Seasonal Timing of Tree Death Shapes Early Saproxylic Beetle Assemblages on *Pinus sylvestris*

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January 2026

Abstract

Dead wood creation in managed forests is an increasingly used tool in the facilitation of biodiversity. As most logging activities, including dead wood creation, are done in winter to avoid the breeding season, I investigated whether this timing impacts the course of the beetle species assemblages on dead wood. In five scot's pine forests on sandy soils of a glacial ridge in the Netherlands, trees were felled beginning from December till June, each eight weeks apart resulting in four treatments. Two cross-flight interception traps were placed on all trees and emptied every four weeks. When sampling all trees at the same time, the felling timings showed no significant effects on species richness, but fungivores increased as trees were dead for a longer time. The species assemblages also differed between felling timings, while the assemblages significantly differed every four weeks on the fresh trees due to phenology. Therefore, results show different courses of species assemblages on the trees for the different treatments, which is assumed to be the result of differences in phenology, functional groups and species assemblage divergence. Priority effects cannot be proven with certainty as there were more factors that were different between the felling treatments. Additionally, the findings suggest that a diversity of seasonal timings is an important tool for maximizing the effectiveness of dead wood creation for biodiversity conservation in forest ecosystems.

Introduction

Seasonality in ephemeral habitats

Ephemeral resource patches (ERPs) are shortly available resources that appear, change and disappear on ecological timescales and are complex sources of biodiversity as they provide a wide variety of microhabitats throughout many stages of succession (Lettenmaier et al., 2025; Butterworth et al., 2022). Seasonality can strongly shape the species assemblages on ERPs such as dung (Latha, 2019), carrion (Matuszweski et al., 2009) and dead wood (Foit, 2012). This is caused by differences in species activities (phenology) as well as differences in temperature and moisture.

Ecological importance of dead wood

Dead wood serves many important roles in the ecosystem including facilitating biodiversity by providing a wide range of habitats, nutrient cycling and forest dynamics (Siitonen, 2001; Stokland et al., 2012). In Europe, a significant share of species in forest biodiversity (20%-25%) is dependent on dead wood (so called 'saproxylic organisms') (Siitonen, 2001). This includes lichens, mosses, fungi, beetles, other invertebrates and vertebrates. These organisms use dead wood in varying ways, from nesting, hibernation or as their primary reproduction substrate (Colijn & Burgers, 2022; Stokland et al., 2012). During the decomposition, dead wood releases carbon and nitrogen back into the soil, driving the soil development (Harmon et al., 1986).

Dead wood creation and forest management

Past forest management practices have had a negative impact on the dead wood volume in the forests and their associated habiting (saproxylic) biodiversity in Europe (Seibold et al., 2014). This resulted in dramatically low saproxylic diversity, compared to non-managed forests (Laaksonen et al., 2020). Changes in forestry practices in the 1990s and 2000s have in most forests increased the volume of dead wood and therewith saproxylic presence and diversity (Jagers op Akkerhuis et al., 2005; Seibold et al., 2016). Dead wood creation has become a common practice in forestry to improve the functioning of forest ecosystems (Siitonen, 2001; Sandström et al., 2019). Currently, many forest managing organisations are incorporating dead wood creation in their management plans, and some have set ambitious targets for the presence of dead wood volume (Natuurmonumenten, n.d.; Bosgroepen, 2024). The dead wood volume in Dutch managed forests is still way below non-managed forests, with obvious consequences for saproxylic species and the trophic levels above (Jagers op Akkerhuis et al., 2005). For many foresters, the question remains what the most effective way of dead wood creation is to improve biodiversity and revitalise forest ecosystems.

Colonization and succession in dead wood

When a tree dies, chemical decomposition starts, and a new opportunity arises for many organisms for a new food source (Jonsell et al., 2007). The dead tree releases certain Volatile Organic Compounds (VOC's) that saproxylic invertebrates use to locate and colonize it (Schütz et al, 2012). Saproxylic beetles play a key role in natural dead wood decomposition and occur in high diversity, making them an often-used group for the studying dead wood ecosystems (Seibold et al., 2019). Species that are adapted to fresh deadwood, where cambium and chemical defenses are still present, arrive first (Ulyshen, 2014). In these early phases, the structure of the bark is a strong filter of species on the ensuing species assemblage (Zuo et al., 2016). Most saproxylic beetle species deposit their larvae in dead wood and disperse as imago after which they lay eggs in dead wood (Gimmel et al., 2018). Over time, the change in species composition slows down consecutively when different assemblages of saproxylics, specialized on different phases of decomposition, take the tree to further stages of decay (Stokland et al., 2012; Lettenmaier et al., 2025). Within these saproxylic beetle assemblages, there are three primary functional groups: wood consumers, fungivores and predators (Colijn & Burgers, 2022). All organisms associated with dead wood, including saproxylic beetles, change the structural and chemical environments in the wood (Ulyshen, 2014). They may thus create different environments that that draw in different assemblages of species - namely fungi, arthropods and bacteria - that interact with one another and contribute to the dead wood associated diversity. Throughout the entire decomposition process, species also interact with one another and can therewith be dependent on the presence or absence of other species (Schroeder et al., 1994). Examples of this are specialized predator only occurring when its prey species is present or a fungivore preferring habitats with certain fungal species.

Additionally, the order in which species arrive plays a key role in the development of species assemblages (Foit, 2015; Seibold et al., 2015; Jacobsen et al., 2015; Weslien et al., 2011). For example, some saproxylic beetle species are known to carry spores of fungi, which alter the structure of the dead wood and thereby impact the suitability of the habitat for other species (Seibold et al., 2019a). Such a "priority effect" can have long lasting effects on the species assemblages on dead wood masses (Weslien et al., 2011; Lettenmaier et al., 2025).

Succession of functional groups in early decay stages

Functional group composition -the proportions of predators, wood-eaters and fungivores- shifts across stages in the decay process, which in turn determine the resulting species assemblages (Laaksonen et al., 2020a; Ulyshen & Hanula, 2010). From the start of decomposition, fungal colonisation increases, providing more feeding opportunities for fungivores (Stokland et al., 2012; Ulyshen & Hanula, 2010). As a result, trees that have been dead longer generally support higher fungivore abundances, especially because prolonged availability increases the chance of colonisation during seasonal peaks in fungal activity (Brabcová et al., 2022). In these early stages, no decline in wood-eaters is expected: ample resources remain, including tissues that only become accessible once the tree's defensive compounds have sufficiently degraded (Yang, 2021; Stokland et al., 2012). Furthermore, the low nutrient content of dead wood limits the number of wood-eaters that can complete development, regardless of colonisation pressure (Filipiak, 2018), contributing to their relatively stable abundance. Together, the rise in fungivores and the steady presence of wood-eaters increase prey availability, which can lead to a slight increase in predator abundance, which is consistent with field observations by Ulyshen & Hanula (2010).

These increases in the abundance of fungivores and predators are expected to correlate with increases in species richness, as higher numbers of individuals often coincide with higher richness due to greater niche availability (Haddad et al., 2001). This increase of individuals being paired with an increase in species has been observed in field experiments (Knuff et al., 2020) and in large-scale Dutch inventories of saproxylic beetles (Moraal, 2014). The increase in species richness over time would also be in line with the concept that over time, a more homogenous wood mass becomes more heterogeneous, creating more microhabitats and therewith increasing species richness (Stokland et al., 2012; Lettenmaier et al., 2025).

Drivers of saproxylic biodiversity

Tree level factors

The initial chemical and structural aspects of a dead tree, such as chemical defenses, wood density, bark structure and nutrient content, are proven to affect the saproxylic species composition (Stokland et al, 2012; Guo et al., 2016). In particular, the tree species of origin of the dead wood strongly affects these factors. As decomposition proceeds, the decay process alters the chemical and structural aspects, resulting in different habitats in different stages of decay (Seibold et al., 2022). Consequently, species assemblages change in a successional sequence, from early colonizers to fungivores and late-stage soil mixers. Furthermore, the local climate is an important driver of species composition, as sun exposure, temperature and rainfall impact the internal moisture and temperature dynamics of the dead wood (Romo et al., 2019). Similarly, the position of the wood (lying or standing) also influences internal temperature and moisture dynamics (Stokland et al., 2012). Additionally, stumps are known to inhibit different species assemblages compared to stems, with there even being differences between high stumps and low stumps (Staff, 2015). High stumps are higher up in the canopy and therefore more sun-exposed, changing the internal chemical and physical properties as well as warming the microclimate, which is expected to increase the numbers of individuals on high stumps (Lackner et al., 2024; Stokland et al., 2012).

Stand level dead wood factors

On a larger scale, dead wood volume, and diversity (in size and decay stages), play a key role in forest biodiversity (Lassauce et al., 2011). A higher local volume and size (diameter and length) diversity in dead wood results in more saproxylic species (Seibold & Thorn, 2018). Current forest management affects this volume and diversity in deadwood habitat saproxylic through dead wood removal, fragmentation and retention (Gossner et al., 2013; Laaksonen et al., 2020).

Landscape factors

Equally important, the history of the forest ecosystem influences species assemblages; for instance, in forests with a long history of dead wood retention, more species are conserved, resulting in different current assemblages (Laaksonen et al., 2020). The landscape context also limits the pool of potential colonizers: in isolated forests with little dead wood in surrounding areas, there are few saproxylic species and therewith few potential colonizers (Stokland et al., 2012). Moreover, connectivity of forest habitats further shapes the potential species pool (Ranius et al., 2001).

Natural patterns of tree mortality

In natural forest ecosystems in temperate regions, tree mortality occurs in waves of disturbance and is dependent on extreme weather events, while tree age also plays an important role (Harmon et al., 2020). The two primary natural drivers of tree death are droughts and storms (Neumann et al., 2017). Tree deaths from droughts occur almost exclusively in some years during summer, while tree death from storms primarily occur at random between November and April (Batlori et al., 2020; Neumann et al., 2017). These events can also cause damage to trees, resulting in a later death. This results in differing patterns of tree death throughout the years, with peaks in summer and winter (Neumann et al., 2017).

Role of seasonality in dead wood ecology

Seasonality is an important aspect of dead wood species assemblage development. Saproxylic beetle species differ drastically in the seasonal timing of their life cycle (phenology) (Gillespie et al., 2018). Some species disperse as soon as temperatures become suitable in spring (e.g., *Tomicus minor*), whereas others develop as larvae or pupae during spring and disperse in late summer (e.g., *Arhopalus rusticus*). The peak in activity of saproxylic beetles in spring can be explained by the natural patterns of tree death because the winter is too cold for most beetles to colonise trees and many trees that die in winter, become available for the first time in spring (Bartlori et al., 2020). Other species capitalise on the trees that die during summer and are active in late summer. As a result of these different strategies, different species peak in number at different times throughout the year, leading to seasonal variation in the composition of active imagines- the life stage during which beetles colonize, disperse and reproduce on new dead wood sources (Moraal, 2014; Foit, 2012). Consequently, it has been hypothesised that the seasonal timing of tree death influences the initial saproxylic assemblage, with potential cascading effects on subsequent dead-wood decay processes (Foit et al., 2015), as discussed later. Yet, such seasonal change may partially be driven by seasonality in the physical and chemical state of dead wood (Stokland et al., 2012). In addition to the saproxylic beetle assemblages, fungal assemblages also show strong seasonal dynamics, with peaks in activity that influence the abundance and behaviour of fungivores (Brabcová et al., 2022).

Seasonal timing of tree death also affects functional group composition, even in the early decay stages. Foit (2012) hypothesised that freshly created dead wood may require several weeks before reaching optimal conditions for saproxylic colonisation. Because this “colonisation window” may not align with seasonal peaks in beetle activity, the timing of tree death could influence which species successfully establish. If, like Foit (2012) suggests, this window were to start a few weeks after felling and end after a few months, the species richness would be the highest on trees felled in winter.

Knowledge gaps

In the Netherlands, and in many other regions, most forest management (including dead wood creation by felling) is carried out in winter to avoid the breeding season (Audubon New York, 2017; Staatsbosbeheer, 2022). However, the ecological implications of this seasonal timing, and more broadly the timing of tree death, have been investigated only a handful of times (Foit, 2012; Foit, 2015; Ferro & Gimmel, 2014). Existing studies show that seasonal timing can significantly influence the ensuing beetle assemblage (Foit, 2012; Foit, 2015; Ferro & Gimmel, 2014). Two mechanisms are proposed in the literature. First, trees differ physiologically depending on whether they die during the growing season or while overwintering, which affects their defensive and structural properties (Nilsson, 2022). Second, seasonal variation in beetle activity means that the species active while tree death are the ones that colonize it (Foit, 2012). Thus, trees felled in spring may attract different initial colonizers than trees felled in summer (Foit, 2015).

Although the order of species arrival is known to influence subsequent succession, it remains unclear how priority effects occur in this succession. A priority effect would imply that early-arriving species modify the habitat in ways that shape the trajectory of later assemblage assembly (Foit, 2012). If such an effect exists, trees felled in different seasons would follow distinct assemblage development pathways as they decay. Whether this mechanism operates in saproxylic beetle assemblages has not yet been demonstrated, however it has been described in primary succession of vegetation (Durbeck et al., 2023).

Although expected, it is uncertain whether functional group composition follows the same order of succession when the trees are felled at different seasonal timings. No study has directly tested whether different felling seasons lead to different functional group dynamics in the early decay stages. Mechanisms such as successional changes and increasing habitat heterogeneity over time are known to influence species richness and functional group abundances (Stokland et al., 2012; Ulyshen & Hanula, 2010), but it is unknown whether these processes occur at the same speed on trees felled at different seasons. For instance, variation in seasonal activity of fungi could affect the proportion of fungivores (Brabcová et al., 2022) and the differing temperatures throughout the year can affect the speed of the shifts in functional group composition (Romo et al., 2019; Stokland et al., 2012).

Objectives and predictions

When these knowledge gaps are adequately adressed, the findings would have implications for forest management as a potentially optimal felling-timing regime for biodiversity could be worked out. In other words, with differing timing of intervention, ephemeral habitats are in alternative stages of development during the same seasons, thereby increasing habitat heterogeneity and supporting a greater diversity of saproxylic beetle species.

This research has two objectives. 1. Find out what impact seasonal timing of tree death has on the saproxylic beetle assemblage, species richness and functional group composition in artificially created deadwood habitat. 2. Find out whether different felling timings lead to different courses of species composition resulting from the different orders of arrival of the colonizing species, proving or disproving the priority-effect. 3. Demonstrate whether there are differences in species richness, abundance and diversity between stumps and logs.

I formulated three predictions: the first addresses the third objective, the second and third relate to the second objective, and the fourth relates to the first objective.

1. Compared to stems, stumps provide different microhabitats, resulting in higher species richness, numbers of individuals and Shannon diversity.

2. Because of phenological patterns, saproxylic beetle assemblage composition on fresh dead wood will differ throughout the year

3. At a fixed moment in time, the saproxylic beetle assemblages will differ significantly between trees felled in different months.

4. With time, decay of dead wood creates more habitat heterogeneity, resulting in a higher abundance of fungivores (a), stability in the number of wood-eaters (b) and higher abundance of predators (c), which results in a higher species richness (d) that is attracted to the tree at a specific moment in time.

The outcomes of this study will help to deepen the understanding of the development of species assemblages on dead wood and dead wood ecology. The study will also have management implications as from the results it can be (1) concluded how seasonal timing impacts the dead wood species composition, species richness and functional group composition and (2) advised on when to fell trees for an improved facilitation of biodiversity. An experiment will be set up where saproxylic beetles are sampled on trees felled at different seasonal timings.

Methodology

Study site

The study was conducted on the south side of the Veluwe, in the nature reserve Planken Wambuis (2123 hectares), consisting of forest, heathland and drifting sand on dry sandy soils (Büisma, 2006). Much of the forested area is covered with Scot's pine (*Pinus sylvestris L. (1753)*) production forests, as well as old beech (*Fagus sylvatica L. (1753)*) forests and younger birch (*Betula pendula, Roth*) forests with, more occasionally, also larch (*Larix kaempferi (Lamb.) Car. 1856*) and douglas fir (*Pseudotsuga menzieszi (Mirb.) Franco. 1950*) plots. The five selected sampling sites were in pine dominated forests of similar age (around 50 years old), relatively closed canopy and similar in local dead wood volume. The study area is characterized by a temperate climate with an annual average temperature of 11.2°C, with temperatures in winter as low as -2°C and in summer as high as 33°C, while the annual precipitation is around 900mm (Knmi, n.d.).

Experimental design

Following a complete randomized block design, in the five selected areas, five locations trees were randomly selected, each being at least 100 meters apart (See figure 1). At these five locations, a Scot's pine tree was selected that matched 5 criteria, namely (1) a 30 centimetres dbh, (2) no odd shape of stem or crown, (3) no local open canopy, (4) no local high dead wood volume and (5) no high numbers of nearby other tree species. Of these five locations, one was selected as a control tree, meaning it was not felled and remained alive. The control trees were part of the design to ensure that the sampled beetles were attracted by the treatments and not caught by randomness. The other four trees were felled every eight weeks using high stump cutting (at around 1.30 meters) on December 8th, 2024 (T1), February 4th, 2025 (T2), March 31st, 2025 (T3), and May 26th, 2025 (T4) (see figure 1). This resulted in 5 trees at 5 different locations that were selected, which is 25 in total, of which, 20 were felled at 4 different timings, and 5 remained alive as control trees.

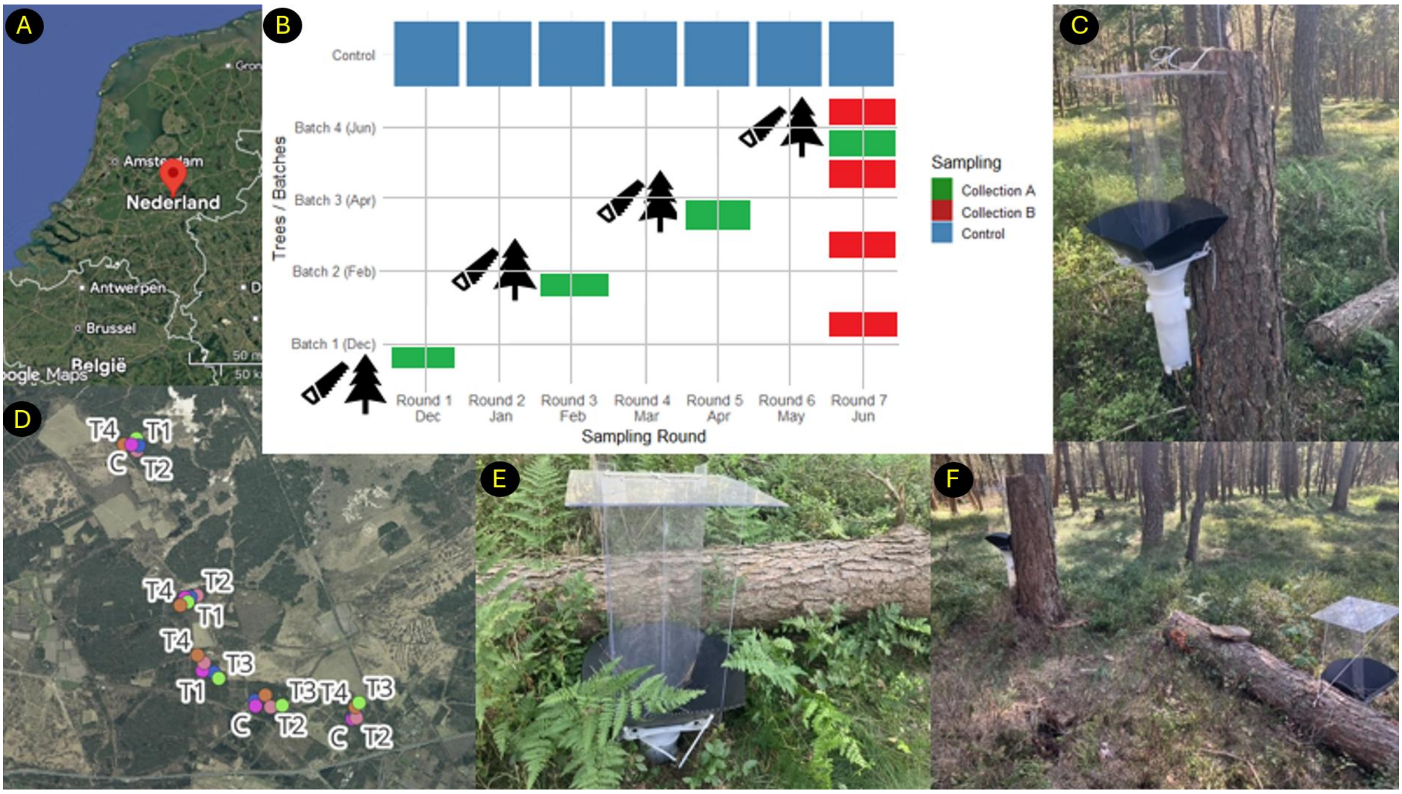

Figure 1. Study site location (panel A) and the locations of the treatment trees (panel D), with "C" as control and "T1" till "T4" indicating the different felling timings. "T1" trees were felled in December, "T2" in February, "T3" in April and "T4" in June. The experimental setup on the treatment trees (panel F) including the trap position on stumps (S) (panel C) and the trap position on the logs (L) (panel E). Lastly on the top (panel B), the timeframe of the entire experiment with sampling collection A consisting of four weeks of sampling on the most recently felled trees, sampling collection B consisting of all samples taken during June and the control trees samples every four weeks. Every rectangle is equal to a sample on a stump and a sample on a log for every location, meaning that for sampling collection A, there are 7 samples (for the 7 rounds), two positions and five locations, resulting in a total of 70 samples. For sampling collection B, there are four felling timings, five locations and two trap positions resulting in a total of 40 samples. On every control tree, just one trap was placed, therefore resulting in a five samples per round and a total of 35 samples across the experiment

Insect sampling

Insects were sampled using cross-window flight interception traps, following the design described by Gossner et al. (2013) (Figure 1). This sampling method was selected because it allows repeated, non-destructive sampling of individual trees, in contrast to methods that require destructive sampling of the substrate (e.g. Foit, 2015) or use in-situ emergence and therefore prevent further colonisation of the trees (Hjältén et al. 2010).

Trap placement

At the treatment trees, two window traps were installed. One trap was attached to the high stump, facing away from the stem, while the second trap was placed on the south-facing side of the stem at approximately one meter above the start of the stem (Figure 1). Trap position on a tree can influence the beetle assemblages captured (Graf et al., 2021). Although this was considered by using two trap positions per tree, trap position itself was not a primary research objective. Therefore, for all analyses, arthropod counts from both traps were combined to represent the assemblage associated with each tree.

At the (living) control trees, one window trap was installed from the start of the experiment. These traps were hung on the south-facing side of the stem at approximately one meter height.

Sampling scheme and collections

Sampling was conducted over seven rounds of four weeks, resulting in three distinct sampling collections (Figure 1). Control trees were sampled continuously every four weeks throughout the experiment. Trees that were felled most recently were sampled during the first four weeks and the subsequent four weeks following their death, except for the tree felled in June, which was sampled only during June. These samples together formed sampling collection A. In addition, four trees felled at different times were all sampled during the same four-week period in June, constituting sampling collection B. For the tree felled in June, sampling collections A and B overlapped (Figure 1).

Identification and sample selection

All invertebrates were identified to order level. Saproxylic beetles, based on Colijn & Burgers (2022), were identified to species level, except for Staphylinidae, Throscidae, and the genus *Epurea* spp. (Nitidulidae). Identifications were carried out using a binocular microscope and relevant literature (Lompe, n.d.). All individuals were counted and recorded in a spreadsheet.

Sampling collection A was used to assess the initial insect assemblage for prediction 3. Sampling collection B was used to test differences in species composition, species richness, and functional groups among different felling timings for predictions 1 and 2. Samples from control trees were used to characterize background insect assemblages and to distinguish species attracted specifically to felled trees.

Field measurements

To correct for environmental factors that may influence the assemblages attracted to the traps, four covariates were measured on all 20 treatment trees. These covariates were selected because they are measurable in the field and have been shown to influence saproxylic and forest-associated assemblages in multiple studies (Foit, 2012; Larrieu et al., 2017; Stokland et al., 2012). The covariates were canopy cover, dead wood volume, tree-related microhabitat (TReM) diversity, and living ground plane. Below, the field measurements and subsequent calculation of the four covariates are described in detail.

Canopy cover

Canopy cover was measured to quantify light exposure at each trap location. Measurements were taken directly above the trap on stump using the mobile application *Canopy Cover* (Easlon, n.d.), a method shown to provide accurate canopy cover estimates (Schweizer et al., 2024). For consistency, all measurements were conducted using the same smartphone, the default app settings, and the built-in spirit level to ensure the phone was held perfectly horizontal.

Dead wood and TReM surveys

Local dead wood volume can be measured using field surveys. Diversity in dead wood habitats can be measured using TReMs. TReMs (Tree Related Microhabitats) are an upcoming way to quantify the diversity of microhabitats (Larrieu et al., 2017). These microhabitats such as fungi, rotholes or dead branches result from the before-mentioned factors such as, among others, decomposition stage and species composition. Both dead wood volume and TReM diversity were assessed using combined surveys of standing and lying dead wood within a 30 m radius around each treatment tree.

Standing tree survey

Standing trees were surveyed following a method heavily inspired by Roy et al. (2024). From a fixed point between the tree stump and the dead log, a piece of cardboard (1 cm thick) with a stretched rope (42 cm) attached was held next to the eye. This setup ensured that all trees with a diameter of at least 30 cm within a 30 m radius were included. The observer closed one eye and slowly rotated 360°, recording all trees that appeared thicker than or equal to the cardboard.

For each recorded tree, the following information was noted: species, diameter at breast height (DBH), living or dead status, decay stage (1–5, if dead), whether the tree was a stump, and the presence of tree-related microhabitats (TReMs), such as woodpecker holes, trunk cavities, and perennial fungal fruiting bodies (Roy et al., 2024; Larrieu et al., 2017). The complete list of recorded TReMs is provided in appendix 5.

Lying tree survey

For the full-area sampling, all lying dead trees with a diameter larger than 30 cm, that were at least half within a 30 m radius around the treatment tree, were recorded. For each recorded log, species, diameter at breast height, diameter at halfway, total length, decay stage, and TReMs (using the same classification as for standing trees) were noted.

Calculation of covariates

Field data were processed into four covariates:

1. *Canopy cover*

   Canopy cover values (in % sky covered) were used directly without further processing.

2. *Dead wood volume*

   Dead wood volume was calculated by summing standing and lying dead wood. Volumes of lying logs from the full-area sampling were calculated using the Newtonian formula (Li et al., 2015). Newtonian formula:

$$V = \frac{L}{6}(D_s^2 + 4D_m^2 + D_l^2)$$

Standing dead wood volume was calculated using a cylindrical approximation based on DBH and a fixed length of 18 m. Volumes of standing and lying dead wood were then summed to obtain total dead wood volume per location.

3. *TReM diversity*
TReM counts from standing and lying dead wood surveys were combined for each location, based on protocol of Roy et al. (2024). Simpson's diversity index was then calculated using the diversity function from the *vegan* package (Oksanen et al., 2025). In Bouget et al. (2023), TReM diversity was also calculated and correlated with ecological results.

4. *Living ground plane*
The living ground plane was calculated using the diameters of all living trees recorded in the standing tree survey. For all living trees in the survey, basal areas were calculated and summed, treating each tree as a circle. Living ground plane represents the density of the forest, which could affect saproxylic assemblages (Stokland et al., 2012).

Analysis

All analyses were conducted in R (version 4.4.0; R Core Team, 2024). Only saproxylic beetle species present in the dataset of Colijn & Burgers (2022) were included in the analyses. For each sample, species richness, number of individuals and Shannon diversity were calculated, which was used in prediction 1. Standing and trap on stem specimens were combined for all other analysis as counting them separate would mean pseudo replication and combining them results in more species data overall. Species richness was calculated on these combined samples. For functional group analyses, species were assigned to three main functional groups: xylophagous (wood-feeding), mycetophagous (fungus-feeding), and zoophagous (predatory). Classification of species into functional groups followed Colijn & Burgers (2022). This classification was used to aggregate species abundances per guild for subsequent analysis of functional group–specific responses to deadwood availability and felling date (Prediction 1).

Preliminary analyses and data preparation

Prior to testing the study predictions, preliminary analysis was conducted.

First, samples from felled treatment trees were compared with standing samples from living control trees to confirm that tree death affected saproxylic beetle assemblages. Species richness from control trees and sampling collection B was compared using paired *t*-tests when assumptions of normality were met, and Wilcoxon signed-rank tests otherwise. Forest was included as a blocking factor. As significant differences were detected, control tree samples were excluded from all subsequent analyses, which focus exclusively on comparisons among felled trees.

For visualisation purposes of the species assemblages, non-metric multidimensional scaling (NMDS) was additionally performed, as it provided a clearer representation of assemblage differences.

Effects of stumps and stems on species richness, number of individuals and Shannon diversity (Prediction 1)

Prediction 1 states that traps on stumps sample significantly higher species richness, abundance and diversity. To test this, for every stump and stem sample combination (using both sampling collection A and B), these variables of interest were calculated and the pairs were compared.

Species richness, total abundance, and Shannon diversity were compared between trap positions using paired *t*-tests when data met normality assumptions, and Wilcoxon signed-rank tests otherwise. This procedure was run for each round and on all sample pairs.

Phenological shifts in early coloniser assemblages (Prediction 2)

Prediction 2 states that due to phenological patterns, beetle assemblage composition on freshly deadwood substrates will differ throughout the year. To test this, analyses focused on sampling collection A, which captured beetle assemblages shortly after tree felling, representing the first month of species assemblages.

Species composition was analysed using constrained ordination, with forest included as a blocking factor. This approach ensured that deadwood age remained constant (recently felled), while the sampling moment within the season varied. Detrended correspondence analysis (DCA) indicated a relatively short gradient length (DCA1 = 2.79), suggesting predominantly linear species responses. Capscale ordination with Bray-Curtis dissimilarities was chosen as the appropriate ordination method for statistical testing as it allows for blocking factors and covariables, was suitable for the next prediction, and the axis length was not too far off.

Effects of felling timing on species assemblages (Prediction 3)

Prediction 3 states that at a fixed moment in time, species assemblages will differ significantly between trees felled in different months. To test this, analyses were conducted using sampling collection B, which was collected simultaneously across all trees, i.e. a fixed sampling moment.

Species composition was compared among trees with different felling dates using constrained ordination, like Foit (2012). DCA indicated short gradient lengths (DCA1 = 1.89), supporting the assumption of linear species responses. Capscale ordination with Bray–Curtis dissimilarities was therefore applied.

This method allows for the inclusion of both blocking factors and covariates; forest was included as a blocking factor, and canopy cover, dead wood volume, TReM diversity, and living tree ground plane were added as covariates. Significance of the full constrained model was tested using ANOVA, after which pairwise PERMANOVA tests (*adonis2*; *vegan* package) were conducted to compare individual felling treatments. An NMDS model was made for visualisation.

Effects of felling timing on functional groups and species richness (Prediction 4)

Prediction 4 states that when a dead wood habitat has been available for increasingly longer, greater habitat heterogeneity develops, leading to a higher abundance of predators and fungivores, with a constant number of wood-eaters, which in turn results in higher species richness at a specific moment in time. To test this prediction, generalized linear mixed models (GLMMs) were fitted using the *lme4* package (Bates et al., 2003), based on data from sampling collection B.

1. Model 1: Fungivores ~ Treatment + Deadwoodvolume + (1 | Location)
2. Model 2: Wood-eaters ~ Treatment + Tremdiversity + (1 | Location)
3. Model 3: Predators ~ Treatment + Canopy + (1 | Location)
4. Model 4: Species richness ~ Treatment + Tremdiversity + (1 | Location)

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Species richness was used as the primary response variable, with felling date as a categorical predictor representing the duration of deadwood availability. Forest was included as a random blocking factor, and a Poisson error distribution with log link was applied. Canopy cover, dead wood volume, tree-related microhabitat (TReM) diversity, and living tree ground plane were included as covariates when significant. Model predictions were generated for the response variables excluding random effects.

To explicitly test the proposed mechanism underlying Prediction 1, the same modelling workflow was repeated using the abundance of fungivorous wood-eating and predatory species as response variables. Functional group assignments followed Colijn & Burgers (2022). In this way, both the direct effect of deadwood availability on functional group abundance (Predictions 1a, 1b and 1c) and the resulting pattern in overall species richness (Prediction 1d) were evaluated.

Results

General overview of species composition

In total, 6.245 saproxylic beetles were collected, representing 116 species across 40 families. Species abundances were highly uneven, and species assemblages were dominated by a small number of common species and a large proportion of rare taxa (Figure 2): *Hylastes attenuatus* was the most abundant species (1374 individuals), closely followed by *Tomicus piniperda* (1268 individuals), while 51 species were represented by a single individual.

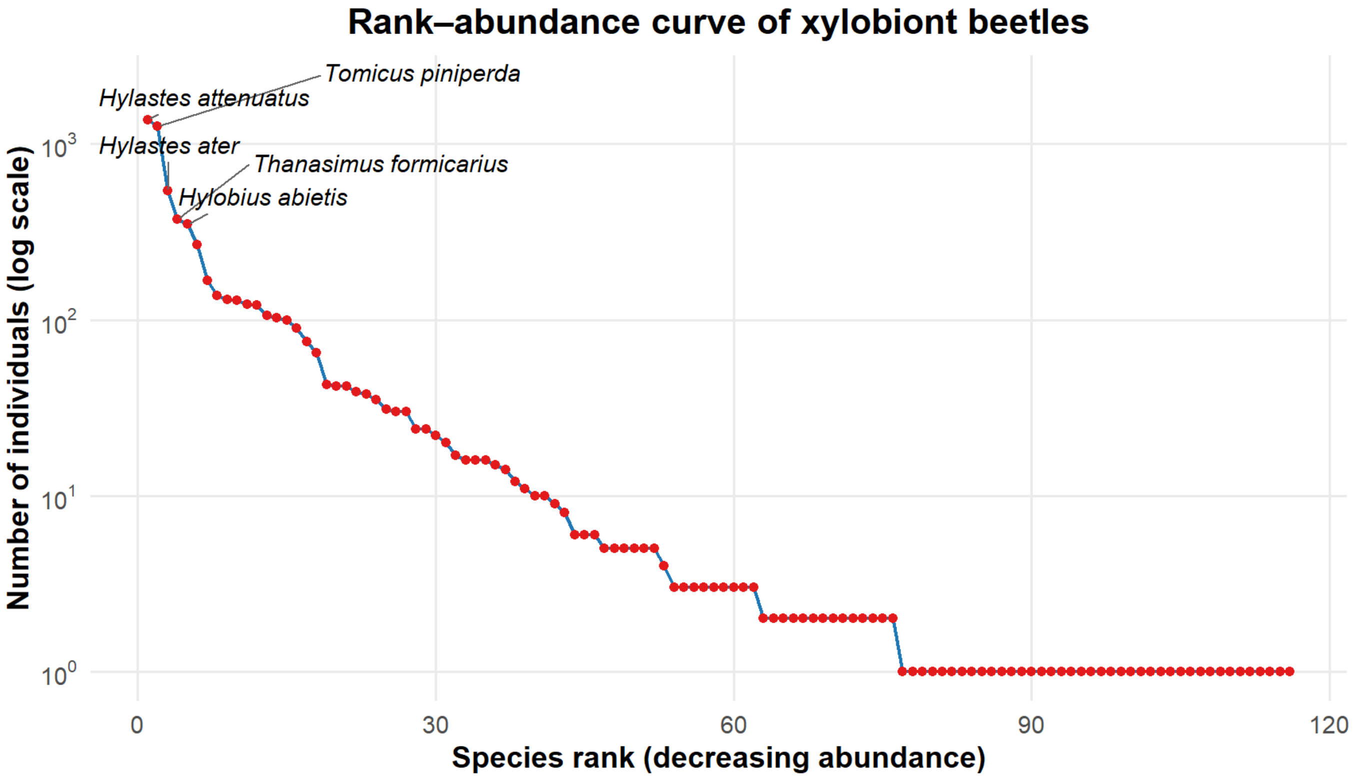

Figure 2. Rank–abundance curve of saproxylic beetle species across all samples. Species are ordered by decreasing abundance on the x-axis, with the number of individuals plotted on a logarithmic scale. The five most abundant species accounted for 62% of all individuals and are highlighted.

Preprocessing

Traps on felled trees outperformed control trees in all three ecological metrics (see figure 4). Although the statistical tests were not significant, the low p-values combined with the low sample size indicate a strong correlation with a higher abundance of saproxylic beetles on felled trees across all rounds, except 1, which was in winter, during a period of low activity.

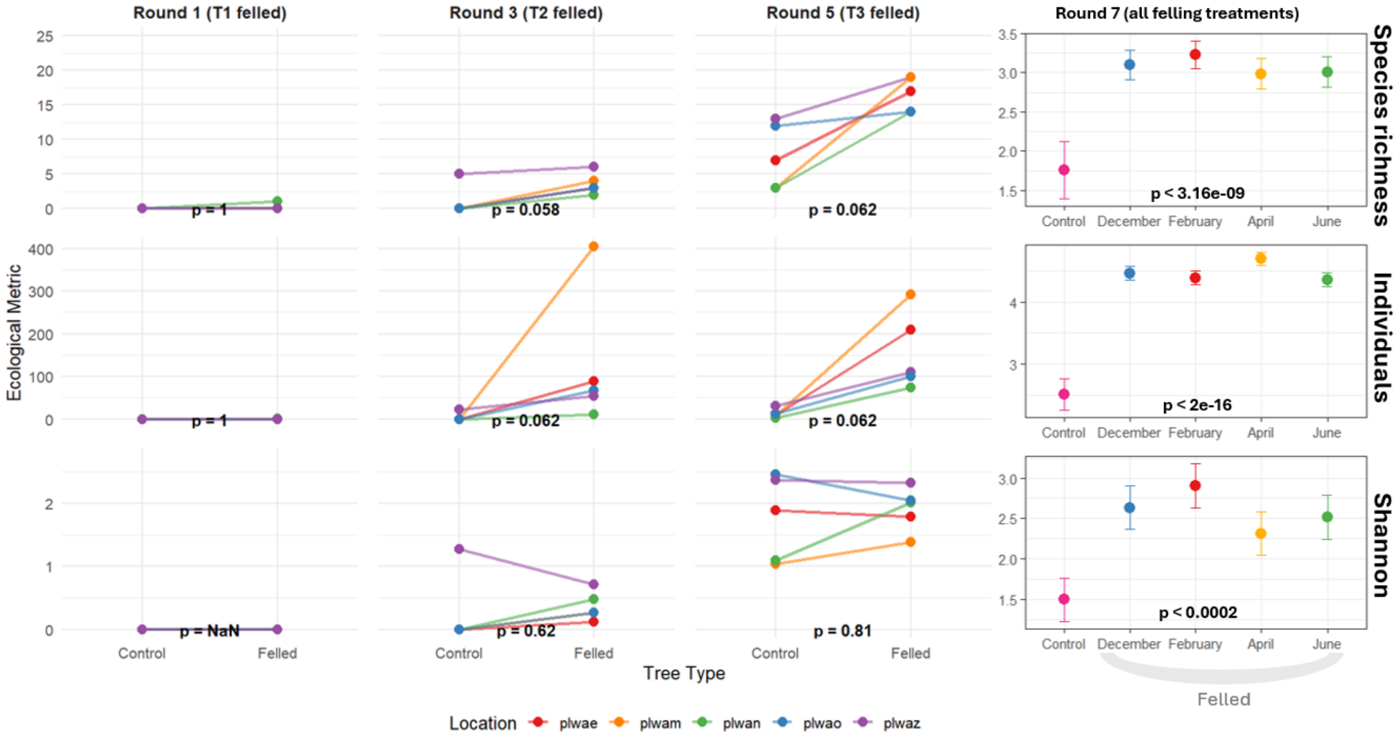

Figure 3: Disturbance validation: The figure shows comparisons between living control trees and felled trees across four rounds and three ecological metrics: species richness, number of individuals and Shannon-Wiener diversity index. For the first three rounds, data from the most freshly felled trees are shown, for Round 7, data from all felling treatments in relation to control trees is shown. For the first three rounds, the lines connect samples from the same location, as do the colours. P-values (calculated with pairwise Wilcoxon rank sign test) are near significant and indicate a strong effect of felling. For Round 7, locations are not distinguished, while the highest p-values are shown from a GLMM that has control as reference, the treatments as explanatory variables and blocks for location. The effect size of the comparisons is 5 as only five control trees were sampled each round (Round 1 is in winter: December, Round 3 in February, Round 5 in April and Round 7 in June).

Comparisons between stumps and stems (Prediction 1)

Trap position

Traps on stumps significantly outperformed traps on stems in all three ecological metrics (see figure 4). Some comparisons were not significant because of a small sample size or absence of saproxylic beetles altogether. During round 1 in winter saproxylic activity was limited and only few beetles were sampled. This pattern persisted somewhat into round 3. When all round pairs are combined, all three ecological metrics differ significantly between stumps and stems (N = 27, Species richness: p= 3.449e-06, Individuals: p= 1.82e-06, Shannon diversity: p= 0.004939). The species accumulation curve suggests that traps on stumps can reach higher levels of species richness.

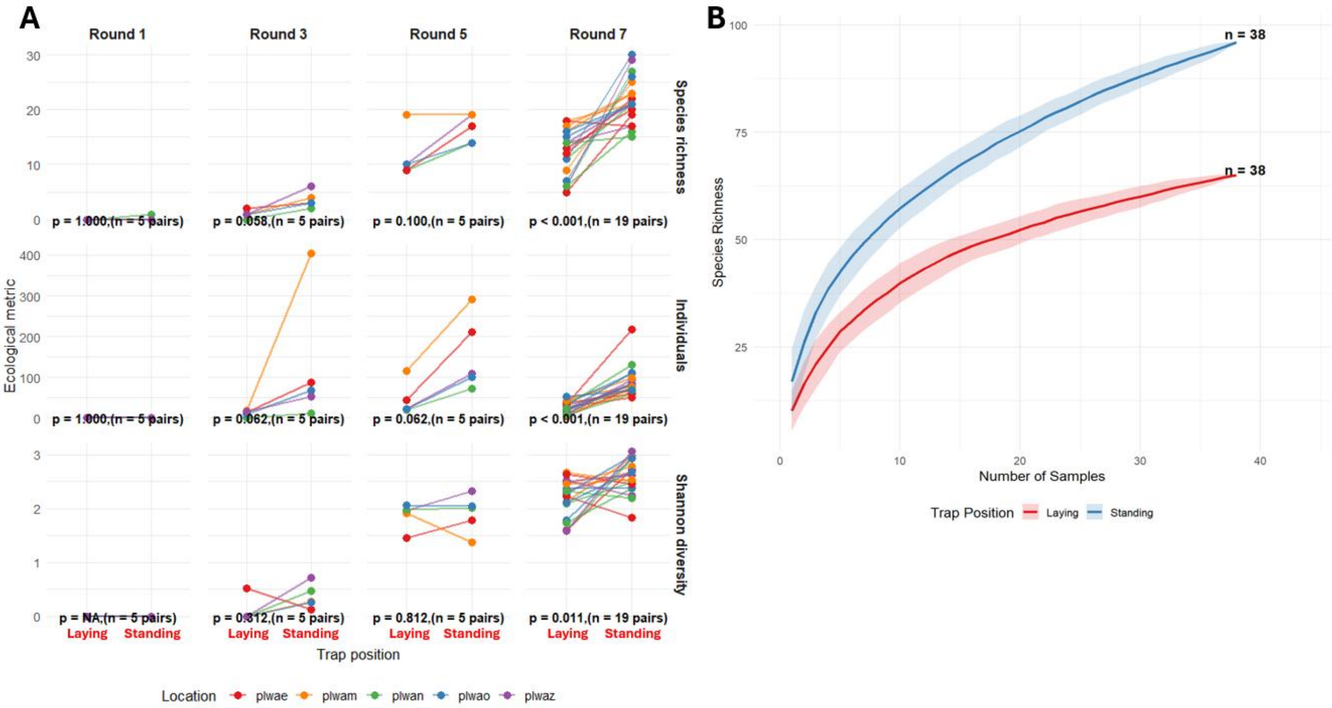

Figure 4: Trap position validation and sampling efficiency. ***A:*** *Paired comparisons of Laying (on stems) and Standing traps (on stumps), subdivided per round and three ecological metrics: Species richness, number of individuals and Shannon-Wiener diversity index. Connected lines mean that the samples were taken at the same tree. Coloured by location. P-values (calculated with pairwise Wilcoxon rank sign test) and sample sizes are shown per panel.* ***B:*** *Sample-based rarefaction curve for laying (red) and standing (blue) traps. The shade marks 95% confidence intervals. Standing traps clearly captured more species.*

Effect of felling date on start assemblages (Prediction 2)

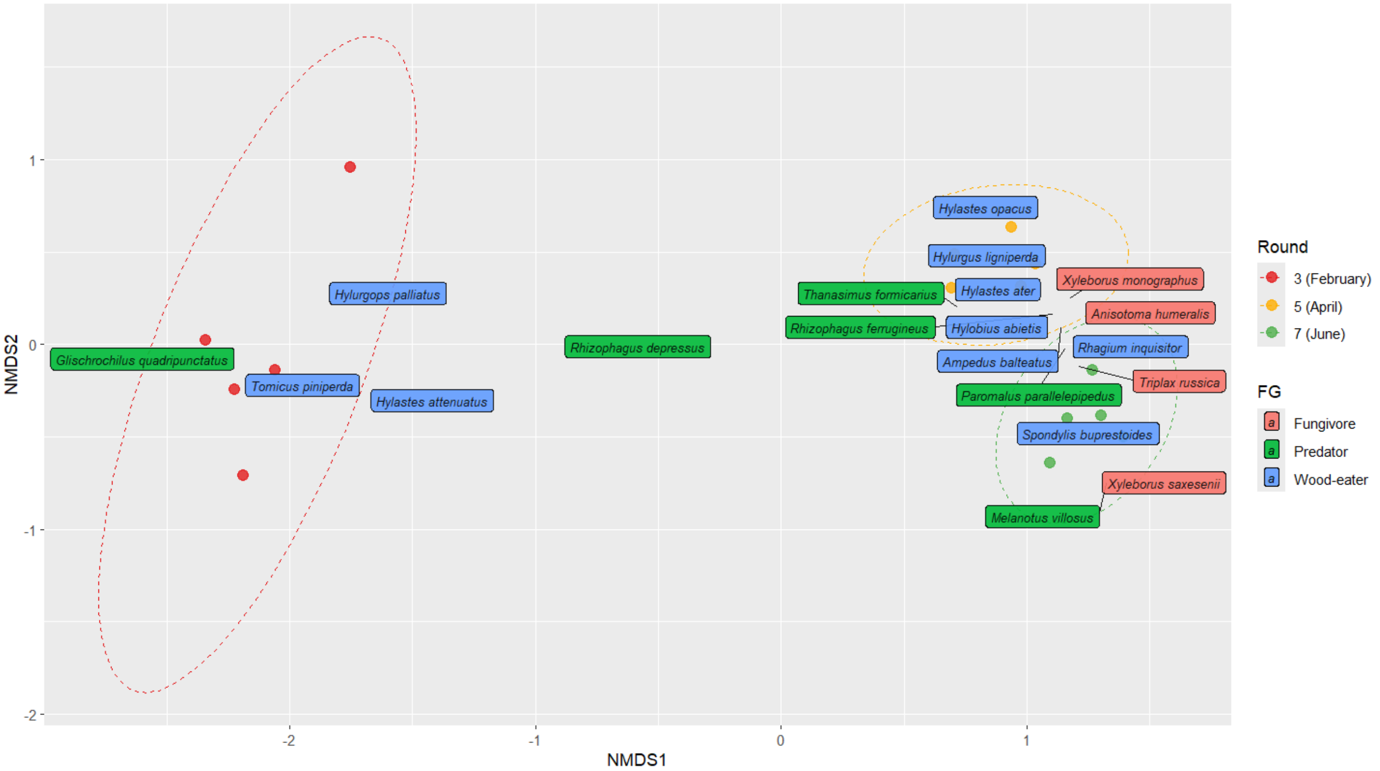

Figure 5: NMDS ordination (Based on Bray-Curtis dissimilarity) of saproxylic beetle assemblages of freshly cut trees across rounds. Points represent beetle assemblage sampled on a single tree and ellipses show 95% confidence intervals. Species labels highlight the top 20 most abundant species, color-coded by functional group (following the division by Colijn & Burgers (2022)): red for Fungivores, green for Predators and blue for Wood-eaters. Round (excluding round 1 as it contained only one saproxylic beetle) had a significant effect on the species assemblage (PERMANOVA, p = 0.001). Comparing the rounds, a pairwise PERMANOVA based on Bray–Curtis dissimilarity (using adonis2 from the vegan package) revealed significant differences in species composition between all sampling rounds. Round 3 (February) differed significantly from 5 (April) and 7 (June) (Padj = 0.015), with relatively high effect sizes (R^2 = 0.43–0.55). Similarly, round 5 differed from round 7 (R^2 = 0.41: Padj = 0.015), which together concludes that all pairwise comparisons were significant and thus all rounds had significantly different assemblages.

It was predicted that phenological patterns would lead to changes in saproxylic beetle assemblage composition on fresly felled trees. This phenological effect was isolated by sampling freshly felled trees for the first month at different seasonal timings. Assemblage composition differed significantly across rounds (PERMANOVA: R^2 = 0.28, p = 0.001). Pairwise comparisons are significant between all rounds and the visualisation shows a clear clustering of assemblages by sampling round and a gradient across time (Figure 7). The results strongly support the prediction that the first assemblages across different months are distinct. Fungivores seem to be less active during the earlier spring.

Effect of felling date on species composition (prediction 3)

Species composition of sampling collection B differed significantly between trees felled at different times (prediction 2; See figure 6). Therefore, felling date had a significant effect on species assemblage composition. Constrained ordination (Capscale) showed that felling treatments explained significant parts of the variation in species assemblage for the different treatments after correcting for location (ANOVA $p = 0.001$; figure 7). None of the covariables added explanatory value to the variation of the species composition in the capscale model (Canopy cover $p = 0.396$; TReM diversity $p = 0.698$; Living tree ground plane $p = 0.414$; dead wood volume $p = 0.618$).

The pairwise comparisons based on the distances of the capscale model show significant differences between felling treatments. Assemblages from trees felled 7 months prior differed from those felled 3 months ($R^2 = 0.24$, $p = 0.01$) and 1 month ($R^2 = 0.35$, $p = 0.01$) prior. Similarly, trees felled 5 months prior differed from those felled 1 month prior ($R^2 = 0.25$, $p = 0.02$). Other differences between treatments are weaker and not significant (see appendix 2). These results indicate a gradual turnover of assemblages.

To visualise these patterns, an NMDS ordination based on Bray-Curtis dissimilarities showed clustering of assemblages based on month of felling, while similar treatments overlapped. A global PERMANOVA on this visualisation confirmed the significant differences between felling months ($R^2 = 0.28$, $p = 0.001$). Both analyses show differences in beetles' assemblages because of felling timing and suggest a gradient of assemblages along the similarity of the treatments.

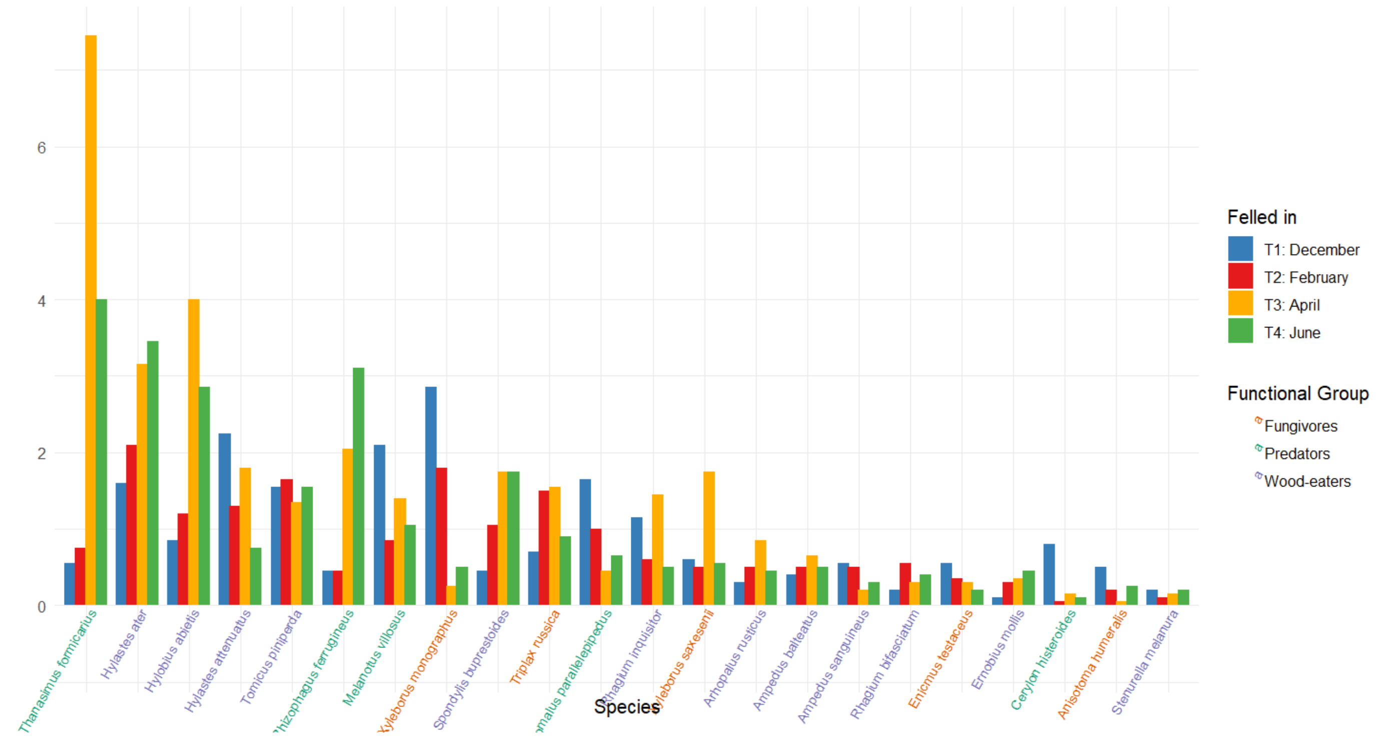

Figure 6: Average abundance of the most abundant beetle species (at least 10 individuals) across four tree-felling timings (December, February, April, June). Bars represent mean individual counts per tree, grouped by felling month. Species names are color-coded by functional group: Fungivores (blue), Wood-eaters (orange), and Predators (green). Species are ordered from most to least abundant across all treatments.

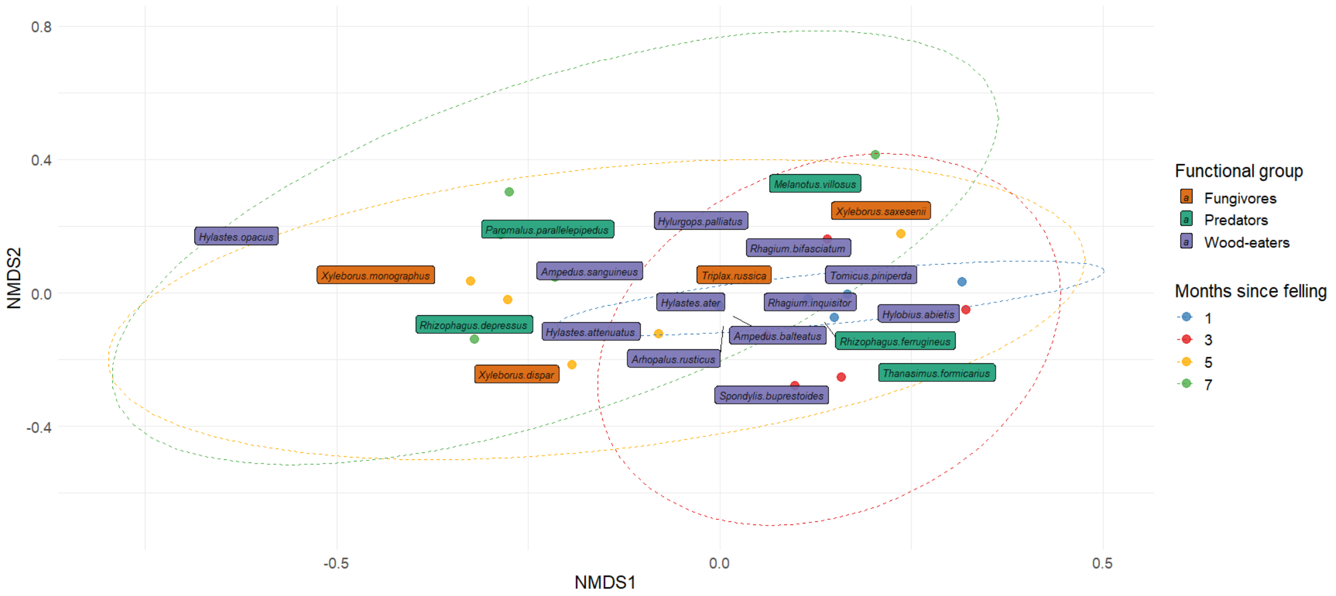

Figure 7: NMDS of saproxylic beetle assemblages and felling timing during June (Sampling collection B). Species labels highlight the top 20 most abundant species, color-coded by functional group: red for Fungivores, green for Predators and blue for Wood-eaters. Ellipses indicate 95% confidence areas per felling treatment. Saproxylic beetle assemblages differed significantly among felling treatments (PERMANOVA: $R^2 = 0.28$, $p = 0.001$), supporting the prediction (2) that trees felled at assemblages shift with felling timings.

Effect of felling date on species richness and functional groups (prediction 4)

Looking at the functional group abundances and the species richness, the GLMMs showed clear patterns in fungivore and predator abundance, while wood-eaters and species richness showed no significant differences among felling timings (Figure 5). In most cases, the covariables had no significant explanatory value. The results each variable of prediction 4, including covariates, will now be explained in detail.

Fungivores

Fungivore abundance increased strongly with time since felling. Compared to 7 months, abundances were 37–73% lower at earlier stages (1 month: $\beta = -1.30$, $p < 0.00001$; 3 months: $\beta = -0.45$, $p = 0.0013$; 5 months: $\beta = -0.46$, $p = 0.00027$). Dead wood volume had a positive effect ($\beta = 0.52$, $p < 0.00001$), so the other covariables were excluded from the model. Although not in the figure, fungivore species richness was not significantly affected by felling treatment or by any of the covariables, although the difference between 1 month and 7 months was almost significant ($\beta = -0.49880$, $p = 0.05239$; all other $p > 0.101$).

Wood-eaters

Wood-eater abundance peaked at 5 months after felling ($\beta = 0.274751$, $p = 0.00300$), with all other treatments not differing significantly ($p > 0.63$). TrEM diversity was the only covariable with a significant, surprisingly negative, effect on wood-eater abundance ($\beta = -1.925526$, $p = 0.00886$). Wood-eater species richness remained constant, with no significant differences between treatments or effects of covariables ($p > 0.30$).

Predators

Compared to 7 months, predator abundance peaked at 3 months ($\beta = 0.52$, $p < 0.00001$) and bottomed at 5 months ($\beta = -0.44$, $p = 0.00059$). Canopy cover had a negative effect ($\beta = -2.01$, $p = 0.0023$), suggesting predators prefer more open conditions. None of the treatments or covariates had significant effects on predator species richness ($p > 0.102$).

Species richness

Overall species richness did not differ significantly between the different felling treatments (all $p > 0.29$). The only significant covariate was TreM diversity, which had a significant negative effect ($\beta = -2.03$, $p = 0.018$).

Overall, the increase in fungivores with dead wood availability time is in line with prediction 1. Wood-eaters remained stable. The predators are also sensitive to dead wood availability time, but do not increase linearly but peak at 3 months, while increasing again at 7 months. These patterns did not result in any differences in species richness.

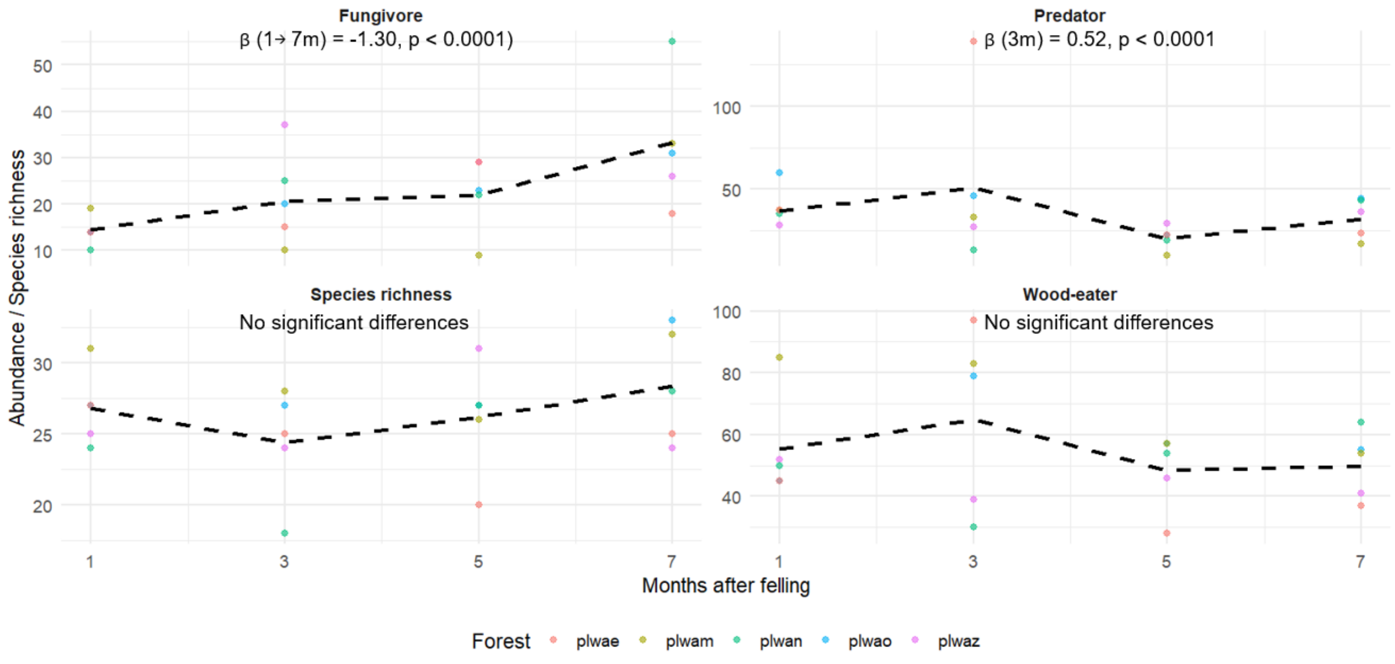

Figure 8: Felling time dependent trends in beetle guilds (following the division by Colijn & Burgers (2022)) with GLMM predictors. Abundance of fungivores, wood-eaters, predators, and overall species richness across four time points (1–7 months after felling), color-coded by location. Dashed lines represent GLMM predictions averaged across locations. Fungivore abundance increased significantly over time (β (Estimate) = -1.30 to -0.45, p < 0.001), and predator abundance peaked at 3 months (β = 0.52, p < 0.001). Species richness and wood-eater abundance showed no significant differences across time points. These patterns support the hypothesis that longer deadwood availability result in more habitat heterogeneity within the treatment tree, although it did not result in higher species richness.

Discussion

1. Key findings

In this ecological experiment, I tested the effect of felling date on saproxylic species richness, functional group composition and assemblage development on artificially felled Scots pine trees. Felling date significantly affected the initial assemblages, the assemblage composition observed, and the abundance of fungivores, which was higher on trees that had been felled for a longer time at the June sampling. Species richness, predators and wood-eaters remained stable across treatments.

Predictions

Stumps versus stems (prediction 1)

The expectation of higher species richness, number of individuals and Shannon diversity on stems, was strongly supported. In contrast to this research, other studies did not see increases in species numbers, individuals and diversity on high stumps (Hjältén et al., 2010; Lackner et al., 2024; Staff, 2015). The crucial difference between this study and the other studies is that this study used flight-interception traps as opposed to bark-peeling. Flight interception traps measure activity instead of presence and only sample at a fixed location (Gossner et al., 2013), while bark peeling measures exact presence equally on the entirety of the dead wood source. This makes flight-interception traps more susceptible to the microclimate, which was very different between the high stumps and the stems. The high stumps were more exposed to sun, resulting in a warmer microclimate and therewith more specimens in total and thus more richness, individuals and diversity. The mechanism is entirely methodological.

The other studies testing this hypothesis did however see differences in the species assemblages between stumps and stems (Hjältén et al., 2010; Lackner et al., 2024; Staff, 2015), which was not tested in this study, but highlights the added value of high stumps as they create different microhabitats with different species compared to stems.

Assemblage composition for start assemblages (prediction 2)

The prediction of differences in species assemblages on fresh trees in their first month was supported by the results. These seasonal differences in species assemblages have widely been documented (Sawoniewicz, 2015) and many species have distinct periods of activity during the year (Zeegers & Heijerman, 2008).

The absence of saproxylic beetles on the freshly felled trees in December can be explained by the low temperatures resulting in little to no beetle activity.

Because of the life cycles of saproxylic beetles on *pinus sylvestris* taking at least 50 days (Hlávková & Doležal, 2022), it can be assumed that all beetles that were caught in sampling collection A came from surrounding dead wood: none developed on the treatment trees.

The primary mechanism behind the different assemblages is phenology and the resulting variation in beetle species activity. This is clearly visible in the results as some species (such as *Arhopalus Rusticus* in the earlier months) were completely absent in some months, which is consistent with the knowledge of their phenology (Zeegers & Heijerman, 2008). Secondary explanatory value comes from a few other factors that differ between months. These are:

1. Fungal activity: throughout the year, fungal activity for different species varies, resulting in varying suitability for the species associated with them throughout the year, which can affect their activity.
2. Temperature and moisture: different months have different temperature and moisture levels, which typically means that the dead trees will be dryer in summer. This has undoubtedly impact on the activity of species the trees will attract.

The species assemblages on the first round that had sufficient activity (round 3), had few fungivores compared to later rounds (Figure 5). This suggests that fungivores may have alternative phenology compared to wood-eaters, a pattern that was also observed in Lenzi et al. (2025). This pattern suggests that functional group phenology follows the annual distribution of that functional group's resources.

Assemblage composition when sampled at the same time (prediction 3)

Different felling timings resulted in distinct species assemblages, confirming that the timing of tree death strongly shapes subsequent species assemblages.

Mechanisms

Previous studies (Foit 2012; Foit 2015) identified colonization windows as a key mechanism, and this explanation fits the patterns observed here. Trees that were in the "right" window during peak activity were likely colonized earlier, taking away resources for the species that came later.

Because the initial colonizing communities were different, priority effects may contribute, but they cannot be identified as the primary driver because treatment trees differed in multiple other ways. Differences in assemblages likely also arose from two factors inherent to the differences in timeframe:

1. Development time: Trees that were dead for a longer time, were visibly decayed and had more fungivores. This suggests that differences between the treatments could be down to differences in development time, not just the colonizer species. The different colonizing species had different lengths of time to alter the dead wood object. In the current design, it is impossible to distinguish which part of the differences in later assemblages were caused by the colonizing species and the time since tree death. Longer development time is known to result in different species assemblages and functional group compositions (Stokland et al., 2012). That pattern was also observed in the wood-eaters, who remained stable in total abundance but shifted in species identity, with recently felled trees hosting more Scolytinae (Appendix 3).
2. Microclimatic events; Trees that were felled earlier, experienced weather events differently compared to still-living trees, influencing internal conditions and therewith early assemblage development. Moisture and temperature are known to affect dispersal activity, metabolism and therewith saproxylic species assemblages (Romo et al., 2019; Hagge et al., 2024).

Ecologically, the results show that the timing of tree felling limits subsequent species assemblages, which are likely to remain different in later stages.

Functional group composition and species richness (Prediction 4)

Prediction 4 proposed that longer availability of dead wood would increase within-object habitat heterogeneity, leading to higher abundances of fungivores (1a) and predators (1c), stability in wood-eaters (1b) and ultimately higher species richness (1d).

Felling date had a clear positive effect on fungivore abundance, whereas predator abundance showed a non-linear pattern, peaking at three months and declining at five months before increasing again at seven months. Species richness did not differ among felling dates.

Fungivores

The increase in fungivores on older dead wood aligns with the expectation that fungal colonisation progresses with decay stage, creating more resources and microhabitats for fungivores. Such successional increases in fungivores are well documented in dead-wood systems (Mlynarek et al., 2018; Wende et al., 2017; Seibold et al., 2022). Fresher wood typically supports relatively less fungivores, because fungal development is still limited, resulting in fewer niches for fungivores.

Wood-eaters

Following expectations, wood-eaters remained stable in numbers and a gradual shift in species was visible with less Scolytinae and more Cerambycidae on the trees felled more recently. This pattern aligns with the expectation of a stability in resources for wood-eaters and a gradual shift in the nature of the dead wood habitat in the first few months. The shift in species within the wood-eaters is most likely caused by the shift in nature of the dead wood object by the damage of earlier wood-eaters, which happens in single months (Marini et al., 2013).

Predators

Predators did not increase as expected, the pattern was weak or absent. The peak at three months and decline at five months suggest that predator responses may lag behind fungivore increases or may be influenced by short term fluctuations in prey availability or microclimatic conditions as saproxylic beetles are known to be highly sensitive to microclimatic patterns (Seibold et al., 2015). The peak of predators on the trees that were felled 3 months before sampling, is likely explained by one outlier, namely a sample that had a disproportionally large number of *Thanassimus formicarius*. When excluding this outlier, the distribution of predators is more constant. The original reasoning for an increase in predators was an increase in prey because the fungivores were expected to increase, while the wood-eaters were expected to remain constant. Both these patterns were the case; however, this did not translate to significantly more predators. Although saproxylic predators are proven to prefer wood-eaters over fungivores, it is known that predators respond more strongly to changes in wood-eaters (Brin & Bouget, 2018; Wende et al., 2017). When looking at the individual forests that were sampled, a gradual increase in predator abundance over months since felling can be noticed on two out of five trees. The absence of this pattern could be attributed to a weakness in this pattern and fluctuations in microclimate and moisture.

Species richness

Field observations indicated that trees that were dead for a longer time, were more structurally heterogeneous (e.g., bark loss, woodpecker holes), consistent with the assumption that dead-wood age increases microhabitat diversity (Stokland et al., 2012). However, this increased heterogeneity did not translate into higher species richness in the trap catches. A factor could be that an increase in species that are associated with the very early phase of decomposition, such as sap-feeders (Stokland et al., 2012), resulted in higher species richness in the samples of trees that were felled more recently. Another explanation could be that species richness responds more slowly to changes in decay stage, considering that the difference between treatment was at most 7 months. Also, the richness differences may have been too subtle to detect with the sampling method used.

The hypothesis of Foit (2012) of “colonisation windows”, would translate into higher species richness on the trees felled in winter as these trees would be in the right window and the trees felled more recently would not be in the right window yet. That was the pattern observed by Foit (2012). Athough the increase in richness was not observed, colonisation windows can still play a role given the differences between species assemblages. If the entire first year of species assemblages on dead trees felled in different seasonal timings were to be documented, colonisation windows would suggest a higher cumulative species richness in this first year.

Overall, Prediction 1 was only partially supported: fungivore abundance increased with dead-wood age as expected, but predator abundance and species richness did not show the predicted positive responses.

Additionally, Gillespie et al. (2017) suggests that functional group and functional trait compositions shift throughout the year as resources and microclimates fluctuate throughout the year in a predictable fashion. An example of this is that larger species have shorter imago activity windows as they need resources that are different in nature compared to smaller species- namely larger resources, available for longer time. The results from prediction 2 support this reasoning: in March (Round 3), few fungivore species were active, potentially because that time of year does not offer suitable resources for fungivores.

2. Covariates

Simpson diversity of TreMs had a significant negative correlation with both species richness and wood-eater abundance, which are surprising results as TReM diversity is expected to increase diversity because it leads to more microhabitats. These observed patterns could be caused by inconsistencies in the measurements of the TReMs or there is an unknown mechanism behind this. Another aspect to consider are the limitations of the index in which specific information on the TReM type is lost. A direct analysis, where the unique TreMs are considered, was beyond the scope of this research.

Dead wood volume positively correlated with the number of fungivores, which is in line with literature on dead wood assemblages (Stokland et al., 2012). Oddly though, the other functional groups and species richness are also expected to be correlated positively, considering what is known from prior research. The absence of this pattern could be down to the selection of the treatment trees, during which the local dead wood volume was considered and therefore sites were chosen that were like one another regarding dead wood volume.

The canopy cover had a significant negative effect on predator presence, which is consistent with another study that found an effect of canopy cover on functional groups (Schmidl & Bussler, 2008). Higher canopy cover is also known to decrease the abundance of saproxylic beetles (Stokland et al., 2012; Seibold et al., 2016). There are no signs of inconsistencies in the data, although there are more robust techniques of measuring canopy cover (Von Meijenfeldt et al., 2025).

The relatively few cases of significant effects of the covariables indicate that the experiment was properly standardized for the measured covariates. Potential other, less influential, factors of influence are described in appendix 3.

3. Integrated findings

Regarding the first research aim. the results show that delayed seasonal timing of tree death shapes the subsequent species assemblages and their functional group composition with decreases in fungivores and stability in wood-eaters and predators as well as stability in species richness.

Priority effects

The second research aim was to assess whether priority effects occur in this system. The results show that trees felled at different times hosted different start assemblages (Prediction 2) and that these differences persisted into later sampling (Prediction 3). This pattern is consistent with priority effects, in which early colonisers influence subsequent species assemblage development.

However, alternative explanations cannot be ruled out. Differences in microclimate, decomposition stage, and seasonal species pools, which are all inherent to the felling-date treatments, may also drive divergent successional trajectories. Priority effects have been documented in dead wood systems, convincingly in interactions between early colonizing beetles and later fungal communities (Jacobsen et al., 2015) and are well established in vegetation ecology (Durbeck et al., 2023). Yet in dead wood systems, unlike in vegetation studies, manipulation of first colonizers, is harder to test. Without such manipulation, priority effects cannot be isolated from other factors correlating with felling date.

Thus, while the observed patterns are consistent with priority effects, they cannot be primarily attributed to them. Experimental introduction of primary colonisers would be required to distinguish priority effects from other factors that influence species assemblage.

4. Methodological considerations

This study used, like in Gossner et al., 2013, flight-interception traps, which could have led to biases in the data as this method measures activity instead of exact presence. Foit (2012) and Foit (2015) had a similar setup to this study, but used bark sampling instead of traps, which measures exact presence on the trees of interest. Because of the usage of the traps, species in their larval phase at the time of sampling are not caught, potentially explaining the lack of proof for prediction 4.

Only the beginning of decay was researched, but the pattern is expected to continue (Foit, 2012; Jacobsen et al., 2015). This experiment will continue with more rounds of window traps throughout the first year of development of every treatment tree.

Practical and logistical issues are always associated with field studies, and this one was no different. In round three, one sample (both the laying and trap on stumps) was missing, in round 5, one control tree sample was missing and in round 7, one laying sample on a treatment tree was vandalised. There are no indications that these incidents had a significant impact on the results and the following conclusions.

5. Management implications

Since different felling timings lead to different species compositions, it could be assumed that the highest diversity is created overall when the timing of dead wood creation is varied, however that is not proven. Evidence suggests that a more diverse timing of dead wood creation will lead to a wider range of ephemeral habitats and a wider range of species that will benefit. A management regime of dead wood creation that varies in seasonal timing would also

The advise to vary with seasonal felling timing is consistent with Laaksonen et al., (2020a), which found that because of the short window of suitable microhabitat, certain saproxylic species need a continuous sequence of dead wood sources to maintain their presence.

The strong effects of felling dates on species assemblages suggest that seasonal timing of tree death in forest ecosystems could also be used to protect endangered species such as *Cucujus cinnaberinus*. Optimal management practices with the goal of protecting certain endangered saproxylic species are already researched (Horák et al., 2011). In vegetation assemblage ecology, priority effects are already being planned for by sowing certain species to induce desired assemblages (Durbeck et al., 2023).

6. Future research

The experimental setup of this research will continue with the treatment trees being sampled for a longer time and new trees being felled every two months to document the development of species assemblages of six different felling timings in the first year. Consistent with other studies (Weslien et al., 2011), I expect the pattern of different courses of species assemblage developments to continue throughout the first year, although the effect will barely be visible during the colder months because of limited activity.

To definitively prove the priority effect, the factors that differed between the treatments of this experiment besides colonizer species, must be somehow removed. This can be done by packing trees for periods of time and allowing beetles experimentally so that only desired beetle species will make it in. This would not correct for fungal colonisation or differences in climatic factors. Another option could be releasing species different colonizer species on similar trees and validating that these species do colonise the trees. Such a study would have to prove the success of colonisation by the desired species after release.

Furthermore, for colonisation windows, stronger evidence could rome from a full documentation of all species in the first year on trees with varying felling timings. If colonisation windows would exist as understood in this research, the cumulative species richness over a year should be higher on trees that were felled in winter compared to trees felled in spring.

This research successfully prove that seasonal timing of tree death filters the potential species assemblages, which suggests that variation in felling timing would create optimal conditions for a wider range of species. Although my research did not find significant differences in species richness, similar experiments did, suggesting that certain felling timings benefit more species than others (Foit, 2012; Foit, 2015). The continuation of my experiment can give the necessary data to create a forest management regime where biodiversity is maximized using an optimal combination of seasonal timings of tree death.

Conclusion

This study shows that the seasonal timing of tree death partially determines saproxylic beetle assemblages on *Pinus sylvestris*. Multiple mechanisms help explain why felling treatments differed in initial colonizers, subsequent assemblages and functional group composition. These mechanisms include phenology, functional group development, and species altering habitats.

At the same time of sampling, species assemblages differed between trees felled at a different moment. The same was true at the very start of decay, confirming that trees felled in different months begin and continue their development with different species pools. These early differences were mostly driven by phenology. These early differences combined with differences in decay, resulted in subsequent differences in species assemblages. Therefore, the trees had different courses of species assemblages, which strongly suggest priority effects and colonisation windows in dead wood ecology. Differences in development across multiple mechanisms on different timeframes seem the primary driver ofifferences resulting from different felling timings.

From a management perspective, varying the seasonal timing of dead wood creation will benefit species in two primary ways: 1 create a wider range of diversity in dead wood decay stages across the forest, benefitting a wider range of species and 2 keep a more constant flow of new dead wood habitats so that microhabitats across all decay stages are supported and more species are supported. Ultimately, this study underscores the importance of temporal heterogeneity in ephemeral resource patches as a tool for maintaining and enhancing biodiversity.

Final remarks

This study was conducted in cooperation with Natuurmonumenten. During the preparation of this work the author used Copilot (version GPT-5.1) and Chatgpt (version GPT-4) for generating R code that was used in the analysis and for literature search. After using these toosl/services, the author thoroughly reviewed and edited the content as needed and takes full responsibility for the content of the publication. A full list of all ai conversations, with prompts, links and output, is provided in Appendix 4.

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Appendix 1

response	group1	group2	test	statistic	df	p	effsize	effsize_name	effsize_ci	n1	n2
Species Richness	Control living	Felled	t-test	-7.525	14.021	0.0000027500	*	*	*	5	39
Individuals	Control living	Felled	Wilcoxon rank-sum	20.000		0.0044000000	*	*	*	5	39
Shannon	Control living	Felled	t-test	-4.292	4.824	0.0084300000	*	*	*	5	39
NumSpecies	Laying	Standing	t-test	-7.172	36.679	0.0000000176	-2.30	Cohen's d	[-3.107, -1.474]	19	20
Individuals	Laryng	Standing	Wilcoxon rank-sum	1.500		0.0000001270		Rank-biserial r	[-0.996, -0.984]	19	20
Shannon	Laying	Standing	t-test	-3.825	35.387	0.0005110000	-1.23	Cohen's d	[-1.911, -0.536]	19	20

*Table 1 Prior analysis identifying the effect of felling and trap position on species richness, number of individuals and species diversity. *The effect size was not calculated for these comparisons as they were very lopsided (1 group way larger than the other), resulting in unreliable effect sizes.*

Appendix 2

Comparison of treatments Trees felled in	*R-square*	*P-value*
7 months vs 5 months	0.13	0.35
7 months vs 3 months	0.24	0.01
7 months vs 1 months	0.35	0.01
5 months vs 3 months	0.17	0.10
5 months vs 1 month	0.25	0.02
3 months vs 1 month	0.09	0.77

Table 2 Results from the pairwise comparison of assemblage compositions grouped by felling dates, using a PERMANOVA (Bray–Curtis distance, 999 permutations, blocked by location, using adonis2 from the vegan package). Significant differences in red (α < 0.05).

Appendix 3: Other factors of influence

Not all the factors determining dead wood species composition as written in the introduction were measured. The first potentially missing factor is the species pool available in the different forests in which the research was conducted. Because these forests potentially had differences in species composition throughout, the pools of potential colonizers could be different. The broader landscape context regarding dead wood including species, forest age and forest management is another factor of influence that is difficult to measure (Stokland et al., 2012). These factors were somewhat corrected for in the block design with different forests, however, these factors can vary within the forests.

Additionally, there could be differences in chemical and physical composition of the wood, cambium and bark between individuals of the same tree species, which was corrected for as much as possible when selecting treatment trees. Not all these differences are visible. No two trees are ever the same regarding moisture content, shape, pathogen presence, initial fungal colonizers, chemical defense and the VOC's released. Differences might persist, which could be measured by taking wood samples, which is sometimes done but no study found any effects when comparing dead wood bodies of the same species.

Overall, these factors are unlikely to have played major roles because the felling treatments mostly had significant effects. If these factors were to be influential, they would have to correlate with the treatments.

Appendix 4: Use of AI

For this thesis, AI was used for 2 purposes:

1. For assistance with writing the code for the analysis

Prompt: “can you give me code for a species accumulation curve?”

https://chatgpt.com/c/694e62e6-7d3c-8327-858f-20bca233a6c5

It gave the code for the species accumulation curve in the results

Prompt: Very detailed explanation of dataset structure, request for a paired line plot comparing trap positions.

https://copilot.microsoft.com/shares/4dXFxxeVfgMGyUqhryU55

The code was used for the chart in the results and adapted for the chart for control trees

Prompt: old linear model code was pasted with the request for species numbers per functional group.

https://copilot.microsoft.com/shares/GA4pyqXBGD653FgneUZMk

It gave code for an updated version of the code for the glmm that included species numbers per functional group across treatments. This analysis was mentioned in the results.

2. For literature search

Prompt: “zijn er voorbeelden van een toename bij insecten van zowel soorten als abundantie in dood hout ecosystemen? wetenschappelijke artikelen graag”

https://copilot.microsoft.com/shares/MC16XEBGTBXgMAoh1fFvi

It gave journal articles that were read and used.

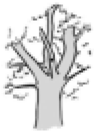
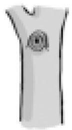
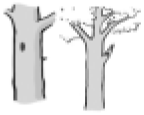
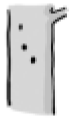
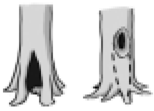
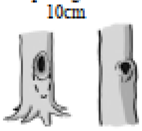
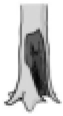
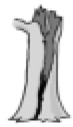
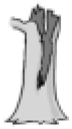
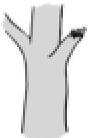
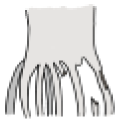
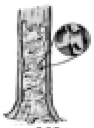
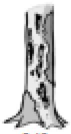
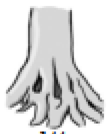
Prompt: “is this true?: any scientific sources?:

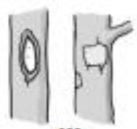
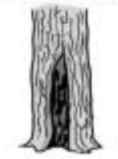
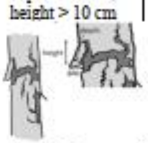
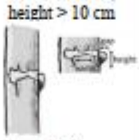
The shifts in functional group composition throughout the early phases of dead wood development (i.e. the first year), are poorly understood, yet plays a key role in the resulting species assemblages.”

https://copilot.microsoft.com/shares/oeipHXN1wL1tgDMBbB5MC

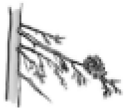
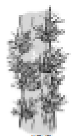
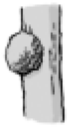
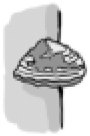
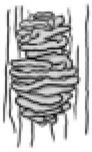
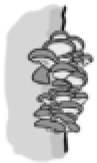
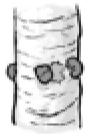
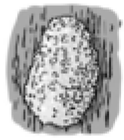
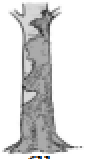
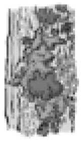
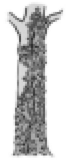
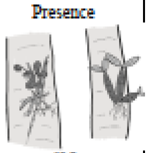
It gave scientific sources to backup the mechanism that I reasoned.

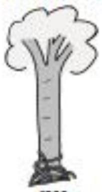
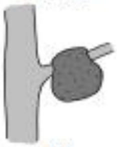
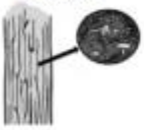
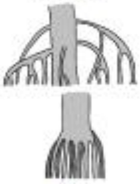
Appendix 5: List of TrEMs

Form	Group	Types				
Cavitites l. s.	Woodpecker breeding cavities	**Small woodpecker breeding cavity** Entrance Ø <4cm  **111**	**Medium-sized woodpecker breeding cavity** Entrance Ø = 4-7cm  **112**	**Large woodpecker breeding cavity** Entrance Ø >10cm  **113**	**Woodpecker flute** Entrance Ø > 3cm  **114**	
	Rot-holes	**Trunk base rot-hole (closed top, ground contact)** Opening Ø > 10cm  **121**	**Trunk base rot-hole (closed top, no ground contact)** Opening Ø > 10cm  **122**	**Semi-open trunk rot-hole** Opening Ø > 30cm  **123**	**Chimney trunk base rot-hole** Opening Ø > 30cm  **124**	**Chimney trunk rot-hole** Opening Ø > 30cm  **125**
		Hollow branch Opening Ø > 10cm  **126**	**Broken Stiltroot** Depth >10cm, Ø > 5cm  **127**			
	Insect galleries	**Insect galleries and bore holes** Hole Ø > 2cm or area >300cm²  **131**				
	Concavities	**Woodpecker foraging excavation** Depth >10cm, Ø > 10cm  **142**	**Trunk bark-lined concavity** Depth >10cm, Ø > 10cm  **143**	**Root-buttress concavity** Entrance Ø > 10cm  **144**		

	Concavities by leaves or fruits	**Furled leaf concavity** Entrance Ø > 10cm  151	**Leaf tent**  152	**Dry / Old fruits with cavitites**  153	**Dead leaves frill** Multiple layers of leaves  154	
	Dendrotelms	**Dendrotelm** Ø > 15cm  161	**Bromeliads** Presence  162			
Tree injuries and exposed wood	Exposed sapwood only	**Bark loss** Area > 300 cm²  211	**Fire scar** Area > 600 cm²  212	**Bark shelter** Gap > 1 cm, depth > 10 cm, height > 10 cm  213	**Bark pocket** Gap > 1 cm, width > 10 cm, height > 10 cm  214	
	Exposed sapwood and heartwood	**Stem breakage** Ø > 10 cm at break point  221	**Limb breakage** Exposed heartwood > 300 cm²  222	**Crack** Length > 30 cm, width > 1 cm, depth > 10 cm  223	**Lightning scar** Length > 30 cm, width > 1 cm, depth > 10 cm  224	**Fork split at insertion** Length > 30 cm  225
Crown deadwood	Crown deadwood	**Dead brances** Branch Ø > 10 cm, or Branches Ø >3 cm and > 10 % of the crown is dea  311	**Dead top** Ø > 10 cm at the base of the piece or deadwood  312	**Remaining broken limb** Broken end Ø > 20 cm, length of the remaining piece > 0.5 m  313		

2

Excrescences	Twig tangles	**Witch broom** Largest Ø > 50 cm  **411**	**Epicormic shoots** >5 twig clusters  **412**			
	Burrs and cankers	**Burr** Largest Ø > 20 cm  **421**	**Canker** Largest Ø > 20 cm or large part of the trunk covered  **422**			
Fruiting bodies of saproxylic fungi and slime moulds	Perennial fungal fruiting bodies	**Perennial polypore** Largest Ø > 5 cm  **511**				
	Ephemeral fungal fruiting bodies	**Annual polypore** Largest Ø > 5 cm or cluster of > 10 fruiting bodies  **512**	**Pulpy agaric** Largest Ø > 5 cm or cluster of > 10 fruiting bodies  **513**	**Large Pyrenomycete** Stroma Ø > 3 cm or stroma cluster covering > 100 cm²  **514**	**Myxomycetes** Largest Ø > 5 cm  **515**	
Epiphytic and epixylic structures	Epiphytic and parasitic crypto- and phanerogams	**Bryophytes** > 10 % of the trunk area covered  **611**	**Foliose and fructicose lichens** >10 % of the trunk area covered  **612**	**Ivy and lianas** >10 % of the trunk area covered  **613**	**Ferns** > 5 fronds  **614**	**Orchids** Presence  **615**

		Mistletoe Largest Ø > 20 cm  **617**	**Hemiepyphyte**  **618**	**Strangler Fig around living tree**  **619**	**Strangler Fig around dead tree**  **6110**	**Dead Lianas**  **6111**
	Nests	**Vertebrate nest** Ø > 10 cm  **621**	**Invertebrate nest** Presence  **622**	**Cartonnest** Presence  **623**		
	Microsoils	**Bark microsoil** Presence  **631**	**Crown microsoil** Presence  **632**	**Dead leaf** >1 m  **633**		
Exudates	Exudates	**Sap run** Cumulative length > 10 cm  **711**	**Heavy resinosis** Cumulative length > 10 cm  **712**			
Root formations	Root formations	**Stiltroots**  **811**	**Buttressroots**  **812**			