Variations of saproxylic beetle assemblages within the same white spruce logs across early and
advanced decay classes

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Advisor   Second Reader

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ABSTRACT

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Keywords: abundance, advanced decay, Alberta, beetles, community structure, conservation, early decay, niche partitioning, richness, saproxylic, spatial aggregation, white spruce

Saproxylic species play a multitude of essential ecological roles within the forest ecosystem by undergoing a distinct succession as deadwood decays in the early to late successional stages. As of 2024, knowledge regarding saproxylic beetle community drivers, in terms of biotic interactions and larval niches, is still minimal. Striving to understand the structure, function, drivers of community assembly, and spatiotemporal dynamics of saproxylic fauna in forest ecosystems is necessary to ensure the conservation of saproxylic biodiversity. This study investigates whether there are patterns of diversity, abundance, and composition of saproxylic beetles within sections of the same white spruce log and whether there are differences or similarities between the early decay class (DC2) and advanced decay class (DC5) of white spruce logs. The study was carried out in a 10-ha non-harvested white spruce [(Picea glauca (Moench) Voss)] stand (56°79′N, 118°36′W, 758 m a.s.l.) located at the Ecosystem Management Emulating Natural Disturbances (EMEND) research site in northwestern Alberta. Both DC2 and DC5 white spruce logs were cut into five bolts, 60 cm long, with 60 cm intervals between each bolt. A total of 30 white spruce bolts were transported to Berlese funnels where saproxylic beetles were collected, and later identified to species and feeding guild. The data collected was analyzed using Excel and RStudio, using Generalized Linear Model (GLM) to compare species richness and abundance and Non-metric Multidimensional Scaling (NMS) ordination to understand community structure. Results from this study indicated that mean species richness did not differ significantly within and between decay classes. However, saproxylic beetle abundance was significantly highest in bolt two, second from the stump, and gradually declined in abundance towards bolts situated higher in the tree. Even though species richness did not differ significantly within and between decay classes, DC2 showed less similarity in species composition across the log replicates than DC5. These results indicate that saproxylic beetle assemblages are spatially aggregated within the same decay class of log. This study revealed that log sections closest to the stump are recommended to be left post-harvest to aid saproxylic beetle population persistence rather than leaving treetops. Most importantly, understanding the niche partitioning of saproxylic species at different decay stages of deadwood, in terms of competition and co-existence, can contribute to developing forest management strategies that have the least impact on saproxylic beetle populations.

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INTRODUCTION

Saproxylic insects depend on dead woody material, wood-inhabiting fungi, or other saproxylic species during all or part of their lifecycle (Speight 1989; Hammond et al. 2004; Horak 2021). They are taxonomically diverse with many important trophic roles and significantly contribute to overall forest biodiversity (Jacobs et al. 2007; Onodera et al. 2017). In fact, most boreal taxa are less diverse than forest arthropod communities (Hammond et al. 2004). Saproxylic insects, in particular, play a multitude of essential ecological roles within the forest ecosystem, such as decomposing coarse woody materials, nutrient cycling, and contributing to food web dynamics (Hammond et al. 2001; Jacobs et al. 2007; Onodera et al. 2017). This group of organisms comprises a large portion of biodiversity associated with deadwood (Siebold et al. 2023).

Deadwood remnants play structural roles in forest ecosystems, such as regulating geomorphic processes like soil erosion and interrupting litter and water movement on slopes (Hammond et al. 2001) Deadwood provides habitats for forest organisms by holding moisture, providing substrates for growth, and contributing nutrients to forest soils over the long term (Hammond et al. 2001; Lee et al. 2014). Deadwood is a key functional ecosystem attribute for biodiversity as its decomposition takes several months to decades, offering a variety of microhabitats for large and diverse assemblages of forest organisms (Jacobs et al. 2007; Lee et al. 2014; Siebold et al. 2023). Maintaining the quantity and quality of deadwood is considered one of the most important attributes in forest ecosystems to sustain saproxylic diversity (Jacobs et al. 2007; Janssen et al. 2011). Saproxylic beetle assemblages are sensitive to environmental disturbances that affect the quality and quantity of deadwood, in terms of size, wood traits,

climatic conditions, and the decomposer community (Jacobs et al. 2007; Siebold et al. 2023). The distinct succession of saproxylic beetles as deadwood decays demonstrates the importance of conserving all decay classes of deadwood post-disturbance to sustain biodiversity levels (Jacobs et al. 2007). In managed forests, the creation and retention of deadwood has been recommended to reduce habitat loss for saproxylic species (Onodera et al. 2017).

To sustain the biodiversity of deadwood-dependent species in managed forest ecosystems, a better understanding of the drivers of their community assembly is needed (Seibold et al. 2023). Efforts to understand the structure, function, and spatiotemporal dynamics of saproxylic fauna in forest ecosystems are necessary to ensure the conservation of saproxylic biodiversity (Hammond et al. 2001). Identifying a species' position in the ecosystem, in terms of its biotic interactions and abiotic habitat requirements, requires an understanding of its ecological niche (Horak 2021). The decay rate of deadwood is influenced by the association between insects and decay fungi, due to the vectoring of decay fungi by saproxylic beetles (Hammond et al. 2001). Understanding the niche partitioning of saproxylic species at different decay stages of deadwood, in terms of competition and co-existence, can contribute to the development of forest management strategies that minimize impacts on populations of saproxylic beetles (Hammond et al. 2001). As of 2024, knowledge regarding saproxylic beetle community drivers, in terms of biotic interactions and larval niches, is still minimal (Horak 2021). The overall goals of this study are to understand variations and diversity patterns of saproxylic beetle assemblages within five sections of the same stem in both early and advanced decay classes of white spruce logs and to compare structures of beetle assemblages between the early and advanced decay classes.

OBJECTIVE

To discover and describe variations of saproxylic beetle assemblages within five sections of the same stem in both the early decay class (DC2) and advanced decay class (DC5) white spruce logs and to compare saproxylic assemblages between the early and advanced decay classes of deadwood. The study intends to understand the drivers of saproxylic beetle community structures by determining whether there are patterns of saproxylic beetles across the five deadwood sections within and between decay classes.

HYPOTHESES

The null hypothesis states that there are no similarities in saproxylic beetle assemblages within each section of the same stem, attributing any similarities to stochasticity in beetle aggregation within deadwood. The alternative hypothesis proposes that saproxylic beetle assemblages within each section of the same stem are similar.

A secondary hypothesis states that early decay classes of logs exhibit less variation in saproxylic beetle assemblages within the same log compared to advanced decay classes. This could be attributed to the larger variety of niches provided by advanced decay classes of deadwood, such as sections decomposing at different rates due to the growth of mosses and plants accelerating the decay of certain sections. Additionally, advanced decay stages may attract a broader range of saproxylic beetles that are generalists across multiple stages of decomposition.

LITERATURE REVIEW

SAPROXYLICS

Canada is home to approximately 30 percent of the world's boreal forests, which host an estimated 22,000 species of insects (Langor et al. 2006). Nearly half of these species remain undescribed and are forest generalists found in other forest types (Langor et al. 2006). Saproxylics exhibit the highest diversity and most characteristic assemblages of all boreal forest arthropods (Langor et al. 2006). The term saproxylic refers to the nature of biodiversity associated with deadwood (Stokland et al. 2012). Saproxylic invertebrates, best defined by Speight (1989), are species that depend on dead or dying woody material, wood-inhabiting fungi, or other saproxylics during some or all stages of their lifecycle. Fungi and insects constitute most of the wood-inhabiting biodiversity associated with decayed wood, with wood-inhabiting insects predominantly found in four key orders: Coleoptera, Diptera, Hymenoptera, and Isoptera (Stokland et al. 2012). Lepidoptera and Hemiptera comprise fewer species that inhabit wood (Stokland et al. 2012).

Within boreal forests and northern temperate regions, beetles are the principal invertebrate decomposers of deadwood, while brown-rot fungi are the main fungal decomposers of coniferous wood (Stokland et al. 2012). The dispersal ability of only a few saproxylics is currently understood, and this ability allows species to persist in changing environments, affecting population dynamics, extinction risk, and species distributions (Feldhaar and Schauer 2018). Dispersal ranges can vary from a few metres by walking, characteristic of saproxylics

using persistent habitats with longer longevity, to 100 kilometres in some flying bark beetles, characteristic of saproxylics using more transient habitats (Feldhaar and Schauer 2018).

Saproxylic invertebrate species fulfill a magnitude of functional roles within the forest ecosystem, including those of detritivores, fungivores, predators, scavengers, and parasitoids, with a variety of symbiotic relationships (Stokland et al. 2012; Lee et al. 2018). The diversity of trophic levels associated with saproxylics is due to the high spatial variability within stands and the microhabitat variability (Langor et al. 2006). The saproxylic food web comprises detritivores that consume decaying plant material, bacteria, or fungi that brought about the decay (Stokland et al. 2012; Ulyshen and Šobotník 2018). Most saproxylics feed within the cambium zone due to the tissue rich in sugars, while others feed on easily digestible cytoplasm, rich in proteins, lipids, and starches (Stokland et al. 2012). Insects with a specialized enzyme apparatus feed on cell walls that are more difficult to digest, which are rich in cellulose, hemicellulose, and lignin (Stokland et al. 2012). Understanding the intricate details of saproxylics is imperative for designing forest management plans and conservation strategies aimed at preserving saproxylic populations (Feldhaar and Schauer 2018).

Saproxylic beetles often initiate the process of decomposition as they are among the first to colonize dying trees (Janssen et al. 2011). Dying or dead trees emit volatiles such as ethanol and terpenes, which attract saproxylic species (Hammond et al. 2001). Primary saproxylic species penetrate and tunnel through un-populated portions of the wood, as they are responsible for the mechanical breakdown of deadwood by slowly digesting cell walls and cell contents (Speight 1989; Hammond et al. 2004). Phloeophagous and xylophagous beetles, which feed on the phloem and xylem of the tree, are among the primary saproxylics to colonize, feed, and breed in recently dead or dying trees (Speight 1989; Webb et al. 2008). Saproxylic species indirectly

break down woody materials by vectoring and facilitating decay fungi and other microorganisms that humify wood (Hammond et al. 2004). Speight (1989) states that populations of saproxylic organisms increase as primary saproxylic species establish a wider array of habitats. This is due to secondary saproxylic species that cannot tunnel or rely on substrates somewhat decomposed, depending upon primary saproxylics to access and initiate the decomposition of uncolonized wood (Speight 1989). Insects within the mycetophagous and predaceous feeding guild, including fungivorous insects and insects that prey on other saproxylics, are among the secondary saproxylics that are characteristic of deadwood in advanced decay classes (Speight 1989; Lee et al. 2014).

DEADWOOD

Large-scale disturbances and treefalls create spatial heterogeneity of deadwood across the forest floor, producing a variety of microhabitats that can be classified as snags, logs, coarse woody material, and fine-woody material (Hofgaard 1993). Understanding the definitions of each type of deadwood is essential for understanding saproxylic niches. For the purpose of this thesis, 'deadwood' represents the dead tissue of fallen trees, including the bark and wood (Wood 2012). 'Logs' and 'coarse woody material' or 'debris' are terms related to deadwood and will be used interchangeably (Lee et al. 2014), while 'snags' are considered standing dead trees (Onodera et al. 2016). In this thesis, 'coarse woody material' refers to larger deadwood on the ground, such as logs, whereas 'fine woody material' is considered as twigs and branches. Both vertebrate and invertebrate species use deadwood and snags as habitats for breeding and other purposes, which is of ecological importance for their population persistence (Stokland et al. 2012).

Deadwood undergoes both physical and chemical changes as decay advances (Stokland et al. 2012). Understanding and predicting these changes to bark cover, wood density, and moisture content can help understand the niches required by the wide diversity of saproxylic insects, as deadwood has a large impact on their biodiversity (Wood 2012). The inner bark is the first to be consumed once a tree dies, while the wood becomes soft and nitrogen-rich from fungal decay, and moisture content increases steadily (Stokland et al. 2012). Prior to decay, wood is a nitrogen-poor resource (Stokland et al. 2012). However, once wood is infiltrated by fungal decay, nitrogen levels increase rapidly as fungal mycelium contains seven to ten times more nitrogen than wood (Stokland et al. 2012). Rates of decomposition are significantly influenced by lignin abundances and carbon-to-nitrogen ratios (Lasota et al. 2018). Conifers have a higher lignin content, in quantity and qualitative composition than broadleaved trees, making them more resistant to microbial degradation (Stokland et al. 2012). The lignin composition found in conifers also influences the fungal host-tree preferences, as most brown-rot fungi are confined to coniferous trees (Stokland et al. 2012). Unlike broadleaved trees, conifers also have a resin defence system that can seal wounds, preventing some saproxylic species from attacking (Stokland et al. 2012).

To comprehend the relationship between saproxylic species and various deadwood decay classes, characterized by their physical attributes, wood softness, nutrient dynamics, and biomass loss, a classification system for deadwood decay is needed (Stokland et al. 2012; Lee et al. 2014). This study employs a similar classification system to Hofgaard's (1993) proposal, which includes eight classification degrees. In this system, a DC1 log is newly fallen with needles, while a DC8 log is unrecognizable due to complete humification. This thesis will analyze saproxylic beetle assemblages in decay classes two (DC2) and five (DC5) of white spruce logs, representing early and advanced decay, respectively.

DC2 deadwood is characterized by bark loose or falling off, decay penetrating less than three cm into the wood, initial mycelium growth beneath the bark, weakly decayed, and typically occurring 10 years post-tree death (Stokland et al. 2012). Advanced decay deadwood is nearly decomposed, characterized by a heavily fragmented stem outline, disintegration upon lifting, there is a presence of wood mould in cavities, and typically occurs 80 to 100 years post-tree death (Stokland et al. 2012). The decomposition of deadwood comprises heterotrophic respiration, biological transformation, physical fragmentation, and leaching (Lasota et al. 2018). This process is segmented into three phases driven by saproxylic beetles: colonization, decomposition, and humification (Speight 1989).

During the colonization phase, primary saproxylics capable of cellulose digestion, infiltrate the intact wood of recently deceased trees, carving tunnels through the bark and wood (Speight 1989). Decomposition rates of deadwood are influenced by factors such as temperature, moisture, substrate quality, and tree species, particularly their lignin richness and the carbon-to-nitrogen ratio (Lasota et al. 2018).

In the decomposition phase, secondary saproxylics feed on or off the activities of the primary saproxylics, accelerating the decomposition process as more organisms exploit previously inaccessible resources (Speight 1989). The thickness and decomposition quality of deadwood, rather than its quantity, are crucial for the survival of various organisms (Lasota et al. 2018). Saproxylics, both primary and secondary, often transport symbiotic fungi between deadwood, introducing fungi that increase supplies of decaying tissue, while saproxylic larvae feed on the fungal spores (Speight 1989).

During decomposition, strongly decayed logs leach carbon while fungi and bacteria advance decay and enrich the concentration of other macronutrients, such as nitrogen,

phosphorus, potassium, calcium, and magnesium (Bade 2015; Lasota et al. 2018). Prior to the humification phase, deadwood becomes a relatively rich substrate due to the colonization by fungi, bryophytes, lichens, and higher plants (Bade 2015). Nutrient leaching from a recently dead log slows as water penetrates deadwood but accelerates with the advancement of decay and involvement of microorganisms decomposing polymers (Lasota et al. 2018).

During the final humification phase, soil organisms replace saproxylics and feed on the bacteria or micro-fungi responsible for wood humification (Speight 1989).

NICHE PARTITIONING

Ecology fundamentally seeks to comprehend species interactions and overlapping niches (Horak 2021). Documenting patterns among coexisting species and discovering the underlying assembly rules is an ongoing endeavour in community ecology (Zhang et al. 2009). Saproxylic communities, a significant component of deadwood-associated biodiversity, depend on the composition of preceding and concurrent communities (Siebold et al. 2023). Horak (2021) hypothesizes that smaller organisms have more competitive interactions. Community assembly species co-existence patterns were initially thought to result from interspecific competition for identical resources (Zhang et al. 2009). However, studies on resource partitioning, spatial aggregation, temporal segregation, and assemblage diversity suggest these mechanisms may facilitate species co-existence, challenging the theory that species co-existence results solely from interspecific competition (Zhang et al. 2009; Kadowaki 2010).

The neutral theory of biodiversity proposes that species diversity in natural communities is primarily controlled by the neutral drift of species abundances, structuring community

assemblages (Horak 2021). In contrast, the traditional successional niche partitioning theory assumes that different species use different resources, fulfilling niches requiring different developmental and/or life stages of a resource through competitive coexistence (Kadowaki 2010). The neutral theory aligns with spatial aggregation, suggesting that if different species are spatially aggregated in patches, there will be patches with few or no individuals, creating spatial refuges for inferior competitors (Wertheim et al. 2000; Kadowaki 2010).

According to the competitive exclusion principle, when two coexisting populations occupy the same ecological niche, the dominant species will replace the other to reduce competition (Zhang et al. 2021). Typically, less dominant species with overlapping ecological niches will evolve to utilize other resources, a process described as niche differentiation (Zhang et al. 2021). Competitive coexistence can be explained through niche partitioning, where species divide available resources to minimize competition, contributing to spatial mechanisms in patchy systems, where saproxylic species display gregarious behaviours (Kadowaki 2010; Horak 2021). Spatial and temporal resource partitioning and ecological displacement are mechanisms of niche differentiation (Zhang et al. 2021).

Spatial variation has a stronger effect on co-existence than temporal variation, where different species have their highest recruitment at different times (Wertheim et al. 2000). Under the spatial aggregation theory, constraints on metabolic, developmental, digestive, searching abilities and detoxication mechanisms of insects govern the optimal utilization of available resources, rather than niche partitioning (Wertheim et al. 2000). Zhang et al. (2021) classify these constraints as extrinsic competition, in terms of searching efficiency and reproduction ability, while intrinsic competition relates to larval development. Horak (2021) noted that aggregated occurrence patterns may result from poor dispersal capacity and should be considered when

studying saproxylics. The debate in community ecology continues as species co-occurrence analyses are completed, questioning whether communities are random assemblages under the spatial aggregation theory, or whether they are the result of deterministic mechanisms, such as interspecific competition and the competitive exclusion principle (Zhang et al. 2009).

Analyzing species co-existence patterns is crucial to understanding saproxylic community drivers as habitats constantly change. Siebold et al. (2023) suggest that host specialization peaks during early decay stages due to high concentrations of secondary metabolites related to plant defence post-tree death. As deadwood progressively decays and other microorganisms are introduced to accelerate the decay process, habitat heterogeneity becomes a key factor in shaping saproxylic communities (Zhang et al. 2009). Host specialization diminishes with ongoing succession associated with advanced decay, and generalists become more prevalent in advanced decay stages (Siebold et al. 2023). Kadowaki (2010) noted that generalist species exhibit lower population persistence than specialists, possibly due to increased habitat heterogeneity from accelerated decay advancement as a larger diversity of microorganisms invade the CWD (Hammond et al. 2004). Siebold et al. (2023) hypothesize that biotic homogenization escalates with CWD decomposition advancement due to decreased CWD spatial beta diversity. Fungivorous insects within the mycetophagous feeding guild, predaceous insects, and parasitoids are most abundant in the final stages of decomposition (Lee et al. 2014). Habitat heterogeneity, evolutionary history, and stochastic processes are all valid explanations for species co-occurrence patterns, rather than interspecific competition (Zhang et al. 2009).

Horak (2021) examined fire-coloured beetle assemblages and found that both niche partitioning and the neutral drift theory influenced species co-existence. Kadowaki (2010) discovered that resource partitioning and spatial aggregation both drive community assemblage

in mycophagous insect communities on diverse, patchy resources. However, temporal variation, studied using fungal sporocarps with a wide range of temporal variation, was not identified as a driver of community assemblage (Kadowaki 2010). Niche partitioning occurs when one species avoids others in a resource-rich environment where all species have similar dietary preferences (Horak 2021). Wertheim et al. (2000) found that spatial aggregation alone maintains species diversity in a mycophagous insect community, disproving that resource partitioning aids species co-existence. The utilization of resources was a random association, as saproxylics exhibit gregarious behaviours, validating the spatial aggregation theory (Wertheim et al. 2000; Horak 2021). Shorrocks and Sevenster (1995) also found that resource partitioning does not contribute to co-existence and that aggregation is the dominant force maintaining diversity. Horak (2021) noted as well that the lack of strong niche partitioning in their study could be due to the neutral drift theory. Wertheim et al. (2000) reiterate that spatial aggregation contributes to co-existence and diversity, is sufficient and necessary to stabilize co-existence, and that interspecific competition does not select for specialization nor character displacement when resource utilization differences are considered. Zhang et al. (2021) studied niche differentiation of two pupal parasitoid wasps with overlapping ecological niches and found that interspecific competition influenced the coexistence of the species through niche differentiation due to extrinsic competition, as one of the wasps had increased searching ability for hosts and better penetrable ability into substrates (Zhang et al. 2021).

MATERIALS AND METHODS

LOCATION

The research was conducted in a 10-ha non-harvested white spruce stand in the 'G block' (56°79′N, 118°36′W, 758ma.s.l.) at the Ecosystem Management Emulating Natural Disturbance (EMEND) research site, established between 1998 and 1999 (Lee et al. 2014). Collections occurred within the "control" compartment of the EMEND experiment's 'G block', situated approximately 90 kilometres northwest of Peace River in the Lower Foothills eco-region of northwestern Alberta. (Lee et al. 2014). The study area, originating from a mixed-severity wildfire regime, currently comprises boreal mixed-wood forests with patches of mesic upland stands (Lee et al. 2022). The 'G block' control compartment's understory is characterized by mosses and lichens with a shrub layer dominated by *Rosa acicularis* Lindl. and *Viburnum edule* (Michx.) Raf., and the common vascular plants including *Cornus canadensis* L., *Linnaea borealis* L., *Rubus pubescens* Raf. and *Epilobium angustifolium* (L.) Holub (Lee et al. 2014). The overstory primarily includes trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and white spruce, with sporadic occurrences of black spruce (*Picea mariana*), lodgepole pine (*Pinus contorta*), balsam fir (*Abies balsamea*), and paper birch (*Betula papyrifera*) (Lee et al. 2022). The mean daily temperatures in Peace River, Alberta for January and July were -9.3°C and 17.6°C respectively, with total precipitation of 1.4 millimetres and 91.5 millimetres in the respective months (Government of Canada 2023).

SAMPLING DEADWOOD

Saproxylic beetle assemblages from the same stem of fallen deadwood in early (DC2) and advanced decay classes (DC5) of white spruce logs were sampled to analyze assemblage distribution within and between decay classes (Figure 1). All figure photos were taken by Dr. Seung-Il Lee in 2011 during the sampling period.

Figure 1. A representative cross-section of the early (left) and advanced (right) decay class logs.

Early and advanced decay class white spruce logs were segmented into five 60 cm bolts, spaced 60 cm apart. The first bolt within the stem is located 1 m above the root collar. This experimental design, with an equal number of bolts cut from the DC2 and DC5 white spruce logs, was replicated thrice, resulting in a total of 30 white spruce bolts from six different logs within the two different decay classes (Figure 2).
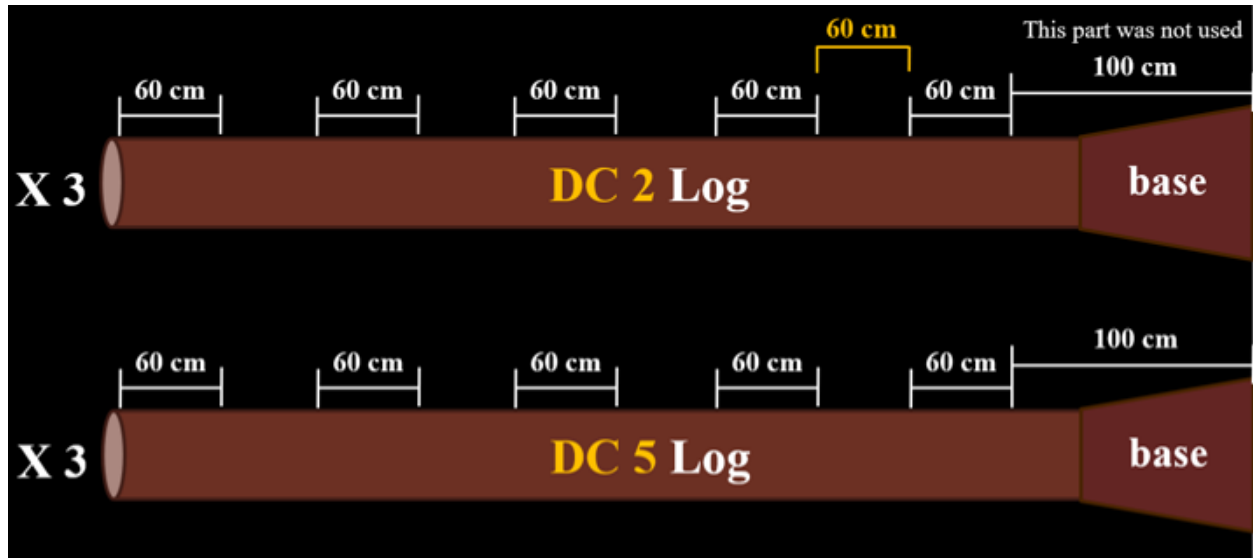
Figure 2. The experimental design to collect the bolts for the saproxylic insect collection.

BERLESE FUNNEL AND BEETLE SAMPLING

Five collections from the 30 bolts were made between July 15th, 2011, and September 12th, 2011, using Berlese funnels. Saproxylic insects were classified into family, genera, and species and categorized into their respective feeding guilds; detritivorous, mycetophagous, phloeophagous, phytophagous, predaceous, xylophagous, and an unknown category. A table of raw data is presented in Appendix I.

The 30 white spruce bolts were transported to Berlese funnels at the Mercer Peace River warehouse. DC2 bolts were halved if they exceeded the Berlese funnel capacity (Figure 3). The Berlese funnels, made from plastic, featured a cylindrical portion (40.6cm tall and 47 cm in diameter), attached at the bottom, allowing beetles to pass through due to a course metal hardware cloth (2 cm × 2cm) supporting wood samples above the funnel (29 cm tall) (Wood

2012). The funnel's base was equipped with a Whirl-PakTM bag containing around 50 mL of propylene glycol for beetle euthanasia and preservation (Wood 2012). Each funnel was sealed with a tight lid featuring a plastic rim and a central opening covered by a 2 mm by 2 mm metal mesh (Wood 2012). A 100-watt light bulb was suspended about 1 to 2 cm above each funnel lid, illuminating continuously throughout the extraction period (Wood 2012). The captured beetles were transferred into 70% ethanol for storage (Wood 2012).

Figure 3. Berlese funnels used for the saproxylic beetle collection at the Mercer Peace River warehouse in Peace River, Alberta. Beetle collection from the early and advanced decay class is seen in the left two images and the right image, respectively.

Beetles captured and preserved in ethanol were examined under a dissecting microscope for species identification (Figure 4).

Figure 4. Microscopic image of a few of the saproxylic insects sampled in early decay class and preserved in 70% ethanol.

STATISTICAL ANALYSIS

The raw data, with beetle identification to family, genus, species and feeding guild, from the 30 white spruce bolts within DC2 and DC5, was analyzed using Excel and RStudio (RStudio Team 2020). Singletons and doubletons were included in all analyses due to their high abundance. Most analyses used Generalized Linear Modeling (GLM) with Gaussian distribution, as the raw data was often square-root or double square-root transformed, resulting in continuous data. GLM, an extension of familiar regression models was preferred over the traditional Analysis of Variance (ANOVA) or standard General Linear Model due to its effectiveness and versatility. To comprehend the significance of the results for the abundance and richness graphs, the 'MASS' package in RStudio was installed to use the "glm.nb" function, addressing over-dispersed data. The 'MASS' package supports Venables and Ripley's MASS functions and datasets. The Shapiro-Wilk normality test was subsequently applied to assess data normality. The 'multcomp' package was employed to run the "glht" function, providing simultaneous inference in general parametric models. Multiple comparisons were conducted using Tukey's Honest Significant Difference test to determine significant differences in beetle abundance in each pair of log sections or decay classes, such as between log replicates in the early decay class. The alpha level was set at 0.05 for all GLM and multiple comparison tests.

To analyze saproxylic community structure across log replicates and decay classes, Nonmetric Multidimensional Scaling (NMDS) was performed using the 'vegan' package, a community ecology package, with the 'metaMDS' function and the Bray-Curtis dissimilarity index applied for two dimensions. NMDS is a technique used to visualize the similarities between individual cases in a multivariate dataset. The final stress value, reported using the "nms.final$stress" script, was acceptable for reliable interpretation.

RESULTS

In 2011, a total of 1023 saproxylic beetles were collected from three DC2 and three DC5 white spruce logs, within the 10-ha non-harvested white spruce stand located at the EMEND research site in northern Alberta. The collection comprised 570 species from the DC2 logs and 453 species from the DC5 logs, discovered within 30 bolts. A total of 90 species were identified across both decay classes, with 48 species in DC2 and 42 in DC5. Of these, 19 families were found in DC2, and 12 families in the DC5 logs, totalling 23 different families. The four most common species identified were phloeophagous *Polygraphus rufipennis* (Kirby) with 305 individuals of the Curculionidae family, predaceous *Lasconotus complex* (LeConte) with 76 individuals of the Colydiidae family, mycetophagous *Pteryx* sp.1 with 270 individuals of the Ptiliidae family, and predaceous *Tachyporus borealis* with 20 individuals of the Staphylinidae family.

SPECIES RICHNESS AND ABUNDANCE

The general trend of mean saproxylic beetle species richness across the three log replicates within DC2 and DC5 did not differ significantly, even though the main GLM result was statistically significant ($P = 0.04755$), subsequent pairwise comparisons did not reveal any significant differences among the log replicates. In DC2 and DC5, log replicates B and A tended to be highest in species richness, respectively (Figure 5). Log replicates A in DC2 and C in DC5 tended to be lowest in mean species richness. In terms of total species richness per log replicate in DC2 and DC5, no clear pattern emerged, other than the existence of rich species richness

within both decay classes (Figure 5). The mean and total species richness identified in each log

replicate is high, indicating high species diversity among decay classes.
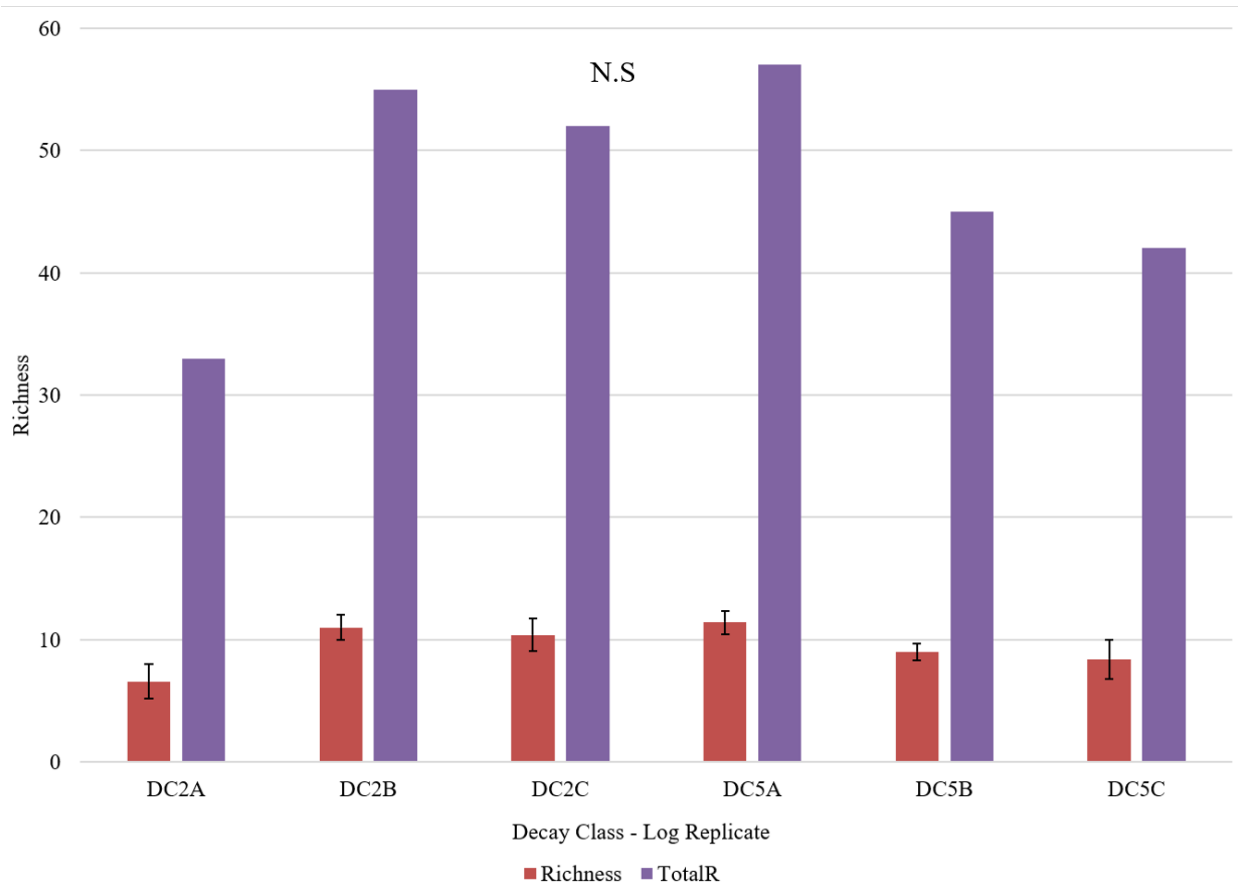
Figure 5. Average saproxylic beetle richness per bolt for each log replicate across decay classes two and five (Red) with total species richness per log replicate (Purple). Error bars for mean species richness represent SE for five bolts per log replicate among each decay class. N.S. represents 'no significant difference' between mean species richness (Red) using Tukey's honestly significant difference test, $P < 0.05$).

Mean species richness between bolts did not differ significantly across decay classes two

and five ($P = 0.1757$). Saproxylic beetle richness tended to be highest in bolt four within both

DC2 and DC5 (Figure 6). Species richness tended to be lowest in bolt two in DC2 and bolt three

in DC5. No clear trend in richness across bolts within decay classes and between decay classes

was apparent (Figure 6).

Figure 6. Mean saproxylic beetle richness within the five bolt replicates within their respective decay classes, DC2 (Blue gradient) and DC5 (Red gradient). Error bars represent the SE for the three log replicates. N.S. represents 'no significant difference' between mean bolt richness using Tukey's honestly significant difference test, $P < 0.05$).

        Mean saproxylic beetle abundance differed significantly within and across decay classes ($P = 1.107e\text{-}05$). Multiple comparisons revealed that beetle abundance was lowest in log replicate A for both DC2 and DC5 (Figure 7), while log replicate C in DC2 showed the highest abundance. No significant difference was observed in abundance between log replicates across decay classes, except for log replicate C in DC2. However, log replicates B and C in DC5 showed no significant differences from log replicates C in DC2.
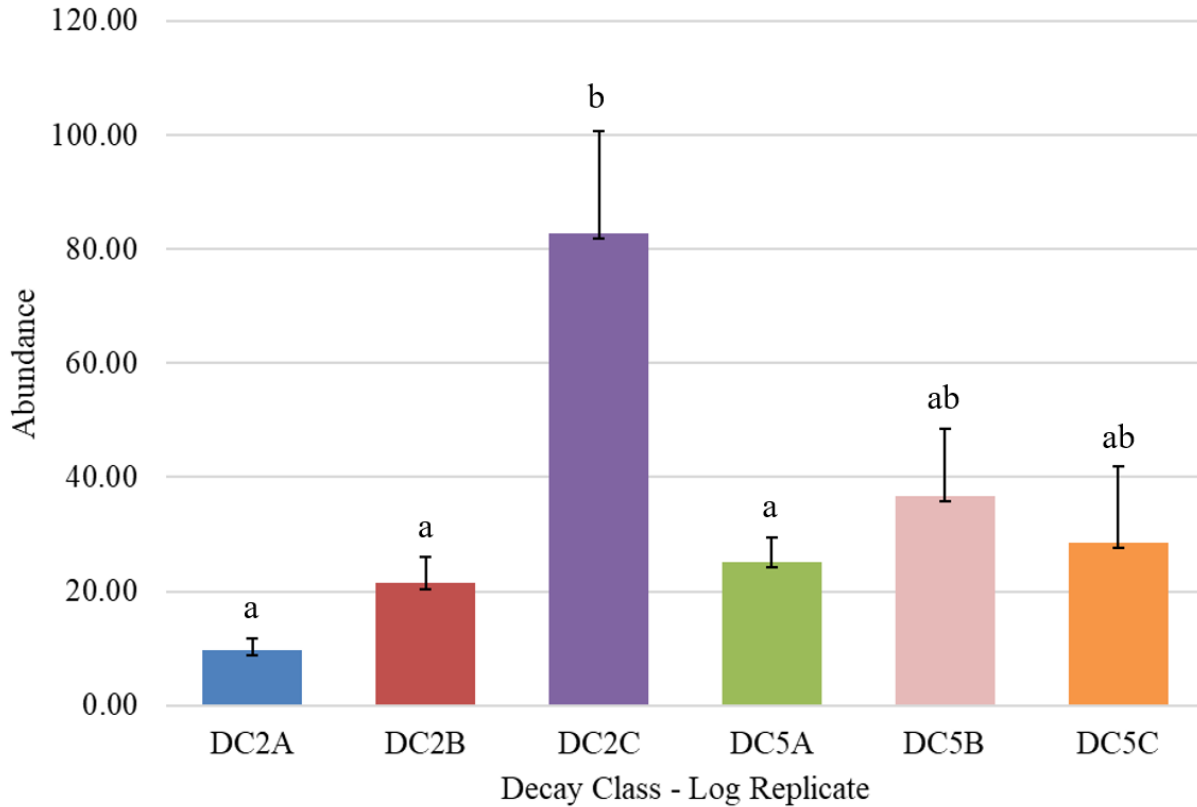
Figure 7. Mean saproxylic beetle abundance within the three log replicates within their respective decay classes, DC2 and DC5. Error bars represent the SE for the five bolts within a log replicate. Significant post-hoc results are displayed by different lowercase letters (Tukey's honestly significant difference test, $P < 0.05$).

Mean abundance between bolts did not significantly differ across decay classes two and five ($P = 0.2262$). However, saproxylic beetle abundance tended to be highest in bolt two within DC2, and bolt four in DC5 had the highest mean saproxylic beetle abundance (Figure 8). The lowest beetle abundance was observed in bolt five in DC2 and bolt one in DC5. No strict pattern in abundance across bolts was apparent, other than a gradual decrease in abundance after bolt two in DC2 for bolts three to five, which is not statistically supported. DC5 appeared to exhibit an opposite pattern of abundance compared to DC2 (Figure 8).
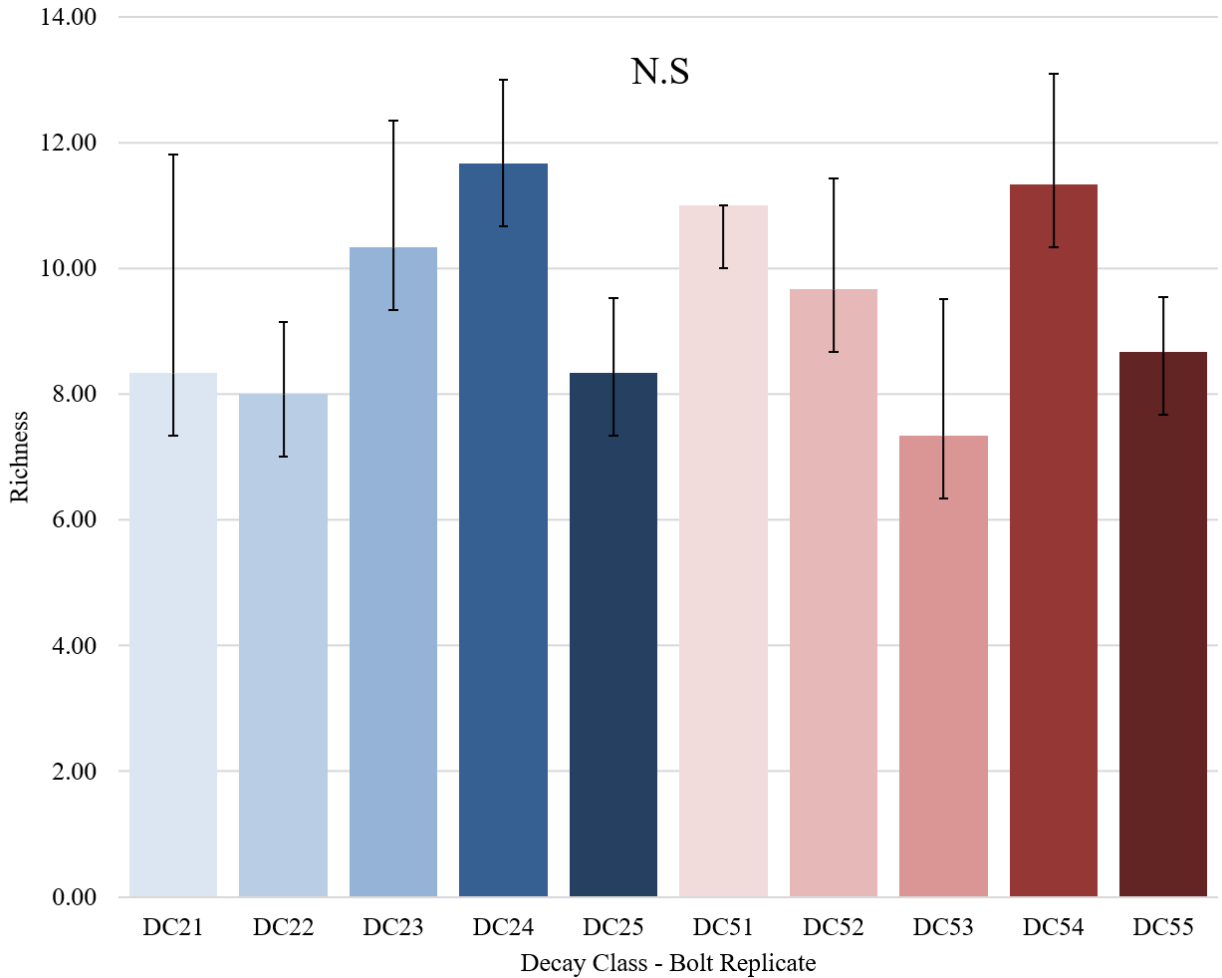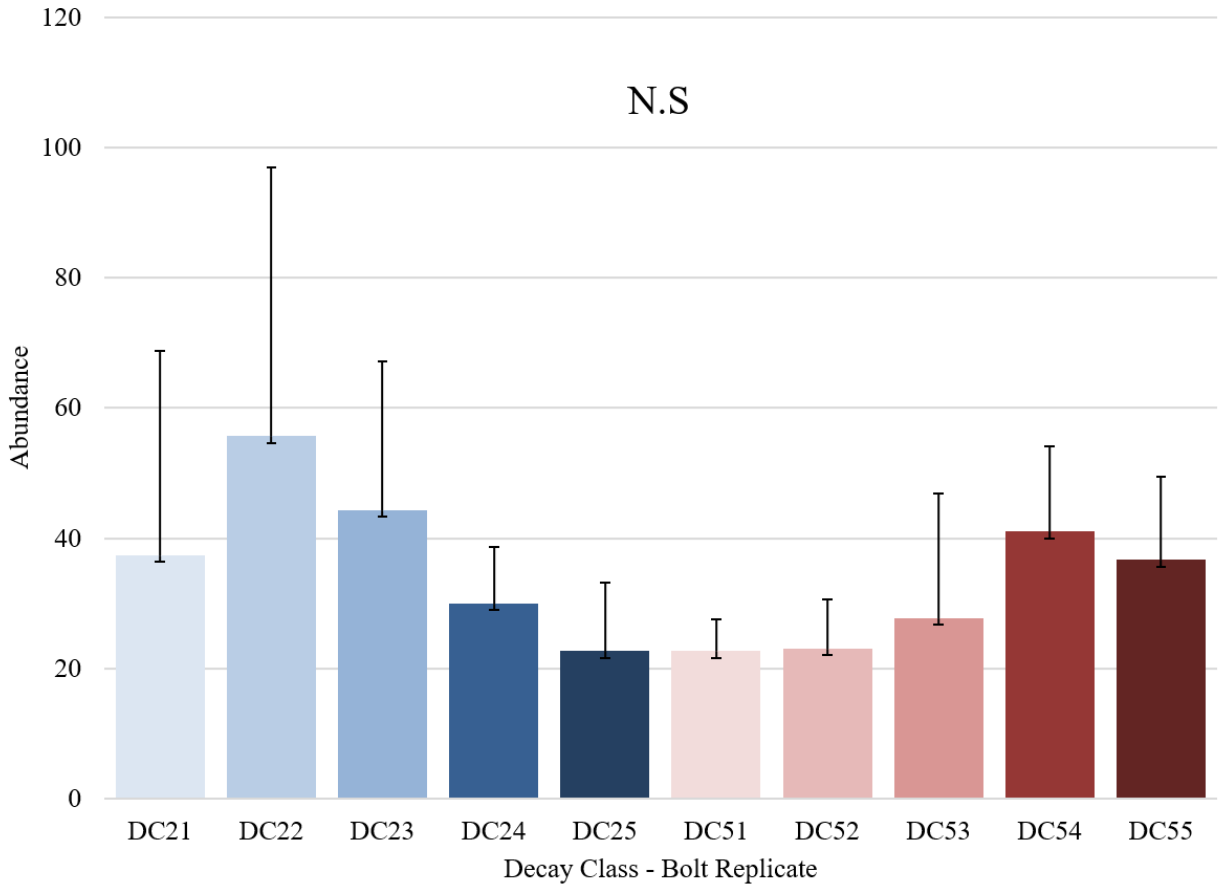
Figure 8. Mean saproxylic beetle abundance within the five bolt replicates within their respective decay classes, DC2 (Blue gradient) and DC5 (Red gradient). Error bars represent the SE for the three log replicates. N.S. represents 'no significant difference' between mean bolt abundance using Tukey's honestly significant difference test, $P < 0.05$).

The abundance of *Polygraphus rufipennis* (Figure 9A) and *Lasconotus complex* (Figure 9B) significantly differed between the log replicates in DC2 (Figure 9A. $P = 3.604e^{-06}$; Figure 9B. $P = 0.003796$). Log replicate C had the highest abundance for both species, while log replicate A had the lowest (Figures 9A and 9B). *Pteryx* sp.1 (Figure 9C) and *Tachyporus borealis* (Figure 9D) did not significantly differ between the log replicates in DC5 (Figure 9C. $P = 0.5311$; Figure 9D. $P = 0.3652$). Log replicate B and A in DC5 tended to have the highest abundance for *Pteryx* sp.1 and *Tachyporus borealis*, respectively. Whereas log replicates A and B

tended to have the lowest abundance for *Pteryx* sp.1 and *Tachyporus borealis*, respectively

(Figure 9).
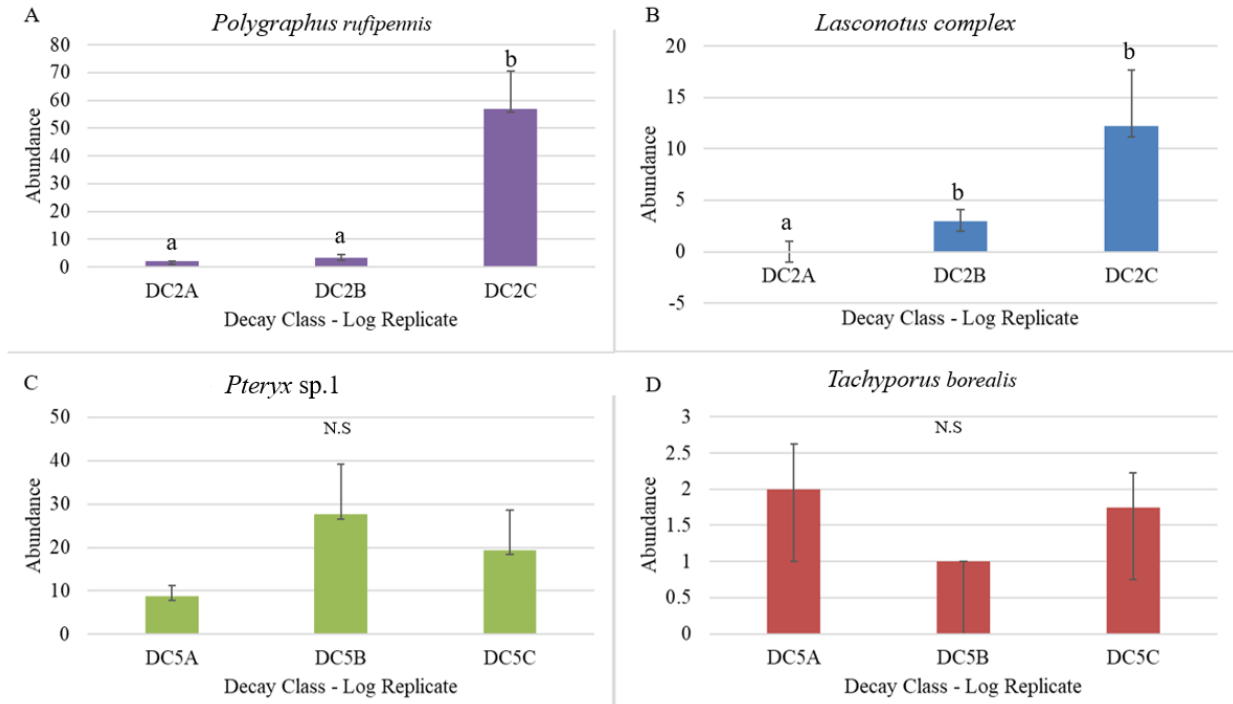
Figure 9. Mean beetle abundance for the two most abundant species in DC2 (A. *Polygraphys rufipennis;* B. *Lasconotus complex*) and DC5 (C. *Pteryx* sp.1; D. *Tachyporus borealis*), across the three log replicates in their respective decay class. Error bars represent the SE for the five bolts within a log replicate. Significant post-hoc results are displayed by different lowercase letters (Tukey's honestly significant difference test, $P < 0.05$), while N.S. represents 'no significant difference' between mean species abundance across log replicates in their respective decay classes.

SPECIES COMPOSITION

NMS ordination was conducted using all saproxylic beetle data, including singletons and doubletons, to accurately represent species composition within and between log replicates, and across decay classes. Saproxylic beetle assemblages associated with DC2 and DC5 were distinctly separate (Figure 10). The final stress for the three-dimensional solution was 12.9%,

indicating a reliable interpretation of results. DC2A exhibited the highest variation in species

composition, whereas the other two DC2 log replicates showed minimal variations in species

composition. The overlapping of DC2B and DC2A indicates similar species composition.

Species composition for DC5 was notably similar due to overlapping ellipses of DC5A, DC5B,

and DC5C, suggesting similar species composition across log replicates in DC5 (Figure 10).
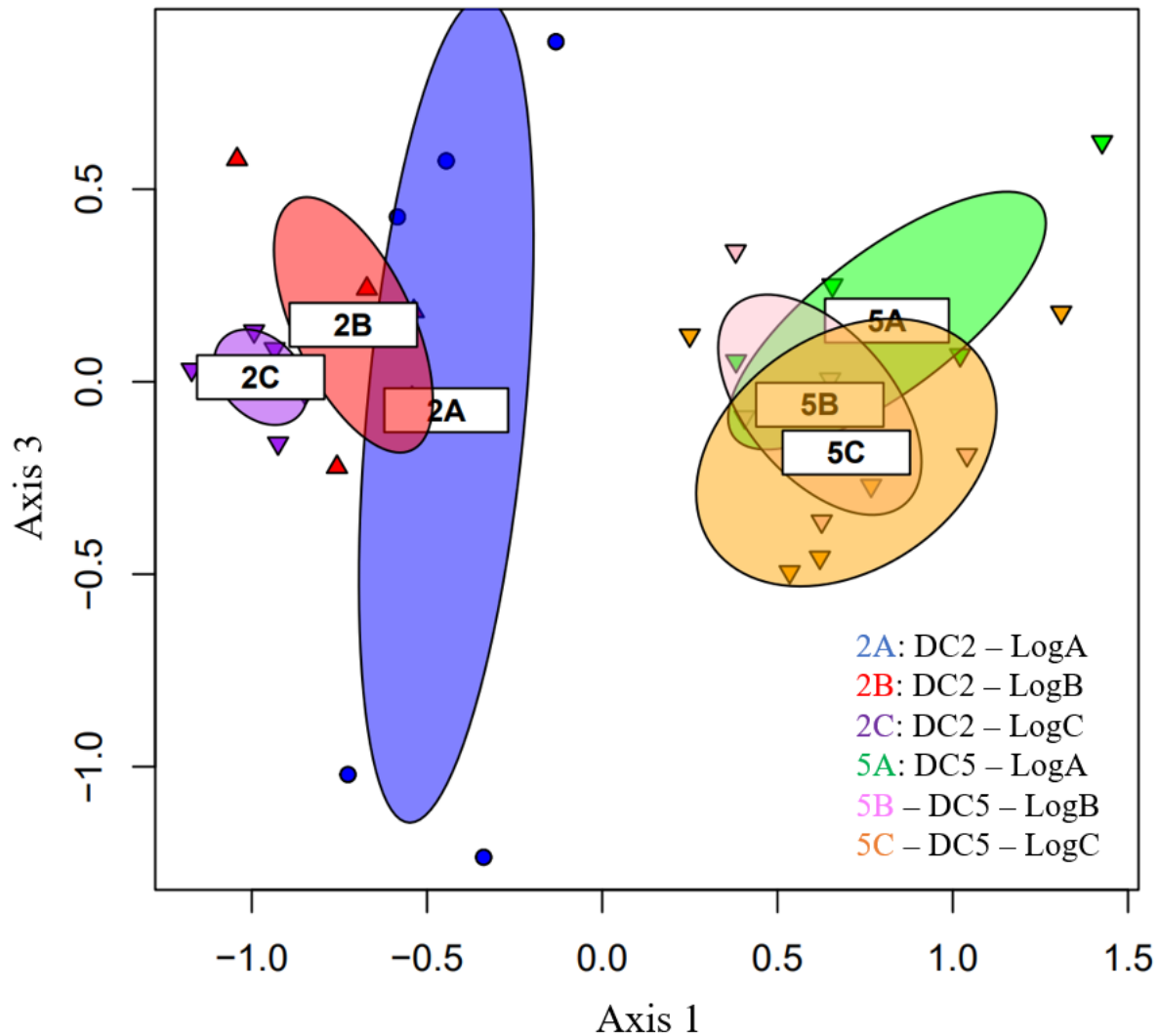
Figure 10. Non-metric multidimensional scaling ordination of saproxylic beetles grouped by decay class (2; 5) and log replicate (A; B; C). Singletons and doubletons were included, and the data was square root transformed prior to analysis. Final stress for a three-dimensional solution = 12.9%. Similar coloured five dots or triangles to their respective coloured ellipse represent the five bolts per log replicate.

CHANGES IN FEEDING GUILDS

The feeding guild structure significantly changes between DC2 and DC5, with 58% of the total abundance in DC2 phloeophagous beetles and 72% of the total abundance in DC5 mycetophagous beetles (Figure 11). *Polygraphus rufipennis* and *Pteryx* sp.1, with 305 and 270 individuals collected in DC2 and DC5 respectively, constitute the majority of the phloeophagous and mycetophagous feeding guilds (Table 1). The predaceous feeding guild showed an 8% increase in abundance from DC2 to DC5. *Lasconotus complex* dominated the DC2 predaceous guild, with 76 individuals, while species within the Staphylinidae family dominated the DC5 predaceous guild, with 102 individuals. The phloeophagous community disappeared by DC5. Most species constituting 22% of the mycetophagous guild in DC2 belong to the Latridiidae family, with 99 individuals collected, while the Ptiliidae family dominated 72% of the mycetophagous guild in DC5, with 272 individuals collected (Table 1).

Figure 11. Changes in saproxylic beetle feeding guild abundances, represented as percentages, from DC2 and DC5. Unknown feeding guild is most likely to be either mycetophagous or predaceous.

SPECIES DISTRIBUTIONS BETWEEN DC2 AND DC5

A high diversity of saproxylic beetles was identified across each bolt over the six log replicates, with numerous singletons and doubletons identified in both DC2 and DC5. A few specialists seen across dec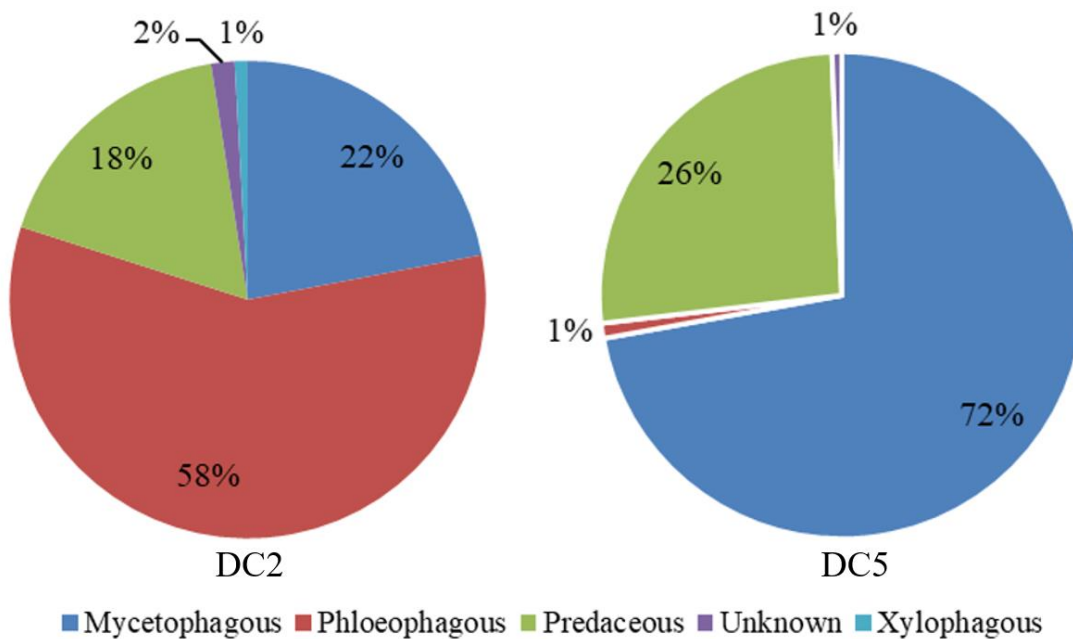ay classes included the top four most abundant species, *Polygraphys rufipennis*, *Lasconotus complex*, collected within DC2, and *Pteryx* sp.1, and *Tachyporus borealis*, collected within DC5 (Table 1). Ten generalists overlapped between decay classes. The two most abundant generalists were *Latridius minutus* and *Cartodere constricta*, with 14 and 29 individuals collected in DC2, and 10 and 11 individuals collected in DC5, respectively.

Table 1. Saproxylic beetle abundance in DC2 and DC5 of white spruce logs.

Family	Species	FG	DC2	DC5	Total
Curculionidae	*Polygraphus rufipennis*	PHL	305	1	306
Colydiidae	*Lasconotus complex*	PRE	76		76
Latridiidae	*Cartodere constricta*	MYC	29	10	39
Latridiidae	*Corticaria ferruginea*	MYC	20	8	28
Latridiidae	*Corticaria* sp.1	MYC	19	5	24
Curculionidae	*Dryocoetes affaber*	PHL	17		17
Latridiidae	*Latridius minutus*	MYC	14	11	25
Latridiidae	*Corticaria rubripes*	MYC	12	2	14
Staphylinidae	*Phloeopora* sp.1	PRE	7		7
Mycetophagidae	*Typhaea stercorea near.*	MYC	6	1	7
Cucujidae	*Pediacus fuscus*	PRE	5		5
Corylophidae	*Clypastraea* sp.1	MYC	4		4
Staphylinidae	*Nudobius cephalus*	PRE	4		4
Corylophidae	*Orthoperus scutellaris*	MYC	4	1	5
Latridiidae	*Cortinicara gibbosa*	MYC	3		3
Curculionidae	*Crypturgus borealis*	PHL	3		3
Laemophloeidae	*Leptophloeus* sp.1	MYC	3		3
Curculionidae	*Tychius stephensi*	UNK	3		3
Cryptophagidae	*Atomaria* sp.3	MYC	2		2
Curculionidae	*Carphonotus testaceus*	XYL	2		2
Latridiidae	*Enicmus fictus*	MYC	2	1	3
Curculionidae	*Otiorhynchus ovatus*	XYL	2		2
Curculionidae	*Pissodes rotundatus*	PHL	2		2
Curculionidae	*Xylechinus montanus*	PHL	2		2
Staphylinidae	*Aleocharinae* sp.1	UNK	1		1

Table 1.2.
(Continued)

Staphylinidae	*Aleocharinae* sp.2	UNK	1		1
Carabidae	*Amara* sp.1	PRE	1		1
Staphylinidae	*Atheta graminicola*	PRE	1		1
Staphylinidae	*Boreophilia islandica*	UNK	1		1
Carabidae	*Carabidae* sp.1	PRE	1		1
Staphylinidae	*Carpelimus* sp.1	UNK	1		1
Staphylinidae	*Carpelimus* sp.2	UNK	1		1
Cryptophagidae	*Cryptophagus acutangulus*	MYC	1		1
Cryptophagidae	*Cryptophagus tuberculosus*	MYC	1		1
Silvanidae	*Dendrophagus cygnaei*	MYC	1		1
Dermestidae	*Dermestes lardarius*	DET	1		1
Ciidae	*Dolichocis manitoba*	MYC	1		1
Coccinellidae	*Microweisea misella*	PRE	1		1
Staphylinidae	*Mocyta breviuscula*	PRE	1		1
Eucinetidae	*Nycteus* sp.1	MYC	1		1
Staphylinidae	*Oligota* sp.1	PRE	1		1
Staphylinidae	*Olisthaerus megacephalus*	PRE	1	4	5
Trogossitidae	*Peltis fraterna*	MYC	1		1
Staphylinidae	*Phloeostiba lapponica*	PRE	1		1
Salpingidae	*Sphaeriestes virescens*	UNK	1		1
Cerambycidae	*Tetropium cinnamopterum*	XYL	1		1
Cleridae	*Thanasimus undatulus*	PRE	1		1
Trogossitidae	*Thymalus marginicollis*	MYC	1		1
Ptiliidae	*Acrotrichis* sp.1	MYC		2	2
Staphylinidae	*Aleocharinae* sp.3	UNK		1	1
Staphylinidae	*Athetini* sp.1	PRE		7	7
Cryptophagidae	*Atomaria ephippiata*	MYC		1	1
Cryptophagidae	*Atomaria* sp.2	MYC		1	1
Byrrhidae	*Byrrhus cyclophorus*	UNK		1	1
Carabidae	*Calathus advena*	PRE		2	2
Byrrhidae	*Cytilus mimicus*	UNK		1	1
Staphylinidae	*Gabrius brevipennis*	PRE		8	8
Cryptophagidae	*Henoticus serratus*	MYC		1	1
Staphylinidae	*Ischnosoma splendidum*	PRE		7	7
Staphylinidae	*Lathrobium fauveli*	MYC		11	11
Staphylinidae	*Lathrobium washingtoni*	MYC		15	15
Leiodes	*Leiodes* sp.1	MYC		1	1
Staphylinidae	*Liogluta aloconotoides*	MYC		12	12
Staphylinidae	*Myrmecocephalus* sp.1	PRE		1	1
Staphylinidae	*Oxypoda frigida*	PRE		15	15
Staphylinidae	*Oxypoda operta*	PRE		2	2
Staphylinidae	*Philhygra* sp.2	PRE		1	1

Table 1.3.
(Continued)

Carabidae	*Platynus decentis*	PRE		4	4
Cerambycidae	*Pogonocherus penicillatus*	XYL		1	1
Ptiliidae	*Pteryx* sp.1	MYC		270	270
Staphylinidae	*Quedius labradorensis*	PRE		1	1
Staphylinidae	*Quedius rusticus*	PRE		3	3
Monotomidae	*Rhizophagus remotus*	PRE		1	1
Curculionidae	*Scierus annectans*	PHL		1	1
Staphylinidae	*Seeversiella globicollis*	PRE		3	3
Staphylinidae	*Stenus austini*	PRE		4	4
Carabidae	*Stereocerus haematopus*	PRE		4	4
Staphylinidae	*Tachyporus borealis*	PRE		20	20
Carabidae	*Trechus apicalis*	PRE		6	6
Curculionidae	*Trypodendron lineatum*	MYC		1	1
		Grand Total	570	453	1023

DC, decay class; FG, feeding guilds; MYC, mycetophagous; PHL, phloeophagous; PRE, predaceous; UNK, unknown; XYL, xylophagous; DET, detritivorous.

Key findings aiding our hypotheses include the lack of significant difference in mean species richness within and between decay classes, and the significant similarity in mean abundance within and between decay classes, except for log replicate C in DC2. Bolt2 in DC2 exhibited the highest abundance, which gradually declined as bolts higher in the tree were reached. *Pteryx* sp.1 and *Tachyporus borealis*, collected in DC5, showed no significant difference in abundance across log replicates, unlike *Polygraphus rufipennis* and *Lasconotus complex* collected in DC2. NMS demonstrated that the three log replicates in DC5 have similar species composition, while DC2 showed less similarity across log replicates. As decay progresses, the phloeophagous feeding guild disappeared, and the mycetophagous and predaceous feeding guilds dominate. Notable changes in families associated with feeding guilds from DC2 to DC5 included a shift from Latridiidae to Ptiliidae within the mycetophagous feeding guild, Colydiidae to Staphylinidae within the predaceous feeding guild, and the disappearance of the Curculionidae family in the phloeophagous feeding guild. Species with

distinct specializations to their respective decay class included *Polygraphys rufipennis* and *Lasconotus complex*, collected within DC2, and *Pteryx* sp.1 and *Tachyporus borealis*, collected within DC5. Common generalists overlapping between decay classes were *Latridius minutus* and *Cartodere constricta*.

DISCUSSION

The study aimed to understand variations in saproxylic beetle assemblages within five sections of the same stem in both early and advanced decay classes of white spruce logs and to contrast beetle assemblage structures between these decay classes. Mean species richness and abundance did not significantly differ within and between decay classes, except for a single log replicate (BoltC in DC2). A trend was observed where beetle abundance was highest in bolt two across the three log replicates in the early decay class, declining gradually as bolts higher in the tree were reached. This trend, however, lacked statistical support. In terms of saproxylic beetle assemblages, there was greater variability in community structure across the log replicates in the earlier decay class than in the advanced decay class. This trend may align with the simultaneous dominance of phloeophagous, mycetophagous, and predaceous feeding guilds in the earlier decay class, while only the mycetophagous and predaceous feeding guilds dominating in the advanced decay class. This may correlate with the most abundant species collected in the earlier decay class, *Pteryx* sp.1 and *Tachyporus borealis*, lacking similarities in abundance across log replicates. In contrast, *Polygraphus rufipennis* and *Lasconotus complex,* the most abundant species collected in the advanced decay class, displayed similarities in abundance across log replicates.

HYPOTHESIS 1 – Richness and Abundance

Lee et al. (2014) found no significant differences in species richness and abundance between advanced and intermediate decay stages, a pattern that persisted in this study when analyzing bolts evenly displaced across log replicates within their respective decay class. This contrasts with Stokland et al. (2012), who found species richness peaking after tree death and gradually declining with decay advancement. A trend observed in the earlier decay class, with the highest beetle abundance in bolt two, may align with a study by Onodera et al. (2016), who found the greatest species abundance in the basal stem of a snag. For clarity, bolt2 is located 2.2 to 2.8 metres above the ground level while Onodera et al. (2016) classified the basal stem as 0 to 2.5 metres above ground level. However, species richness did not show significant differences among vertical log positions, consistent with this study and Lee et al. (2014). This pattern contradicts previous studies that identified higher saproxylic species richness at positions closer to the ground level (Hammond et al. 2004). Interestingly, Onodera et al. (2016) noted that saproxylic assemblages associated with the basal stem may persist to fallen logs, aligning with this study in terms of abundance and richness. However, it's important to recognize that the orientation of decay wood, such as snags compared to fallen logs, influences the fauna present due to differing moisture and temperature conditions (Hammond et al. 2004). Snags, exposed to sunlight, create higher subcortical temperatures, and enhance the emanation of volatiles from newly deadwood (Hammond et al. 2004). Snags tend to have higher abundance, whereas species richness tends to be higher in stumps and logs (Hammond et al. 2001). The higher species richness in logs may correlate to the environment provided by the forest canopy cover (Hammond et al. 2004). The forest floor, being shadier and moister, provides a higher diversity of microhabitats (Hammond et al. 2004).

HYPOTHESIS 2 – Community Structure

The study found that the community structure in the early decay class exhibited more variability than in the advanced decay class. There was limited similarity in community structure across log replicates in the early decay class. In the early decay class, the community structure in log replicate C was notably different from replicates A and B, which shared few similarities. In contrast, DC5 showed significant resemblances in community structure across its three log replicates. Factors influencing species composition in the early decay class could include varying co-occurring species of fungi, moisture and temperature conditions, or the quality and diameter of the log (Jacobs et al. 2007). However, early decay classes typically offer a lower diversity of microhabitats, with intact nutrient-rich resources in the form of phloem and sapwood, compared to advanced decay classes (Hammond et al. 2004). Hammond et al. (2004) characterize freshly killed aspen wood as decay class one, while a decay class two log has notably loose or falling bark with initial mycelium growth beneath the bark. This might account for the high diversity in community structure found within the early decay class. Colonizing bark beetles, which are more aggressive and less diverse, inhabit freshly killed woody material (Stokland et al. 2012). Once the tree is dead, non-aggressive bark beetles, which are more diverse, find their niche within the log (Stokland et al. 2012). The aggressive, early boring species are suggested to "precondition" the wood for succeeding species (Hammond et al. 2001). Hammond et al. (2001) noted that beetle richness and abundance were higher once the succeeding species established themselves after the colonization of early wood-boring insects.

The phloeophagous feeding guild dominated the earlier decay class with 58% of the species collected being phloeophagous beetles, closely resembling the study conducted by Lee et al. (2014). These wood and bark-boring beetles require fresh host material, have excellent host-

find capabilities, and disperse well (Hammond et al. 2001). I propose that saproxylic beetle assemblages in the earlier decay class were variable due to the presence of early boring species and the newly colonized succeeding species. Siebold et al. (2023) found that beta diversity was unexpectedly higher during the early years of succession from highly abundant species, specialized species, and rare species, attributing this to stochasticity in early saproxylic beetle communities. Highly specialized species typically dominate the early stages of decay due to the high concentration of secondary metabolites associated with plant defence immediately after tree death, and gradually transition to generalists as decay progresses (Seibold et al. 2023). Hammond et al. (2004) also note that an increase in microhabitat diversity and species richness is expected as deadwood transitions from DC1 to DC2, due to the presence of wood-decaying fungi. These fungi provide fungal structures such as fruiting bodies, hyphae, and spores for food or oviposition, attracting frugivorous groups of Staphylinidae and Ciidae (Hammond et al. 2004), both of which were present in this study in the early decay class. The mycetophagous feeding guild co-dominates along with the phloeophagous feeding guild in the early decay class, comprising 22% of the collected species.

The similarity in community structure across log replicates in the advanced decay class could be due to the similar abundance of fungivorous species, with 72% of the species collected within the mycetophagous feeding guild. The presence of fungivorous species, along with predators and parasitoids within the predaceous feeding guild, is typical in assemblages associated with advanced decay stages (Lee et al. 2014). Total habitat availability and diversity increase in moderately to heavily decayed wood (Hammond et al. 2004). In contrast, host specialization decreases with ongoing saproxylic beetle succession along with the advancement of deadwood decay (Seibold et al. 2023). Since generalists are more common in advanced stages

of decay, this could account for the similarity in community structure found in the advanced decay class.

NICHE PARTITIONING

Understanding the drivers that shape community assembly for saproxylic species is crucial for their conservation in post-disturbance or managed forest ecosystems (Seibold et al. 2023). The question arises whether saproxylic community structures are driven by niche partitioning or spatial aggregation. Evidence of niche partitioning in species with similar dietary preferences is the avoidance of certain species from others with different dietary preferences (Horak 2021). Based on the analysis of species presence and absence in this study, richness remained consistently high across the log replicates, potentially indicating spatial aggregation. If there was no correlation between species presence and absence, this type of co-occurrence would suggest the community structure is driven by niche partitioning (Horak 2021). Shorrocks and Sevenston (1995) argue that the presence of patches with high local densities and nearby patches of low density indicates strong intraspecific competition. Kadowaki (2010) further suggests that patch-level total insect biomass would increase linearly with richness in the absence of interspecific competition. However, if interspecific competition is present, patch-level biomass and species richness would peak due to resource depletion (Kadowaki 2010). In the current study, richness remains similar across log replicates and decay classes, with abundance varying more depending on the log replicate. This could indicate resource depletion and a case of spatial aggregation due to species stochasticity or the neutral theory.

Kadowaki (2010) examined four specialist species in a mycophagous community and determined that niche partitioning explained the successional sequence and spatial distribution of these species over time. This might align with the theory proposed by Hammond et al. (2001), stating that bark and wood borers precondition deadwood for colonization by other. This form of niche partitioning can be observed with the advancement of deadwood decay as the phloeophagous feeding guild in the early decay class dissipates into the mycetophagous feeding guild in the advanced decay class. However, both Kadowaki (2010) and Horak (2021) found that resource partitioning and spatial aggregation both contribute to driving species co-existence on diverse, patchy resources.

Supporting the neutral drift theory of species abundance, Horak (2021) suggested that saproxylic community assembly was not driven by niche partitioning, given the nutrient-rich and diverse microhabitats provided by deadwood. Shorrocks and Sevenston (1995) introduced the aggregation model of competition, highlighting 'probability refugees', competitively inferior species thriving in ephemeral patches. Kadowaki (2010) further noted that while successional niche partitioning influences the direction of competitive interactions, it doesn't ensure coexistence. Mycophagous insects exemplify the aggregation model of coexistence, displaying specialist species with higher population persistence than generalists (Kadowaki 2010). Specialist species, such as *Pteryx* sp.1 and *Lasconotus complex* in the early decay class, are more abundant than generalist species like *Latridius minutus,* supporting the aggregation model of competition. Wertheim et al. (2000) argued that resource partitioning doesn't reduce competitive interactions, indicating that interspecific competition doesn't provide the selection pressure needed for specialization. Intraspecific aggregation allows mycophagous insects to coexist with their competitors (Wertheim et al. 2000), as seen in the advanced decay class where beetles

within the predaceous feeding guild coexist with beetles within the mycetophagous community. Wertheim et al. (2000) concurred that it's unlikely that competitive interactions select for specialization or character displacement, while spatial aggregation does. Many studies have concluded that spatial aggregation is both necessary and sufficient to stabilize coexistence and species diversity in saproxylic communities (Shorrocks and Sevenster 1995; Wertheim et al. 2000; Horak 2021). Shorrocks and Sevenster (1995) conducted a particularly relevant study on fruit flies (*Drosophila* spp.) that exploit patchy and ephemeral resources characteristic of deadwood. They declared that spatial heterogeneity was a strong driver for maintaining diversity in these communities, aligning with this study due to the changes that occur to deadwood as decay advances (Shorrocks and Sevenster 1995).

If spatial aggregation is indeed necessary and sufficient to stabilize saproxylic beetle coexistence in community structures, resource types are likely governed by constraints on metabolic, developmental, digestive, and searching abilities, detoxification mechanisms of the insects, and the presence of fungi (Wertheim et al. 2000). Feldhaar and Schauer (2018) further suggested that saproxylic species dispersal strategies are shaped more by spatial and temporal variability of deadwood, feeding strategy, resource competition, kin competition, and inbreeding avoidance. Overall, the net effects of resource utilization of saproxylic communities inhabiting deadwood are a random association, where competitive interactions are not necessary for coexistence (Wertheim et al. 2000).

LIMITATIONS

Several limitations must be considered when assessing the accuracy of the current data and its subsequent analysis. Evaluating phloem abundance in early decay class logs poses challenges. The selection of log replicates for sampling significantly impacts the observed phloem abundance. Even subtle differences between log replicates can influence the composition of the associated fauna and their successional stages. To mitigate biases related to over and under-sampling, future studies should prioritize collecting additional log replicates from the early decay class. By doing so, we can minimize discrepancies in phloem abundance estimates. For instance, log replicate C yielded 414 beetles, whereas log replicate A yielded only 49 beetles. The under-sampling of log replicate A may have distorted the Non-Metric Multidimensional Scaling (NMS) graph, as RStudio relies on relative abundance for processing. Unfortunately, environmental data associated with the log replicates remain unavailable.

CONCLUSION

The study aims to understand saproxylic beetle assemblage variations within five sections of the same white spruce log, comparing early decay and advanced decay classes. Key findings indicate a high abundance of beetles in bolt two of the early decay class deadwood. Onodera et al. (2016) propose that assemblages linked to the basal stem of a snag may persist within fallen logs, aligning with our study. Forest management practices focused on timber production detrimentally impact saproxylic communities by removing essential deadwood habitats (Siebold et al. 2023). In intensively managed plantation forests, deadwood is often overlooked and removed due to its lack of economic value (Onodera et al. 2017). Prioritizing biodiversity

conservation necessitates leaving remnants of deadwood post-harvest, supporting the diverse arthropod community (Hammond et al. 2004). The basal stem of logs can be retained post-harvest to support saproxylic diversity. As the basal stem decays, it becomes a hub of high diversity, with increased beetle richness and abundance as succeeding species establish themselves after early wood-boring insect colonization. Preserving both early and advanced decay deadwood is crucial due to its unique community structures. Saproxylic beetles exhibit spatial aggregation in early and advanced decay classes. Leaving remnants of the basal stem post-harvest provides a habitat for these beetles, as resource utilization within saproxylic communities tends to be a random association, not reliant on competitive interactions for coexistence (Wertheim et al. 2000). Integrating timber production with biodiversity conservation is essential for advanced plantation management, minimizing impacts on ecosystem structure and function while safeguarding saproxylic fauna in forest ecosystems (Hammond et al. 2001; Onodera et al. 2017). Future studies should explore the economic value of biodiversity within deadfall and determine the spatial distribution of basal stems needed to sustain saproxylic populations in new plantations.

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