



Fire-emulating tree veteranization as an alternative restoration measure to prescribed burning:

effects on beetle communities in boreal forests

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Fire-emulating tree veteranization as an alternative restoration measure to prescribed burning: effects on beetle communities in boreal forests

Brandefterliknande trädveteranisering som en alternativ restaureringsåtgärd till naturvårdsbränning: effekter på skalbaggsamhällen i boreala skogar

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Abstract

In this study, fire-emulating tree veteranization was compared with prescribed burning in its effects on beetle communities in boreal forests. In Ejheden Ekopark in northern Dalarna, Sweden, a stand previously subjected to prescribed burning was compared with an adjacent stand where trees had been veteranized through girdling or bark stripping, with additional stem-base burns applied to selected trees in 2025. Beetle communities and habitat characteristics were assessed in 2024 and 2025, with the first sampling conducted 1-2 years after the initial restoration treatments and before the additional stem-base burns, and the second sampling conducted after the stem-base burns in the veteranized stand. Temporal changes were first compared between 2024 and 2025 for bark-stripped and girdled pine trees and for prescribed-burned trees (pine and birch). Treatment differences in 2025 were then assessed among bark-stripped, bark-stripped-and-burned, girdled-and-burned, and burned-only pine trees, as well as prescribed-burned pine and birch trees. Beetle abundance and species richness increased in the veteranized tree treatments between 2024 and 2025, with particularly large increases occurring in bark-stripped and girdled trees combined with stem-base burning. Shannon diversity also increased between sampling years but did not show treatment-specific temporal differences. By 2025, abundance was significantly higher in the girdled treatment than in the prescribed-burned treatment, while species richness no longer differed between the approaches. Reduced tree vitality was further associated with higher beetle abundance and species richness, greater char height with higher abundance, and greater deadwood availability with higher Shannon diversity. Community composition differed among stand-level restoration approaches, sampling years, and tree-treatment types, with temporal shifts being more pronounced in the veteranized stand. Moreover, pyrophilous and red-listed beetles increased between sampling years in the veteranized stand. These findings highlight the potential of fire-emulating tree veteranization, particularly when combined with targeted stem-base burning, to create heterogeneous fire-affected and deadwood-related habitat conditions utilized by disturbance-associated and conservation-relevant beetles. Veteranization may therefore complement prescribed burning within broader fire-based restoration strategies, although longer-term monitoring is needed to determine whether these responses persist and how different restoration approaches develop over time.

Keywords: boreal forests, saproxylic beetles, tree veteranization, prescribed burning, ecological restoration, deadwood, fire disturbance, biodiversity

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Abbreviations

Abbreviation	Description
B	Burned-only
BS	Bark-stripped
BS+B	Bark-stripped-and-burned
G	Girdled
G+B	Girdled-and-burned
GLMM	Generalized linear mixed model
n.d.	No date
NMDS	Non-metric multidimensional scaling
PB birch	Prescribed-burned birch
PB pine	Prescribed-burned pine
SLU	Swedish University of Agricultural Sciences
VFM	Department of Wildlife, Fish, and Environmental Studies

1. Introduction

1.1 Fire regimes in boreal forests

In boreal forests, fire is one of the most important natural disturbance processes, driving structural heterogeneity that is fundamental for maintaining biodiversity across the landscape (Ramberg 2020; Wein 1993). Historically, recurring fires shaped boreal forests across Fennoscandia as heterogeneous landscapes characterized by a mosaic of successional stages. Fire-return intervals varied among forest types and regions, with pine-dominated forests generally experiencing more frequent fires than spruce-dominated stands (Esseen et al. 1997; Zackrisson 1977). This pattern reflects differences in fire tolerance among tree species, as Scots pine (*Pinus sylvestris*) was able to persist under recurring fire regimes, whereas the expansion of Norway spruce (*Picea abies*) was restricted by frequent fire disturbance (Bradshaw 1993). In Sweden, however, this fire regime was substantially altered beginning in the late nineteenth century due to increasing fire suppression associated with the development of industrial forestry (Östlund 1993; Zackrisson 1977). Fire-scar reconstructions from northern Sweden demonstrate the magnitude of this change, with fire frequency during the mid-nineteenth century exceeding present-day lightning ignition rates by more than tenfold (Niklasson & Granström 2000). Whereas approximately 1% of forest area burned annually under historical fire regimes, only around 0.01% of productive forest area burns annually in Sweden today (Granström 2001).

1.2 Consequences of fire suppression

Forest fire generates a variety of habitat structures, including deadwood, canopy openings, and a range of post-fire substrates, thereby increasing structural heterogeneity in boreal forests (Esseen et al. 1997; Ramberg 2020). Early post-fire successional stages are characterized by abundant deciduous trees such as birch and aspen and represent highly diverse habitats supporting many threatened species across Sweden (Berg et al. 1994; Esseen et al. 1997). The suppression of the natural fire regime in the boreal landscape has therefore reduced the availability of fire-created habitats, while promoting a shift towards late-successional forests dominated by spruce at the expense of previously mixed stands of Scots pine, birch and aspen (Bradshaw 1993; Zackrisson 1977). This habitat loss has contributed to declines in biodiversity, particularly among pyrophilous species, including plants, fungi, lichens, and insects associated with fire and recently burned habitats (Esseen et al. 1997; Hjältén et al. 2018).

Among these affected organisms, saproxylic beetles, which depend on dead or decaying wood or associated organisms during at least one stage of their life cycle, comprise a taxonomically and functionally diverse component of forest biodiversity (Jacobs et al. 2006; Speight 1989). Within this group, pyrophilous species are closely associated to fire-related habitats and may rely on or benefit from fire-created structures such as fire-

damaged trees and fire-scarred wood, as well as recently burned areas (Bell 2023; Wikars 1997). Standing and fallen deadwood provide essential breeding substrates for saproxylic beetles, with different species specializing in particular decay stages (Samuelsson et al. 1994; Samuelsson & Ingelög 1996; Siitonen 2001). Fire-created canopy openings further enhance the exposure of deadwood to sunlight, creating important habitat conditions for many saproxylic species (Dahlberg & Stokland 2004; Hjältén et al. 2018). In managed forests, the availability of deadwood has been substantially reduced, while deadwood volume, diversity, and continuity represent key structural features shaping biodiversity in boreal forest landscapes (Hekkala et al. 2016; Sandström et al. 2019). The loss and fragmentation of such fire-created habitats have contributed to declines in saproxylic beetles, including pyrophilous species, many of which are currently of conservation concern (Bell 2023; Cálix et al. 2018; SLU Artdatabanken 2026).

1.3 Beetle communities as indicators

In this context, pyrophilous beetles represent an important target group for efforts aimed at restoring fire-associated habitat conditions in boreal forests (Hjältén et al. 2018). As pyrophilous beetles are closely associated with fire and include species with specialized adaptations for detecting and colonizing recently burned areas, they can serve as indicators of post-disturbance habitat quality and restoration outcomes (Bell 2023; Evans 1966; Fredriksson et al. 2020; Wikars 1997). Their occurrence reflects both the presence of fire-created structures, such as deadwood substrates and fire-damaged trees, and the availability of suitable habitats in the surrounding landscape (Hjältén et al. 2018). Fire-created structures contribute to habitat conditions supporting a variety of associated plant and animal communities across multiple taxonomic groups beyond their role for beetle communities (Esseen et al. 1997). Therefore, evaluating beetle diversity and community composition provides valuable metrics for assessing whether restoration measures recreate habitat conditions associated with natural fire regimes (Fredriksson et al. 2020).

1.4 Restoration approaches

To counteract the loss of fire-created habitats and the associated decline in biodiversity, ecological restoration in boreal forests aims to recover structural elements historically generated by fire and thereby emulate natural disturbance regimes (Fries et al. 1997). For saproxylic beetles, particularly pyrophilous species, maintaining or emulating post-fire structural features is crucial for recreating habitat conditions associated with historical fire regimes (Siitonen 2001). Since the Forestry Act of 1993, Swedish forest policy has increasingly emphasized management approaches that resemble natural disturbance regimes, including prescribed burning and the addition of deadwood, to promote biodiversity conservation and habitat restoration (Johansson et al. 2013; Kyraschenko et al. 2022).

Prescribed burning is increasingly used as a conservation and restoration measure to reintroduce natural disturbance processes and recreate post-fire habitat structures that have largely disappeared following long-term fire suppression (Granström 2001; Eales et al. 2018; Ramberg 2020). Specifically, prescribed burning has been shown to increase structural heterogeneity through the creation of deadwood, fire scars, and multilayered forest structures, while facilitating successional processes including deciduous tree recruitment (Hardenbol et al. 2020; Ramberg et al. 2026). These effects can in turn enhance biodiversity by restoring habitat conditions suitable for pyrophilous and saproxylic species (Eales et al. 2018; Hjältén et al. 2018). For saproxylic beetles, responses to prescribed burning include increases in abundance and species richness, as well as shifts in community composition towards early successional species associated with fire-created habitats (Hyvärinen et al. 2009; Hjältén et al. 2018).

However, the effectiveness of prescribed burning in achieving conservation objectives depends substantially on stand characteristics, weather conditions, seasonal timing, and landscape context, and some burns may not fully recreate key fire-related structures (Ramberg et al. 2026). Despite its ecological benefits, prescribed burning remains logistically demanding and costly, requiring skilled personnel for implementation (Halme et al. 2013; Hjältén et al. 2023). Moreover, a recent comparison of wildfires and prescribed burns showed that prescribed burns may not fully emulate wildfire conditions in terms of tree mortality, deadwood production, and the resulting habitat suitability for beetle species associated with old-growth habitats (Fredriksson et al. 2025). Together, these constraints limit the extent to which prescribed burning alone can reproduce the spatial and structural variability of historical fire regimes (Halme et al. 2013; Niklasson & Granström 2000). These limitations have led to increasing interest in complementary restoration approaches targeting specific fire-associated habitat structures.

Veteranization treatments aim to accelerate the formation of tree-related microhabitats, such as wounds and decay structures, that develop naturally in veteran trees and provide habitat for diverse saproxylic communities (Cizek et al. 2025). Within this framework, fire-emulating veteranization techniques such as girdling, bark stripping, and stem-base burning have been proposed as complementary approaches to prescribed burning (SCA 2026). These interventions aim to recreate structural characteristics of veteran and fire-damaged trees by generating deadwood, bark injuries, and fire scars that resemble habitat features found in old-growth and fire-related habitats (Cizek et al. 2025; Munters 2025). While young managed stands typically contain little deadwood, natural recovery in boreal forests may take decades without restoration. As restoration methods differ in the quantity and quality of deadwood they generate, they may complement one another in restoring structurally diverse habitats (Hekkala et al. 2016). Numerous studies show that interventions such as girdling and prescribed burning can support saproxylic insect and fungal communities by increasing deadwood availability (Bernes et al. 2015; Sandström et al. 2019).

By generating different habitat conditions, disturbance types can therefore support distinct saproxylic beetle assemblages, suggesting that fire and non-fire disturbances may not be ecologically equivalent (Boucher et al. 2012). This may partly be related to differences in tree damage and mortality processes, which influence the characteristics of resulting substrates (Toivanen & Kotiaho 2010). Fire-emulating veteranization techniques may create dead and wounded wood with different qualities, including variation in damage extent and resin impregnation patterns among treatments (Munters 2025). Such variation in damage characteristics and resulting substrate properties may contribute to differences in saproxylic beetle colonization (Hägglund 2016; Toivanen & Kotiaho 2010).

This highlights the importance of considering not only the structures created by restoration measures, but also the processes through which these structures develop. However, because some pyrophilous insects possess adaptations specifically linked to fire and post-burn environments, approaches that emulate disturbance without fire may not fully recreate the conditions required by these species (Bell 2023). Although fire-emulating veteranization techniques have gained increasing attention as restoration approaches in boreal forests (SCA 2025), empirical evidence on their effects on fire-associated biodiversity remains limited. In particular, it is unclear how different veteranization treatments influence beetle diversity and community composition, and whether incorporating fire enhances their ability to recreate habitat conditions comparable to prescribed burning. Combining fire-emulating veteranization techniques with stem-base burning may therefore provide a complementary approach by integrating fire-created habitat features with the structural characteristics induced by veteranization. This study evaluates how different fire-emulating veteranization treatments influence beetle diversity and community composition compared with prescribed burning to assess their potential for restoring fire-structured forest biodiversity.

1.5 Research question and hypotheses

To address these knowledge gaps regarding the effects of fire-emulating veteranization treatments on fire-associated forest biodiversity, the following research question and hypotheses were formulated:

How do fire-emulating tree veteranization treatments and additional stem-base burning influence beetle diversity in boreal forests compared with prescribed burning?

H1. Beetle abundance, richness, and diversity are expected to vary among treatment types and to increase from 2024 to 2025, with greater responses in the veteranized stand following the addition of stem-base burns.

H2. Beetle community composition is expected to differ between sampling years, between stand treatments, and among tree-treatment types.

H3. Treatment types are expected to differ in their effects on tree vitality, with girdling combined with stem-base burning expected to result in the greatest reduction in tree vitality. Beetle abundance and species richness are expected to be higher on trees with reduced vitality.

H4. Beetle alpha diversity is expected to be higher with increasing deadwood availability and char height.

H5. The abundance and richness of pyrophilous and red-listed beetles are expected to increase from 2024 to 2025 in the veteranized stand, with greater temporal responses in the veteranized than in the prescribed-burned stand following the addition of stem-base burning. Abundance and richness are also expected to differ among tree-treatment types, with higher values in treatments combining mechanical veteranization and stem-base burning.

2. Material and methods

2.1 Study area

Ejheden ekopark was established in 2007 by Sveaskog, a state-owned company and Sweden's largest forest owner. Located in northern Dalarna in Sweden, the ekopark covers a total of 6,891 hectares and consists of a mosaic of forests, mires, and lakes shaped by natural fire regimes. The following description of the ekopark is based on the management plan published by Moberg (2007), which provides an overview of the area based on inventories conducted approximately 20 years ago.

The ekopark is dominated by *Scots pine* forests, followed by deciduous-rich coniferous forests. A major forest fire in the late 19th century promoted the natural regeneration of deciduous species, resulting in an unusually high proportion of deciduous trees (22.5% of the ekopark's forests contain at least 10% deciduous trees). Birch is the dominant deciduous species in the ekopark and commonly occurs in fire-influenced pine forests, providing valuable habitats for insects and birds. Such fire-influenced forest conditions are therefore considered important for pyrophilous insect species (Moberg 2007).

The ekopark is characterised by a high proportion of mature and old-growth forest (with many stands containing pine trees older than 150 years and birch trees older than 100 years). Approximately 80% of the forest area exceeds the harvest maturity age, while 51% is classified as old-growth forest (>1.5 times the minimum harvest age). These structurally complex forests contribute to a high proportion of key habitats (key biotopes or areas of high conservation value), covering more than one third of the forested area. According to the Ekopark plan, deadwood availability is high, with an average of 49.8

standing dead pines and 91.9 pine logs per hectare, measured for trees and logs >15 cm in diameter (Moberg 2007).

The ekopark follows a multifunctional management approach aiming to balance production and conservation, with parts of the forest remaining under timber production (originally 65% = 4,476 ha). The long-term goal of the ekopark concept is to designate at least half of the area for nature conservation. Of the designated conservation forests, one fifth was initially classified as low-value restoration forests intended to develop over time and improve habitat connectivity. According to Moberg (2007), restoration targets include 9.2% of productive forest land, focusing on stands with the potential to develop high nature values, among which pine forests represent the largest share (5.6%).

Restoration efforts aim to mimic the natural disturbance dynamics of fire to enhance ecological functionality. Management practices include both passive restoration (allowing natural succession) and active measures such as prescribed burning (Moberg 2007). In 2018, a 260-ha prescribed burn was conducted within the ekopark, described as one of the largest prescribed burns in Sweden (Sveaskog 2019). In addition, three large pine core areas and one birch core area have been established to support fire-adapted species (Moberg 2007).

2.2 Study design

The study was conducted in two adjacent forest stands in ekopark Ejheden: a prescribed-burned stand and a veteranized stand, each comprising eight experimental plots (Figure 1). Prescribed burning was done in 2022, and beetle communities were sampled using flight interception traps during two consecutive years, 2024 and 2025 (Appendix 1).

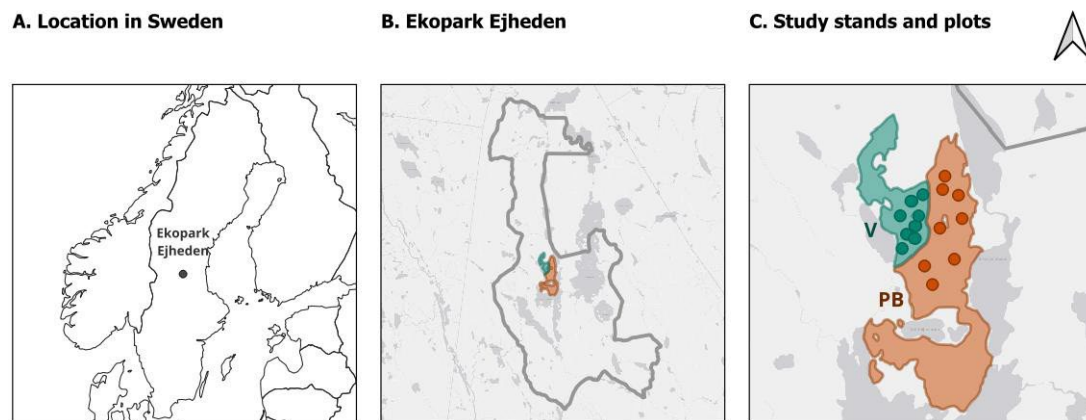


Figure 1. Study area of the restoration project in Ekopark Ejheden, northern Dalarna, Sweden. (A) Location of Ekopark Ejheden in Sweden. (B) Location of the two study stands within Ekopark Ejheden, shown in green for the veteranized stand and brown for the prescribed-burned stand. (C) Spatial arrangement of the experimental plots within the veteranized (V) and prescribed-burned (PB) stands, comprising eight plots per stand. Map created by the author using QGIS, with country boundaries from Natural Earth (2026) and the basemap from Esri (n.d.).

In the prescribed-burned stand, each plot contained two birch and two pine trees, resulting in 32 sampled trees in each sampling year. In the veteranized stand, treatments were

applied at the tree level within plots. In 2024, four pine trees per plot were sampled, of which two were girdled and two were bark-stripped in 2023 as fire-emulating veteranization treatments. In 2025, four additional pine trees per plot were included, resulting in eight sampled trees per plot (Figure 2). Six trees per plot received additional stem-base burns in the early spring of 2025 when there was still snow on the ground, including two previously bark-stripped trees, two previously girdled trees, and two non-veteranized control trees. The two remaining veteranized trees were not subjected to stem-base burns and consisted of two bark stripped trees. Overall, 64 trees were sampled in the veteranized stand in 2025, of which 48 received stem-base burns. As a result, the 2025 sampling design comprised six tree-level treatment types, with two trees representing each treatment type per plot: bark-stripped, bark-stripped-and-burned, girdled-and-burned, and burned-only pine, as well as prescribed-burned pine, and prescribed-burned birch (Appendix 1).

Overall, the study design enabled two complementary comparisons. First, a temporal comparison between 2024 and 2025 was conducted based on treatment types that were present in both years, allowing assessment of changes associated with the application of stem-base burns in the veteranized stand. Second, all treatment types sampled in 2025 were compared to assess differences among treatments.

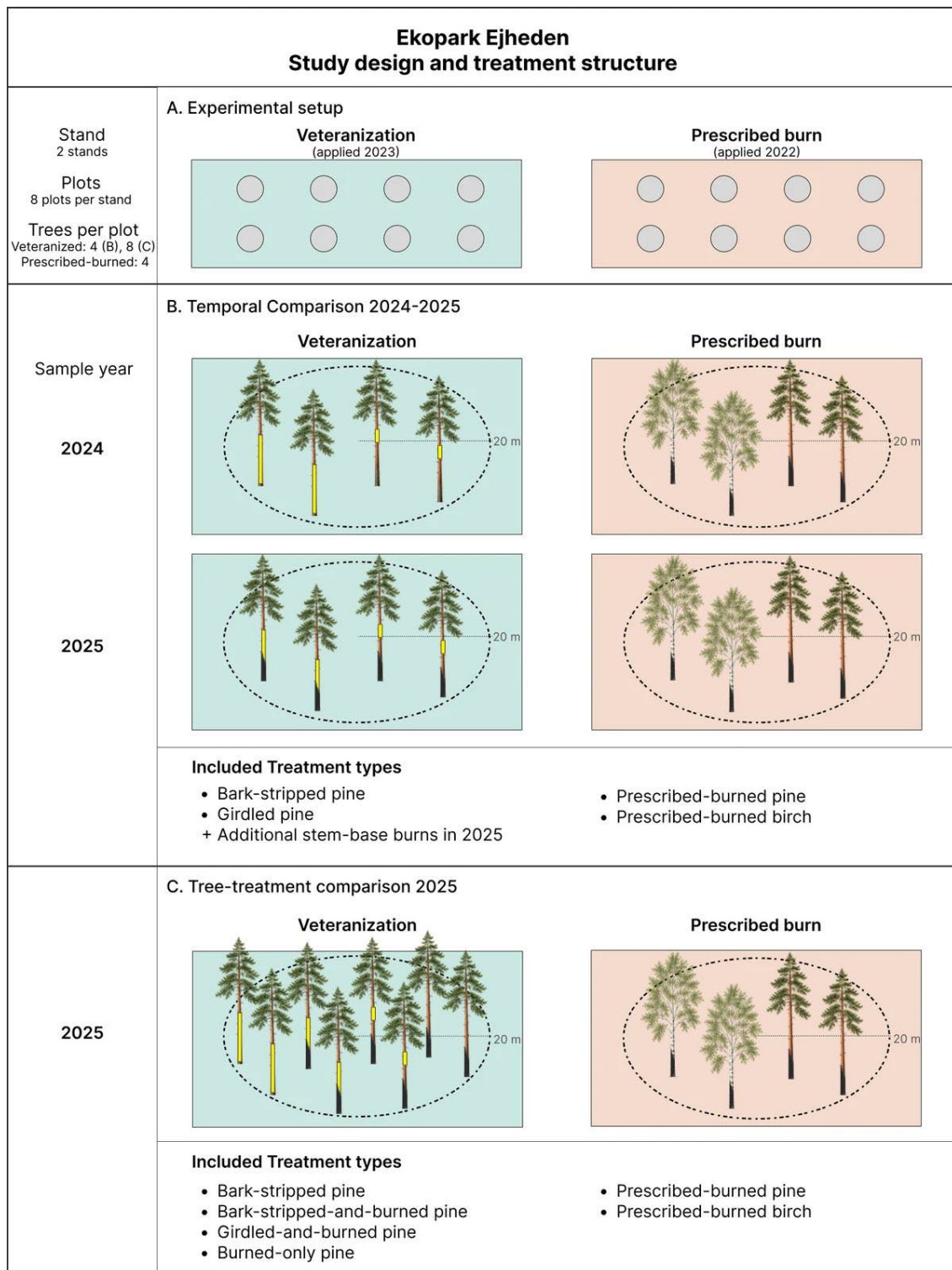


Figure 2. Study design and treatment structure of the restoration project in Ekopark Ejheden, evaluating beetle community responses to fire-emulating tree veteranization and prescribed burning treatments. (A) Experimental setup showing the spatial arrangement of the veteranized and prescribed-burned stands and their experimental plots. (B) Representative plot layout and included treatment types used for the temporal comparison between 2024 and 2025 based on comparable treatments across years. (C) Representative plot layout and included treatment types used for the 2025 comparison among all sampled treatment types. Figure created by the author using Figma and Canva, with tree icons adapted using Canva AI.

2.3 Sampling and measurements

Beetle sampling was conducted in the summer of 2024 (before stem-base burning) and repeated in 2025 (after stem-base burning) using small flight-intercept traps attached to the stems of the study trees following Bergmark et al. (2024). Each trap consisted of a vertically mounted Plexiglas panel with a 1000 ml plastic container positioned below at breast height (130 cm). All traps were consistently oriented towards the south. The containers were filled with a solution of 60% propylene glycol and water, with a small amount of detergent added to reduce surface tension, allowing insects to sink and thereby be preserved. In each sample year, the traps were positioned from May to early June and emptied twice during the sampling period, first in July and a second time in late August. The collected samples were sorted, and taxa were identified by a taxonomist, with beetle species (order *Coleoptera*) forming the basis of the analyses. Pyrophilous categories according to Wikars (2006), saproxylic classifications (VFM beetle database), and conservation status based on the Swedish Red List 2020 (SLU Artdatabanken 2020) were assigned at the species level. Functional group and conservation classifications were corrected where necessary using Artfakta (SLU Artdatabanken 2025). Pyrophilous beetles were classified into four fire-association categories: 1 = fire-dependent, 2 = strongly fire-favoured (rarer species), 3 = strongly fire-favoured (more common species), and 4 = fire-favoured. Red-listed species included those classified as Near Threatened (NT) or Vulnerable (VU) according to the Swedish Red List 2020, as no Endangered or Critically Endangered species occurred in the dataset. In this study, pyrophilous and red-listed beetles were considered species of conservation concern.

In addition to beetle sampling, tree- and plot-level variables were recorded during the study period. Tree-level variables were assessed in both 2024 (before stem-base burning) and 2025 (after stem-base burning). For each tree, species, height, and the diameter at breast height (DBH) were measured. Char height was estimated as the vertical extent of visible charring on tree stems and used as an indicator of fire intensity for both stem-base burns and prescribed burns. Tree vitality was classified as either alive (green foliage), of reduced vitality (partially yellow foliage), or dead (completely yellow or absence of foliage). At the plot-level, structural variables were recorded in 2024, including basal area of living pine and birch, canopy cover (photo-based), and the proportion of burned vegetation, humus, and exposed mineral soil.

Depending on deadwood abundance and accessibility, circular plots with a radius of 10, 15, or 20 meter from the plot centre were used for deadwood assessment. A 20 m radius was applied in plots with low and easily accessible deadwood to ensure that at least 10 pieces could be included in the assessment. In all other cases, radii of 10 or 15 meters were used. Deadwood pieces were counted if their base or, in cases where the base was missing their widest section, was located within the plot. Only deadwood pieces meeting the minimum size criteria of 1.3 m in length, 5 cm in diameter at the thinnest part, and 10 cm in diameter at the widest part were recorded. For volume estimations, the height,

length, smallest and largest diameters alongside tree species and type of deadwood (log or snag) were noted.

2.4 Deadwood volume estimation

To estimate local deadwood volume, allometric and geometric equations were applied for logs and snags, respectively. Log volume was calculated using the formula for a truncated cone, based on length, minimum and maximum diameter. Snag volume was calculated using taper-equations following Näslund (1947). Separate species-specific equations were applied for deciduous and coniferous tree species (Equations 1 and 2), incorporating diameter at breast height (D , cm) and tree height (H , m).

$$0.03715 \times DD^2 + 0.02892 \times DD^2 + 0.004983 \times DD \times HH^2 \quad (\text{Equation 1})$$

$$0.09314 \times DD^2 + 0.03069 \times DD^2 + 0.002818 \times DD \times HH^2 \quad (\text{Equation 2})$$

For broken snags, original tree height was estimated using a linear regression based on measured heights of intact snags. Subsequently, volume estimates were reduced according to the proportion of height loss through breakage following Ollas (1980). Volume reductions were conducted at thresholds of ≥ 0.1 , 0.3, 0.5, and 0.7 proportion of height loss, corresponding to increasing volume reduction factors of 0.3, 0.5, 0.75, and 0.9, respectively.

2.5 Statistical analyses

All analyses were conducted in R (version 4.6.1) using RStudio (version 2026.06.0+242). Prior to statistical analyses, data were cleaned and harmonized, with beetle abundance data from 2024 and 2025 subsequently merged with corresponding tree- and plot-level variables. A high abundance of *Trypodendron lineatum* recorded in one sample in 2025 was excluded from diversity analyses as an extreme outlier. All statistical tests were assessed at a significance level of $\alpha = 0.05$.

The analyses followed two complementary approaches: (1) a temporal comparison between 2024 and 2025, and (2) a tree-treatment comparison including all treatment types sampled in 2025. The temporal comparison included four combinations of treatment type and tree species that were present in both years: bark-stripped pine, girdled pine, prescribed-burned pine, and prescribed-burned birch. This allowed evaluation of temporal changes following the additional stem-base burning of previously veteranized trees in 2025 relative to their initial treatment state in 2024. In contrast, the 2025 tree-treatment comparison incorporated all six treatment types present following the application of additional stem-base burning in the veteranized stand: bark-stripped, bark-stripped-and-burned, girdled-and-burned, burned-only, prescribed-burned pine, and prescribed-burned birch.

Alpha-diversity metrics were calculated at the trap level, with abundance and species richness additionally evaluated in relation to tree vitality at the same scale. Community composition was analysed based on species-by-trap abundance matrices, with trap-year combinations used as sampling units for temporal comparisons. For ordination and statistical testing, samples were grouped according to sampling year-stand treatment combinations. Plot-level variables describing canopy openness and deadwood volume, as well as tree-level measurements of vitality and char height, were assigned to the corresponding trap records prior to model fitting.

Alpha diversity was quantified using abundance, species richness, and Shannon diversity. Species records were aggregated by trap and species before calculating diversity metrics. Total abundance was calculated as the number of individuals per trap, species richness as the number of unique species, and Shannon diversity was calculated using the Shannon index implemented in the *vegan* package (Oksanen et al. 2026).

Effects of treatment type and additional environmental or structural variables on alpha diversity were evaluated using generalized linear mixed models fitted with *glmmTMB* (Brooks et al. 2017). Total abundance and species richness were modelled using generalised linear mixed models with negative binomial error distribution (GLMMs; family = *nbinom2*) to account for potential overdispersion in count data, whereas Shannon diversity models were analysed using mixed-effects models with normal error distribution (family: Gaussian). Plot identity was included as a random intercept to account for the hierarchical sampling design in all models.

For the temporal comparison, models included sampling year, treatment type, their interaction, and tree species as fixed effects. Canopy openness and deadwood volume were considered as potential environmental covariates and evaluated using Akaike information criterion (AIC), with a cut-off of 2 units. Deadwood volume was retained only for the Shannon diversity model, where it improved model fit. For the tree-treatment comparison in 2025, treatment type represented the main predictor, with tree vitality and char height included as additional structural predictors.

In the alpha-diversity models, prescribed-burned pine was used as the reference category for the 2025 tree-treatment comparison. For the temporal comparison, prescribed-burned and pine were used as reference levels for treatment type and tree species, respectively. Estimated marginal means and post-hoc pairwise contrasts among relevant factor levels were obtained from the fitted models using the *emmeans* package (Length & Piaskowski 2026).

Model diagnostics were evaluated using simulation-based residual diagnostics implemented in *DHARMA* (Hartig 2026), including tests for overdispersion and outliers. Despite the use of negative binomial models, significant residual overdispersion remained in both abundance models, particularly in the temporal comparison model (dispersion = 4.00, $p < 0.001$), and to a lesser extent in the 2025 tree-treatment model (dispersion = 2.44, $p = 0.024$). Alternative model specifications were evaluated but did not substantially

improve model diagnostics. Therefore, abundance model results were interpreted with caution. Diagnostics for species richness and Shannon diversity models showed no significant indications of overdispersion or outliers.

Community composition was analysed using non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities calculated from species-abundance matrices. NMDS was performed using the *metaMDS()* function implemented in the *vegan* package (Oksanen et al. 2026). Two-dimensional solutions were generated using 200 random starts, and stress values were used to evaluate ordination quality, with values around 0.2 commonly considered acceptable (Clarke 1993).

Differences in community composition were tested using PERMANOVA with the *adonis2*-function in the *vegan* package (Oksanen et al. 2026) with 999 permutations. In the main PERMANOVA analyses, permutations were constrained within plots to account for the repeated sampling structure within plots. For the temporal comparison, the models included sampling year, stand treatment, and their interaction to evaluate differences among combinations of sampling year and stand treatment. Within the prescribed-burned stand, additional analyses evaluated whether community composition varied with tree species and sampling year. For the tree-treatment comparison in 2025, treatment effects were assessed across all treatment types. Significant results were further explored using pairwise PERMANOVA comparisons with p-value adjustment according to the Benjamini-Hochberg method (Benjamini & Hochberg 1995). Homogeneity of multivariate dispersion was assessed using the *betadisper()* function in the *vegan* package (Oksanen et al. 2026), with significance tested using the *permutest()* function with 999 permutations. Dispersion patterns were considered when interpreting differences in community composition, and significant differences in dispersion were further evaluated using Tukey HSD tests.

Differences in tree vitality among treatment types in 2025 were evaluated using a Kruskal-Wallis test based on ordinal vitality classes, with classes ordered as alive, reduced, and dead. Significant overall differences were followed by pairwise Wilcoxon rank-sum tests with Benjamini-Hochberg correction.

Abundance and species richness of pyrophilous and red-listed beetles were summarised at the plot level for the temporal comparison and at the trap level for the 2025 tree-treatment comparison. Wilcoxon rank-sum tests were used to evaluate differences between sampling years and stand treatments. Differences among tree-treatment types were assessed using Kruskal-Wallis tests followed by pairwise Wilcoxon rank-sum tests with Bonferroni correction.

Data processing and visualisation were performed using the R packages *dplyr*, *tidyr*, *tibble*, *forcats*, *ggplot2*, and *patchwork*.

3. Results

Across all samples collected in 2024 and 2025, a total of 7,149 beetle individuals representing 316 species were recorded. Of these, 247 species were classified as saproxylic, 33 as pyrophilous, and 15 as red-listed (NT or VU). Detailed pairwise comparisons and exact test statistics are provided in Appendix 2.

3.1 Temporal comparison (2024 vs. 2025)

3.1.1 Alpha diversity

For the temporal comparison of beetle alpha-diversity between 2024 and 2025, treatment types comprised bark-stripped and girdled trees in the veteranized stand, both of which received additional stem-base burning in 2025, as well as pine and birch trees in the prescribed-burned stand. Beetle abundance increased significantly from 2024 to 2025 in all treatment types (all $p < 0.001$; Figure 3). In the prescribed-burned treatment, predicted abundance increased from 21.3 to 48.5 individuals (2.3-fold increase), whereas the girdled and bark-stripped treatments showed greater increases, from 13.3 to 94.0 individuals (7.1-fold increase) and from 13.3 to 74.0 individuals (5.6-fold increase), respectively. The magnitude of these temporal changes differed among treatment types, with significant interactions between sample year and treatment type for both girdled and bark-stripped treatments relative to the prescribed-burned treatment (Table 1). Pairwise comparisons showed no significant differences in abundance among treatment types in 2024, whereas the girdled treatment had significantly higher abundance than the prescribed-burned treatment in 2025 ($p = 0.001$).

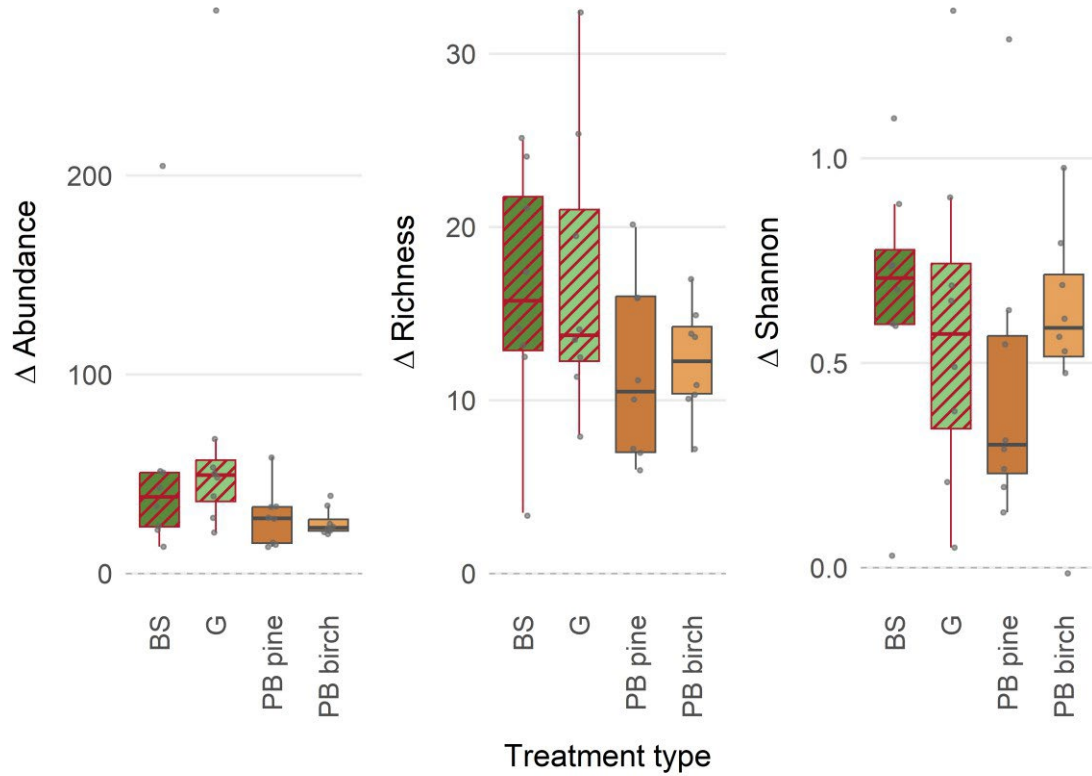
Species richness displayed a similar temporal pattern, with significant year-by-treatment interactions for both girdled and bark-stripped treatments relative to the prescribed-burned treatment (Table 1). Species richness also increased significantly between years in all treatment types (all $p < 0.001$), with increases from 13.8 to 25.7 species in the prescribed-burned treatment, 10.1 to 28.7 species in the girdled treatment, and 10.0 to 27.7 species in the bark-stripped treatment. In 2024, the prescribed-burned treatment showed higher richness than the girdled and bark-stripped treatments ($p = 0.031$ and $p = 0.023$, respectively). However, these differences were no longer evident in 2025, with no significant differences among treatment types following the additional stem-base burning treatment in the veteranized stand.

Shannon diversity also increased significantly between sampling years (Table 1). However, no interaction between sample year and treatment type was detected, indicating a consistent temporal increase in Shannon diversity across treatments. Deadwood volume had a significant positive effect on Shannon diversity (Table 1). Pairwise comparisons revealed no significant differences among treatment types. In addition, birch trees showed slightly higher abundance and species richness than pine trees, whereas Shannon diversity was not significantly affected by tree species (Table 1).

Table 1. Summary of generalized linear mixed models assessing temporal changes in beetle abundance, species richness, and Shannon diversity between 2024 and 2025. Temporal comparisons of alpha diversity included three tree-treatment types: bark stripped, girdled, and prescribed burn, with the veteranized trees additionally subjected to stem-base burning in 2025 and prescribed-burned trees comprising both pine and birch. Tree species and, where applicable, plot-level deadwood volume were included as additional predictors. The reference levels were prescribed-burned trees for treatment type, pine for tree species, and 2024 for sampling year. Estimates, standard errors (Std. Error), z-values, p-values, and model families are provided for each predictor.

Predictor	Estimate	Std. Error	z value	p value	Family
Total Abundance					
Intercept (PB, pine, 2024)	2.922	0.131	22.355	< 0.001	Negative binomial GLMM, log link
Year	0.825	0.132	6.236	< 0.001	
Treatment: Bark stripped	-0.472	0.202	-2.340	0.019	
Treatment: Girdled	-0.466	0.202	-2.302	0.021	
Tree species	0.270	0.132	2.043	0.041	
Year x bark stripped	0.895	0.236	3.792	< 0.001	
Year x girdled	1.128	0.238	4.744	< 0.001	
Species Richness					
Intercept (PB, pine, 2024)	2.543	0.074	34.315	< 0.001	Negative binomial GLMM, log link
Year	0.622	0.080	7.759	< 0.001	
Treatment: Bark stripped	-0.325	0.123	-2.633	0.008	
Treatment: Girdled	-0.312	0.123	-2.531	0.011	
Tree species	0.166	0.079	2.096	0.036	
Year x bark stripped	0.399	0.147	2.713	0.007	
Year x girdled	0.421	0.146	2.879	0.004	
Shannon index					
Intercept (PB, pine, 2024)	2.134	0.084	25.273	< 0.001	Gaussian GLMM
Year	0.574	0.061	9.409	< 0.001	
Treatment: Bark stripped	-0.099	0.088	-1.136	0.256	

Treatment: Girdled	-0.195	0.088	-2.225	0.026
Tree species	0.075	0.086	0.873	0.383
Deadwood Volume	0.045	0.014	3.171	0.002



Additional stem-base burning in 2025  No  Yes

Figure 3. Change (Δ) in beetle abundance, species richness, and Shannon diversity between 2024 and 2025 for four treatment types sampled in both years. Diversity metrics on tree-treatment level were averaged within plots before calculating temporal changes (2025 – 2024). Boxplots show the distribution of plot-level changes, with individual plots represented as jittered points. Red outlines indicate veteranized treatment types that received additional stem-base burns in 2025. Abbreviations: BS = bark-stripped; G = girdled; PB = prescribed burn.

3.1.2 Community composition

Beetle community composition was compared between the veteranized and prescribed-burned stands in 2024 and 2025, resulting in four combinations of sampling year and stand treatment visualised in the following NMDS ordination (Figure 4). Community composition differed significantly among the four combinations of sampling year and stand treatment ($p = 0.001$, $R^2 = 0.194$). A significant interaction between sampling year and stand treatment indicated that temporal changes in community composition depended on stand treatment, although the interaction explained only a small proportion of the

variation ($p = 0.001$, $R^2 = 0.027$). Multivariate dispersion also differed among the four groups ($p = 0.001$), indicating differences in within-group variability.

Pairwise comparisons showed that all combinations of sampling year and stand treatment differed significantly in community composition (all $p = 0.001$). Temporal changes were significant within both stand treatments, with a greater shift in the veteranized stand ($R^2 = 0.181$) compared with the prescribed-burned stand ($R^2 = 0.136$). Differences between stand treatments were also significant within both sampling years, with greater separation between veteranized and prescribed-burned stands in 2025 ($R^2 = 0.121$) compared with 2024 ($R^2 = 0.042$).

Additional analyses within the prescribed-burned stand showed that tree species significantly affected beetle community composition, explaining 4.2% of the variation ($R^2 = 0.042$, $p = 0.001$). However, the interaction between sampling year and tree species was not significant ($R^2 = 0.020$, $p = 0.056$), indicating that temporal changes in community composition did not differ between pine and birch trees.

Post-hoc comparisons revealed lower within-group variability in the 2025 veteranized stand compared with all other groups (all $p < 0.05$), whereas dispersion did not differ between the prescribed-burned stand across years or between stand treatments in 2024.

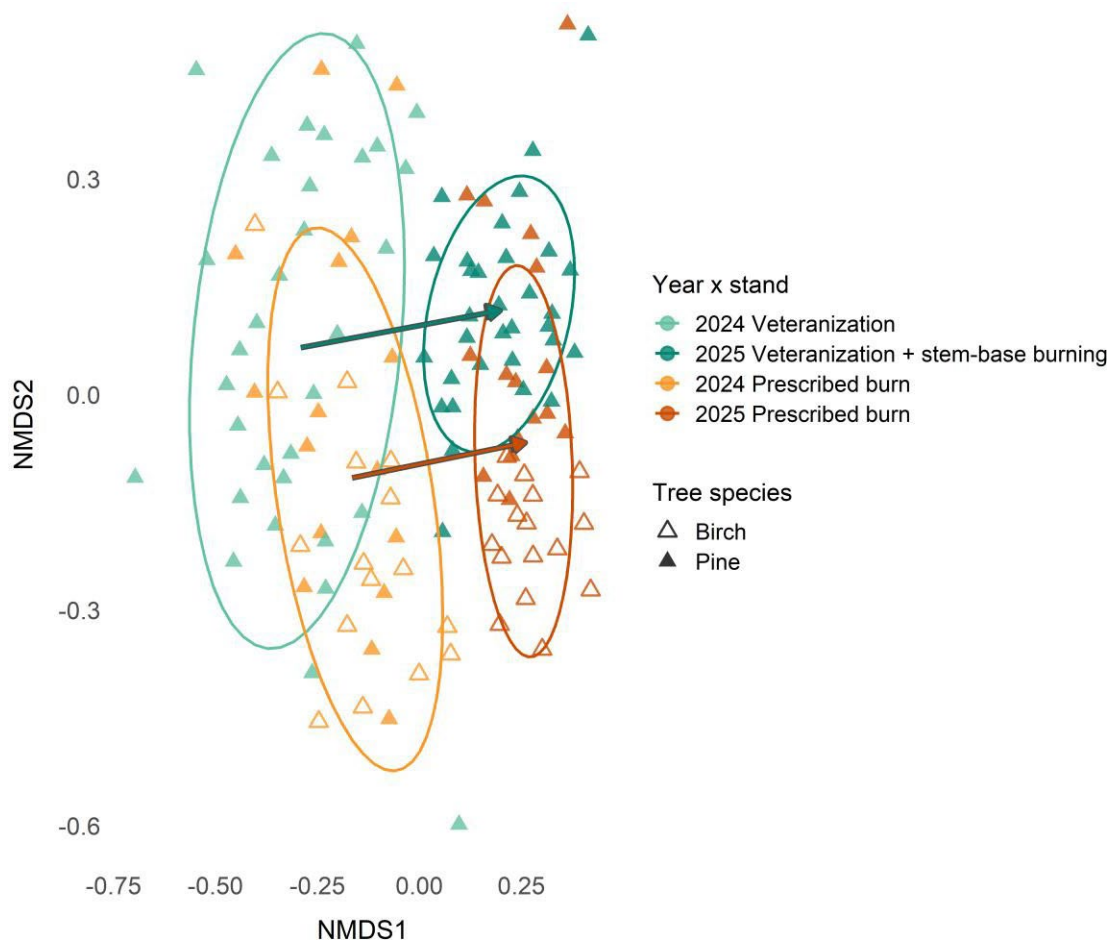


Figure 4. Non-metric multidimensional scaling (NMDS) ordination of beetle community composition across combinations of sampling year and stand treatment (2024 and 2025; veteranized and prescribed-burned stands) based on Bray-Curtis dissimilarities (stress = 0.283). Colours indicate stand-treatments, with lighter and darker shades distinguishing sampling years. Symbol filling indicates tree species (pine and birch). Each point represents a trap sample from an individual treated tree in a given sampling year. Arrows indicate the temporal shift in community centroids from 2024 to 2025 within each stand-treatment.

3.2 Tree-treatment comparison in 2025

3.2.1 Alpha diversity

For the 2025 tree-treatment comparison of beetle alpha diversity, six treatment types were distinguished: bark-stripped, bark-stripped-and-burned, girdled-and-burned and burned-only pine in the veteranized stand, together with prescribed-burned pine and prescribed-burned birch. Beetle abundance varied among treatment types and was additionally associated with tree vitality and char height (Table 2; Figure 5). Compared with living trees, trees with reduced vitality and dead trees showed higher beetle abundances (Table 2). Additionally, beetle abundance increased with increasing char height (Table 2). Model estimates indicated higher abundance in most treatment types compared with prescribed-burned pine. However, after Tukey correction, only bark-stripped-and-burned pine showed significantly higher predicted abundance than prescribed-burned pine, with approximately two-fold higher abundance ($p = 0.009$). No other pairwise comparisons among treatment types were significant.

Species richness was mainly associated with tree vitality, while treatment effects were comparatively weak. Similar to beetle abundance, richness increased with decreasing tree vitality, with higher values in trees with reduced vitality and dead trees (Table 2) compared with living trees. In contrast, char height had no significant effect on species richness.

Shannon diversity was not associated with tree vitality or char height (Table 2). Pairwise comparisons revealed lower diversity in girdled-and-burned pine compared with prescribed-burned birch ($p = 0.015$), whereas no other treatment comparisons were significant.

Table 2. Summary of generalized linear mixed models assessing differences in beetle abundance, species richness, and Shannon diversity among six tree-treatment types in 2025. The 2025 treatment comparison included bark-stripped, bark-stripped-and-burned, girdled-and-burned, burned-only, prescribed-burned pine, and prescribed-burned birch trees. Tree vitality and char height were included as additional predictors. The reference levels were prescribed-burned pine trees for treatment type and alive trees for vitality. Estimates, standard errors (Std. Error), z-values, p-values, and model families are provided for each predictor.

Predictor	Estimate	Std. Error	z value	p value	Family
<i>Total Abundance</i>					
Intercept (PB pine, alive)	3.019	0.223	13.516	< 0.001	Negative binomial GLMM, log link
Bark stripped	0.487	0.258	1.887	0.059	
Bark stripped + burned	0.646	0.191	3.381	< 0.001	
Girdled + burned	0.538	0.219	2.452	0.014	
Burned only	0.529	0.226	2.337	0.019	
Prescribed-burned birch	0.373	0.174	2.150	0.031	
Vitality: Reduced	0.488	0.147	3.331	< 0.001	
Vitality: Dead	1.609	0.308	5.221	< 0.001	
Char height	0.215	0.087	2.486	0.013	
<i>Species Richness</i>					
Intercept (PB pine, alive)	2.928	0.137	21.409	< 0.001	Negative binomial GLMM, log link
Bark stripped	0.077	0.158	0.489	0.625	
Bark stripped + burned	0.178	0.117	1.511	0.131	
Girdled + burned	0.039	0.127	0.303	0.762	
Burned only	0.109	0.139	0.783	0.433	
Prescribed-burned birch	0.207	0.099	2.091	0.037	
Vitality: Reduced	0.268	0.085	3.159	0.002	
Vitality: Dead	0.535	0.172	3.118	0.002	
Char height	0.042	0.050	0.844	0.399	

Shannon Index

Intercept				Gaussian GLMM
(PB pine, alive)	2.892	0.149	19.343	< 0.001
Bark stripped	-0.209	0.176	-1.184	0.236
Bark stripped + burned	-0.073	0.143	-0.511	0.609
Girdled + burned	-0.350	0.152	-2.312	0.021
Burned only	-0.237	0.159	-1.489	0.137
Prescribed-burned birch	0.140	0.099	1.412	0.158
Vitality: Reduced	0.153	0.092	1.666	0.096
Vitality: Dead	0.279	0.192	1.449	0.147
Char height	-0.081	0.050	-1.625	0.104

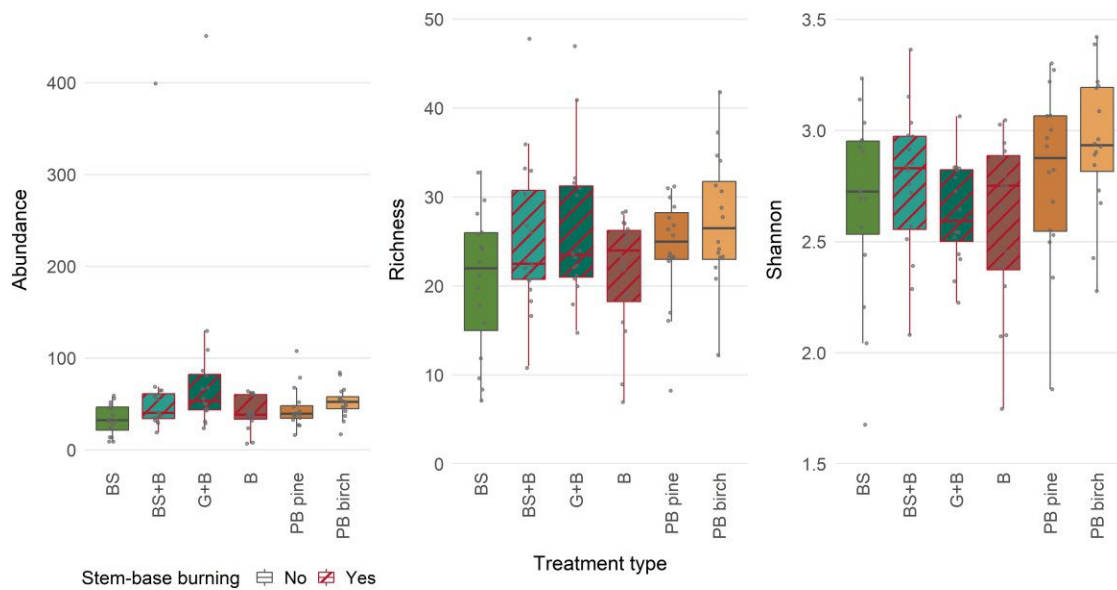


Figure 5. Beetle abundance, species richness, and Shannon diversity across seven treatment types in 2025. Diversity metrics were calculated for sampled trees. Boxplots show distributions of tree-level values, with each observation represented as a jittered point. Red outlines indicate treatment types that received additional stem-base burns in 2025. Abbreviations: BS = bark-stripped; BS+B = bark-stripped-and-burned; B = burned-only; G+B = girdled-and-burned; PB = prescribed burn.

3.2.2 Community composition

Differences in beetle community composition among the six treatment types in 2025 are visualised in the NMDS ordination (Figure 6). Community composition differed significantly among the six treatment types in 2025 ($p = 0.001$, $R^2 = 0.164$). Multivariate dispersion did not differ among treatment types, indicating that PERMANOVA results primarily reflected differences in community composition rather than differences in within-group variability.

Pairwise comparisons revealed significant differences for 11 of the 15 treatment contrasts (all $p \leq 0.021$). Prescribed-burned birch differed significantly from all other treatment types, whereas prescribed-burned pine differed from all treatment types except bark-stripped pine. Additional significant differences were observed between girdled-and-burned and bark-stripped ($R^2 = 0.098$) as well as burned-only pine ($R^2 = 0.082$). Furthermore, bark-stripped-and-burned differed from bark-stripped ($R^2 = 0.061$) and burned-only pine ($R^2 = 0.055$).

The bark-stripped treatment did not differ significantly from burned-only, girdled-and-burned, or prescribed-burned pine. Likewise, community composition in bark-stripped-and-burned and girdled-and-burned pine did not differ significantly.

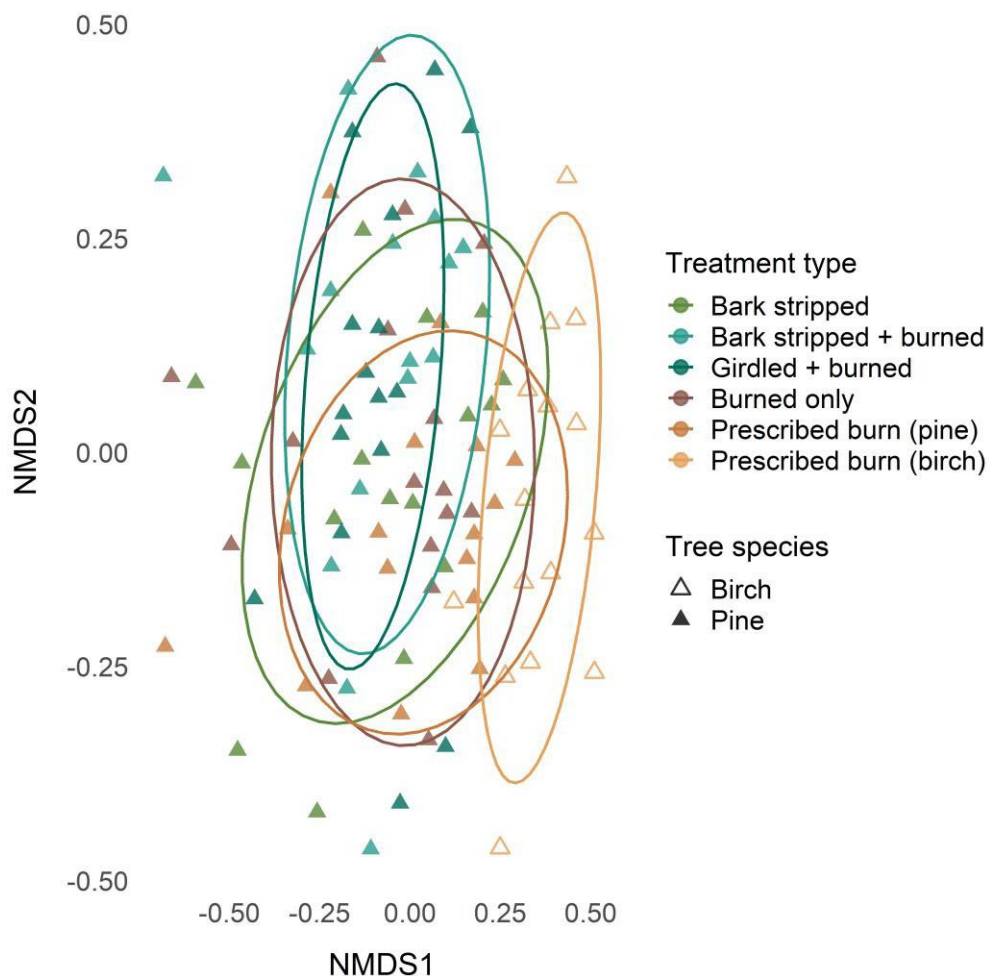


Figure 6. Non-metric multidimensional scaling (NMDS) ordination of beetle community composition across tree-treatment types in 2025 based on Bray-Curtis dissimilarities (stress = 0.293). Colours indicate tree-treatment types and symbol filling indicates tree species (pine and birch). Each point represents a trap sample from an individual treated tree.

3.3 Tree vitality

The distribution of tree vitality differed significantly among treatment types ($\chi^2 = 43.21$, $p < 0.001$; Figure 7). Pairwise comparisons showed that girdled-and-burned trees differed significantly from all other treatment types ($p < 0.05$), with 14 of 16 trees classified as having reduced vitality, one as dead, and one as alive.

Within the prescribed-burned treatment, pine and birch trees showed intermediate vitality distributions, with reduced-vitality and dead trees occurring in both groups. Prescribed-burned pine additionally differed from bark-stripped and burned-only pine, whereas prescribed-burned birch showed no further differences beyond the contrast with girdled-and-burned trees. In contrast, bark-stripped and burned-only pine exhibited similar vitality patterns, consisting exclusively of alive individuals in 2025. Bark-stripped-and-burned pine showed intermediate patterns and did not differ from any treatment other than girdled-and-burned pine.

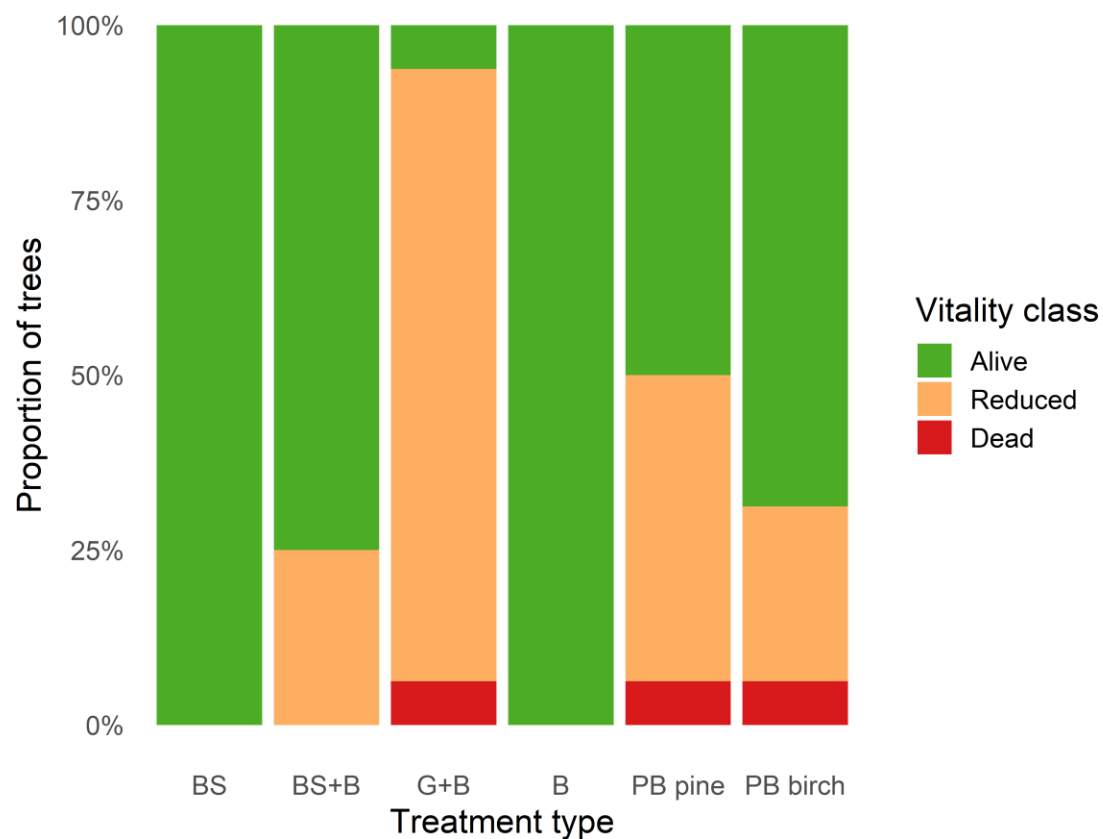


Figure 7. Proportions of trees classified as alive, reduced vitality, and dead across treatment types in 2025. Each treatment type includes 16 trees sampled across eight plots (two trees per plot). Abbreviations: BS = bark-stripped; BS+B = bark-stripped-and-burned; B = burned-only; G+B = girdled-and-burned; PB = prescribed burn.

3.4 Species of conservation concern

The abundance and richness of pyrophilous and red-listed beetle species were compared across sampling years, stand-treatments, and tree-level treatment types to assess responses to fire-emulating restoration measures. Between sampling years, pyrophilous beetle abundance did not differ significantly, whereas species richness increased significantly from a mean of 4.6 to 8.6 species between 2024 and 2025 ($p < 0.001$). Red-listed beetles showed significant temporal changes, with both abundance and species richness increasing between years (both $p < 0.001$). Mean abundance increased from 0.6 to 7.1 individuals per plot, while mean richness of red-listed beetles increased from 0.5 to 2.7 species per plot.

Differences between stands were assessed within each sampling year (Figure 8). In 2024, pyrophilous beetle abundance and species richness differed significantly between stands ($p = 0.006$ and $p < 0.001$, respectively), with approximately two-fold higher abundance and richness in the prescribed-burned stand compared with the veteranized stand (22.3 vs. 10.6 individuals; 6.1 vs. 3.1 species). In 2025, abundance still differed between stands ($p = 0.010$), but the pattern reversed, with higher abundance in the veteranized stand than in the prescribed-burned stand (27.8 vs. 16.6 individuals). At the same time, species richness of pyrophilous beetles no longer differed between stands in 2025. Within-stand comparisons showed that pyrophilous beetle abundance and species richness increased significantly between 2024 and 2025 in the veteranized stand (both $p < 0.001$), while no significant temporal changes were detected in the prescribed-burned stand (Figure 8).

Red-listed beetle abundance and richness did not differ between stands in 2024. However, both metrics differed significantly in 2025 (both $p = 0.008$), with higher values in the veteranized stand. Mean abundance increased from 0.1 individuals in 2024 to 12.5 individuals in 2025 in the veteranized stand. In 2025, mean abundance was then approximately seven-fold higher in the veteranized stand than in the prescribed-burned stand (12.5 vs. 1.75 individuals), while richness was about 2.5-fold higher (3.9 vs. 1.5 species). In the veteranized stand, abundance and richness of red-listed beetles also increased significantly between sampling years (both $p < 0.001$), while neither metric changed significantly over time in the prescribed-burned stand (Figure 8).

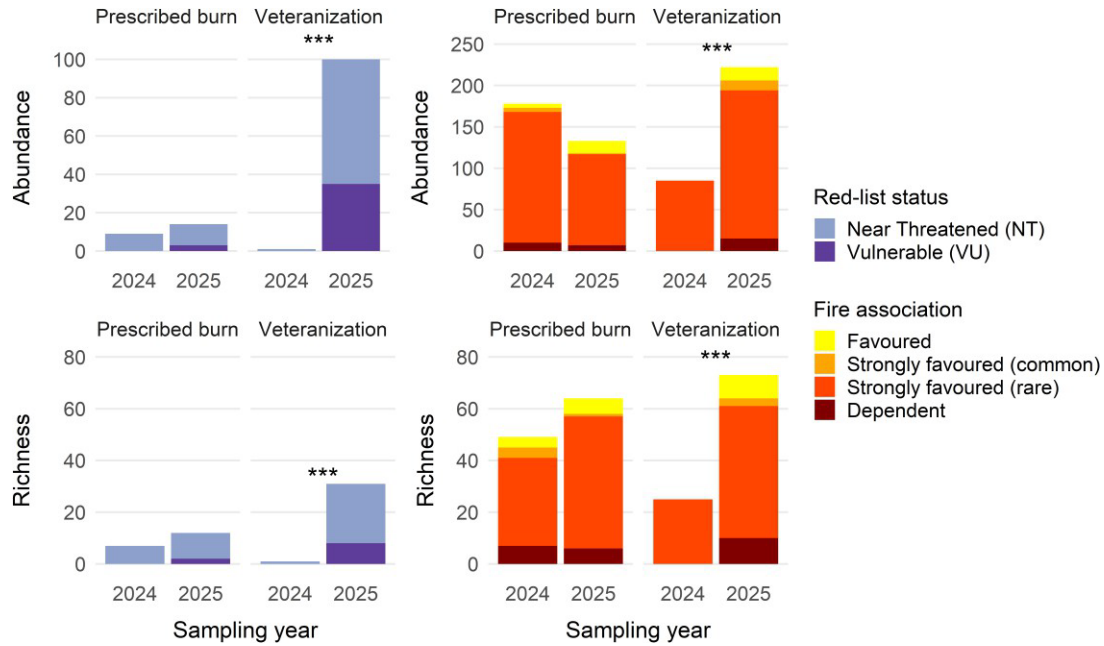


Figure 8. Changes in red-listed and pyrophilous beetle abundance and species richness between 2024 and 2025 across veteranized and prescribed-burned stands. Only comparable treatment types present in both years were included for temporal comparisons. Stacked bars show plot-level values, representing species-level red-list categories (NT and VU) or fire-association categories. Asterisks indicate significant differences between sampling years within stand-treatments (Wilcoxon rank-sum tests, all $p < 0.001$).

At the tree-treatment level in 2025 (Figure 9), neither abundance nor richness of pyrophilous beetles differed significantly among treatment types ($p = 0.066$ and $p = 0.082$, respectively). In contrast, both abundance and richness of red-listed beetles differed significantly among treatment types (both $p < 0.001$). The highest mean abundance and richness values were recorded in bark-stripped-and-burned pine (3.5 individuals; 1.44 species), followed by girdled-and-burned pine (2.75 individuals; 0.88 species).

Pairwise comparisons revealed the same overall pattern for both metrics. Bark-stripped-and-burned pine supported significantly higher abundance and richness of red-listed beetles than bark-stripped pine, burned-only pine, and prescribed-burned birch (all $p < 0.05$ for both metrics). Likewise, girdled-and-burned pine showed significantly higher values than prescribed-burned birch. However, no significant differences were evident between bark-stripped-and-burned and girdled-and-burned pine, or between either of these treatments and prescribed-burned pine.

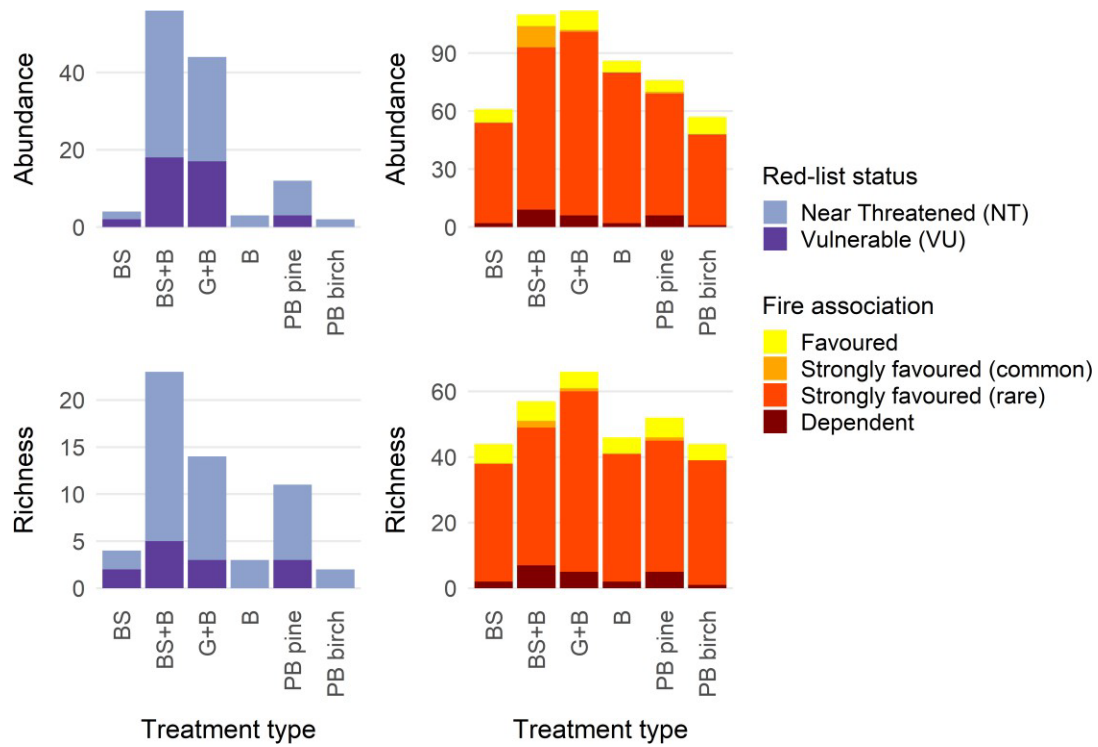


Figure 9. Red-listed and pyrophilous beetle abundance and species richness across treatment types in 2025. Stacked bars show sampled-tree-level values, representing species-level red-list categories (NT and VU) or fire-association categories. Abbreviations: BS = bark-stripped; G = girdled; PB = prescribed burn.

4. Discussion

4.1 Temporal dynamics of beetle communities following restoration

Beetle alpha diversity increased between 2024 and 2025, but the magnitude and treatment dependence of this change differed among metrics. Abundance and species richness increased to a greater extent in the veteranized treatments than in the prescribed-burned treatment, whereas Shannon diversity increased consistently across treatments. Although abundance did not differ among treatments in 2024, the subsequent increase in the veteranized treatments resulted in higher abundance in the girdled treatment than in the prescribed-burned treatment in 2025. The initial richness advantage of the prescribed-burned treatment was likewise no longer evident in 2025. These patterns indicate larger temporal changes in abundance and richness in the veteranized treatments. Between-year variation in weather conditions and successional turnover may have contributed to the overall temporal changes (Boucher et al. 2012; Fredriksson et al. 2020). However, the differing magnitude of change among treatments coincided with the addition of stem-base burning in the veteranized stand in 2025, suggesting a contribution of treatment-related habitat development to the observed trajectories.

The temporal trajectories are closely related to the intervention histories of the two restoration approaches. The prescribed burn occurred two years before the first beetle sampling, allowing fire-created resources to develop and become available for colonization (Boucher et al. 2012). In contrast, the veteranized trees had already been mechanically injured and were undergoing structural changes as vitality declined before stem-base burning introduced new charred and fire-affected structures (Munters 2025; SCA 2026). The response in the veteranized treatments may therefore partly reflect colonization of newly created fire-related resources in addition to microhabitats already generated by mechanical tree injury (Boucher et al. 2012; Cizek et al. 2025). The two approaches were consequently sampled at different stages of habitat development, limiting direct comparison of their temporal trajectories.

Changes in alpha diversity were accompanied by shifts in community composition. The significant interaction between year and stand-treatment indicates that beetle communities followed different temporal trajectories in the veteranized and prescribed-burned stands, with greater compositional differentiation between the approaches in 2025 than in 2024. This increasing differentiation coincided with the addition of stem-base burning in the veteranized stand, although background temporal variation cannot be excluded. The continued overlap among communities indicates that the stand treatments remained partly similar in composition. The pattern suggests increasing divergence between stand treatments rather than complete separation of their beetle assemblages.

Host-tree identity provides an additional consideration when interpreting these stand-level differences. Pine and birch supported different beetle communities within the prescribed-burned stand, whereas veteranization was applied only to pine. Some differences between the stand treatments may therefore reflect host-tree composition in addition to restoration treatment (Bütler et al. 2025; Frostgård et al. 2026). The lower multivariate dispersion of veteranized communities in 2025 indicates reduced within-group variability but does not by itself imply higher ecological quality (Clarke 1993).

Overall, H1 was partially supported: abundance and species richness showed the predicted temporal increase and greater responses in the veteranized treatments following the addition of stem-base burning, whereas Shannon diversity increased across treatments. The temporal differences in community composition between stand treatments provide partial support for H2, while the tree-treatment differences provide further support for this hypothesis, as discussed below.

4.2 Drivers of beetle responses: restoration treatments and habitat structure

The treatment-level patterns suggest that beetle responses were associated more directly with habitat conditions created by the treatments than with treatment identity itself. Tree vitality was associated with abundance and species richness, char height with abundance,

and plot-level deadwood volume with Shannon diversity. Together with the compositional differentiation among treatment types, these relationships indicate that different restoration treatments generated structural conditions associated with different dimensions of beetle diversity (Sandström et al. 2019).

Both abundance and species richness increased with decreasing tree vitality, with higher values on reduced-vitality and dead trees than living trees. Damaged and declining trees can provide exposed woody tissue, altered bark structures and developing deadwood that become available at different stages of deterioration (Jacobs et al. 2006; Siitonen 2001). The association of reduced vitality with abundance and richness therefore suggests that beetles responded not only to complete tree mortality but also to habitat conditions developing during tree decline. Shannon diversity was not associated with tree vitality, indicating that the changes in abundance and richness were not necessarily accompanied by changes in the relative distribution of individuals among species.

The treatments generated a range of vitality stages rather than a uniform progression towards mortality. Girdled-and-burned trees showed the greatest reduction in vitality, whereas bark-stripped-and-burned trees showed an intermediate response and bark-stripped and burned-only trees remained alive. This variation is consistent with the different effects of mechanical injury and burning on tree condition (Jacobs et al. 2006; Pasanen 2017). The positive associations of reduced vitality with abundance and richness suggest that weakened and declining trees may provide beetle habitat before complete mortality occurs (Samuelsson et al. 1994; Siitonen 2001). Because vitality was itself influenced by treatment, however, it is best interpreted as a potential pathway linking treatments to beetle responses rather than an independent causal effect. These findings support H3, as treatment types differed in their effects on tree vitality, with girdled-and-burned trees showing the greatest reduction in vitality, while beetle abundance and species richness were higher on trees with reduced vitality.

Despite these habitat associations, treatment-specific differences in alpha diversity were limited. Bark-stripped-and-burned pine showed higher abundance than prescribed-burned pine, but most other treatment contrasts were not significant. Species richness and Shannon diversity likewise showed limited treatment differentiation. In contrast, community composition differed among the six tree-treatment types in 2025, with 11 of 15 pairwise comparisons significant. Thus, treatments supporting similar levels of abundance, richness or Shannon diversity could nevertheless support different beetle assemblages. Girdled-and-burned and bark-stripped-and-burned pine differed compositionally from bark-stripped pine without burning and from burned-only pine, while prescribed-burned pine differed from most treatment types except bark-stripped pine. These patterns suggest that community responses were associated with combinations of mechanical injury and stem-base burning and the resulting habitat-development stages, rather than with a uniform effect of veteranization or burning alone. The tree-treatment differentiation provides further support for H2, although not all treatment types differed significantly.

Partial overlap among treatment-specific communities indicates that treatments generated both shared and distinct habitat conditions. Mechanical injury can initiate tree decline and expose woody substrates, while stem-base burning adds charred and fire-affected structures (SCA 2026). Different combinations of these features may therefore provide overlapping but not identical resources, allowing partly similar assemblages to occur under different habitat configurations (Toivanen & Kotiaho 2010). Non-significant differences between some treatment combinations should not be interpreted as evidence that the treatments created identical habitats.

Char height provided further evidence that fire-related habitat characteristics were associated with beetle responses. Abundance increased with increasing char height, whereas species richness and Shannon diversity were not associated with char height. Fire-related structures have been linked to beetle responses in boreal forests (Hekkala et al. 2014; Hyvärinen et al. 2006), and the positive association with abundance is consistent with charred structures providing relevant resources for pyrophilous beetles (Hjältén et al. 2018; Ramberg et al. 2026). However, the absence of corresponding relationships with richness and Shannon diversity highlights that char height should not be interpreted as a general proxy for beetle diversity.

Deadwood availability showed a different pattern, being positively associated with Shannon diversity but not with abundance or species richness. This suggests that deadwood availability was more closely related to variation in the distribution of individuals among species than to the total number of individuals or species recorded (Sandström et al. 2019; Siitonen 2001). The different associations of tree vitality, char height and deadwood volume with diversity metrics further indicate that no single habitat characteristic explained all dimensions of beetle diversity. Because deadwood volume was measured at plot level, this relationship reflects an association between stand-level habitat availability and Shannon diversity rather than a direct tree-level effect.

Taken together, the habitat relationships provide partial support for H4. Beetle alpha diversity increased with increasing char height for abundance and with increasing deadwood availability for Shannon diversity. The predicted positive associations were therefore metric-specific rather than consistent across abundance, species richness and Shannon diversity. Different combinations and developmental stages of habitat structures may consequently support different beetle assemblages without producing consistent differences in overall alpha diversity. Rather than maximizing a single habitat characteristic, restoration may therefore benefit from maintaining a heterogeneous set of tree conditions and fire-affected structures (Hjältén et al. 2017; Sandström et al. 2019; Toivanen & Kotiaho 2010).

4.3 Responses of species of conservation concern

Responses of pyrophilous and red-listed beetles provide a more functionally specific perspective on restoration responses. Both groups showed temporal changes in the veteranized stand, but the responses differed between stand-level and tree-treatment comparisons. This indicates that fire-emulating restoration created habitat conditions utilized by both pyrophilous and red-listed beetles, although responses varied between ecological groups and scales of comparison (Bell 2023; Hyvärinen et al. 2006; Tälle et al. 2026).

Pyrophilous beetles increased in both abundance and species richness between 2024 and 2025 in the veteranized stand following the addition of stem-base burning, whereas no significant differentiation among individual tree-treatment types was detected in 2025. The absence of treatment-level effects should nevertheless be interpreted cautiously given the limited number of pyrophilous individuals and species available for analysis. The stand-level increase is consistent with the rapid utilization of newly fire-affected habitat reported for pyrophilous beetles (Boucher et al. 2012). H5 was therefore partially supported for pyrophilous beetles, with the predicted greater temporal response in the veteranized stand but no evidence for treatment-level differences.

Red-listed beetles showed a more consistent response. Their abundance and species richness increased between 2024 and 2025 in the veteranized stand, whereas no significant temporal changes occurred in the prescribed-burned stand. At the tree-treatment level, both measures differed among some treatments, with the highest mean values in bark-stripped-and-burned and girdled-and-burned pine. However, neither combined veteranization treatment differed significantly from prescribed-burned pine, suggesting comparable responses between these treatments. Thus, H5 was also partially supported for red-listed beetles.

The group-level responses nevertheless do not imply that all pyrophilous (Wikars 2006) or red-listed species (SLU Artdatabanken 2020) responded similarly, as increases in group-level abundance or richness may be driven by a subset of species associated with particular habitat conditions (Boucher et al. 2012; Ranius 2011). The species-level patterns help explain these group-level responses. *Stephanopachys linearis* showed the clearest increase, from one individual on prescribed-burned pine in 2024 to six individuals on both prescribed-burned and bark-stripped-and-burned pine in 2025, with a further four on girdled-and-burned pine. The species develops in the inner bark of recently burned conifers, particularly Scots pine, and is commonly associated with fire scars on living, fire-damaged trees (Lundberg 1984; SLU Artdatabanken 2025; Wikars 1997, 2006). Its high abundance in burned veteranized trees is therefore consistent with the creation of fire-affected bark habitat. *Stephanopachys substriatus*, another fire-dependent and vulnerable species, was likewise recorded only in veteranized treatments in 2025, with one individual each on bark-stripped, bark-stripped-and-burned and girdled-and-burned pine. Its close association with burned inner bark and fire scars, together with the

rarity of records from unburned trees, provides further, although limited, evidence that veteranized trees can provide habitat used by pyrophilous beetles (Lundberg 1984; SLU Artdatabanken 2025; Wikars 1997, 2006).

Other species illustrate that the response was not restricted to strictly fire-dependent beetles. The vulnerable, fire-favoured *Tragosoma depsarium* occurred on bark-stripped, bark-stripped-and-burned and prescribed-burned pine in 2025. Its larval development is primarily associated with older, sun-exposed lying Scots pine deadwood, which can be promoted by disturbances such as fire (Ehnström & Axelsson 2002). Its occurrence across bark-stripped and bark-stripped-and-burned pine therefore suggests that restoration may also benefit conservation-relevant beetles through the development of suitable deadwood structures rather than fire-specific substrates alone. Similarly, the fire-dependent *Euracmaeops septentrionis* and strongly fire-favoured *Acanthocinus griseus* were recorded in the stem-base-burned veteranization treatments, further indicating use of recently injured and fire-affected parts of declining conifer trees (Ehnström & Axelsson 2002; Hedgren 2004; Palm 1957, 1984; SLU Artdatabanken 2025).

Together, these species-level patterns reinforce the community-level evidence that fire-emulating veteranization created habitat used by both disturbance-associated and conservation-relevant beetles. At the same time, the low abundance of most individual species and the different intervention histories limit species-specific causal inference. For species of conservation concern, H5 was therefore partially supported, with short-term responses evident, although the results do not establish long-term conservation benefits.

4.4 Management implications, strengths, limitations and future research

The findings support the potential of fire-emulating tree veteranization as a complementary restoration measure for creating selected fire-associated and deadwood-related habitat structures (Bernes 2015; SCA 2026). The short-term beetle responses are consistent with evidence that newly created disturbance habitats can be utilized relatively rapidly (Boucher et al. 2012), particularly where mechanical tree injury is combined with targeted stem-base burning. However, veteranization operates at the level of individual trees and selected structures and cannot reproduce the broader ecological effects of prescribed or natural fire (Fredriksson et al. 2025). It should therefore complement rather than replace landscape-scale fire-based restoration (Angelstam 1998; Hjältén 2023; Svensson et al. 2023).

The results suggest that management should focus on maintaining a diversity of habitat conditions rather than maximizing tree mortality or a single treatment characteristic. The differing associations of beetle responses with tree vitality, char height and deadwood availability, together with compositional differentiation among treatment types, indicate that different structural conditions may support different beetle assemblages (Jacobs et

al. 2006; Sandström et al. 2019 Siitonen 2001). Veteranization may therefore be particularly useful where targeted creation of fire-associated structures is desirable or prescribed burning is difficult to implement (Halme et al. 2013; Hjältén et al. 2023), while remaining embedded within a broader restoration strategy. Restoration outcomes should consequently be assessed using multiple structural and biological indicators, because overall beetle diversity, pyrophilous beetles and red-listed species captured different aspects of the restoration response (Fredriksson et al. 2020; Tälle et al. 2026).

Strengths and limitations

A major strength of the study was its multi-scale approach, combining temporal stand-level comparisons, tree-level treatments, habitat characteristics and functionally defined beetle groups. The prescribed-burned stand provided a relevant reference for evaluating veteranization against an established fire-based restoration measure, while the combination of community-level and functionally specific responses allowed the study to assess both overall beetle responses and conservation-relevant taxa. The study also contributes to the still limited empirical evidence on fire-emulating veteranization, particularly where mechanical tree injury is combined with targeted stem-base burning.

The main limitation was the short and temporally uneven study design. The prescribed-burned stand had been burned in 2022, whereas stem-base burning in the veteranized stand occurred shortly before the 2025 sampling. The two approaches were therefore assessed at different stages of habitat development, and the temporal response in the veteranized stand may partly reflect early colonization of newly created fire-affected structures (Boucher et al. 2012). The 2025 comparison included a burned-only treatment, providing a within-year reference for burning in the absence of mechanical veteranization. However, the study did not use a fully factorial design combining mechanical injury and burning, and pre-treatment data were unavailable. The temporal response in the veteranized stand can therefore not be attributed to stem-base burning alone, while the absence of pre-treatment sampling limits causal separation of treatment effects from background temporal variation. A replicated BACI design would provide a more robust basis for resolving these effects (Hjältén et al. 2017). These limitations constrain interpretation of the greater temporal response in the veteranized stand and do not allow conclusions that veteranization had a persistent or superior effect relative to prescribed burning.

Generalization is also constrained by the single study site and experimental spatial scale. Beetle responses may depend on regional species pools, surrounding habitat and landscape connectivity, particularly for rapidly colonizing pyrophilous species (Boulanger et al. 2026; Fredriksson et al. 2020; Svensson et al. 2023). Multi-site and longer-term studies are therefore needed to assess whether the observed patterns are consistent across environmental and landscape contexts.

Several analytical limitations should also be considered. Residual overdispersion remained in the negative-binomial abundance models despite testing alternative specifications, so abundance results should be interpreted cautiously. The main PERMANOVA results were unchanged when permutations were constrained within plots, supporting the robustness of the detected community-composition patterns with respect to repeated plot structure. As the NMDS stress values exceeded 0.2, the ordinations were interpreted as exploratory representations of broad community patterns rather than precise depictions of fine-scale differences (Dexter et al. 2018).

Finally, the species-level responses show that group-level increases in species of conservation concern were not uniform across species. Some species were represented by only a few individuals, limiting the extent to which species-specific responses and their persistence can be assessed. The observed increases therefore indicate utilization of restoration-created habitats by conservation-relevant beetles at the group level, but do not establish that all species benefited or that these responses will persist as habitat conditions develop.

Future research

Future research should prioritize long-term, repeated monitoring of both beetle communities and the structural development of veteranized trees (Ekström 2025; Hekkala et al. 2014; Pasanen 2017). Tracking vitality, fire-affected structures, tree mortality, deadwood and decay stages over several years would help distinguish temporary colonization from persistent or changing community responses and clarify when follow-up interventions may be required.

Experimental studies across multiple sites should further separate the effects of mechanical injury, burning intensity and intervention timing. Factorial and replicated designs could disentangle additive and interactive effects of these components and determine whether their combination affects beetle groups differently (Seibold et al. 2015). Such studies could also assess how landscape context and regional species pools influence beetle responses (Boulanger et al. 2026; Svensson et al. 2023).

An important longer-term research objective is to determine how veteranization can best be integrated with prescribed burning and other fire-based restoration measures to provide complementary habitat conditions across spatial and temporal scales (Angelstam 1998; Svensson et al. 2023). Rather than treating these approaches as interchangeable, future research should investigate whether and under which conditions targeted tree-level interventions complement landscape-scale fire in maintaining the continuity and diversity of fire-associated habitat (Hekkala et al. 2016).

6. Conclusion

This study demonstrates that fire-emulating tree veteranization can contribute to beetle diversity in boreal forests, particularly when mechanical tree injury is combined with additional stem-base burning. The greater temporal increases in abundance and species richness in the veteranized treatments, together with changes in community composition, indicate a pronounced short-term response of beetle communities. This response was also evident among pyrophilous and red-listed species, particularly in the veteranized stand, suggesting that the combined restoration approach provided habitat conditions utilized by conservation-relevant beetles. In contrast, mechanical tree veteranization without additional burning showed more limited treatment-level responses, emphasizing the role of the stem-base burning component in the beetle responses observed in this study.

More broadly, the results suggest that targeted tree-level restoration interventions can complement prescribed burning by creating fire-affected and deadwood-related habitat structures at tree and local stand scales. The different associations of beetle responses with tree vitality, char height and deadwood availability further indicate that restoration benefits are likely to depend on maintaining a diversity of habitat conditions rather than maximizing any single structural feature. Restoration outcomes should therefore be assessed using multiple biological and structural indicators rather than a single measure of habitat development. Fire-emulating veteranization may be particularly valuable as a complementary measure where targeted development of fire-associated structures is desirable or prescribed burning is difficult to implement. By providing habitat features at a smaller spatial scale, such interventions may also complement broader efforts to restore fire as an ecological process by increasing the diversity and spatial continuity of these microhabitats.

The different intervention histories and absence of pre-treatment sampling limited the ability to isolate the individual contribution of stem-base burning to the observed temporal response from the ongoing effects of mechanical veteranization. Nevertheless, the results indicate short-term utilization of the resulting habitat by beetle communities. Veteranization should not be considered a substitute for prescribed or natural fire, but rather as a complementary tool within broader fire-based restoration strategies. Longer-term and multi-site studies are needed to determine whether habitat created by veteranization with stem-base burning continues to support beetle communities over time and how tree-level interventions can best complement landscape-scale fire restoration.

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Popular science summary

Long-term fire suppression has greatly reduced the occurrence of natural fire in boreal forests, making fire-related habitats rare and threatening species associated with burned and fire-affected structures. Prescribed burning is increasingly used to restore these habitats, but its application can be constrained by environmental conditions, landscape context and implementation requirements. Fire-emulating tree veteranization has therefore emerged as a complementary approach, but empirical evidence on its effects on fire-associated biodiversity remains limited. This study investigated whether tree veteranization can support beetle biodiversity, how it compares with prescribed burning, and to what extent additional stem-base burning influences beetle responses. The study was conducted in Ekopark Ejheden in northern Dalarna, Sweden, where beetles were sampled in 2024 and 2025 using flight-interception traps in a veteranized stand and an adjacent prescribed-burned stand. Veteranized trees were girdled or bark-stripped, with additional stem-base burning applied to selected trees in 2025.

Beetle abundance and species richness increased between 2024 and 2025, with greater increases in the veteranized treatments after mechanical injury was combined with stem-base burning. Shannon diversity also increased between years, but across treatments rather than in a treatment-specific pattern. Community composition differed between sampling years, stand treatments and tree-treatment types, indicating partly different beetle assemblages. Beetle responses were also associated with different habitat characteristics: lower tree vitality was associated with higher abundance and species richness, greater char height with higher abundance, and greater deadwood availability with higher Shannon diversity. Pyrophilous and red-listed beetles increased between years in the veteranized stand, although responses varied among individual species. Overall, mechanical veteranization without additional burning showed more limited treatment-level responses, whereas the clearest short-term responses were observed where veteranization was combined with stem-base burning.

These findings highlight the potential of targeted stem-base burning as a component of fire-emulating veteranization for creating fire-associated habitat structures that can support beetle diversity. More broadly, tree-level veteranization can complement prescribed burning by creating fire-affected and deadwood-related habitat structures at a smaller spatial scale, thereby contributing to greater diversity of fire-associated microhabitats. Veteranization should therefore complement rather than replace prescribed or natural fire and be considered within broader fire-based restoration strategies. Longer-term and multi-site studies are needed to determine whether habitats created by veteranization with stem-base burning continue to support beetle communities over time and how tree-level interventions can best complement landscape-scale fire restoration.

Declaration of AI use

Artificial intelligence (AI) tools were used during the preparation of this thesis as a supplementary tool. Their use included support with literature exploration, the development and organisation of ideas and thesis structure, the discussion and contextualisation of results, language editing, and the development and refinement of graphical elements. AI-generated suggestions were critically evaluated and verified by the author. All data analyses, scientific interpretations, conclusions, and final written content remain the responsibility of the author. Sources suggested by AI tools were independently checked for relevance and accuracy. AI tools were not used to generate scientific results or to replace the author's own analysis and academic judgement.

Appendix 1



Figure 10. Flight interception trap attached to a selected tree for beetle sampling.

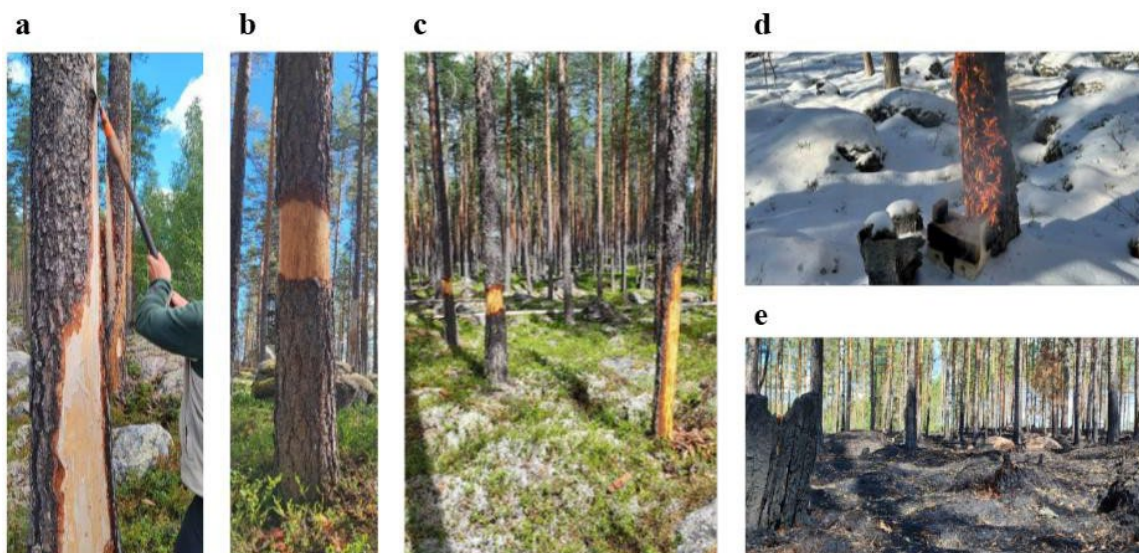


Figure 11. Examples of the restoration treatments. (a) Bark-stripped tree, (b) girdled tree, (c) veteranized stand with bark-stripped and girdled trees, (d) stem-base burning, and (e) prescribed-burned stand. Photographs (a-c, e) by Emelie Fredriksson; photograph (d) by Sveaskog.

Appendix 2

Table 3. Pairwise PERMANOVA comparisons between years and stand treatments (2024 vs. 2025).

Group 1	Group 2	F	R ²	p	p-adjusted
2024 veteranized	2025 veteranized	13.701	0.181	0.001	0.001
2024 veteranized	2024 prescribed burn	2.730	0.042	0.001	0.001
2024 veteranized	2025 prescribed burn	10.849	0.149	0.001	0.001
2025 veteranized	2024 prescribed burn	15.221	0.197	0.001	0.001
2025 veteranized	2025 prescribed burn	8.564	0.121	0.001	0.001
2024 prescribed burn	2025 prescribed burn	9.731	0.136	0.001	0.001

Table 4. Pairwise PERMANOVA comparisons among treatments in 2025.

Group 1	Group 2	F	R ²	p	p-adjusted
bark stripped pine	girdled burned pine	3.245	0.098	0.001	0.001875
bark stripped pine	prescribed burn birch	4.649	0.134	0.001	0.001875
bark stripped burned pine	prescribed burn pine	3.290	0.099	0.001	0.001875
bark stripped burned pine	prescribed burn birch	7.272	0.195	0.001	0.001875
burned control pine	prescribed burn birch	6.232	0.172	0.001	0.001875
girdled burned pine	prescribed burn pine	4.175	0.122	0.001	0.001875
girdled burned pine	prescribed burn birch	7.878	0.208	0.001	0.001875
prescribed burn pine	prescribed burn birch	3.284	0.099	0.001	0.001875
burned control pine	girdled burned pine	2.688	0.082	0.002	0.003333
burned control pine	prescribed burn pine	1.985	0.062	0.006	0.009000
bark stripped pine	bark stripped burned pine	1.960	0.061	0.009	0.012273
bark stripped burned pine	burned control pine	1.732	0.055	0.025	0.031250
bark stripped pine	burned control pine	1.511	0.048	0.083	0.095769
bark stripped burned pine	girdled burned pine	1.366	0.044	0.131	0.140357
bark stripped pine	prescribed burn pine	1.290	0.041	0.153	0.153000

Table 5. Pairwise comparisons of tree vitality among treatments in 2025.

Comparison	BH-adjusted p
bark stripped pine – bark stripped burned pine	0.13803
bark stripped pine – burned control pine	1.00000
bark stripped pine – girdled burned pine	<0.001
bark stripped pine – prescribed burn pine	0.00612
bark stripped pine – prescribed burn birch	0.07230
bark stripped burned pine – burned control pine	0.13803
bark stripped burned pine – girdled burned pine	0.00068

Comparison	BH-adjusted p
bark stripped burned pine – prescribed burn pine	0.25526
bark stripped burned pine – prescribed burn birch	0.80150
burned control pine – girdled burned pine	<0.001
burned control pine – prescribed burn pine	0.00612
burned control pine – prescribed burn birch	0.07230
girdled burned pine – prescribed burn pine	0.02973
girdled burned pine – prescribed burn birch	0.00226
prescribed burn pine – prescribed burn birch	0.49737

Publishing and archiving

☒ YES, I, Kira Koopmann, have read and agree to the agreement for publication and the personal data processing that takes place in connection with this

☐ NO, I do not give my permission to publish the full text of this work. However, the work will be uploaded for archiving and the metadata and summary will be visible and searchable.