



Deadwood restoration in boreal forests benefits saproxylic beetles

Effects of prescribed burning and tree girdling

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Keywords: deadwood, saproxylic beetles, prescribed burning, tree girdling, boreal forests, Pinus sylvestris

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Abstract

Forest management in Fennoscandia has nearly eliminated natural disturbances, such as fire, from forest ecosystems. This affects the composition of tree species, the availability of deadwood, and saproxylic beetle communities. Restoration methods such as prescribed burning and tree girdling aim to replenish the deadwood supply in boreal forests. Prescribed burning creates habitats that benefit fire-dependent beetles and influences successional patterns that benefit Scots pine (*Pinus sylvestris*). Tree girdling adds to already existing deadwood pools and provides a high variety in decay classes that benefit many generalist beetles. Both methods were applied at three treatment areas per method across three years (2022, 2023 and 2024) in Ekopark Ejheden, an area with a long history of fire.

Deadwood volumes of six individual treatment areas, three for each treatment method and year, were calculated separately for snags and logs. Deadwood volumes, abundance, richness, diversity and composition values were used to compare between treatment methods. No significant differences in deadwood volumes were found. Deadwood abundance, richness and diversity were significantly higher in burnt plots at three years post-treatment than in girdled plots. Deadwood composition differed significantly between treatment methods and years. The indicator deadwood category composition showed that stands treated with prescribed burning produced logs and snags in intermediate decay classes. Stands treated with tree girdling produced logs in a wider range of decay classes, including very early to late decay stages.

Ecletror traps were used to sample saproxylic beetles and abundance, species richness and diversity values were used to compare treatment methods. Beetle abundance and species richness were shown to be significantly higher in areas treated with prescribed burning than in tree girdled areas at one and two years post-treatment. Beetle diversity was significantly higher for prescribed burning at two years post-treatment. At three years post-treatment, no significant differences were detected. Beetle composition differed significantly between treatment method and time since treatment. Indicator species analysis showed 19 beetle species that were almost exclusively associated with prescribed burning and three species that were exclusively associated with tree girdling.

My results show that both prescribed burning and tree girdling are effective tools for increasing the deadwood supply in boreal forests. Prescribed burning and tree girdling produce different deadwood categories, which can be interpreted in terms of how the methods act across the plot. Prescribed burning is shown to be clearly favoured by fire-associated beetle species, supporting the argument that fire as a disturbance is irreplaceable by any other method. Regardless of this, tree girdling is a valuable method for promoting the accumulation of deadwood in boreal forest ecosystems. This method should be regarded as an additional benefit rather than a replacement of prescribed burning.

Keywords: deadwood, saproxylic beetles, prescribed burning, tree girdling, boreal forests, *Pinus sylvestris*

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Abbreviations

Abbreviation	Description
SLU	Swedish University of Agricultural Sciences
BOKU	University of Natural Resources and Life Sciences

1. Introduction

1.1 Deadwood and Fire

In modern times, economic interests in forestry have increased, leading to forestry being considered as one of the main drivers for a global decline in biodiversity through habitat loss, degradation and species extinction (IPBES 2019).

Deadwood has always been an important part of a forest ecosystem, providing specific ecological niches and serving as a key element in the forest food chain (Löfroth et al. 2023).

As economic interest in timber production and forestry practices intensified, the removal of deadwood from the ecosystem became common to avoid waste of economic resources. As these methods were used for forest and pest management, this form of forest degradation went mostly unnoticed by the public. By normalising “cleaned out” forests, the public perception of deadwood in forests changed too. As a consequence, deadwood was now commonly associated with untidiness, chaos and the loss of economic resources (Flint et al. 2009).

Nowadays, the awareness among the public and the forestry community of the importance and therefore the amount of deadwood in an ecosystem has increased in Europe. However, there is still a high demand for more deadwood in uneven-aged and diverse forests to improve biodiversity (FISE 2025).

Forestry in Sweden, as in most parts of central and northern Europe, is primarily centred around timber production, with tree stands of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) (Berghlund & Kuuluvainen 2021). Forest stands with genetically improved trees with short rotations to enable quicker harvesting times are favoured, a strategy that prevents deadwood from developing naturally (Siitonen 2001). Under natural, undisturbed conditions, both tree species would reach ages of several hundred years, allowing for old growth forests with diverse structures that would benefit various forest organisms (Schweingruber & Wirth 2009). Research comparing production forests with forests in natural reserves has shown that forests in protected areas provide almost 10 times higher deadwood volumes and 2,6 times higher deadwood diversity than forests that mostly serve a production purpose. These results can be traced to larger diameter sizes and greater variety in decay stages due to different age classes within natural forests (Bergman et al. 2026). To restore deadwood volumes and diversity in managed landscapes, artificial disturbances like prescribed burning were reintroduced. By creating logs (lying deadwood) or snags (standing deadwood), deadwood became available again to saproxylic species even years after the event (Hjältén et al. 2018).

Structural diversity is considered a key element in ensuring that as many organisms as possible benefit from the deadwood supply in a forest ecosystem.

Different stages of decay, diameters and tree species, for example, host different organisms that rely on these structures in various stages of their life cycle (Vítková et al. 2018; Sandström et al. 2019). Since fire creates very specific conditions for species that depend on this type of disturbance, but others “simply” need a sufficient supply of deadwood structures, deadwood restoration relies on a combination of methods to promote more diversity in the forest ecosystem (Hjältén et al. 2018).

1.2 Fire history in Fennoscandia

Fennoscandia’s history with fire in boreal forests can be tracked back through soil profiles to the 14th century. Before increased human activity in northern Sweden, fires were primarily caused by lightning, leading to large, infrequent fires (Zackrisson 1977).

After human settlement in the area, around the 17th century, fire frequency increased. This has been linked to agricultural methods that were prominent at the time, like pasture burning and slash-and-burn agriculture. Up until that point, around 1% of forest area in Fennoscandia burned each year (Zackrisson 1977). Around 1850, new economic interests in timber production emerged, which ultimately led to stricter restraints on the use of fire in agriculture and to an improved fire management system, resulting in reduced fire frequency (Rolstad et al. 2017; Aakala et al. 2023). This change in forest management practices has led to stand-replacing clear-cutting rather than a stand-replacing natural disturbance, which in turn results in vastly different habitat conditions (Hjältén et al. 2018).

While fire was considered a regular natural disturbance before increased human interference in the fire regime, it is now considered rare, with less than 2000 ha burning annually in Sweden, though occasional exceptions have occurred over the years. That translates to an average of 0.006% of forest area burned annually since the introduction of stricter forest management regimes (Ramberg et al. 2018; Kinnunen et al. 2024). This shift in the fire regime from a regular use of fire to fire suppression has led to a change in tree species composition over the years, resulting in increased numbers of spruce forests with closed canopies instead of open pine forests (Hjältén et al. 2018). These findings show that fire events, or their absence from the ecosystem, actively shape the boreal forest by influencing the diversity of stands through the frequency and severity of the fire (Hjältén et al. 2018; Aakala et al. 2023).

As fire in Fennoscandia is mostly an event of low to moderate intensity, trees that do not die immediately during the fire are very likely to die at a later point in time because of insect damage, creating delayed, long-term sources of deadwood (Eriksson et al. 2013; Sandström et al. 2019; Montoro Girona et al. 2023). These events are characterised by the burning of vegetation on the forest floor and low tree mortality (Montoro Girona et al. 2023). Fire removes ground vegetation,

opens up habitats and creates new substrates in the process (Hjältén et al. 2018). This changes the forest structure and alters the local microclimate through an increase in charred surfaces, that allow more light to be absorbed (Eriksson et al. 2013).

This has a significant impact on maintaining landscape dynamics, structure, composition and biodiversity as well as successional processes in boreal forests. All of these processes produce many different habitat types as fire alters the dead and living wood structures of the forest as well as ground vegetation and soil habitats. The loss of fire in the system therefore affected various species that are adapted to these recurring events (Hjältén et al. 2018). Therefore, artificial methods to enhance deadwood availability in forests, such as prescribed burning, have been used as conservation methods in Fennoscandia for a long time (Aakala et al. 2023).

1.3 Saproxylic beetles

Saproxylic beetles are insects that rely on deadwood in various stages of decay at some point in their lifecycle. They play an important ecological role by processing and breaking down deadwood and recycling nutrients (Calix et al. 2018). Since saproxylic beetles rely on a continuous supply of dead and decaying wood, they are very sensitive to the availability of deadwood within forest ecosystems. Dead and decaying wood provides a multitude of microhabitats where species with very specific environmental requirements can thrive. Saproxylic species can have diverse nutritional preferences and can act as predators of other beetle species, such as bark beetles (Ulyshen & Šobotník 2018). Other factors that influence saproxylic beetle species include canopy openness, host tree species and deadwood volume, decay stage of deadwood, other available microhabitats in the area and fungal species (Cizek et al. 2025).

As of 2018, almost 18% of saproxylic beetle species are considered threatened, making them one of the most threatened insect groups across Europe. Logging, tree loss and wood harvesting are considered the major threats that these species face, resulting from the long history of viewing dead and decaying wood as signs of neglect and poor forestry management (Calix et al. 2018). To maintain saproxylic biodiversity in boreal forests, it is necessary to include diverse measures such as prescribed burning, tree felling and girdling which have been shown to have positive effects in the past (Hjältén et al. 2018; Löfroth et al. 2023).

1.3.1 Fire and saproxylic beetles

Using fire as a restoration tool to increase the amount of deadwood in forests has been part of active forest management Fennoscandia in the past. Oftentimes, these deadwood restoration measures have been carried out to increase the presence of

saproxyllic beetle presence (Hjältén et al. 2018). Beetles that rely on fire for the long-term survival of their species can be categorised as either fire-dependent or strongly fire-favoured beetle species (Wikars 2006; Bell 2023). Fire-dependent insects are defined as species that show a strong behavioural specialisation for fire and occur primarily on recently burned sites. Strongly fire-favoured insects denote species that respond positively to smoke, fire or ash and are significantly more abundant in burnt than unburnt areas (Wikars 2006). As fire has been a natural, regular and recurring event in the past, fire-dependent species have adapted specifically to fire-related disturbances by developing mechanisms that allow them to sense fires and disperse towards them even from great distances (Hjältén et al. 2018). Fire-dependent species colonise areas sometimes even during the fire and disappear relatively fast after the event, ranging from days for flying beetles to 1-3 years for ground-dwelling beetles. These species rely on recently burned areas that cannot be created by other disturbances and they depend on the regular recurrence of fires (Bell 2023).

Other saproxyllic beetles that benefit from large-scale disturbances are often times early colonising species. They benefit from weakened stands and have very general habitat requirements (Bell 2023). Fire-damaged trees therefore provide a great habitat not only for fire-dependent species but also for large amounts of bark beetles, which can result in high economic consequences for the managing party (Kluting et al. 2023; Löfroth et al. 2023). Because of that early colonising pattern, forest conservation measures that promote large-scale deadwood availability are often linked with an increase in bark beetle presence, with research showing that bark beetle abundance was five times higher in burned stands than in areas treated with alternative methods to burning (Kärvemo et al. 2017). These circumstances create a conflict between biodiversity conservation efforts and the timber industry.

1.4 Deadwood management

Landscape diversification has been proposed in previous research as a means to enhance adaptability and resilience of forests. In particular, increasing the functional and structural diversity of forests has been shown to increase the forests' ability to resist and recover from disturbances (Gazzea et al. 2024). To ensure structural diversity in forests, there is an increasing focus on artificially creating deadwood because deadwood levels have declined in the past. Recovery of deadwood supply takes a long time, as it does in growing forests. Therefore, intervention methods such as prescribed burning or tree girdling are used to replenish deadwood supply faster than how it would occur in natural systems (Sandström et al. 2019). Mimicking natural disturbances to support biodiversity in Fennoscandian forests is already a well-accepted concept. However, careful planning of these methods is necessary to achieve outcomes that are acceptable for all parties involved.

Prescribed burning, or conservation burning, has been used in Sweden as a conservation tool since the 1990s. It has become increasingly common to apply prescribed burning in Swedish forests, as it is part of the FSC certification process to restore fire-dependent habitats (Cogos et al. 2020). Prescribed burning is a useful tool for treating areas that are hard to treat with other methods due to lack of infrastructure or economic resources. While fire acts as a damaging force in the first place, these effects are generally considered minor and temporary, as the process brings more benefits than disadvantages to the forest system in the long run. Among other things, it promotes the regeneration of pines, a fire-dependent tree species (Francos & Úbeda 2021). Since prescribed burning not only creates but also destroys pre-existing deadwood, careful planning is required when choosing suitable areas for conservational burning. Especially deadwood in late decay stages is very vulnerable to fire but has high value for red-listed species (Eriksson et al. 2013). Fire intensity and fuel load are therefore variables that can be controlled during the event (Hekkala et al. 2014). In European boreal forests, prescribed burns are mostly carried out at a low to moderate intensity, minimizing damaging effects with long-term consequences (Francos & Úbeda 2021; Montoro Girona et al. 2023). Prescribed burning can be a particularly useful tool for creating environments that benefit saproxylic species, as burned deadwood has supported more indicator species when compared to artificially created deadwood without burning (Sandström et al. 2019; Larsson Ekström et al. 2024).

Another practice widely used in nature conservation is tree girdling. In Sweden this method is called “Katning”. The tree girdling method is part of a broader application called veteranisation, in which trees are damaged to mimic the effects that fire would have on them (SCA 2020). Tree girdling intentionally kills individual trees by removing a strip of bark and cambium around the tree trunk (Hägglund & Hjältén 2018; Dufour-Pelletier et al. 2020). The height of the girdling, tree species and quality of the tree are all factors that have an impact on the aimed conservation goals and need to be considered in the planning phase. Girdled trees do not die immediately after the treatment but can remain alive and, in exceptions, can even continue to grow for up to two years after treatment. Eventually, the roots and consequently the whole tree die due to lack of nutrients (Dufour-Pelletier et al. 2020). Applying this method on stands is considered a relatively low-maintenance approach that yields high rewards in terms of deadwood levels (Vítková et al. 2018).

1.5 Research questions and hypotheses

The aim of this thesis is to compare two forest conservation methods, prescribed burning and tree girdling and their effects on deadwood restoration and saproxylic beetle communities.

I asked these two main questions:

1. Are there any differences in deadwood volume, abundance, diversity, richness and/or composition between treatment methods (burned/girdled) and years?
2. Are there any differences in beetle species abundance, richness, diversity and/or composition between treatment methods (burned/girdled) and years?

For these questions, I have the following hypotheses.

RQ1: Differences in deadwood characteristics across treatment methods and time since treatment:

H1a: Tree girdled plots are expected to host higher deadwood volumes in the early post-treatment stands, as legacy deadwood is present. Burnt plots are expected to produce higher deadwood volumes in the older post-treatment stands due to delayed tree mortality (Harmon 2009; Nirhamo et al. 2023)

H1b: Tree girdled plots are expected to have a higher abundance of deadwood than burnt plots in the early post-treatment stands because of legacy deadwood that is present in the plots (Sandström et al. 2019; Lutz et al. 2020). Abundance in the plots of both treatment methods will be highest in the oldest post-treatment plots, as more deadwood is added through delayed tree mortality (Nirhamo et al. 2023).

H1c: Tree girdled plots are expected to produce higher deadwood richness than burnt plots in the early post-treatment stands (Sandström et al. 2019). Richness is expected to be higher in older post-treatment plots, with burnt plots showing higher richness due to the broad spectrum of dead trees resulting from fire (Harmon 2009).

H1d: Tree girdled plots are expected to have higher deadwood diversity than burnt plots in the early post-treatment stands. Older burnt plots are expected to have higher diversity than tree girdled plots because of delayed tree mortality (Harmon 2009).

H1e: More homogeneous deadwood composition with a high variety of decay classes is expected amongst tree girdled stands since all plots share a similar baseline of legacy deadwood that is increased through girdling (Augustynczyk et al. 2024). For burnt areas, a lower variety of decay classes and greater heterogeneity between stands occur as fire acts simultaneously across the whole

plot and the treated stands develop similarly over time (Angers et al. 2011; Sandström et al. 2019).

RQ2: Differences in beetle characteristics across treatments and years:

H2a: Prescribed burning is expected to produce an initial peak in beetle abundance in the early post-treatment stands because of early colonising and fire-associated species that decline as these species leave again since the specific required conditions are no longer available (Kärvemo et al. 2017; Fredriksson et al. 2020). Tree girdling produces lower beetle abundance in early post-treatment stands and increases over time as more dead wood becomes available (Hägglund & Hjältén 2018).

H2b: Prescribed burning is expected to produce a higher richness in earlier post-treatment stands as fire-associated species are still present (Toivanen & Kotiaho 2010; Bell 2023). Richness in girdled plots is high and increases over time as the supply of deadwood increases and diversifies (Hägglund & Hjältén 2018).

H2c: Prescribed burning is expected to have higher diversity in early post-treatment plots because of fire-associated species, this is expected to decrease as the treated plots start to recover and lose their specific habitat requirements (Toivanen & Kotiaho 2010). Later post-treatment girdled plots are expected to have higher diversity than early post-treatment plots as the supply of deadwood increases and diversifies (Hägglund & Hjältén 2018).

H2d: Both treatment methods are expected to share a similar baseline of beetle species, with prescribed burning specifically hosting fire-associated species that do not occur in girdled plots (Sandström et al. 2019). Later post-treatment burnt stands are expected to host a similar species composition to that of tree girdling (Heikkala et al. 2016).

2. Methods and Materials

2.1 Study Area and Design

The study area for this thesis is Ekopark Ejheden in the county of Dalarna in central Sweden. Ekopark Ejheden is owned by Sweden's largest state-owned forest company, Sveaskog (Moberg 2007). The purpose of these Ekoparks is to preserve and develop forest landscapes of high conservation value, such as Ejhedens long history with forest fires and pine trees, while still practising forestry. About 14% of Sweden's forests are owned and managed by Sveaskog in line with the FSC and PEFC certifications. According to this certification, regular conservation burns have to be carried out to benefit species that rely on burned areas (Sveaskog 2026). Ekopark Ejheden was founded in 2007 as the first ecopark in the county and spans 6,900 hectares, of which 4,500 are considered productive forest. Traces of humans can be dated back to the Stone Age and to more prominent interactions with fire through slash-and-burn agriculture in the 1800s. The forests in Ekopark Ejheden are reported to consist of 80% older forests (older than 80 years), including 487 stands with pines components over 150 years old. Especially in areas affected by fire events, pine deadwood (snags and logs) is documented as very dominant (Moberg 2007).

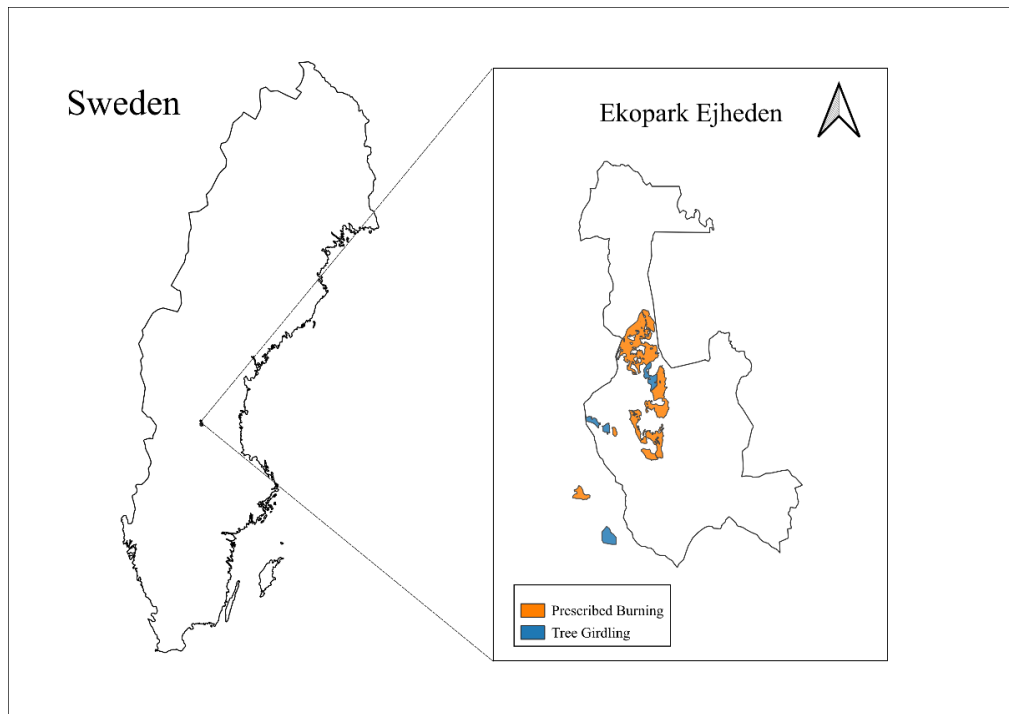


Figure 1: Map showing the location of Ekopark Ejheden and areas where plots were selected for treatment with either prescribed burning or tree girdling

In this study, two treatment methods were applied in the study area: prescribed burning (Burn22, Burn23 and Burn24) and tree girdling (Girdling22, Girdling23 and Girdling24). For each treatment method, three treatment areas were selected that were treated either in 2022, 2023 or 2024. Observations about the development of the plots can therefore only be made on the basis of a chronosequence and not a time series. This means that the treated sites all share similar environmental conditions but are treated at different times and therefore differ in age. Within the prescribed burn treatment, there were five or six individual plots per treatment area, while ten or eleven plots were sampled for each treatment area within the tree girdling method. Other veteranisation methods such as bark stripping (“Katning”) and felling were also applied in the girdled plots, but for lack of comparability only girdled trees were sampled. Elector traps were put up on already dead pines at the end of May 2025 and taken down at the end of September of the same year. These traps are used to collect beetles from specific substrates, such as deadwood, because they enclose and darken a portion of the habitat. Once the beetles emerge from the deadwood, they move towards the light and get trapped in a collecting box at the end, where they can be collected later (Alinvi et al. 2007).

2.2 Deadwood characteristics, inventory and analysis

To investigate the effects of burning and girdling on deadwood characteristics, 48 plots with radii of either 10, 15 or 20 meters were selected within the six different treatment areas. The number of sampled trees varied across plots and treatments. Pine trees (*Pinus Sylvestris*) were the dominant tree species, with some birch (*Betula pendula*) and spruce trees (*Picea abies*) scattered throughout the study plots. For this thesis, only pines were considered. Each piece of deadwood was classified as a log or a snag and measured accordingly. Specifically, for snags, the diameter at breast height (DBH), the height and the decay stage for coniferous snags were recorded. The decay stage classes for snags were determined according to Thomas’s (1979) classification system from classes 1-9. Stages 1-3 represent the stage of vitality (1= alive, 2 = declining vitality, 3 = dead), whereas stages 4-9 describe the state of decay (Thomas 1979). For logs, the base and top diameters, length of the log and the decay stage were recorded. The decay stage for coniferous logs was determined using a mix of visual assessment (stages 1 and 2) and recording the depth of penetration of a knife (stages 3-6) into the log (Siitonen & Saaristo 2000). For both logs and snags, the proportion of burned bark was recorded in percentage after a visual assessment.

The deadwood volume was first calculated for each individual plot within the treatment and then summed up per treatment. For logs, the formula for truncated cones, using the length of the log in meters and the base (R_{max}) and top diameter

(Rmin) in meters, was used. For snags, the taper equation for conifers (Näslund 1947) was used.

Log volume: Formula for a truncated cone

$$V = \frac{1}{3} * \pi * L * (Rmax^2 + Rmax * Rmin + Rmin^2)$$

Snag volume: Formula taper equation (Näslund 1947)

$$V = 0,0914 * D^2 + 0,03069 * D^2 + 0,002818 * D * H^2$$

After the deadwood volume was calculated for each plot, it was averaged over one hectare and summarized by treatment. This value is called Mean Deadwood (m³/ha) in Table 2. The same was done for Log and Snag (m³/ha). The different plot sizes were considered in this process. Total Deadwood (m³) refers to the sum of deadwood volumes per treatment method before averaging over one hectare. The same was done for Log and Snag (m³).

Deadwood abundance, richness and diversity were calculated per plot and per treatment area using individual deadwood pieces. Deadwood abundance was defined as the total number of individual deadwood pieces per plot and treatment area. Deadwood richness was calculated by creating 71 deadwood categories based on decay stages for coniferous logs and snags, diameter classes (0-10 cm, 10-20 cm, 20-30 cm and ≥30 cm) and proportion of burned bark (0%, 0-25%, 25-50% and 50-100%). Deadwood richness therefore is defined as the number of different deadwood categories per plot and treatment area. Deadwood diversity was calculated per plot and treatment area using the Shannon index, which accounts for the number of deadwood categories and the evenness of their distribution.

All statistical analyses were done using R, Version 4.5.2. (R Core Team 2025). Deadwood volume, abundance, richness and diversity were modelled using generalized linear mixed models in glmmTMB (McGillucuddy et al. 2025) with treatment method, time since treatment and their interaction as fixed effects. While abundance was modelled with a negative binomial error distribution, richness, diversity and volume were modelled using a Gaussian error distribution. The random effect for plots was excluded from the model, as each plot had its own individual plot ID and was only tested once. The fit of the model was assessed using Dharma (see Figure 8-10) (Hartig et al. 2024). Pairwise post hoc Tukey tests were performed in emmeans (Lenth et al. 2026) and marginal R² values were calculated using the delta method in MuMIn (Bartoń 2026). Deadwood category composition tests were carried out using PERMANOVA with

Bray-Curtis dissimilarity, followed by betadisper to test homogeneity of dispersion. Deadwood category composition was visualised using NMDS ($k = 2$) in the vegan package (Oksanen et al. 2026). Indicator deadwood categories were identified using the indicspecies package (De Cáceres & Legendre 2009).

2.3 Beetle characteristics, inventory and analysis

The eclector traps were mounted on dead pine trees at the end of May 2025 and the beetles were collected in September of the same year. Afterward, the trapped beetles were identified to the species level by a Finnish expert, and the red list category was therefore assigned based on the Finnish red list. As this thesis focuses on a Swedish study area, the red-list categories were later transferred according to the Swedish red list (SLU Artdatabanken 2026j).

In total, 180 traps were installed across 48 plots, including three traps that were empty upon collection (Table 1). While it was possible to match the traps to their corresponding treatment areas, it was not possible to match them at the plot level within those areas because the GPS data was missing. This meant that no tests on the connections between deadwood and beetle characteristics could be made because a sample size of six treatment areas was insufficient.

Table 1: Number of beetle traps per treatment and time since treatment.

Treatment method	Time since treatment	Number of traps
Prescribed Burning	1 year post	33
	2 years post	32
	3 years post	27
Tree Girdling	1 year post	30
	2 years post	30
	3 years post	28

Beetle abundance was defined as the total number of individuals caught per trap and summed up per treatment, species richness was calculated as the number of unique species caught per trap and treatment area and the diversity index “Shannon” takes species richness and the distribution of the evenness of abundance into account, this was also calculated at the trap and treatment level (Table 7). Richness and the Shannon diversity index were calculated in the vegan package in R (Oksanen et al. 2026) and modelled later using a generalized linear mixed model in the glmmTMB package (McGillcuddy et al. 2025). To determine which species were mainly associated with specific treatments, an

indicator species analysis was carried out across all 6 treatment areas and only the two main treatment methods, prescribed burning and tree girdling (De Cáceres & Legendre 2009). Additionally, the 10 most abundant species per treatment method were determined, using the previously determined abundance values (Appendix, Table 13). Fire dependency of beetles was based on Wikars (2006). In this thesis, mostly beetle species in category 1 “fire dependent” and category 2 “strongly fire favoured, 0-5 years post treatment, rare species” were found. Category 4 “strongly fire favoured, >5 years post treatment, rare species” was recorded twice. The Finnish red list was compared with the Swedish one (SLU Artdatabanken 2026j).

All statistical analyses were done using R, Version 4.5.2. (R Core Team 2025). Beetle abundance, richness and diversity were modelled using generalized linear mixed models in glmmTMB (McGillucuddy et al. 2025) with treatment method, time since treatment and their interaction as fixed effects. Trap ID was used as a random effect since trap numbers were reused across treatments. While abundance and richness were modelled using a negative binomial distribution, Shannon diversity was modelled using a Gaussian distribution. The fit of the model was tested with Dharma (see Figure 11-13) (Hartig et al. 2024). Pairwise post hoc Tukey tests were performed in emmeans (Lenth et al. 2026) and marginal R^2 values were calculated using the delta method in MuMIn (Bartoń 2026). A beetle species composition test across treatments was conducted using PERMANOVA with Bray-Cutris dissimilarity, followed by betadisper to test homogeneity of dispersion. This was visualised using NMDS ($k=2$) in the vegan package (Oksanen et al. 2026). Indicator species were identified using the indicpecies package for the two treatment methods and for treatment method and years (De Cáceres & Legendre 2009).

3. Results

3.1 Deadwood

3.1.1 Deadwood volume

Calculations of the deadwood volume showed the highest volumes for both treatment methods at three years post-treatment. At one and two years post-treatment, tree girdling produced higher deadwood volumes than prescribed burning. In burnt areas, snag volumes were recorded to be higher than log volumes. For girdling, an opposite pattern was observed. Log volumes higher in the treatment areas at three and one year post-treatment. Snag and log volumes at two years post-treatment were very similar (Table 2).

Table 2: Deadwood volume per treatment, divided into log and snag components. Total Deadwood (m^3) is the log and snag volumes of the individual plots added together and summed up for each treatment. Mean Deadwood (m^3/ha) is the deadwood volume that was calculated for each plot averaged over one hectare and summarized by treatment.

Treatment	Total Deadwood (m^3)	Log (m^3)	Snag (m^3)	Area (ha)	Mean Deadwood (m^3/ha)	Log (m^3/ha)	Snag (m^3/ha)
Burn22	15.642	3.493	12.149	0.589	26.555	5.931	20.624
Burn23	6.019	2.237	3.782	0.644	9.346	3.474	5.872
Burn24	7.224	2.984	4.240	0.628	11.497	4.749	6.748
Girdling22	23.699	22.340	1.359	1.233	19.220	18.117	1.102
Girdling23	11.783	5.699	6.084	1.037	11.365	5.497	5.868
Girdling24	15.704	11.082	4.621	1.147	13.695	9.665	4.030

Deadwood volume did not differ significantly between treatment methods but did vary significantly within treatment methods and years since treatment (Figure 1). Both prescribed burning (Burn2022) and tree girdling (Girdling2022) have shown significantly higher deadwood volumes at 3 years post-treatment compared to younger stands at 1 and/or 2 years post-treatment (Table 3). Although not statistically significant, early post-treatment girdled plots showed higher volumes than young, burned plots, providing weak support for H1a (Figure 2). For prescribed burning, deadwood volume increased significantly over time. Tree girdling showed a similar pattern, though the increase was statistically significant only when comparing stands at two and three years post-treatment. These findings suggest that both treatments are comparable in terms of deadwood accumulation over time, contradicting H1a.

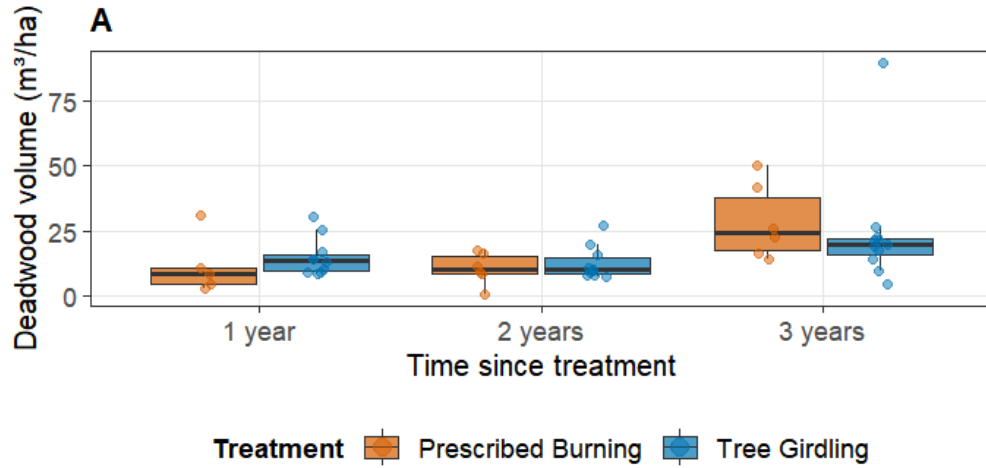


Figure 2: Values of mean deadwood volume (m^3/ha) for prescribed burning and tree girdling for plots at 1, 2 and 3 years post-treatment. Jitter points represent individual plot values.

Table 3: Model coefficients and marginal R^2 for GLMM of deadwood volume (Gaussian) in response to treatment type (Burn vs. Katning) and time since treatment. Reference level: Burned, treated 2022 (3 years post-treatment).

Response variable	Term	Estimate	SE	z	p
Volume	Intercept	2.607	0.282	9.233	<0.001
	Treatment: Katning	-0.453	0.351	-1.289	0.197
	Year: 2023 (2 yrs post)	-1.604	0.399	-4.017	<0.001
	Year: 2024 (1 yr post)	-1.162	0.419	-2.775	<0.01
	Katning $\times$ 2023	0.628	0.501	1.253	0.21
	Katning $\times$ 2024	0.578	0.516	1.120	0.263
	R^2 (delta)	0.371			

3.1.2 Deadwood abundance, diversity and richness

Each bar of the graph below represents the proportion of surveyed logs and snags that fall into the decay stages present in this area of the survey (Figure 3). Decay classes were assigned to each deadwood piece during the survey conducted in Summer 2025.

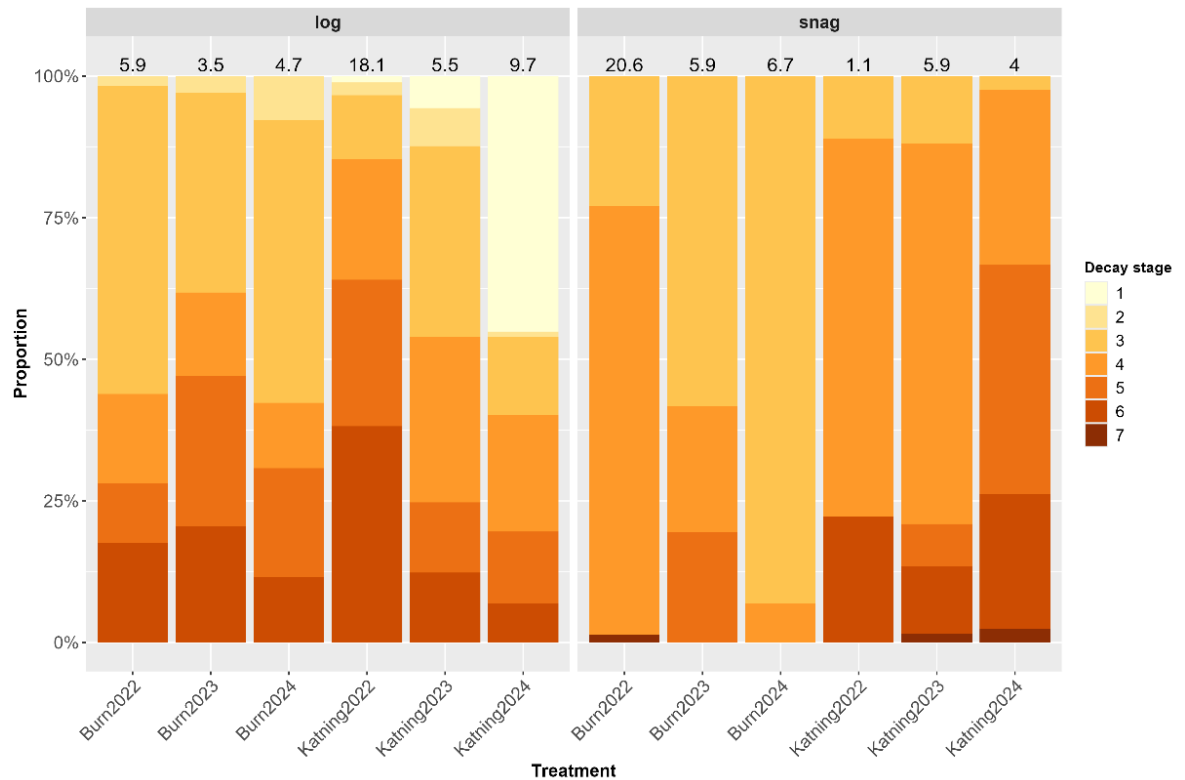


Figure 3: Proportional distribution of decay stages for logs and snags across all six treatment groups, separated by deadwood type. Numbers above bars indicate mean deadwood volume (m³/ha) per treatment group.

Prescribed burning produces a high proportion of burned of deadwood that fall into decay stage 3- 7, with stage 3 being the most prominent across all burned plots regardless of age. Burned logs show more variety in decay classes, ranging from class 2 to 6, coupled with lower volumes than snags, which are dominated by decay class 3 and 4. Tree girdling produces deadwood that shows a balanced amount of decay classes ranging from 1 to 7, with decay class 4 being the most prominent one. Girdled logs, regardless of age, show more variety between decay classes (1-6), coupled with higher volumes than snags, which show high amounts of decay class 4.

Table 4: Deadwood metrics per treatment Total deadwood abundance, deadwood category richness and Shannon diversity per treatment and time since treatment.

Treatment ID	Time since treatment	Total abundance	Deadwood richness	Shannon diversity (H')
Burn22	3 years post	131	28	2.668
Burn23	2 years post	70	29	3.136
Burn24	1 year post	55	23	2.646
Girdling22	3 years post	98	19	2.502
Girdling23	2 years post	156	21	2.394
Girdling24	1 year post	144	21	2.389

In total, 654 pieces of deadwood were recorded across six different treatment areas. In burnt areas, the treatment area at three years post-treatment had the highest deadwood piece abundance and the area most recently treated, had the lowest (Table 4). For prescribed burning, stands at three years post-treatment had twice the deadwood abundance as stands at one or two years post-treatment (Figure 4). For girdled areas no similar pattern in deadwood abundance was observed. Deadwood richness stayed consistent throughout the girdled areas, whereas higher deadwood richness was recorded for older burnt plots compared to younger burnt plots.

Overall, prescribed burning resulted in significantly higher deadwood abundance and richness at three years post-treatment than tree girdling. Deadwood diversity is significantly higher in the burnt than girdled plots at three years post-treatment. However, at two years post-treatment, girdled plots show a significantly higher deadwood diversity than burnt plots. Diversity showed similar patterns, with the oldest stand at three years post-treatment also having higher diversity compared to stands at one or two years post-treatment. Within the tree girdling method, deadwood abundance and richness were higher in younger stands compared to the stand at three years post-treatment (Table 5).

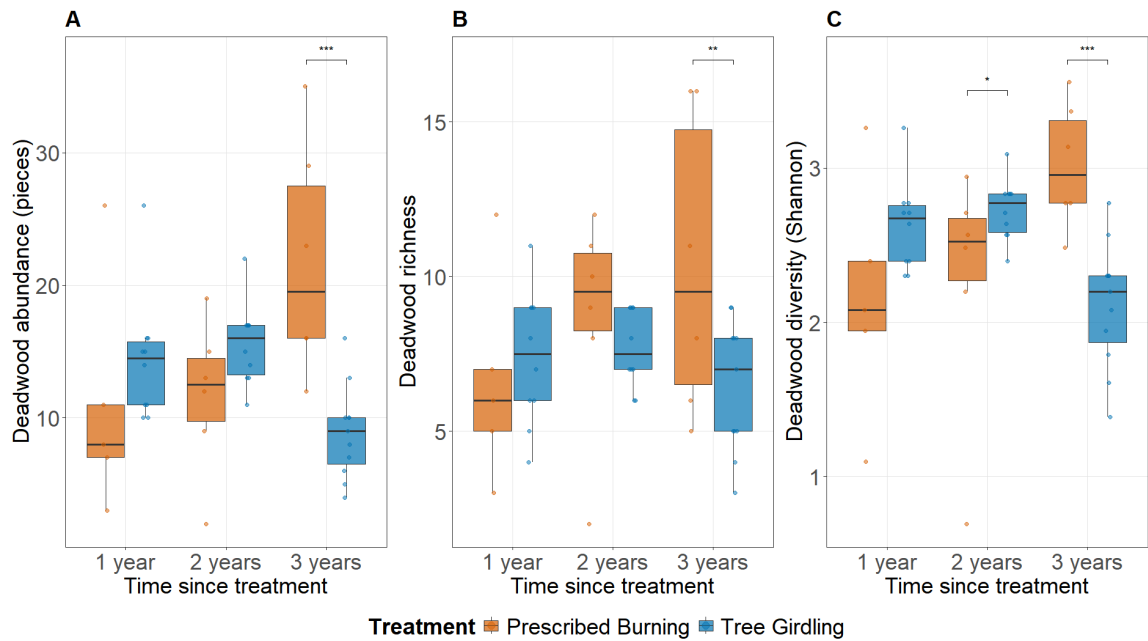


Figure 4: Raw values of deadwood abundance (A), richness (B) and Shannon diversity (C) for prescribed burning and tree girdling at 1, 2 and 3 years post-treatment. Jitter points represent individual plot values. Significance brackets indicate significant pairwise differences between treatment methods at each time point based on Tukey-adjusted emmeans contrasts: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Table 5: Model coefficients (estimate, SE, z, p) and marginal R^2 for GLMMs of deadwood abundance (negative binomial), richness and diversity (both Gaussian) in response to treatment type (Burn vs. Katning) and time since treatment. Reference level: Burned, treated 2022 (3 years post-treatment at time of measurement)

Response variable	Term	Estimate	SE	z	p
Abundance	Intercept	3.046	0.138	22.071	<0.001
	Treatment: Katning	-0.890	0.188	-4.735	<0.001
	Year: 2023 (2 yrs post)	-0.628	0.211	-2.973	<0.01
	Year: 2024 (1 yr post)	-0.712	0.227	-3.141	<0.01
	Katning $\times$ 2023	1.198	0.272	4.398	<0.001
	Katning $\times$ 2024	1.195	0.286	4.183	<0.001
	R^2 (delta)	0.373	—	—	—
Richness	Intercept	10.333	1.066	9.696	<0.001
	Treatment: Katning	-3.879	1.325	-2.928	<0.01
	Year: 2023 (2 yrs post)	-1.667	1.507	-1.106	0.269

Response variable	Term	Estimate	SE	z	p
Diversity	Year: 2024 (1 yr post)	-3.733	1.581	-2.362	<0.05
	Katning × 2023	2.912	1.890	1.541	0.123
	Katning × 2024	4.679	1.949	2.400	<0.05
	R ² (delta)	0.182	—	—	—
	Intercept	3.015	0.180	16.753	<0.001
	Treatment: Katning	-0.901	0.224	-4.026	<0.001
	Year: 2023 (2 yrs post)	-0.749	0.254	-2.944	<0.01
	Year: 2024 (1 yr post)	-0.859	0.267	-3.217	<0.01
	Katning × 2023	1.365	0.319	4.277	<0.001
	Katning × 2024	1.371	0.329	4.164	<0.001
	R ² (delta)	0.346	—	—	—

3.1.3 Deadwood composition

PERMANOVA results show significant differences in deadwood category composition between treatment method, years and their interaction, indicating that the deadwood composition varies as stands age post-treatment (Table 6). The treatment ellipses show no overlap, confirming the strongly significant PERMANOVA results (Figure 5). The blue ellipse for tree girdling is the more compact, tightly clustered one. The burned, orange ellipse is larger and the points are more spread out, suggesting more variability between the burned plots which is confirmed by the significant betadisper results ($p = 0,022$). The significant betadisper result ($p = 0,013$) for the Treatment and Year interaction indicates that some combinations of Treatment and Year are more heterogeneous than others. For both treatment methods, the oldest stands treated in 2022 can be visually distinguished from earlier post-treatment stands, which suggests changes in deadwood composition as the stands age. Earlier post-treatment plots show more overlap, implying similarities in deadwood composition.

Table 6: Deadwood category composition PERMANOVA results (p -value of PERMANOVA and Betadisper, R^2 of PERMANOVA and NMDS stress) comparing treatment method (Prescribed Burning / Tree Girdling), year and their interaction. Values in bold denote significant results ($p < 0.05$). NMDS stress based on $k = 2$ dimensions.

Variables	p (PERMANOVA)	R^2 (PERMANOVA)	p (Betadisper)	NMDS stress
Treatment method	0.001	0.284	0.022	0.081
Year	0.001	0.138	0.819	—
Treatment $\times$ Year	0.001	0.112	0.013	—

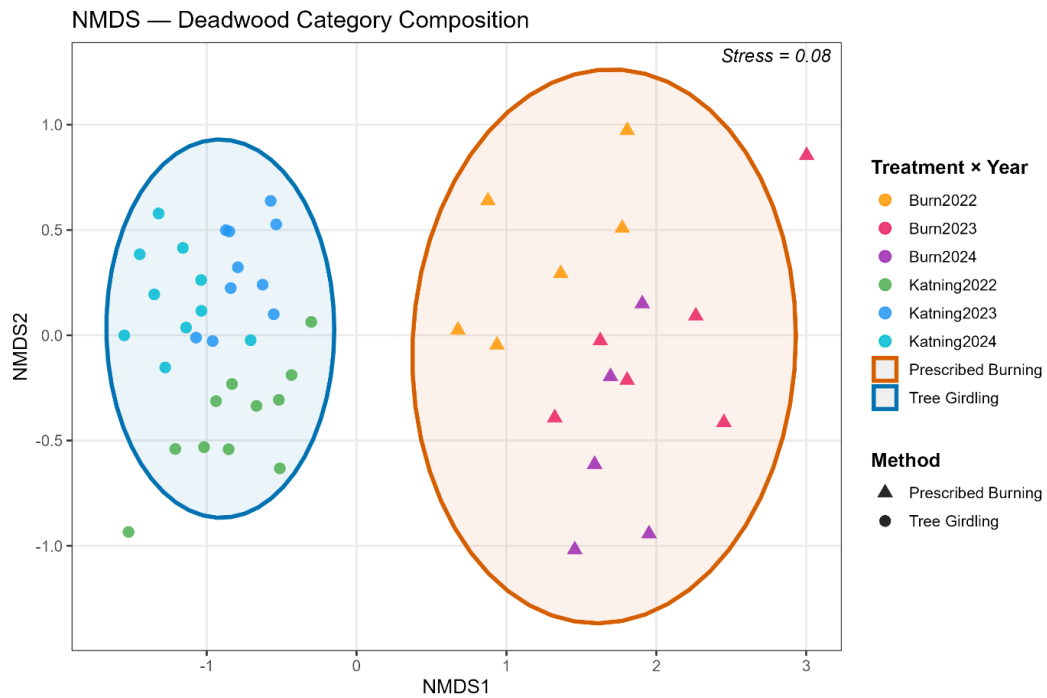


Figure 5: Non-metric multidimensional scaling (NMDS) ordination of deadwood category composition based on Bray-Curtis dissimilarity ($k = 2$, stress = 0.08).

Indicator category analysis identified 17 significant deadwood categories associated with prescribed burning and 11 with tree girdling. All indicator categories showed perfect or near-perfect specificity, indicating that they occur exclusively in their associated treatment method. Burning indicator categories are almost equally divided into logs and snags, with snags being the slightly more dominant type of deadwood. Decay classes 3 and 4 are the most dominant, but more advanced decay classes 5 and 6 are also included. Tree girdling indicator categories are dominated by logs in decay classes 4-6, indicating a more advanced decay pattern than prescribed burning (Appendix, Table 11).

3.2 Beetles

3.2.1 Species abundance, richness and diversity

In total, 6,460 individual beetles were recorded. 5,329 of these individuals were collected within areas treated with prescribed burning, whereas the remaining 1,131 individuals were collected within areas treated with tree girdling. Overall, species richness was also higher in burnt areas, however Shannon diversity was calculated to be in girdled plots than in burnt areas of the same year (Table 7).

Table 7: Beetle characteristics: total beetle abundance, species richness and Shannon diversity (H') per treatment and time since treatment.

Treatment ID	Time since treatment	Total abundance	Species richness	Shannon diversity
Burn22	3 years post	1,015	76	2.244
Burn23	2 years post	670	83	2.986
Burn24	1 year post	3,644	87	2.394
Girdling22	3 years post	669	66	3.187
Girdling23	2 years post	174	46	3.334
Girdling24	1 year post	288	49	2.722

At three years post-treatment, beetle abundance, species richness and Shannon diversity did not differ significantly between treatment methods. However, one and two years after treatment, prescribed burning resulted in significantly higher beetle abundance and species richness. Abundance within the burnt treatment areas was found to be seven times higher at one year than at two years after treatment and five times higher at one year than at three years after treatment. For girdled areas, beetle abundance in stands at three years post-treatment was almost four times higher than at two years post-treatment and twice as high at one-year post-treatment (Figure 6, Table 8). Species richness for burnt areas was significantly higher than in girdled areas at one and two years post-treatment. Within prescribed burning, species richness at one year post-treatment was significantly higher than at two or three years post treatment. For tree girdling treated areas at three years post-treatment showed significantly higher richness than areas at one or two years post-treatment. Species diversity was significantly higher in stands treated with prescribed burning at two years post-treatment. No significant difference in species diversity across years within girdled plots was found.

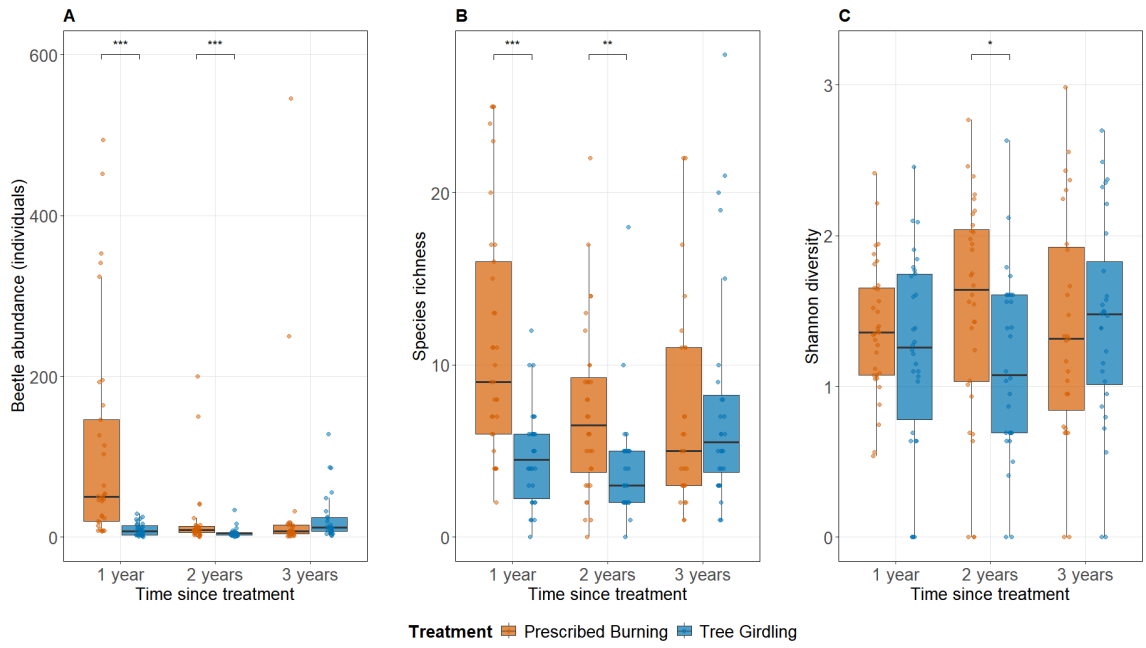


Figure 6: Values of beetle abundance (A), species richness (B) and Shannon diversity (C) for prescribed burning and tree girdling at 1, 2 and 3 years post-treatment. Jitter points represent individual trap values. Significance brackets indicate significant pairwise differences between treatment methods at each time point based on Tukey-adjusted emmeans contrasts: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Table 8: Model coefficients (estimate, SE, z, p) and marginal R^2 for GLMMs of beetle abundance (negative binomial), richness (negative binomial) and Shannon diversity (Gaussian), in response to treatment type (Burn vs. Katning) and time since treatment. Reference level: Burned, treated 2022 (3 years post-treatment). All models include trap as a random effect.

Response variable	Term	Estimate	SE	z / t	p
Beetle Abundance	Intercept	3.103	0.272	11.387	<0.001
	Treatment: Katning	0.021	0.338	0.062	0.95
	Year: 2023 (2 yrs post)	-0.323	0.322	-1.002	0.316
	Year: 2024 (1 yr post)	1.601	0.329	4.866	<0.001
	Katning $\times$ 2023	-1.044	0.444	-2.349	<0.05
	Katning $\times$ 2024	-2.414	0.437	-5.520	<0.001
	R^2 (delta)	0.405	—	—	—
Species Richness	Intercept	1.956	0.132	14.816	<0.001
	Treatment: Katning	0.096	0.184	0.521	0.602

Response variable	Term	Estimate	SE	z / t	p
Shannon Diversity	Year: 2023 (2 yrs post)	0.033	0.179	0.185	0.853
	Year: 2024 (1 yr post)	0.482	0.173	2.780	<0.01
	Katning $\times$ 2023	-0.683	0.260	-2.627	<0.01
	Katning $\times$ 2024	-0.987	0.254	-3.885	<0.001
	R ² (delta)	0.205	—	—	—
	Intercept	1.390	0.126	11.036	<0.001
	Treatment: Katning	0.042	0.176	0.238	0.812
	Year: 2023 (2 yrs post)	0.134	0.171	0.786	0.433
	Year: 2024 (1 yr post)	-0.002	0.170	-0.012	0.99
	Katning $\times$ 2023	-0.426	0.242	-1.755	0.081
	Katning $\times$ 2024	-0.213	0.242	-0.882	0.379
	R ² (delta)	0.039	—	—	—

3.2.2 Beetle community composition

PERMANOVA results show significant differences in beetle community composition between treatment method, year and their interaction. However, the low R² values for each factor suggest high natural variability between traps that is not connected to either factor (Table 9). The strong overlap of the ellipses visually confirms these R² values and suggests that, while both treatment methods share many similar species, each treatment hosts a specific set of indicator species (Figure 7). Betadisper results were non-significant, indicating that neither treatment method nor year is an indicator of differences among traps within the same group.

Table 9: Beetle species composition PERMANOVA results (*p*-value of PERMANOVA and Betadisper, R^2 of PERMANOVA and NMDS stress) comparing treatment method (Prescribed Burning / Tree Girdling) and year (sequential terms). Values in bold denote significant results ($p < 0.05$).

Factor	p (PERMANOVA)	R^2	p (Betadisper)	NMDS stress
Treatment method	<0.01	0.027	0.108	0.209
Year	<0.01	0.038	0.092	—
Treatment $\times$ Year	<0.01	0.051	—	—

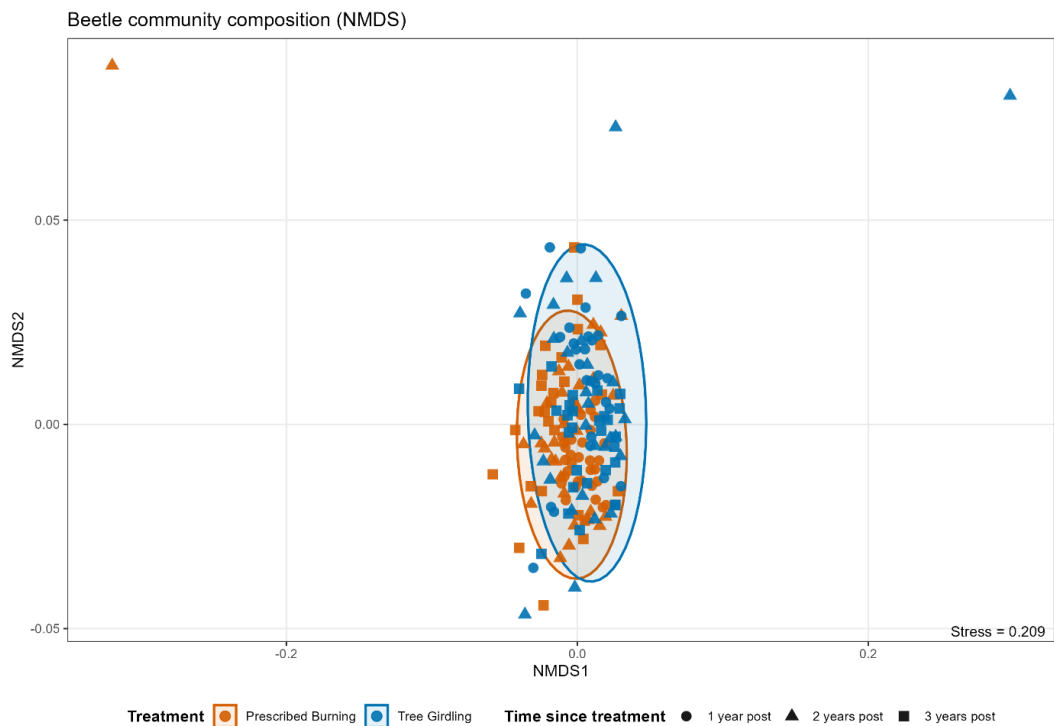


Figure 7: Non-metric multidimensional scaling (NMDS) ordination of beetle community composition based on Bray-Curtis dissimilarity ($k = 3$, stress = 0.209).

The indicator species analysis identified 19 beetle species specifically connected to prescribed burning and three species associated with tree girdling (Table 10). Indicator species for burned plots show dominant patterns of fire-dependent beetle species, bark beetle species and their predators. Tree girdling indicator species include *Pissodes pini*, a pine weevil classified as a forest-damaging species; *Lochmaea suturalis*, a species that is associated with open areas and *Corticarina parvula*, a saproxylic species. The, for the most part, very high Specificity values (A) confirm that these species are tightly connected to their specific treatment method in this study.

Table 10: Indicator species for prescribed burning and tree girdling based on multilevel pattern analysis (multipatt, IndVal.g association function, 999 permutations). Specificity (A) = probability that a site belongs to the target group given the species is present. Fidelity (B) = probability of finding the species in sites of the target group. Only significant associations ($p < 0.05$) are shown.

Treatment	Species	Specificity (A)	Fidelity (B)	IndVal	p
Prescribed Burning	<i>Phloeonomus pusillus</i>	0.860	0.374	0.567	<0.01
	<i>Tomicus piniperda</i>	0.995	0.308	0.553	<0.01
	<i>Hylastes opacus</i>	0.980	0.253	0.498	<0.01
	<i>Thanasimus femoralis</i>	0.837	0.264	0.470	<0.01
	<i>Trypodendron lineatum</i>	0.976	0.209	0.451	<0.01
	<i>Placusa depressa</i>	0.866	0.209	0.425	<0.01
	<i>Dalopius marginatus</i>	0.771	0.220	0.412	<0.05
	<i>Stephanopachys linearis</i>	0.961	0.176	0.411	<0.01
	<i>Strophosoma capitatum</i>	0.761	0.209	0.399	<0.05
	<i>Corticaria ferruginea</i>	0.938	0.132	0.352	<0.01
	<i>Placusa atrata</i>	0.930	0.121	0.335	<0.01
	<i>Xylita laevigata</i>	0.682	0.165	0.335	<0.05
	<i>Enicmus rugosus</i>	0.860	0.121	0.322	<0.01
	<i>Epuraea laeviuscula</i>	0.941	0.099	0.305	<0.05
	<i>Nudobius lentus</i>	0.925	0.099	0.302	<0.05
	<i>Dromius schneideri</i>	0.925	0.099	0.302	<0.05
	<i>Sphaeriestes stockmanni</i>	1.000	0.088	0.296	<0.05
	<i>Platysoma lineare</i>	0.860	0.099	0.292	<0.05
	<i>Tomicus minor</i>	1.000	0.077	0.277	<0.05

Tree Girdling	<i>Pissodes pini</i>	0.807	0.244	0.444	<0.01
	<i>Lochmaea suturalis</i>	0.832	0.140	0.341	<0.05
	<i>Corticarina parvula</i>	1.000	0.058	0.241	<0.05

3.3 Red listed and fire associated beetle species

Out of 161 beetle species found within this study, 13 were red listed as Near Threatened (NT), one was red listed as Vulnerable (VU) and twelve were species assigned a fire class (Appendix, Table 12). Four of the 13 NT species were associated with a fire category, *Acmaeops septentrionis* in category 1 “fire-dependent” and *Dropephylla clavigera* in category 4 “strongly fire-favoured, rare species, found 5 years after fire (Wikars, 2006). The other two species (*Sphaeriestes stockmanni*, *Stephanopachys linearis*) were also classified as fire-dependent and showed up in the indicator species analysis between treatment methods. The beetle classified as VU (*Corticeus longulus*) is not associated with fire and was found with a total abundance of four individuals, with two in a burned plot at three years post treatment and one individual each in the burned plots two and one year post treatment.

The indicator species analysis for the two treatment methods yielded five beetles that were associated with fire. Two were classified as fire-dependent (*Sphaeriestes stockmanni*, *Stephanopachys linearis*) and three as strongly fire-favoured, common species that occurred between 0 and 5 years post-treatment (*Corticaria ferruginea*, *Phloeonomus pussillus*, *Placusa atrata*), with *Phloeonomus pussillus* at 143 individuals also being one of the most abundant species found in burned plots. Another fire-associated species was found in the list of the most abundant species comparing both treatment methods (Appendix, Table 13). *Corticaria rubripes* was the fourth most abundant beetle, with 435 individuals found across all burned plots. It is classified as a common, strongly fire favoured species that occurs within 0-5 years post-treatment. With 159 individuals the species was also the most abundant one within the tree girdling method. Another common strongly fire-favoured beetle (*Hylobius abietis*) was, with 101 individuals, the second most abundant species found in girdled areas, however it was not mainly associated with the method, as it occurred in burned plots across all years as well. The indicator species analysis for treatment method and year (Appendix, Tabel 14) resulted in another two beetle species associated with prescribed burning and one species connected to both prescribed burning and tree girdling. *Asemum striatum*, a common strongly fire-favoured beetle that was only found twice in burned plots at one year post-treatment. *Litargus connexus*, also a common strongly fire-favoured beetle that was only found three times in

burned plots at two years post-treatment. And *Phloeostiba lapponica*, which is also a common strongly fire-favoured beetle was found 11 times in both burned and girdled plots.

4. Discussion

The aim of this thesis was to compare two forest conservation measures, prescribed burning and tree girdling, and their respective deadwood characteristics (volume, composition, abundance, richness and diversity) and saproxylic beetle characteristics (abundance, richness, diversity and composition). Deadwood volumes of both treatment methods were similar, but abundance, richness and diversity values were higher at three years post-treatment for prescribed burning, indicating structural differences. Beetle characteristics were higher in stands at one and two years post-treatment for prescribed burning, indicating the presence of fire-associated beetle species.

4.1 Deadwood characteristics and composition

RQ1: Are there any differences in deadwood volume, abundance, diversity, richness and/or composition in treatment method (burned/girdled) and years?

Ekopark Ejheden is a boreal production forest dominated by Scots pine (*Pinus sylvestris*) (Moberg 2007). The Swedish National Forest Inventory (NFI) provides insights into deadwood availability across the whole country by tree species, averaged over five years. These estimates put pine deadwood at 3,7 m³/ha in Sweden (The Swedish National Forest Inventory (SLU) 2025b; a). Especially at the landscape level, other studies have suggested that an increase in deadwood volume in production forests is recommended to reach amounts of 20 – 50 m³/ha (Bergman et al. 2026). While tree girdling three years post-treatment with 19,2m³/ha, barely falls short of the 20m³ mark, prescribed burning exceeded the mark with 26,5m³/ha at three years post-treatment. It should be noted that these numbers were calculated using only pine deadwood, but as other tree species are scattered throughout the plot, it is likely that other deadwood is present in the treatment areas, adding to these volume counts.

Deadwood volume did not differ significantly across treatment methods or years, which indicates that time since treatment is a stronger predictor of deadwood volume than treatment method. Significant differences in deadwood volume were observed only among the treatment methods, with higher volumes in the stands whose treatment dates back the longest (Burned22 and Girdling22). These results are based on a chronosequence but still reflect observed patterns of tree mortality for both methods. Prescribed burning is typically characterized by an initial pulse of tree mortality, followed by delayed tree mortality, in which burned trees die within the first four years after treatment (Nirhamo et al. 2023). For tree girdling, a similar pattern has been described. Trees do not die off instantly but can remain alive for several years before the stress caused by the

treatment makes the roots and therefore the tree die off (Dufour-Pelletier et al. 2020). Deadwood therefore accumulates over time, which could explain the higher volumes for the forest stands treated in 2022, making them three years post-treatment. It is important to recognize that these methods differ in their interaction with pre-existing, legacy deadwood. Whereas burning acts across the whole stand more or less simultaneously according to fire severity, tree girdling has been described as a precise method, as each tree is treated individually (Angers et al. 2011; Steinebrunner et al. 2025). Prescribed burning therefore unevenly alters the availability of deadwood, as it can consume pre-existing deadwood pieces while producing new deadwood at the same time. This has been shown to result in an overall increase in deadwood after the fire event (Eriksson et al. 2013). Tree girdling, on the other hand, adds the newly created deadwood on top of any preexisting legacy deadwood pools. Tree girdling therefore leaves old supplies intact, where it can continue to age and decompose while a new source of deadwood is added continuously as the girdled trees die off over time (Harmon 2009).

Analysis of deadwood volume, abundance, richness and diversity has shown that, while deadwood volume does not differ significantly between treatments, deadwood abundance, richness and diversity did differ significantly, with burned plots showing higher values for all characteristics at three years post treatment. This could be associated with the fact that girdled plots accumulate deadwood in fewer but larger pieces, while burning produces many smaller to medium-sized individual deadwood pieces at approximately the same time (Lutz et al. 2020). Another possible explanation is differences in fire severity between the treatment years, which could explain the relatively low volume values for 2023 that could potentially mask the increasing trend that could otherwise be assumed. For girdled plots, higher abundance and richness values were observed in younger stands compared to burned stands at the same post-treatment age. The method's ability to maintain legacy deadwood in the stands could be a possible explanation for this pattern. While these differences were not significant, the broader range of decay stages in girdled areas points towards structural advantage between treatment methods, especially in the early post-treatment stages (Figure 3).

Deadwood composition differed significantly between treatment method, year and their interaction in the PERMANOVA analysis. R^2 values indicate that treatment method was more important than treatment year or interaction when it came to determining deadwood categories within the treated areas. The significant Betadisper result for the treatment variable additionally confirms that prescribed burning produces more heterogeneous results within burned plots than tree girdling does. These results confirm my hypothesis that treatment methods produce significantly different deadwood category compositions and that the time since treatment also has a significant influence.

The heterogeneity in burned plots compared to girdled plots can be explained by differences in fire severity, which influence deadwood composition. These mixed-severity events contribute to differences between the type of deadwood that is being created (Nappi et al. 2010). These mechanisms lead to a higher variability within the burned plots and are visually presented in the NMDS plot through the wider ellipse. While the deadwood composition between the burned plots is very heterogeneous, the fire event initially creates similar characteristics for the individual deadwood pieces within each plot. As the treated stand continues to age, the delayed tree mortality will become clearer and will provide new deadwood input over time. This leads to more diverse decay stages and compositions in older stands than in stands treated more recently (Angers et al. 2011). The oldest burned plots additionally support this argument through their clear visual separation from the younger stands, suggesting a clear shift in deadwood category composition at three years post-treatment. As burned trees typically die off within the first few years of treatment, these findings are consistent with comparable studies (Nirhamo et al. 2023). The tighter clustering of the girdled ellipse indicates lower variability of deadwood category composition within tree girdling, which suggests more similarities between girdled plots. This can be explained through the type of application of the method. The precision of the method allows the pre-existing deadwood in the plot to continue to develop naturally. All girdled plots therefore share a similar baseline while being supplemented by new deadwood that is gradually added as the girdled trees begin to die off (Augustynczyk et al. 2024). This results in more homogeneity in deadwood category composition between girdled plots.

The temporal differences between plots treated in different years are also visible in the NMDS results. The partial overlap of the more recently treated plots confirms that stands at one and two years post-treatment share similar deadwood category compositions. Nevertheless, differences in composition are already emerging, possibly driven by the beginning of delayed tree mortality. The oldest plots additionally support this argument through their clear visual separation from the younger stands, suggesting a clear shift in deadwood category composition at three years post-treatment.

The indicator species analysis identified 17 deadwood categories associated with burned areas and 11 categories associated with tree girdled areas. For prescribed burning, indicator deadwood categories consisted of equal amounts of logs and snags in intermediate decay stages, while tree girdling was primarily represented by logs in more advanced stages. Overall, comparisons of decay stages between the treatment methods showed a more uniform pattern of decay for burned areas, while decay classes ranged across the whole spectrum for girdled areas. Snags showed less variety of decay classes for both treatment methods. This could possibly be explained by a decrease in nutrient availability

for standing deadwood that slows down decomposition rates, compared to lying deadwood that is affected by soil moisture through increased ground contact and therefore more susceptible to decomposing organisms (Ylisirniö et al. 2012; Oberle et al. 2018).

These results show that prescribed burning and tree girdling produce stands with significantly different deadwood compositions. Whereas prescribed burning produces more uniform stands in intermediate decay stages, tree girdling provides a large range of different decay stages and combines naturally and artificially created deadwood pieces within the same timeframe.

4.2 Beetle characteristics and composition

RQ2: Are there any differences in beetle species abundance, richness, diversity and/or composition in treatment method (burned/girdled) and years?

At three years post-treatment, beetle abundance, richness and diversity did not differ significantly between treatment methods. Prescribed burning had significantly higher abundance and richness in the stands at one and two years post-treatment and significantly higher diversity at two years post-treatment. Beetle abundance in the girdled stands at three years post-treatment was higher than at one year post-girdling. These findings are in line with my hypothesis H2a.

Prescribed burning creates very specific conditions that benefit species attracted to sunny and open habitats, combined with a lot of fresh deadwood input (Heikkala et al. 2016). Recently burned stands are especially attractive to fire-dependent species that rely on burned conditions for various stages of their lifecycle (Bell 2023). However, other species that are categorised as pest insects, like bark beetles, benefit greatly from large-scale disturbances that produce a lot of dead and dying trees. Bark beetles are primary colonisers of recently damaged areas. They depend on these conditions to reproduce, and their abundance has been described in studies to peak immediately after the disturbance event happens (Toivanen & Kotiaho 2010). As beetle abundance was highest in burned plots at one year post-treatment, this would support the literature stating that collected beetles in year one post-treatment are offspring of the first initial colonisers combined with species that have just started to arrive (Fredriksson et al. 2020). After these initial years, abundance tends to decline as their nutrient source, the phloem and cambium layer, is depleted (Toivanen & Kotiaho 2010). This also provides support for a temporal decline in abundance and species richness for burned plots. Therefore, the factor “time since treatment” is especially valuable to consider when deadwood enrichment measures are taken that aim at benefitting saproxylic beetles. As the burned stands age, the previously very specific habitat conditions change, and the treated area begins to recover and regenerate (Heikkala et al. 2016). These developments were also reflected in my results, as abundance

was found to be seven times higher in the burned stands at one-year post-treatment compared to two years post-treatment. Species richness was also observed to be significantly higher at one-year post-treatment compared to two or three years post-treatment in burned areas. Species diversity for burned areas at two years post-treatment was significantly higher than in girdled areas. This could possibly be explained by reduced competition among species, as the initial peak in primary colonisers tends to decline as the stands age. Another explanation would be that delayed mortality produces more variety in deadwood that benefits a broader spectrum of beetle species (Toivanen & Kotiaho 2010).

Opposite patterns for abundance and richness were observed in tree girdled areas. As the time since treatment increases, a general increase over time is shown through significant increases in abundance and richness. Tree girdling slowly kills a tree, which means that canopies can remain intact for longer times, providing shady conditions and more humid conditions than burned areas for early post-treatment areas. The clear peak in abundance and richness at three years post-treatment suggests that more girdled trees have died off and are utilised by saproxylic beetles. These trends could possibly suggest long-term effects for beetle communities in tree girdled areas as trees continue to die and decompose, which ensures a steady supply of deadwood (Hägglund & Hjältén 2018). Prescribed burning, on the other hand, has been described as a short-term boost for species richness, but it faces the risk of exhausting the deadwood resources in the area rather quickly (Toivanen & Kotiaho 2010).

For the beetle composition, I expected to find species that are associated with fire and early colonising characteristics for burned stands. I also expected many similar species between treatments, especially as the time since treatment increases. This was based on the fact that burned habitats lose their specific conditions as the treated stands begin to regenerate lost vegetation in the fire (Heikkala et al. 2016). While abundance, richness and diversity seem to converge in stands at three years post-treatment, the significant PERMANOVA results indicate differences between treatments, years and their interaction. The non-significant Betadisper results support the significant PERMANOVA results, confirming a difference in composition between the factors. R^2 values are low for each factor, but the treatment and year interaction value suggests that this is the factor that explains a marginally greater proportion of variance between traps than either treatment or year alone.

Girdled plots provide various habitat conditions and substrates within one plot which could explain the lower similarities between each other that characterise traps collected in tree girdled areas (Harmon 2009). The treatment of individual trees with girdling results in many different deadwood options that beetles presumably utilise. As decay stages range from legacy deadwood to continuous fresh inputs from girdling and other natural sources (Augustynczyk et al. 2024),

species composition as a consequence can vary as well. Prescribed burning, on the other hand, provides a more uniform habitat of dead or dying trees that leads to charred wood and a habitat that has been opened to provide sunnier conditions (Angers et al. 2011; Heikkala et al. 2016). While delayed tree mortality for burned plots provides some variety in the deadwood supply, the habitat conditions that are created through burning can still be described as uniform (Francos & Úbeda 2021). These conditions cater to a more specific type of beetles: fire-dependent and primary colonizing beetles (Toivanen & Kotiaho 2010; Bell 2023).

This is also very well represented in the indicator species analysis done to determine which species are almost exclusively associated with one of the two treatment methods. Out of 19 species found mostly in burned plots, five were either fire category 1 or 2, another three species (*Tomicus piniperda*, *Hylastes opacus*, *Tomicus minor*) were classified as bark beetles, three predator species for bark beetles (*Thanasimus femoralis*, *Nudobius lentus*, *Epuraea laeviuscula*) and seven other species (Table 10) were identified. This provides support for the argument that burned areas in the first few years are valuable habitats for fire-dependent beetles and primary colonisers such as bark beetles. The increased presence of bark beetles, especially immediately after the fire, serves as a source of food for beetles that prey on bark beetle species (Hägglund & Hjältén 2018).

For tree girdling, only three species specifically connected to these areas were identified. *Corticarina parvula* is a herbivore and fungivore beetle species that relies on bark and wood as a habitat and consumes fungi and lichen (SLU Artdatabanken 2026b). The availability of advanced stages of decay in girdled areas supports the presence of fungi that serve as a source of nutrition for the beetle species. *Pissodes pini* is described as an herbivorous, cambium-consuming beetle species that feeds on wood and bark, a trait that has led to a characterisation as a pest species in managed forest systems (Hägglund & Hjältén 2018; SLU Artdatabanken 2026h). *Lochmaea suturalis* is a beetle species commonly associated with heather, which suggests structural openness is preferred by this species. It is possible that the individuals ended up in the traps by accident, while seeking shelter, since *Lochmaea suturalis* is not classified as a saproxylic species. Nevertheless, its association with girdled plots might be because tree girdling maintains the presence of heather in the understory, whereas prescribed burning eradicates the ground vegetation during the burning, resulting in less available habitat. The species has previously been recorded in boreal forests (Gillingham et al. 2015).

The strong disparity between indicator species highlights the specific habitat conditions that prescribed burning creates and therefore attracts many species that are primarily connected to burned areas. It has to be noted that prescribed burning creates environments that cannot be recreated through other types of disturbance, as fire-dependent beetles specifically utilised areas affected only by fire

(Sandström et al. 2019). Whereas tree girdling provides more varied substrate conditions that are attractive to a broader generalist community, combined with fewer specific species uniquely associated with girdling. The beetle community was shown to differ between treatment methods, which partially confirms the hypothesis for RQ2, as the species composition between treatment methods did not converge after three years. For older stands similar species compositions were expected as the burned stands were expected to recover enough to be comparable to tree girdling after three years post-treatment.

No indicator species were uniquely associated with burned or girdled plots at three years post-treatment, suggesting both treatments continue to support diverse beetle communities. Burning results in an immediate but declining peak in fire-dependent species, whereas the slower tree death because of tree girdling results in higher abundance and diversity as the stands age. Together, both treatments offer complementary short- and long-term benefits for beetle communities.

4.3 Red-listed and fire-associated beetle species

Burned areas hosted more indicator species overall, with several classified as fire-dependent or strongly fire-favoured. This includes the near-threatened species *Sphaeriestes stockmanni* and *Stephanopachys linearis*, whose decline is closely linked to over two centuries of fire suppression and the resulting loss of early successional forest habitats (Kouki et al. 2012; SLU Artdatabanken 2026c; g). As fire-dependent species, their presence was almost entirely connected to burned plots, which indicates that girdling alone cannot replicate the specific conditions that these specialists require. Other strongly fire-favoured species showed similar patterns. *Phloeonomus pusillus* and *Placusa atrata* were predominantly found in recently burned plots at one-year post-treatment, most likely because of the initial peak in bark beetle abundance that follows a fire disturbance event (SLU Artdatabanken 2026d; f). As a predator species, it seems to track prey availability in the plots rather than responding specifically to a treatment method, therefore benefiting from bark beetle peaks in burned areas in the early years and from the steadily increasing beetle abundance observed in girdled stands over time (Wegensteiner et al. 2015). While small numbers of these species were recorded in girdled plots, their overall association with burned areas suggests that the intensity of prey availability following fire is difficult to replicate through girdling.

Nevertheless, some species were found to be less specific in their habitat requirements and therefore occurred within both treatment methods. *Corticaria rubripes*, one of the most abundant species in the dataset, was found in high numbers in both burned and girdled plots (Appendix, Table 14). Although commonly associated with recently burned areas, its wide distribution across all six individual treatment areas suggests it responds primarily to the general

increase in fresh deadwood availability instead of fire itself (SLU Artdatabanken 2026a). The species presence in girdled plots therefore indicates that tree girdling can provide sufficient habitat conditions for species that are fire-favoured but not strictly fire-dependent. Similarly, *Phloeostiba lapponica*, a carnivorous rove beetle associated with fire, was found across both burned and girdled plots throughout all years (SLU Artdatabanken 2026e). As a predator, it appears to track prey availability rather than treatment type specifically, benefiting from bark beetle peaks in burned areas in early years and from the steadily increasing beetle abundance observed in girdled stands over time (Wegensteiner et al. 2015). Even though *Hylobius abietis* is classified as a strongly fire-favoured species, it was found almost exclusively in girdled areas, where it was the second most abundant species (SLU Artdatabanken 2026i). This might be explained by the species' preference for the cambium layer of dying pines and the larvae's reliance on the roots of freshly dying trees (Bork n.d.). The gradual death of girdled trees could therefore provide a more suitable breeding substrate for this species than the immediate post-fire environment.

Overall, prescribed burning remains essential for supporting fire-dependent beetles, including red-listed species which are unlikely to remain in the area without the regular occurrence of fire. Tree girdling can support species that respond primarily to deadwood enrichment and increased prey availability. This shows the complementary value that both treatment methods contribute to beetle diversity in managed boreal forests.

4.4 Limitations of this thesis

Within this thesis, it was not possible to match the individual deadwood plot values to the information collected from the traps. Because of missing GPS data, a match was therefore only possible on a treatment and year level rather than on an individual plot level. Direct connections between deadwood and beetle characteristics could not be tested on a plot level. However, because of pre-existing studies and research, certain speculations could be made. Connections between the metrics would have been specifically relevant, as decay stage, deadwood volume and deadwood composition were expected to serve as predictors for beetle species richness and diversity. These results could have possibly strengthened any implications made for future management decisions. While the timeframe of this thesis included up to three years post-treatment and could provide important insights into the processes both treatment methods start, no comparisons on changes in beetle assemblage could be made as no pre-treatment data collection was performed. This would have confirmed that observed differences really are connected to the treatment methods rather than preexisting variations between the treatment areas.

The plots studied in this thesis are not connected to each other but provide insight into six individual plots. To better comprehend temporal patterns of deadwood and beetle characteristics, evaluating the same plots over time would provide better insights. Also, more long-term implications of the treatment methods can only be assumed based on similar studies that include a longer timeframe. Especially as beetle abundance and richness in girdled plots were observed to be higher in older plots, it is likely that peak responses to the treatment method are still missing. Future studies would benefit from incorporating larger timeframes to observe larger temporal patterns.

4.5 Conclusions and management implications

Deadwood volumes of 20-50 m³/ha are suggested for boreal production forests if conservation values are to be maintained (Bergman et al. 2026). Specifically, deadwood volume thresholds of 22.4 m³/ha have been calculated to serve as a threshold where the abundance and richness of species with conservation value are significantly higher (Hekkala et al. 2023). At three years post-treatment, prescribed burning with 26,5 m³/ha reached both thresholds, whereas tree girdling with 19,2 m³/ha barely fell short. This suggests that deadwood accumulation in tree girdled areas takes longer, however, the high numbers still indicate a potential for reaching both thresholds as the stands continue to age. These developments might be especially valuable considering that beetle abundance, richness and diversity show higher values in girdled plots at three years post-treatment compared to younger plots. This implies increases in beetle characteristics as time since treatment increases. In burned areas, beetle abundance and richness were lower in older plots and diversity is almost constant, suggesting a decreasing pattern over time. These processes imply that both methods are suitable tools to restore deadwood and benefit saproxylic beetles, but act on two different time scales.

Prescribed burning was found to be essential for supporting fire-associated beetles, as red-listed species are unlikely to remain in the area without the regular occurrence of fire. This shows that the methods complement but don't act as alternatives for each other. The presence of red-listed species in both treatment methods indicates how valuable habitats can be created and maintained in production forests. The relevance of promoting deadwood availability to enhance biodiversity is also portrayed in the EU Forest Strategy for 2030. It states that management practices that ensure sufficient amounts of deadwood are available in production forests in turn ensure long-term environmental and socioeconomic viability of these forests (European Commission 2021). Once sufficient deadwood volumes can be provided, it is important to functionally and structurally diversify forest systems (Gazzea et al. 2024). It has often been suggested by other studies that the quality rather than the quantity of deadwood has a greater impact on the

forest system through different decay classes, diameters and types of deadwood (Bergmark et al. 2024). These measures should not be limited to small plots but should rather span the whole forest system to maintain habitat connectivity and provide continuous habitats for rare and generalist species alike (Siitonen 2001). Active deadwood enrichment through prescribed burning and tree girdling should only be two out of many possible options. Management decisions must be reassessed for each forest stand to take local conditions into account (Hägglund & Hjältén 2018; Sandström et al. 2019).

Lastly, since the decline in deadwood has been associated with public perception of deadwood as untidy and uncontrolled in the past, environmental education programs might be helpful in increasing awareness of its impact on the forest ecosystem (Thorn et al. 2020).

Declaration of AI-use

In the beginning of my thesis, I partially supported my literature search with SciSpace to get an overview of scientific papers that would fit within my study area. After reading the papers I sometimes used NotebookLM to help me summarise and get a clearer understanding of the papers. During the analysis part of my thesis, I used Claude for my R-codes, the descriptive text above tables and underneath figures in the results section and to check for logical inconsistencies within my discussion. After I received feedback from my supervisors and opponents, I also used Claude to suggest ways to shorten the discussion. Before the final hand in of the thesis I used Grammarly to check for spelling or grammar mistakes. Overall, I used the DeepL translator to translate some phrases from German to English or from Swedish to English.

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Popular science summary

Worldwide, forestry is contributing to biodiversity loss. A big part of biodiversity in forests comes from deadwood. Because of economic reasons or for pest management, deadwood is often removed from the system and lots of species, like beetles, that depend on deadwood are now threatened. Fire is a disturbance event that produces lots of deadwood. Up until the 17th century, fire was a natural disturbance event in Sweden, but with increased human settlement, the demand for timber increased too. Forests were now something to protect from fire and stricter fire regimes were put in place. With deadwood and fire mostly gone from forests, beetles that depend on both factors are gone from a lot of forests as well.

But there are ways to support these species and create more deadwood, and they are already very common in Sweden. The two methods I worked with in this thesis are prescribed burning and tree girdling. For prescribed burning, fire is used as a conservation tool that erases the ground vegetation and creates open and light habitats. Its burns are classified as low to moderate, which means that there is not enough fuel for the fire on the ground to burn the whole standing tree, so mostly only the stem chars. This is the case especially for pine forests, as they have canopies that are located in the upper parts of the forests. Tree girdling, on the other hand, acts as a fire-mimicking method. A strip of bark is removed around the stem, which slowly causes the tree to die. This should replicate the way in which a fire makes the tree die off without the charring and fire part. The study area of this thesis is called Ekopark Ejheden and it is located in central Sweden in Dalarna. This Ekopark combines nature conservation and forestry, and it has a long history of fire recurrence in this area. I had six study locations, three for prescribed burning and three for tree girdling. These sites had similar conditions but were treated in different years (2022, 2023 and 2024), making this a study on a chronosequence, not a time series. Deadwood and beetles were sampled in September 2025.

With my data, I calculated the deadwood volumes for standing and lying deadwood separately. I also looked at deadwood abundance, richness, diversity and composition and compared the results between treatment methods and years of treatment. No significant differences in deadwood volumes were found. Deadwood abundance, richness and diversity were significantly higher in burnt areas treated in 2022, which makes them the plots with the longest time since treatment. The composition of deadwood was significantly different for the treatment methods. For prescribed burning, logs and snags were associated in equal amounts with the methods. The deadwood was found to be in the intermediate stages of decay. This is possibly because fire acts uniformly across the treated area and consumes pre-existing deadwood in the process, causing these areas to develop at the same time after treatment. For tree girdling, mostly logs

were associated with the method and the decay stages spanned across the whole spectrum. This is likely because the trees are treated individually and there is already pre-existing deadwood in the plots that gets added to as the girdled trees die off. Eclector traps were used to sample deadwood-dependent beetles and were put up on dead pines. Beetle abundance, richness, diversity and composition were used to compare the treatment methods and years. Beetle abundance and richness were significantly higher in burnt stands treated in 2024 and 2023. Likely because fire-associated beetles and early colonising species like bark beetles were still present. As their source of nutrition is used up and the area begins to recover, they leave again. This is also represented in the beetle composition, which showed significant differences between treatment methods. 19 indicator species were associated with prescribed burning, while only three were connected primarily with tree girdling.

My results on deadwood characteristics indicate that both methods are equally as useful to restore deadwood volumes in boreal forests, with burnt areas creating more structurally diverse habitats. My results on beetle characteristics indicate that prescribed burning supports an immediate peak in beetles shortly after treatment, while tree girdling has more long-term effects. Prescribed burning is clearly favoured by fire-associated beetles and supports the importance of fire reoccurrence for boreal forests in Sweden. Nevertheless, tree girdling is equally as important, as the method supports more generalist beetle species that simply depend on deadwood. These results show that both prescribed burning and tree girdling are valuable tools to support deadwood accumulation and deadwood-dependent species.

Appendix

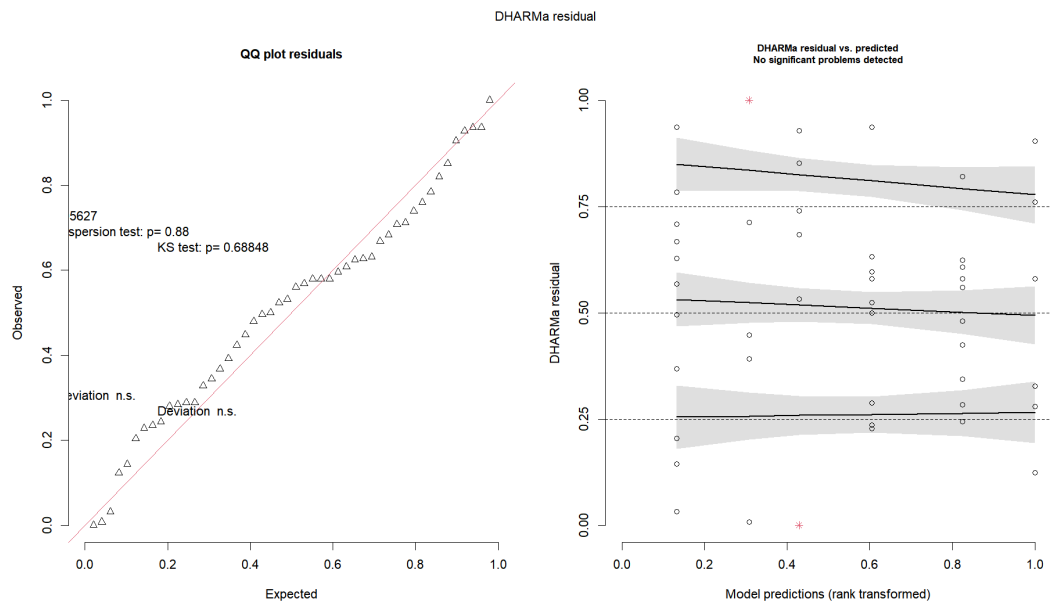


Figure 8: DHARMA results for the Deadwood Abundance model

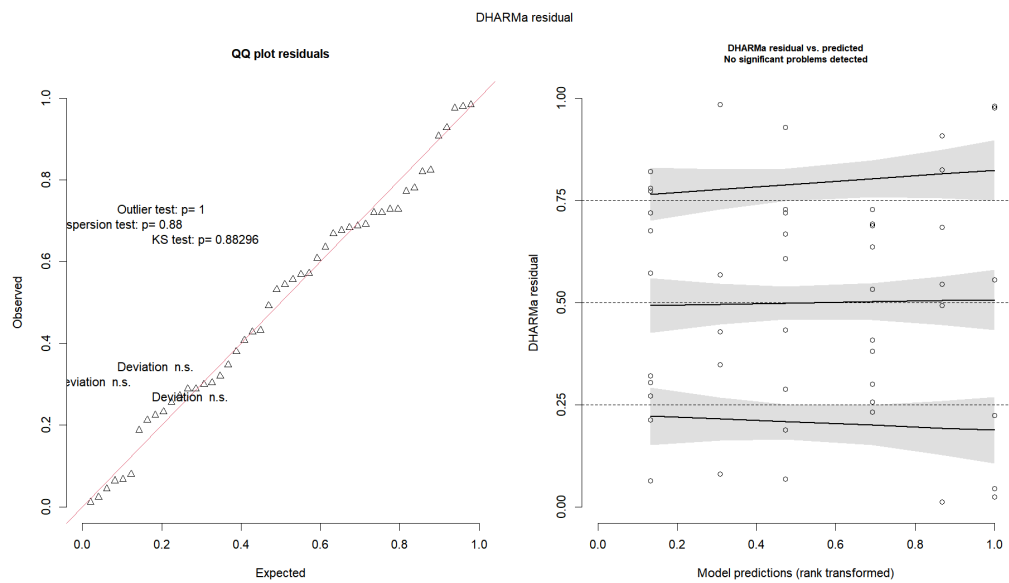


Figure 9: DHARMA results for the Deadwood Richness model

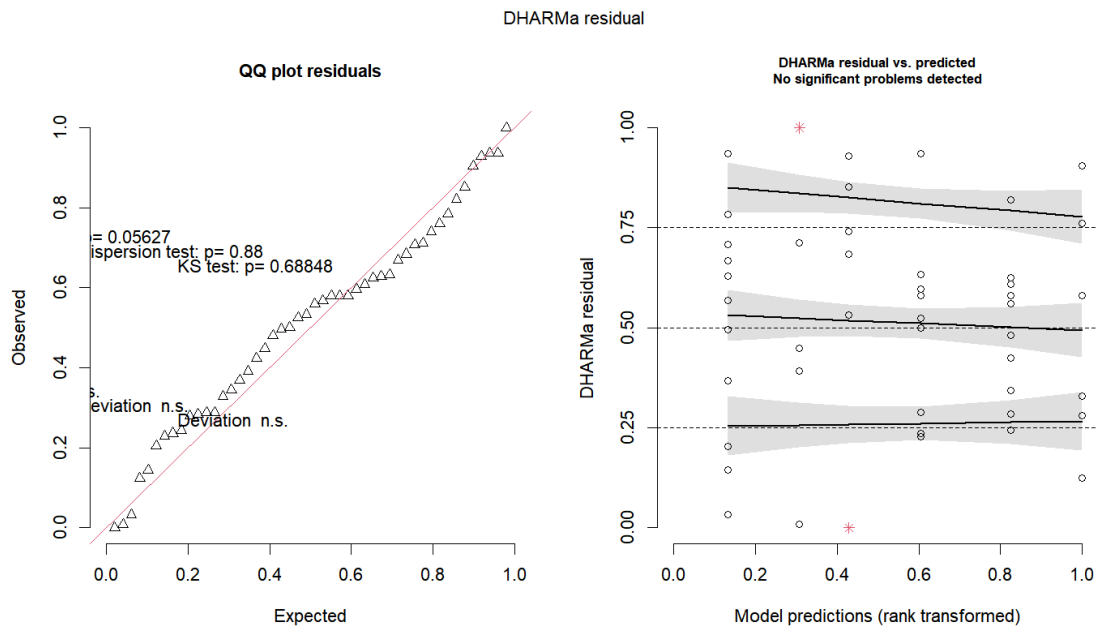


Figure 10: DHARMA results for the Deadwood Diversity model

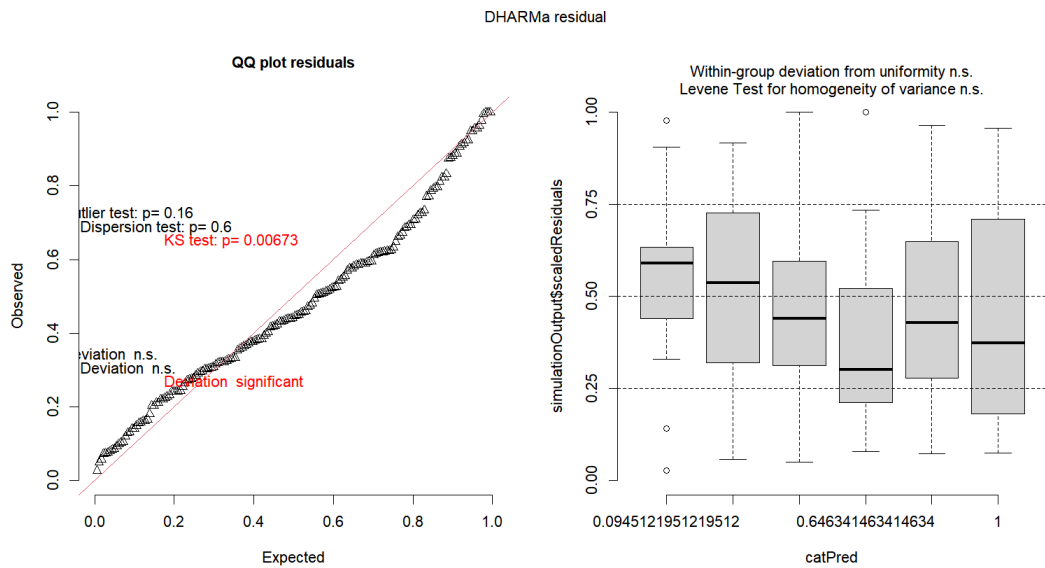


Figure 11: DHARMA results for the Beetle Abundance model

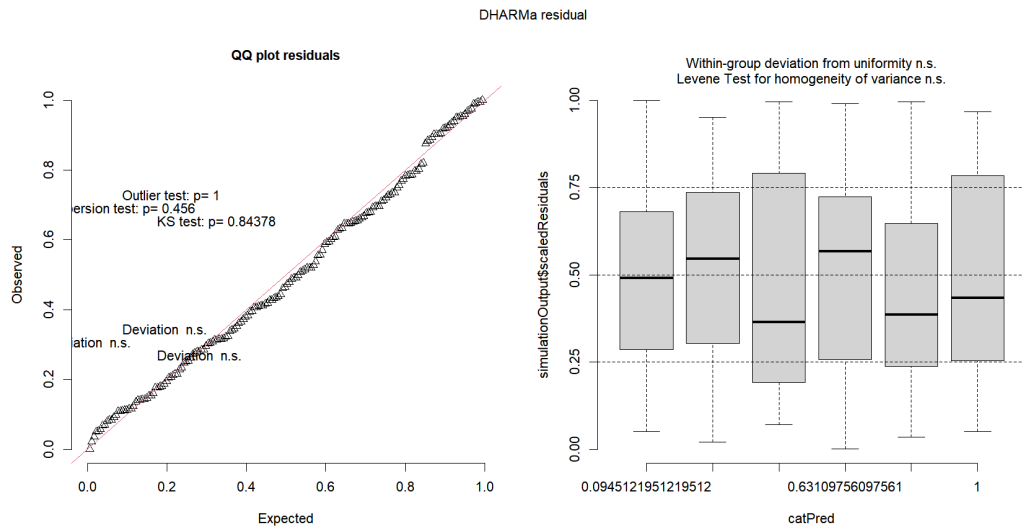


Figure 12: DHARMA results for the Beetle Richness model

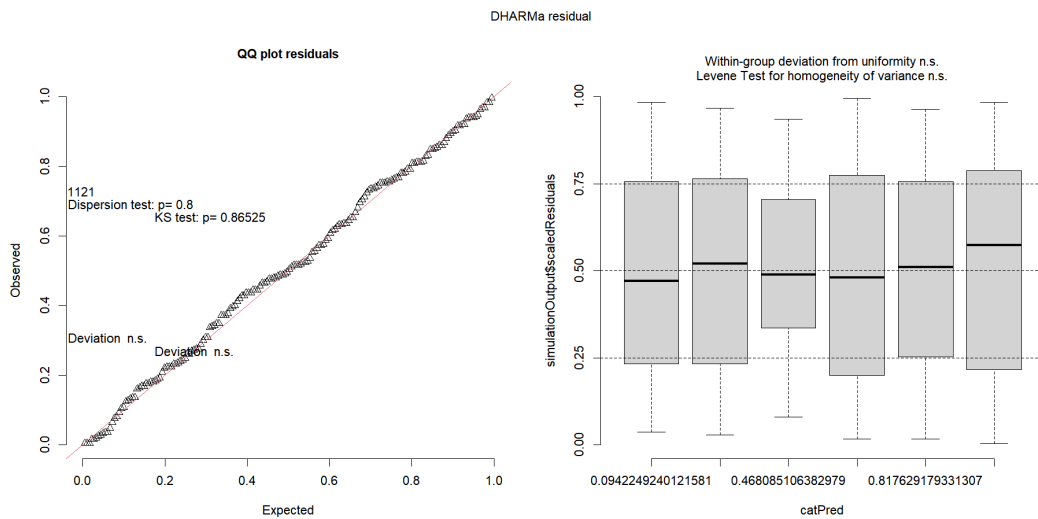


Figure 13: DHARMA results for the Beetle Diversity model

Table 11: Indicator deadwood categories (*IndVal.g*) significantly associated with prescribed burning and tree girdling. Type = log or snag; Decay class; Specificity (A) = proportion of individuals in associated group; Sensitivity (B) = proportion of plots where category occurs; *IndVal* = $\sqrt{A \times B}$. All results significant at $p \leq 0.05$.

Treatment	Category	Type	Decay class	Diameter (cm)	Specificity (A)	Sensitivity (B)	IndVal	p
Prescribed Burning	30	snag	3	10-20	1.000	0.647	0.804	<0.01
	28	log	3	0-10	1.000	0.588	0.767	<0.01
	35	snag	4	10-20	1.000	0.588	0.767	<0.01

Treatment	Category	Type	Decay class	Diameter (cm)	Specificity (A)	Sensitivity (B)	IndVal	p
Tree Girdling	58	log	3	0-10	1.000	0.529	0.728	<0.01
	36	snag	4	20-30	1.000	0.412	0.642	<0.01
	42	log	3	0-10	1.000	0.412	0.642	<0.01
	44	snag	3	10-20	1.000	0.412	0.642	<0.01
	68	log	6	0-10	1.000	0.412	0.642	<0.01
	31	snag	3	20-30	1.000	0.412	0.642	<0.01
	64	log	5	0-10	1.000	0.412	0.642	<0.01
	33	log	4	0-10	1.000	0.235	0.485	<0.05
	46	log	4	0-10	1.000	0.235	0.485	<0.05
	45	snag	3	20-30	1.000	0.235	0.485	<0.05
	47	snag	4	10-20	1.000	0.235	0.485	<0.05
	29	log	3	10-20	1.000	0.176	0.420	<0.05
	49	snag	4	20-30	1.000	0.176	0.420	<0.05
	65	log	5	10-20	1.000	0.176	0.420	<0.05
	9	log	4	0-10	1.000	0.774	0.880	<0.01
	3	log	3	0-10	1.000	0.710	0.842	<0.01
	14	log	5	0-10	1.000	0.613	0.783	<0.01
	11	snag	4	10-20	1.000	0.516	0.718	<0.01
	15	log	5	10-20	1.000	0.484	0.696	<0.01
	21	log	6	0-10	0.908	0.516	0.685	<0.01
	22	log	6	10-20	1.000	0.452	0.672	<0.01
	1	log	1	0-10	1.000	0.387	0.622	<0.01
	23	snag	6	10-20	1.000	0.355	0.596	<0.05
	10	log	4	10-20	1.000	0.290	0.539	<0.05
	13	snag	4	20-30	0.892	0.323	0.536	<0.05

Table 12: Total abundance of fire associated beetle species per treatment and year.
Values represent total number of individuals caught across all traps.

Species	Fire class	Burn24	Burn23	Burn22	Girdling24	Girdling23	Girdling22	Total
<i>Acmaeops septentrionis</i>	1	0	4	0	0	0	0	4
<i>Asemum striatum</i>	2	3	0	0	0	0	0	3
<i>Corticaria ferruginea</i>	2	16	0	0	0	0	1	17
<i>Corticaria rubripes</i>	2	406	21	8	28	27	104	594
<i>Dropephylla clavigera</i>	4	0	0	1	0	0	1	2
<i>Hylobius abietis</i>	2	16	13	7	75	3	23	137
<i>Litargus connexus</i>	2	0	3	0	0	0	0	3
<i>Phloeonomus pusillus</i>	2	105	20	18	0	4	18	165
<i>Phloeostiba lapponica</i>	2	19	12	6	1	3	10	51
<i>Placusa atrata</i>	2	10	3	1	0	0	1	15
<i>Sphaeriestes stockmanni</i>	1	6	6	0	0	0	0	12
<i>Stephanopachys linearis</i>	1	4	21	1	0	1	0	27

Table 13: 10 most abundant beetle species according to treatment method

Treatment method	Species	Total abundance
Prescribed Burning	<i>Tomicus piniperda</i>	1,348
	<i>Trypodendron lineatum</i>	1,201
	<i>Hylurgops palliatus</i>	605
	<i>Corticaria rubripes</i>	435
	<i>Trypodendron laeve</i>	336

Treatment method	Species	Total abundance
Tree Girdling	<i>Phloeonomus pusillus</i>	143
	<i>Tomicus minor</i>	117
	<i>Thanasimus formicarius</i>	98
	<i>Epuraea laeviuscula</i>	84
	<i>Hylastes brunneus</i>	74
	<i>Corticaria rubripes</i>	159
	<i>Hylobius abietis</i>	101
	<i>Hylurgops palliatus</i>	91
	<i>Hylastes brunneus</i>	71
	<i>Pissodes pini</i>	67
	<i>Thanasimus formicarius</i>	58
	<i>Quedius mesomelinus</i>	53
	<i>Epuraea marseuli</i>	46
	<i>Paraphotistus impressus</i>	32
	<i>Melanotus castanipes</i>	28
	<i>Trypodendron lineatum</i>	28

Table 14: Indicator species for Treatment $\times$ Year combinations based on multilevel pattern analysis (multipatt, IndVal.g association function, 999 permutations). Specificity (A) = probability that a site belongs to the target group given the species is present. Fidelity (B) = probability of finding the species in sites of the target group. Years expressed as time since treatment (2022 = 3 yrs post, 2023 = 2 yrs post, 2024 = 1 yr post). Only significant associations ($p < 0.05$) are shown.

Group	Species	Specificity (A)	Fidelity (B)	Indicator value	P
Other	<i>Phloeonomus pusillus</i>	0.126	0.296	0.586	<0.01
	<i>Thanasimus formicarius</i>	0.094	0.222	0.566	<0.05
	<i>Hylobius abietis</i>	0.055	0.259	0.565	<0.01
	<i>Hylastes brunneus</i>	0.172	0.259	0.540	<0.01

Group	Species	Specificity (A)	Fidelity (B)	Indicator value	P
Prescribed Burning 1 yr post + Tree Girdling 3 yrs post	<i>Thanasimus femoralis</i>	0.322	0.296	0.488	<0.01
	<i>Phloeostiba lapponica</i>	0.132	0.148	0.448	<0.05
	<i>Anaspis marginicollis</i>	0.151	0.148	0.395	<0.05
	<i>Xylita laevigata</i>	0.184	0.185	0.389	<0.05
	<i>Corticaria rubripes</i>	0.848	0.951	0.898	<0.01
	<i>Epuraea marseuli</i>	0.856	0.328	0.530	<0.01
	<i>Hylurgops palliatus</i>	0.987	0.246	0.493	<0.01
	<i>Trypodendron laeve</i>	1.000	0.131	0.362	<0.05
	<i>Epuraea angustula</i>	0.932	0.131	0.350	<0.01
	<i>Pytho depressus</i>	0.811	0.148	0.346	<0.05
Prescribed Burning — 1 yr post	<i>Contacyphon padi</i>	0.887	0.131	0.341	<0.01
	<i>Tomicus piniperda</i>	0.761	0.606	0.679	<0.01
	<i>Corticaria ferruginea</i>	0.931	0.364	0.582	<0.01
	<i>Placusa depressa</i>	0.605	0.364	0.469	<0.01
	<i>Placusa atrata</i>	0.641	0.212	0.369	<0.01
	<i>Placusa incompleta</i>	1.000	0.091	0.302	<0.05
	<i>Asemum striatum</i>	1.000	0.091	0.302	<0.05
	<i>Phloeopora nitidiventris</i>	0.824	0.091	0.274	<0.05
Prescribed Burning — 2 & 1 yrs post	<i>Dalopius marginatus</i>	0.727	0.297	0.464	<0.01
	<i>Strophosoma capitatum</i>	0.707	0.266	0.433	<0.05
	<i>Sphaeriestes stockmanni</i>	1.000	0.125	0.354	<0.05
Prescribed Burning — 2 yrs post	<i>Stephanopachys linearis</i>	0.779	0.355	0.526	<0.01
	<i>Litargus connexus</i>	1.000	0.097	0.311	<0.05
Prescribed Burning — 3 & 1 yrs post	<i>Trypodendron lineatum</i>	0.898	0.250	0.474	<0.01

Group	Species	Specificity (A)	Fidelity (B)	Indicator value	p
Prescribed Burning — 3 yrs post	<i>Nudobius lentus</i>	0.737	0.259	0.437	<0.01
	<i>Plegaderus vulneratus</i>	0.831	0.222	0.430	<0.01
	<i>Placusa sp</i>	1.000	0.074	0.272	<0.05
Prescribed Burning — all years	<i>Hylastes opacus</i>	0.980	0.253	0.498	<0.01
Tree Girdling — 1 yr post	<i>Pissodes pini</i>	0.611	0.414	0.503	<0.01
Tree Girdling — 3 yrs post	<i>Quedius mesomelinus</i>	0.750	0.250	0.433	<0.05
	<i>Epuraea pygmaea</i>	1.000	0.071	0.267	<0.05

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