e.g., temperate forests) is necessary to test the generality of our findings. It is also important to underscore the fundamental principle of ecological compensation that applies to all forms of environmental impacts, including urban and infrastructure development. The best approach is to protect the most valuable habitats from irreversible damage (Gardner et al., 2013). Compensatory actions, such as translocation, should be considered only when preservation is not feasible and the societal benefits of the impact clearly outweigh conservation concerns.

## 5. Conclusions

In our study, we observed that translocation of deadwood and associated saproxylic organisms may provide an alternative for restoring habitat elements and biodiversity that would otherwise take decades to develop. At least in a short-term perspective, this approach increased species richness of saproxylic beetles, positively in relation to amount of deadwood translocated. Our findings suggest that increasing diverse types of deadwood, including different species and different decay stages, even the advanced decay deadwood, translocation could be used to accelerate the establishment of species with specific habitat demands that typically takes decades to form. This approach should be tailored based on the initial quality of the compensation area to achieve thresholds in amounts and quality suitable for target species and communities. The long-term outcomes of deadwood translocations for beetle diversity remains to be explored, including assessing the persistence of translocated substrates as functional habitats, and colonization and establishment of local deadwood in the compensation area.

## CRediT authorship contribution statement

**Olov Tranberg:** Writing – original draft, Formal analysis, Data curation, Conceptualization. **Therese Löfroth:** Writing – review & editing, Supervision, Formal analysis, Conceptualization, Data curation, Methodology, Validation, Visualization. **Anne-Maarit Hekkala:** Writing – review & editing, Supervision. **Mari Jönsson:** Writing – review & editing, Supervision, Conceptualization. **Timothy Work:** Writing – review & editing. **Heloise Gibb:** Writing – review & editing. **Lukas Holmström:** Writing – review & editing, Methodology, Formal analysis. **Jörgen Sjögren:** Writing – review & editing, Supervision. **Joakim Hjältén:** Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization.

## Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Joakim Hjalten reports financial support was provided by Boliden Mineral AB. Joakim Hjalten reports financial support was provided by Göran Gustafsson Foundation for the Promotion of Scientific Research. Joakim Hjalten reports financial support was provided by Sveaskog AB. Joakim Hjalten reports was provided by Swedish Research Council Formas. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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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.2025.125448.

## Data availability

Data will be made available on request.

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