UNIVERSITÉ DU QUÉBEC À MONTRÉAL

RESPONSE OF SAPROXYLIC BEETLE COMMUNITIES TWENTY YEARS AFTER CLEARCUT AND PARTIAL CUT HARVESTS IN THE EASTERN BOREAL MIXEDWOOD FOREST

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RÉPONSE DES COMMUNAUTÉS DE COLÉOPTÈRES SAPROXYLIQUES VINGT ANS APRÈS LES COUPES TOTALES ET LES COUPES PARTIELLES DANS LA FORÊT BORÉALE MIXTE

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

RÉSUMÉ

Les pratiques forestières intensives telles que la coupe totale peuvent entraver le rétablissement à long terme de la biodiversité, en particulier la biodiversité saproxylique (dépendante du bois mort). La coupe partielle laisse certains arbres au moment de la récolte, en imitant les perturbations naturelles telles que les chablis ou les épidémies d'insectes. Cela peut permettre le dépôt à long terme de bois mort dans un peuplement et le rétablissement de la biodiversité saproxylique. Nous avons évalué si une coupe partielle d'intensité élevée et faible effectuée dans des peuplements de feuillus au stade de succession précoce, ainsi qu'une coupe partielle d'intensité moyenne effectuée selon différents schémas de coupe dans des peuplements mixtes au stade de succession intermédiaire, permettraient le rétablissement des communautés de coléoptères saproxyliques vingt ans après la récolte. Nos travaux ont été réalisés dans le cadre du projet Sylviculture et Aménagement Forestier Écosystemique (SAFE) dans la Forêt d'Enseignement et de Recherche du Lac Duparquet (FERLD) dans la région boréale mixte de l'ouest du Québec, Canada. Dans les peuplements de feuillus (SAFE 1), à l'hiver 1998-1999, les traitements de récolte suivants ont été répliqués sur 3 blocs de 1 à 3 ha : 1) coupe totale, 2) coupe totale avec brûlage dirigé, 3) coupes partielles dispersées où 2/3 des arbres ont été enlevés (CP2/3) et 4) coupes partielles dispersées où 1/3 des arbres ont été enlevés (CP1/3). Dans les peuplements mixtes (SAFE 3), en 2000-2001, des coupes par trouées de 40%, des coupes dispersées de 40% et des coupes totales ont également été reproduites sur 3 blocs mesurant 1-3 ha. En 2019, nous avons échantillonné du bois mort sur des transects triangulaires (30m de côté) dans chaque bloc de SAFE 1 et 3. En 2019, nous avons installé des pièges d'interception de vol IBL dans SAFE 1 et capturé et identifié 4 842 coléoptères saproxyliques représentant 216 espèces. En 2021, nous avons installé les mêmes pièges dans SAFE 3 et capturé 3 812 coléoptères saproxyliques représentant 185 espèces. En comparant l'abondance, la richesse et la composition de la communauté des coléoptères saproxyliques entre les traitements dans chaque site SAFE, nous avons observé que 20 ans après la récolte, l'abondance globale des coléoptères saproxyliques s'est rétablie dans les CP1/3 au sein des peuplements de feuillus, ainsi que dans les coupes partielles par trouées et dispersées de 40% et les coupes totales dans les forêts mixtes. L'abondance des fongivores était plus faible dans tous les traitements de coupe dans les peuplements de feuillus et mixtes, et l'abondance des xylophages était significativement plus faible dans les coupes totales comparée aux peuplements non coupés. Toutes les guildes alimentaires avaient une abondance réduite dans 2/3 des coupes de feuillus à l'exception des prédateurs. La richesse en espèces dans les coupes partielles était similaire à celle des peuplements témoins non coupés dans les peuplements feuillus et ne différait pas entre les traitements non coupés et témoins dans les peuplements mixtes. La composition de la communauté dans les peuplements de feuillus était similaire entre les peuplements non coupés et les CP1/3 et similaire dans les traitements appliqués dans les peuplements mixtes. Le volume global de bois mort était positivement lié avec l'abondance globale des coléoptères saproxyliques et l'abondance des fongivores et des xylophages dans les peuplements de feuillus. Nous avons conclu que des intensités de récolte partielle de 1/3 à 40% permettent le rétablissement de la plupart des coléoptères saproxyliques 20 ans après la récolte, quel que soit le schéma de coupe (par trouée ou dispersé) si les traitements de coupe sont suffisamment petits (troués d'environ 400 m^2 ou coupes dispersées de ≤50% dans des blocs de 1 à 3 ha). Parce que la réponse entre les guildes alimentaires est variable, les stratégies de conservation pour divers types de faune devront mieux comprendre à quelles variables environnementales ils réagissent. Une récolte partielle de ≤50% est recommandée comme alternative à la coupe à blanc permettant une certaine extraction des ressources parallèlement à la restauration de la biodiversité saproxylique.

Mots clés : sylviculture canadienne, conservation de la biodiversité, effets anthropiques à long terme, conservation des vieux peuplements, succession forestière, récupération des forêts, coupe totale, gestion basée sur l'écosystème, biodiversité saproxylique

ABSTRACT

Intensive forestry practices such as clearcutting may impede long-term recovery of biodiversity, especially saproxylic (deadwood-dependent) biodiversity. Partial cutting leaves some trees behind at time of harvest, in mimicry of natural disturbances such as windthrow or insect outbreak. This may allow long-term deadwood deposition into a stand and recovery of saproxylic biodiversity. We evaluated whether partial harvest of high and low intensity done in early seral stage hardwood stands, as well as partial harvest of mid intensity done in different cutting patterns in mid seral stage mixedwood stands, would allow for the recovery of saproxylic beetle communities twenty years post-harvest. Our work was done as part of the Sylviculture et Aménagement Forestier Écosystemique (SAFE) project in the Lac Duparquet Teaching and Research Forest (FERLD) in the boreal mixedwood region of Western Quebec, Canada. In hardwood stands (SAFE 1), in the winter of 1998-1999, the following harvesting treatments were replicated across 3 blocks measuring 1-3 ha: 1) clearcutting, 2) clearcutting with a prescribed burn, 3) dispersed partial cuts where 2/3 of trees were removed and 4) dispersed partial cuts where 1/3 of trees were removed. In mixedwood stands (SAFE 3), in 2000-2001, 40% gap cuts, 40% dispersed cuts and clearcuts were replicated also across 3 blocks measuring 1-3 ha. In 2019, we sampled deadwood over triangular transects (30m sides) in each block of SAFE 1 and 3. In 2019, we installed IBL flight intercept traps in SAFE 1 and caught and identified 4,842 saproxylic beetles representing 216 species. In 2021, we installed the same traps in SAFE 3 and caught 3,812 saproxylic beetles representing 185 species. Comparing saproxylic beetle abundance, richness and community composition between treatments in each SAFE site, we observed that 20 years post-harvest, overall saproxylic beetle abundance recovered in 1/3 partial cuts in hardwood stands, as well as in 40% gap and dispersed cuts and clearcuts in mixedwood stands. Fungivore abundance was lower in all cutting treatments in hardwood stands and in mixedwood stands, and xylophage abundance was significantly lower in clearcuts compared to uncut stands. All feeding guilds had reduced abundance in 2/3 of hardwood cuts except for predators. Species richness in partial cuts was similar to uncut control stands in hardwood stands and did not differ between cutting treatments and control treatments in mixedwood stands. Community composition in hardwood stands was similar between uncut stands and 1/3 partial cuts and similar in treatments in mixedwood stands. In hardwood stands, overall volume of deadwood was positively related to overall saproxylic beetles, fungivores and xylophages abundance. We concluded that intensities of 1/3-40% partial harvest allow for the recovery of most saproxylic beetles 20 years post-harvest regardless of cutting pattern (gap or dispersed) if cutting treatments are small enough (gaps of ~400m^2 or dispersed cutting of ≤50% in 1-3 ha blocks). Because the response across feeding guilds is variable, conservation strategies for various fauna will need to better understand to what environmental variables they are responding. Partial harvest of ≤50% is recommended as an alternative to clearcutting that allows for some resource extraction alongside recovery of saproxylic biodiversity.

Keywords: Canadian silviculture, biodiversity conservation, long-term anthropogenic effects, old growth conservation, forest succession, forest recovery, clearcutting, ecosystem-based management, saproxylic biodiversity

CHAPTER I

GENERAL INTRODUCTION

1.1 Research Context

Partial cutting can be used in ecosystem-based management in order to recreate and/or emulate elements of natural disturbance regimes (Harvey et al 2002; Franklin et al 2002; Gauthier et al 2023). This component of ecosystem-based management is termed natural disturbance-based management, and although anthropogenic disturbance will differ from natural disturbance, the aim of this technique is to create post-disturbance legacies of living trees, deadwood and canopy cover, supporting recovery of forest stands (Harvey and Brais 2007; Seidl et al 2014). Partial cutting refers to the retention of living trees at harvest that may emulate elements of uncut forests and ecological processes including recruitment of fresh deadwood (Gustafsson et al 2012; Kuuluvainen and Grenfell 2012, Grove 2002; Gauthier et al 2023). This retention can support species assemblages more similar to unmanaged forests (Fenton et al 2013). Partial cuts that maintain high levels of retention (over 50%) better maintain forest leaf litter invertebrates than partial cuts with lower retention (less than 20%) (Jacobs and Work 2012). Spiders (Pinzon et al 2012), carabids (Work et al 2010), bryophytes (Caners et al 2010) and saproxylic beetles (Hjälten et al 2017) are among the organisms that have been shown to benefit from tree retention.

Increased deposition of larger diameter deadwood created after partial cutting will likely further benefit saproxylic (deadwood-dependent) groups such as beetles and fungi which use these substrates as both habitat and a resource. Larger diameter deadwood is more abundant in old-growth forests than younger stands owing to natural disturbance regimes in which natural disturbances target younger, smaller trees in early stages of succession (i.e. competition) and affect older, larger trees in mature forests (e.g. insect outbreaks or windthrow) (Brassard and Chen 2007; Lee et al 1997). In Fennoscandia, intensive forestry practices since the 1950s have depleted forest deadwood supply such that some species have become red-listed (Koivula and Vanha Majamaa 2020). North American boreal forests do not suffer from the same levels of deadwood depletion, but management must prioritize balancing commercial demand with ecological conservation to avoid this problem (Arielle Angers et al 2010). Furthermore, environmental changes caused by harvesting such as increased temperature and decreased relative humidity favour growth rate of wood-feeding beetles and fungi (Barker 2008) and speed decomposition of deadwood in recent clearcuts (Jacobs and Work 2012). In the long-term, reduced volumes of deadwood will support fewer saproxylic beetles in clearcut sites as smaller diameter deadwood quantities are depleted relatively rapidly after harvest.

However, partial cutting, or the retention of a significant number of trees post-harvest (Harvey et al 2002) is a broad category of silvicultural prescriptions that could produce a variety of stand structures or conditions (Montoro Girona 2017; Montoro Girona et al 2023; Bose et al 2013). From a silvicultural perspective, partial cutting has been beneficial in the boreal forest. Experimental shelterwood and seed-tree harvesting combined with scarification have promoted black spruce regeneration in boreal North American stands (Montoro Girona et al 2018). The irregular shelterwood system proposed by Raymond et al (2009) attempts to ensure long rotational periods to allow for the development of later seral stage species. Specific management objectives that would affect stand composition, the distribution of stem diameters and the spatial pattern of retention trees may all affect how well saproxylic communities recover. Greater volumes of larger diameter deadwood maintained in partial cutting may support greater abundance and richness of saproxylic beetles (Joelsson et al 2017) and variety in deadwood should be representative of variety in saproxylic assemblages as specialist taxa will target only specific forms and determine subsequent saproxylic communities (Bouget et al 2012; Hjältén et al 2007; Hjältén et al 2010; Hjältén et al 2012). Jacobs et al (2007) found that 1-2 years following retention treatments, many saproxylic beetle groups reacted to quality and quantity of coarse woody debris more so than the level of retention, except for mycetophagous beetle assemblages, which were significantly correlated with cut intensity. Spatial pattern of retention following partial cutting may also be important in determining conservation of biodiversity. Aggregate retention refers to the retention of tree “islands”, whereas dispersed retention leaves trees scattered at the cut site (Groot et al 2005). Alternatively, we may regard harvest in terms of cut pattern, rather than retention pattern. A gap cut would more closely resemble a clearcut, as a group of trees would be removed in a clump. Dispersed cutting is similar to dispersed retention in that both essentially space out cut and retained trees. Partial harvest may incorporate a combination of both patterns; however, harvest gaps have been shown to impede recovery of biodiversity if the scale is too large. Miller et al (2007) found research plots with harvest gaps of 0.15ha with 10-30% of basal area retention supported lower numbers of Araneae and Collembola than closed canopy plots 8-9 years after harvest.

While often widely advocated for its apparent benefits for biodiversity, a number of limitations to partial cutting should be considered in the context of conservation goals. In stands of commercially valuable black spruce (*Picea mariana* Mill.), partial harvesting may mean increased chance of mortality for residual trees of >12.2cm DBH, which is why it has been recommended that smaller trees be retained or saplings be left as a buffer to protect against windthrow (Moussaoui et al 2020). In experimental shelterwood cutting treatments done on boreal black spruce stands, mortality after 10 years was between 21-43% and with 80% of mortality attributed to windthrow (Montoro Girona 2019). Removal of trees from a stand may promote an environment unsuitable for continued growth of late-successional retained trees, such as black spruce; this situation is usually only a concern in low-retention cuts (e.g. Coates 1997; Ruel et al 2013). Additionally, partial cutting may favour regeneration of one late-successional species over another; balsam fir (*Abies balsamea* L.) will often regenerate faster in response to canopy opening than black spruce, which may in turn affect the structure of saproxylic communities dependent on the two species (Ruel et al 2013; Montoro Girona et al 2023). Additionally, Bose et al (2023) found that partial harvest in mixed-species stands resulted in a 5 year lag in diameter growth for balsam fir, American beech (*Fagus grandifolia* Ehrh.), red spruce (*Picea rubens* Sarg.) and eastern hemlock (*Tsuga canadensis* (L.) Carrière) and a 10 year lag for northern white-cedar (*Thuja occidentalis* L.). Many short- to mid-term partial cutting studies exist, offering promising results for the use of partial cutting as an alternative to clearcutting for biodiversity conservation (e.g. Holmes et al 2004; Work et al 2010;

Hasan et al 2023); however, some existing long-term studies caution against equating the benefits of partial harvest with unmanaged forests. Densities of salamanders in streams within forests managed by partial cutting of various intensities for 50 years were 30% lower than in mature, second-growth forest streams that had been undisturbed for 90 years (Moseley et al 2008). Spider assemblages within stands treated to partial cuts of 75% retention continued to differ from assemblages within unmanaged stands 10 years after partial cutting (Pinzon et al 2016). Recovery of biodiversity may not be apparent even if efforts to maintain the structure of natural forests are made.

I have tested whether partial cutting strategies continue to provide benefits for saproxylic beetles 20 years post-harvest in two types of stands that typify a successional trajectory in eastern boreal-mixedwood forests. Hardwood stands were studied in the context of varying retention intensities, as well as clearcuts with and without a burn treatment. Mixedwood stands were used to compare gap and dispersed retention partial cuts, as well as clearcuts. We aimed to provide recommendations regarding harvesting intensities and patterns that can optimize biodiversity conservation and sustainable forest management.

1.2 State of Knowledge

Fennoscandian forests provide a cautionary example of how intensive harvesting practices such as clearcutting may degrade habitat quality and impact resident biodiversity (Montoro Girona et al 2023). Over 90% of productive Fennoscandian forest land is subject to intensive forest management aimed at maximizing volume of timber production (Halme et al 2013). This has extensive consequences for forest structure, composition and the availability of standing and downed deadwood. Given that approximately one quarter of all forest species are saproxylic (i.e. reliant on deadwood) (Siitonen 2001), it follows that intensive forest management has led to declines in species richness in fungi (Stokland and Larsson 2011) and a large number of insect groups (e.g. Hilszczański et al 2005; Joelsson et al 2017).

1.2.1 Natural Disturbance-Based Management (NDBM) and the Natural Regime of Québec's Boreal Forest

In North America, and particularly in Canada, NDBM has been proposed as an alternative to even-aged harvesting such as clearcutting (Kuuluvainen and Grenfell 2012). NDBM attempts to emulate disturbances such as insect outbreaks (Wilson and MacLean 2015), fire (Hunter 1993) and windthrow (De Grandpré et al 2018) through harvesting activities. It is hoped that silviculture based on natural disturbances will maintain a mosaic of stand age and composition (Bergeron et al 2001) (Figure 1.1). Thus effective emulation of natural disturbances should consider frequency of natural disturbance, size of canopy openings created during disturbance and volume/quantity of standing and downed deadwood left post-disturbance.

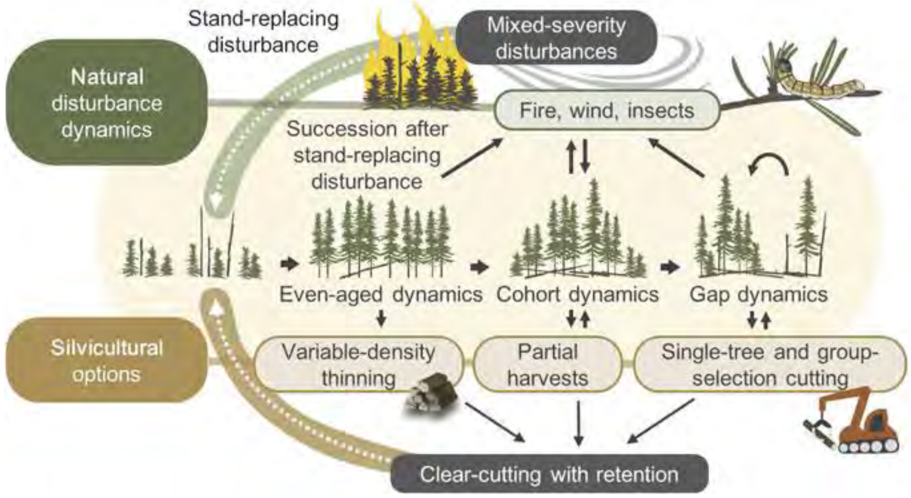

Figure 1.1 A model of silvicultural practices that may emulate natural disturbance and be used as part of a NDBM framework (Montoro Girona et al 2023).

Maintaining a mosaic of stands consistent with historical patterns created by natural disturbance has led to the idea that stand structure can be manipulated as separate tree cohorts that in theory should maintain conditions suitable for resident biodiversity (Bergeron and Fenton 2012). In northwestern Québec, boreal mixedwood forests have been loosely classified into three "cohorts" described by Gauthier et al (2009) that correspond to successional stages occurring post-fire. Initially, following disturbance, stands develop a cohort of shade-intolerant species including jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Tidestr.), balsam poplar (*Populus balsamifera* L.) and white birch (*Betula papyrifera* Marshall) that persist for ca. 100 years. The second cohort is a combination of remaining first cohort stems, shade-tolerant softwood stems that have recruited into the understorey and other species that may establish in gaps (Figure 1.2). This stage occurs every 75-175 years following fire. Eastern white cedar (*Thuja occidentalis* L.), balsam fir and spruce (*Picea* spp. Link) distinguish the third cohort. Additionally, stands in the final stage of succession are characterized by abundant deadwood and few first-cohort species remaining. In later stages of succession, stands are uneven-aged.

Figure 1.2 Mixedwood stands in the Lac Duparquet Research and Teaching Forest, Abitibi-Témiscamingue, Québec.

Forest management plans aspiring to emulate natural disturbances may use a combination of clearcutting or partial cutting. While both types of cutting have been rationalized as mimicking natural phenomena, partial cutting is thought to better maintain biodiversity than clearcutting. Understanding the rationale adopted by a chosen cutting scheme is important if we are to measure and assess the success of the scheme (Montoro Girona et al 2023b). Furthermore, partial cutting has origins in European silviculture, meaning many treatments have been developed to specifically benefit European forests (Montoro Girona et al 2023). Thus, in the following section I will first elaborate on cutting practices currently implemented in Québec's boreal mixedwood forests.

1.2.2 CPRS: Clearcutting in Québec and Associated Consequences

Clearcuts, termed CPRS (Coupe avec Protection de la Régénération et des Sols) in the province of Québec, have been compared to forest fires as both reinitiate succession; yet caution is advised when comparing a clearcut to a fire (Bergeron and Harvey 1997; Larouche et al 2013). Hunter (1993) describes the problem of too-closely emulating a fire disturbance through a clearcut: a clearcut truly resembling a forest fire would need to be much larger and would be more difficult to justify than the smaller clearcuts typically used in forestry. One goal of CPRS is to promote regeneration by providing understorey protection; only merchantable stems are harvested, with a diameter at breast height (DBH) greater than or equal to 9cm (Ruel et al 2013). Stands regenerating after CPRS are typically even-aged and have fewer tree species (Groot et al 2005). Although clearcutting may recover to have some elements of mature stands, such as trees of larger diameter (resulting from the growth of trees left behind), stands that have been clearcut remain structurally distinct from those that have not experienced intensive disturbance for over a century (Bouchard and Pothier 2011). Many populations are negatively affected by clearcutting, and subsequent loss of quality habitat, such as birds and insects (Rosenvald and Lõhmus 2008; Fuller et al 2004). Even-aged silviculture has been associated with the development of stands supporting beetle assemblages distinct from those in reference stands, even after 50 years (Joelsson et al 2017).

To better emulate fire after CPRS, deadwood and logging residuals may be burned post-harvest. In Finnish forests, clearcutting resulted in beetle assemblages that were functionally distinct from those that were observed post-fire (Heikkala et al 2016). While further burning of logging residuals is not a standard practice following CPRS, burning deadwood may attract pyrophilous ("fire-loving") species (Hyvarïnen et al 2006; Toivanen and Kotiaho 2010). Pyrophilous and fire-favoured species use niches created by fire that exclude use by other species owing to specific deadwood characteristics (e.g. colonization by fire-favoured fungi) (Wikars 2002). Initial colonization of these species may lead to an early species-rich community tolerant of open, low-shade conditions; these in turn attract predators and other associated species, facilitating colonization (Heikkala et al 2016). Thus, in the absence of burning, CPRS may not effectively attract pyrophilous species.

1.2.3 The Alternative to CPRS: Partial Cutting in Québec

Partial cutting can include a wide range of retentions. Low retention partial cuts may leave only a few stems whereas high levels of retention may maintain higher stem densities and may show little evidence of impact post-harvest (Bose et al 2013). In contrast to CPRS, partial cutting may be more useful for maintaining heterogeneity in stand structure (Figure 1.3). Partial cutting can be used to emulate smaller openings and understorey recruitment which would otherwise be maintained by natural gap dynamics or windthrow (De Grandpré et al 2000). In Québec, there are many types of partial cutting recognized. Common approaches include "Coupe avec Protection de la Régénération Hautes et de Sols (CPHRS)" and "Coupe avec Protection des Petites Tiges Marchandes (CPPTM). CPHRS retains non-merchantable stems taller than those typically left in CPRS and CPPTM retains merchantable stems (>10-12cm DBH) (Groot et al 2005). Furthermore, there is the irregular shelterwood system. This term encompasses three different partial cutting variants proposed by Raymond et at (2009). All variants involve cuttings introduced with a long regeneration period of over 20% rotation length and with the aim of establishing cohorts of desirable mid-tolerant to tolerant species. Montoro Girona et al (2016) have shown this technique to promote a 41-62% mean increase in radial growth of residual trees 10 years after harvest with a harvest intensity of 50-75%. Individual trees may react differently depending on whether they are edge trees and on height relative to other remaining trees (Montoro Girona et al 2017). Partial cutting may also be classified by cutting pattern: dispersed or gap cutting. Gap cutting consists of clumps of trees removed from within a stand; dispersed retention has been described as "stepping stones" between cut areas (Groot et al 2005).

Figure 1.3 Advantages and disadvantages of partial harvest and clear-cutting (Montoro Girona et al 2023).

Negative consequences of partial cutting can occur if retention levels are low. For example, a 2/3 partial cut meant to mimic dieback of dominant trees in aspen stands may increase mortality of residual trees owing to the low vigour of smaller, unharvested stems (Harvey and Brais 2007). Additionally, dispersed retention in even moderate levels (40%) has been found to be inadequate for forest-dependent arthropod predators (Halaj et al 2008). Spider assemblages in mixedwood and softwood stands continued to differ from unharvested treatments even 10 years after partial cutting with even high retention (75%)(Pinzon et al 2016). Aggregated retention may also be problematic if size of retention patches is not large enough (≤1 ha) to mitigate edge effects, as seen in studies of ground-dwelling invertebrates (Aubry et al 2009; Halaj et al 2008). Retention levels of ≥50% have been suggested as necessary to maintain carabid compositions similar to uncut stands (Work et al 2010). Partial cutting has been found to increase deadwood diversity, or reduce deadwood destruction, in proportion to an increase in the retention level of a stand (Santaniello et al 2016).

1.2.4 Deadwood in Partial Cutting Harvests

Maintaining a variety of deadwood is an important consideration in NDBM. In unmanaged stands, wildfire initiates succession and large volumes of deadwood are recruited (Harper et al 2005). However, post-fire deadwood can degrade quickly and likewise, post-cutting deadwood is decayed in a relatively short span of time. Heikkala et al (2016b) found that ten years after cutting, decomposition of deadwood created at harvest had progressed such that no fresh deadwood was remaining. Jenkins et al (2004) found that the amount of coarse woody debris following harvest declined quickly for the first 14 years after harvest, after which time deadwood leveled off and declined at a slower rate. Self-thinning resulting from stem exclusion contributes a more continuous addition of fresh deadwood that persists through later phases of succession (Harper et al 2005). As the stand begins gap dynamics, coarse woody debris becomes especially abundant owing to the death of the first cohort (Chen and Popadiouk 2002). Older forests can inherit deadwood legacies from earlier successional stages (Bader et al 1995). In stark contrast, logging truncates the potential additions of deadwood that would normally occur as the stand develops (Green and Peterken 1997).

Recruitment of some tree species has been shown to be dependent on specific deadwood substrates (Simard et al 1998). Thus, if these species are reduced or eliminated in a stand, there is a risk succession will produce stands with diminished biodiversity. Partial cutting has been found to benefit deadwood-dependent biota through retention of sufficient deadwood.

1.2.5 Saproxylic Biodiversity in Response to Partial Cutting

Organisms that depend on deadwood in at least one stage of their life cycle are termed saproxylic (Speight 1989). Cavity-nesting birds (Nappi and Drapeau 2011), fungi (Stokland and Larsson 2011), parasitoid wasps (Hilszczański et al 2005) and saproxylic beetles (Hjälten et al 2017) are among the representatives of the forest fauna dependent on fresh deadwood, which may be characterized by persistent bark and wood (Boucher et al 2012). Saproxylic beetles represent a large proportion of forest species (Siitonen 2001): more than twice the number of described species in any other insect order (Grove and Stork 2000). Beetles that initially colonize fresh deadwood initiate decomposition and may determine successive saproxylic communities (Ulyshen and Hanula 2010). Although saproxylic beetles associated with early decay stages are generally comprised of xylophages, predators of early phloem feeders will also be attracted to the sudden pulse of wood colonisers (Lee et al 2014). Saproxylic communities are often distinguished by the decay classes they require, demonstrating that many saproxylic organisms both characterize and are obligatory occupants of only a specific stage of decomposition (e.g. Lee et al 2014, Saint-Germain and Drapeau 2011; Vanderwel et al 2006). Scolytinae (bark beetles) and Cerambycidae (wood-boring beetles) are the predominant xylophages associated with the first stage of wood decay and once deadwood decomposition progresses to a second stage, these beetles and their predators will be replaced by others (Vanderwel et al 2006).

Partial cutting permits forest managers to advance stand structure and composition towards later successional stages or revisit former successional stages (Bose et al 2015). Partial cutting will also likely affect the community of saproxylic organisms, as the type of deadwood available or absent will reflect forest legacies and stand age. The presence of early colonizers observed long-term is relevant because persistence of fresh deadwood-dependent saproxylics may suggest sufficient recruitment of novel deadwood is occurring years after a disturbance-induced deadwood pulse. A continuous influx of fresh deadwood and provision for early saproxylics ensures the persistence of saproxylic species associated with all stages of decay.

Partial cutting with sufficient retention is especially pertinent given that seemingly similar saproxylics may react differently to disturbance. Saint-Germain and Drapeau (2011) determined that after approximately 30 years following disturbance, populations of three cerambycid species, all saprophagous wood-boring beetles, had reacted differently in response to intense logging. Specialization of an insect for one type of deadwood means deadwood retention post-disturbance must leave not just enough deadwood, but enough of the required type. Bark- and wood-boring beetles were shown to better colonize thinned plantations if snags (a population-limiting resource) were supplemented with patches of girdled trees (Thibault and Moreau 2016). Although wood-boring beetles may be attracted to the pulse of deadwood following commercial thinning, their presence will likely indicate visitation rather than colonization if small woody debris is overwhelmingly more abundant than the preferred vertical deadwood (Gandiaga et al 2018). High retention partial cuts can help ensure that living trees eventually provide standing deadwood when they die, thus supporting species that require larger diameter deadwood.

To allow for colonization of cut stands, it is important insects have a means of arrival to the stand. Aggregated retention, if forming an “island” of trees large enough to protect against edge effects, is made more effective if surrounded by dispersed retention that provides connectivity between islands (Lee et al 2017). Using what Lindenmayer et al (2012) refer to as the retention approach, aggregated and dispersed tree retention could be regarded not only as patterns of tree retention but by extension, patterns of deadwood retention if a conscious effort is made to preserve these elements post-harvest. The creation of deadwood corridors within a harvested matrix by using dispersed and aggregated retention in conjunction will promote saproxylic insect conservation (Lee et al 2018).

Partial cutting in the form of small gaps, although resembling a small clearcut, may still allow for recovery of biodiversity if retention of the surrounding stand is sufficient and the gap cut is not too large. Working with rove beetles, Klimaszewski et al (2008) found that composition was increasingly different from uncut stands the larger the gap cut. If gap cuts are small enough, they may present an opportunity for the formation of an ecotone, as species preferring the surrounding forest cover may exist alongside those using the novel open canopy environment (Wiens 1976).

1.3 Objective and Hypothesis

Our objective was to offer recommendations on whether partial cutting of various intensities and cutting patterns could be used as an alternative to clearcutting to allow for the recovery of saproxylic beetles two decades following harvest. We would accomplish this through using IBL flight intercept traps to sample saproxylic beetle communities in cutting treatments done 20 years ago in early seral stage hardwood stands and mid seral stage mixedwood stands (Figure 1.4). Our findings will also contribute to the body of literature that may inform forest management whether natural disturbance-based emulation is observed in what can be inferred from community differences between species. Furthermore, our findings may help us to better understand how saproxylic beetles respond to deadwood availability, and how deadwood availability if affected by treatment, 20 years after cutting.

Figure 1.4 IBL flight intercept trap used to sample saproxylic beetles in hardwood and mixedwood stands of our study.

A simple way to interpret the relative impact of proposed silvicultural treatments is to compare treatments to uncut control stands. Under this approach, differences in abundance of individuals, species or in composition between harvested and unharvested stands would reflect deviations from the ‘natural’ or baseline condition. This approach helps alleviate a common bias in biodiversity research that ‘more is better’ or that maximizing species richness is always the goal of management and increased richness is always desirable. Rather, this assumption is based on an underlying assumption that ‘natural is better’. Under this assumption we would expect that increased tree removal will yield assemblages that are closer in composition to more intensive treatments such as CPRS whereas increased levels of retention will yield communities more similar to control stands. More specifically, with regards to saproxylic beetle abundance, composition and richness, we predicted differences may not be significant between control sites and a partial cut with high retention (1/3 cut). This is based on Joelsson et al (2017), who found uneven-aged, high retention (70%) silviculture supports beetle composition consistent with unmanaged stands based on similar beetle abundance, richness and composition. Similarity to assemblages at control sites implies recovery, and we predicted that 20 years may be sufficient for high retention, 1/3 partial cuts to recover. Because CPRS sites represent the most extreme departure from an uncut site in our study we predicted these will harbour beetle assemblages more distinct from uncut sites than other treatment sites in terms of species composition, species richness and overall community abundance.

We expected that in addition to gradients in standing retention, differences in downed deadwood volume among treatments would affect saproxylic beetle composition. Abundant deadwood volumes are characteristic of mature forests (Kuuluvainen and Laiho 2004) so we expected our control treatments to have greater volumes of deadwood than our cut stands. Deadwood in partial cut stands was expected to be proportionate to retention level; 1/3 partial cuts were expected to have more deadwood 20 years after cutting than 2/3 partial cuts. In addition to overall deadwood volume, the control treatment will presumably have greater diversity of deadwood than any experimental treatment, as trees were not cut at this site and have been allowed to mature and die since the start of the experiment. This translates to the control treatment containing higher volumes of both larger diameter deadwood and deadwood of fresher decay classes.

Logged stands may have decreased availability of large diameter deadwood and deadwood from early decay classes, in turn negatively affecting saproxylic biodiversity (Fischer et al 2015). We expected to see reduced volumes of large diameter deadwood in clearcuts compared with uncut reference stands, as well as reduced volumes of fresh deadwood. Because clearcutting reduces or eliminates deadwood produced from natural tree senescence, deadwood in clearcut stands would be primarily the result of die-off of small diameter trees via self-thinning (Seibold and Thorn 2018). Deadwood predictions correspond with predictions concerning saproxylic beetles. 1/3 cuts were predicted to more closely resemble control stands in saproxylic beetle richness, abundance and composition because the deadwood in 1/3 cuts would also be more similar to the deadwood in control stands (fresher, of greater diameter, and greater volumes of it).

Within mixedwood stands, 40% partial cutting was completed in two different spatial patterns: a gap cut treatment and a dispersed cut treatment. We hypothesized that in our mixedwood stands, saproxylic beetle assemblages from 40% partial gap cuts would be more similar to CPRS treatments than those collected from 40% partial dispersed cuts, which will more closely resemble control stands.

CHAPTER II

FIRST MANUSCRIPT

Response of saproxylic beetle communities twenty years after and partial cut harvests in the eastern boreal mixedwood forest

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Abstract:

Intensive harvesting such as clearcutting poses a risk to saproxylic (deadwood-dependent) biodiversity. Alternatives to clearcutting such as partial cutting may better maintain these species in managed landscapes. Partial cutting may permit for recovery of saproxylic biodiversity through retention of deadwood and living trees. This research aims to evaluate the effects of partial cutting on saproxylic beetle communities. We compared saproxylic beetles collected from a randomized complete block experiment where treatments included 1) clearcutting, 2) clearcutting with a prescribed burn, 3) dispersed partial cuts where 2/3 of trees were removed, 4) dispersed partial cuts where 1/3 of trees were removed and 5) uncut control stands. This study was part of the Sylviculture et Aménagement Forestiers Écosystemique (SAFE) project in the Lac Duparquet Teaching and Research Forest (FERLD) in the boreal mixedwood region of Western Quebec, Canada. We compared beetle communities with deadwood volumes sampled over triangular transects (30m sides) in each treatment x block combination. Using IBL flight intercept traps, we caught and identified 4,842 saproxylic beetles from 216 species. We compared differences in abundance, community composition and species richness between treatments and uncut stands. Abundance of overall saproxylic beetles did not differ between uncut control stands and 1/3 partial cut stands. Extrapolated species richness was higher in uncut, 1/3 cut and 2/3 cut stands than in clearcut stands. Community composition of overall saproxylic beetles was similar in uncut and 1/3 partial cut stands and differed between uncut stands and other treatments. Overall deadwood volume was positively related with overall saproxylic beetle abundance and abundance of fungivores and xylophages. We concluded that saproxylic beetle communities recover more rapidly after partial cutting than clearcutting, and that increasing intensity of cutting negatively

impacts recovery. Our research suggests partial cutting permits long-term recovery of biodiversity while maintaining some timber yield.

Keywords: Canadian forestry, biodiversity conservation, long-term anthropogenic effects, old growth conservation, forest succession

2.1 Introduction

Forest management has shifted from being synonymous with intensive harvesting practices maximizing yield to the integration of conservation strategies for long-term persistence of natural resources and biodiversity (Burton et al 2006; Kuuluvainen et al 2021; Gauthier et al 2023). Forest harvesting that emulates natural disturbances can be used to maintain habitat heterogeneity (Moussaoui et al 2019; Franklin and Forman 1987; Hunter 1993; Montoro Girona et al 2023), ecological legacies including large trees, standing and downed deadwood (Lindenmayer and Laurance 2017; Montoro Girona et al 2016) and biodiversity (Gustafsson et al 2012; Kuuluvainen and Grenfell 2012). In boreal ecosystems, where stand replacing wildfires and large-scale insect outbreaks are frequent (Bergeron and Fenton 2012; Navarro et al 2018), natural disturbance-based management (NDBM) could include a variety of harvesting techniques that could recreate the range and pattern of tree mortality consistent with a forest landscape shaped by these disturbances (Bergeron et al 1999; Montoro Girona et al 2023).

In southern boreal forests in North America, fire is an important disturbance that reinitiates stand succession (Aakala et al 2023). For example, in the Abitibi-Témiscamingue boreal mixedwood forests, in order to maintain a natural landscape mosaic (50% hardwood, 35% mixedwood and 15% softwood) and emulate a fire cycle of 100 years, intensive disturbance such as clearcutting may be necessary (Bergeron and Harvey 1997); however, to rationalize clearcutting as NDBM is controversial. Clearcutting has historically differed from a stand-resetting fire in that a fire will not only leave the soil burnt and chemically altered, but also will leave behind volumes of deadwood and snags not typically retained after a clearcut (Bergeron et al 1999). Clearcutting also homogenizes stand structure with reduced plant and animal biodiversity as seen in Fennoscandian forests subject to decades of even-aged felling (Berg et al 1994; Pawson et al 2006; Keenan and Kimmins 1993; Montoro Girona et al 2023).

In addition to wildfire, windthrow, gap dynamics and insect outbreaks affect forest succession. Insect outbreaks will affect the composition of post-fire successional stages by targeting specific trees. For example, spruce budworm (*Choristoneura fumiferana* Clemens) outbreaks will reduce the softwood trees in a stand, reverting it to a mixedwood composition (Bergeron and Harvey 1997; Lavoie et al 2021; Montoro Girona et al 2018). Windthrow, another gap-creating disturbance in the boreal forest, affects primarily the overstorey (Bergeron et al 1999; Montoro Girona et al 2019). Gap dynamics refer to the continuous mortality and replacement of trees in a stand and this disturbance differs from more severe disturbances in that it maintains and develops a stand rather than initiates it (McCarthy 2001). NDBM may be useful to recreate different successional states in managed landscapes. Group selection cutting may be used to create gaps associated with windthrow damage, careful logging with advanced regeneration and soil protection may be used in mixedwood stands to mimic a return to hardwood stands following insect outbreak and selection cutting in the final, mature cohort can maintain stand composition mimicking gap dynamics (Bergeron et al 1999; Thom and Keeton 2020; Subedi et al 2023).

This management framework has been proposed for the southern boreal mixedwood forest of Québec (Bergeron and Harvey 1997; Burton et al 2006). A cohort model was presented in which NDBM may be used to advance or revert a stand from the present successional cohort to the previous or following one. In the model of Bergeron and Harvey, transition between successional stages is observed by three distinct cohorts: the post-fire hardwoods (*Populus tremuloides* Tidestr. and *Betula papyrifera* Marshall), dominating the stand for the first 100 years; the mixedwood cohort, consisting of hardwoods and softwoods (*Abies balsamea* (L.) Mill. and *Picea glauca* (Moench) Voss); finally, a softwood cohort dominates after 200 years. Manipulation of successional stage, if effectively controlling which cohort is present, should also affect saproxylic (deadwood-dependent) communities dependent on specific cohorts (Löfroth et al 2023).

Partial cutting, or the retention of significant numbers of standing trees post-harvest, can be an effective means to direct future stand composition (Harvey et al 2002), maintain closed-canopy light and microclimatic conditions (Man and Lieffers 1999) and ensure a steady supply of deadwood as standing trees, with time, eventually die and fall to the ground (Bauhus et al 2009). Recruitment of deadwood is important for reintroduction of C into soils (Pan et al 2011), germination sites for mid-shade tree species (Lambert et al 2016; McGee and Birmingham 1997; McGee and Birmingham 1997) and provides habitat for numerous fungal and insect species (e.g. Grove 2002; Speight 1989; Kim et al 2021). Sustained long-term deposition of deadwood is particularly important for maintaining saproxylic insect biodiversity, a group that requires deadwood to complete their development (Hjältén et al 2017; Siitonen 2001; Speight 1989). By maintaining these attributes in partial cuts, it is likely that resident biodiversity will be spared many of the initial impacts associated with more intensive harvesting and may thus recover more quickly.

Saproxylic biodiversity comprises a significant proportion of overall forest diversity, with an estimated 1/4 to 1/3 forest species categorized as saproxylic (Siitonen 2001; Ulyshen and Šobotník 2018). Saproxylic fungi condition the deadwood environment to attract a successive saproxylic community in which fungivorous insects arrive to feed on fungi and attract insects of higher trophic levels (Kaila et al 1994; Jonsell and Nordlander 2004). Beetles (Order Coleoptera) are the most well-studied, diverse order of saproxylic insects, with 65% of families containing saproxylic species (Gimmel and Ferro 2018). Many studies have demonstrated partial cutting can maintain saproxylic as well as epigaeic forest arthropods (Joelsson et al 2017; Lee et al 2018; Pinzon et al 2016). Joelsson et al (2017) found that saproxylic beetle composition did not differ between stands that had been selectively felled (uneven-aged management) after 2-15 years and control stands. North American studies thus far have focused on short- to mid-term effects (e.g. Halaj et al 2008, 5-7 years after treatment; Pinzon et al 2016, 10 years). These studies suggest that the success of partial harvest for biodiversity conservation can be dependent on harvest intensity (Pinzon et al 2016; Work et al 2010), meaning retention levels necessary for effective conservation could be much greater than economically favourable levels of harvest.

Here we evaluate whether partial cutting strategies are effective at maintaining saproxylic biodiversity over longer timeframes. We hypothesized that increasing harvest intensity would have persistent and greater effects on beetle abundance, composition and richness 20 years post-harvest. We anticipated that low intensity 1/3 partial cuts would support similar saproxylic beetle abundance, species richness and composition to uncut control stands. However, we expected 2/3 partial cuts would differ from uncut controls, and resemble clearcut stands. These predictions were based on the hypothesis that 1/3 cut stands would have deadwood volume similar to uncut control stands 20 years after harvest, while 2/3 cut stands would have reduced volumes of deadwood, particularly fresh deadwood. In determining whether beetle communities recovered after 20 years of partial harvest, we sought to offer recommendations for the implementation of partial harvest to maintain diversity by incorporating varying intensities of retention into existing forest management.

2.2. Methods

2.2.1. Study Site

Our project was based in the Lac Duparquet Teaching and Research Forest (FERLD), located in the boreal mixedwood forest in the Abitibi-Témiscamingue region of Québec (48°86’N-48°32’N, 79°19’W-79°30’W) (Brais et al 2004). The study area is located in the mixedwood zone of the boreal shield (Harvey and Brais 2007), in the balsam fir-white birch bioclimatic domain (Larochelle et al 2018). The site receives on average 950mm precipitation and has a mean annual temperature of 0.7°C (Brais et al 2013; Harvey and Brais 2007). A mixed composition of conifers and shade-intolerant hardwood species characterizes the forests in this area. Succession in the region is characterized in early stages by trembling aspen and white birch while balsam fir, eastern white cedar and white birch dominate late successional stands. Aspen stands used in this project originated from a fire in 1923 (Dansereau and Bergeron 1993).

2.2.2 Experimental Design

This study took place as part of the SAFE project. SAFE is a French acronym for “sylviculture et aménagement forestiers écosystemique” or “sylviculture and ecosystem forest management”. In the winter of 1998-1999, replicated harvesting treatments were applied in a randomized complete block design. Experimental treatments were replicated across 3 blocks measuring 1-3 ha. Within the deciduous cohort of the SAFE project, there are 5 experimental treatments which reflect an increasingly intense gradient of stem removal and forest floor disturbance. Stem removal treatments included 1/3 and 2/3 removal of the total basal area through dispersed partial cutting as well as clearcut treatment (Coupe avec Protection de la Régénération et des Sols, or CPRS) where all stems ≥9cm diameter at breast height (DBH) were removed but advanced regeneration was left in place (Ruel et al 2013; Raymond et al 2013). In the 1/3 partial cuts, small non-vigorous stems were cut through low thinning; in 2/3 partial cuts, large diameter, marketable stems were cut using crown thinning (Brais et al 2004). Harvested stands were compared to uncut stands within the experimental block that had pyrogenic origin.

2.2.3 Data Compilation and Measurements

In each block, each experimental treatment contained 5 circular plots measuring 400m^2. For this study, we collected insects from 3 of the 5 plots in each experimental treatment. We sampled saproxylic beetles continuously between May 30 and August 25 in 2019 using IBL intercept traps (Polish IBL2-traps, CHEMIPAN, Warszawa, Poland). IBL traps were emptied regularly at approximately 3-week intervals.

2.2.3.1. Beetle Sampling and Identification

Beetles caught in IBL traps were categorized as saproxylic or non-saproxylic using available literature on species biology. All major groups of saproxylic beetles were identified to species using American Beetles I (Arnett and Thomas 2000) and American Beetles II (Arnett et al 2002) as well as comparison with specimens from the Réné Martineau Insectarium at the Laurentian Forestry Centre (Natural Resources Canada). However, we excluded several families and subfamilies from our analysis owing to difficulty with identification. This was due to a lack of keys available or available keys needing revision, or species identification involving dissection which we were limited in time to perform. We did not include beetles from the following families and subfamilies in our analysis: Cryptophagidae (except for *Antherophagus* sp. (Dejean), *Caenoscelis subdeplanata* (Brisout de Barneville), *Henoticus serratus* (Gyllenhal), *Henotiderus centromaculatus* (Reitter), *Myrmedophila americana* (LeConte) and *Pteryngium crenulatum* (Erichson)), Leiodidae, Epuraeinae (Nitidulidae)(except *Epuraea flavomaculata* (Mäklin)), Ptiliidae, Aleocharinae (Staphylinidae), Pselaphinae (Staphylinidae) (except for *Batrisodes lineaticollis* (Aubé)), Scaphiidinae (Staphylinidae) and Scydmaeninae (Staphylinidae). In the case of smaller beetles, such as ptiliids and aleocharines, traps could contain large numbers that may have altered our findings. As a result, a few hundred beetles that may still be classified as saproxylic are excluded and we acknowledge our findings are not representative of all groups.

2.2.3.2 Downed Deadwood Volume

Deadwood volume was measured, 20 years post-harvest, across all treatments between May and August 2019 using the line-intercept method (Van Wagner 1968). Deadwood was measured over 3, 30m transects oriented in a triangle in the center of each block. Diameter and decomposition class of all pieces of deadwood intersecting the transect were recorded. Deadwood decomposition class was based on classifications by Daniels et al (1997) and consisted of classes 9-13 with 9 being least decomposed deadwood and 13 most decomposed.

2.2.4. Statistical Analysis

We compared abundance of beetles across harvesting treatment using generalized linear models (GLMs) with a model offset to account for minor differences in trapping duration. For these models we used functions from the MASS package (Venables and Ripley 2002). Negative binomial models were used to accommodate highly dispersed count data as negative binomial models are known to perform better than transformations for count data with a large dispersion (O'Hara and Kotze 2010) and models were validated using likelihood ratio chi-squared tests. We also compared abundance of saproxylic beetles or specific feeding guilds (including fungivores, predators, xylophages and decayed wood feeders) to overall volumes of deadwood using similar negative binomial models. Some feeding guilds were included in overall saproxylic beetle analysis, but not analyzed independently as a group owing to low relative abundance (such as slime mold feeders and parasitoids). Traps from each block were pooled for statistical analysis. We compared overall deadwood volume (square root transformed) across treatments using a simple linear model.

We compared species richness between cutting treatments using rarefaction analysis in the iNEXT package (Hsieh et al 2020). Extrapolated and interpolated rarefaction curves were plotted as well as confidence intervals (95%) to determine whether species richness differed 20 years after harvest.

To compare community composition between treatments, nonmetric multidimensional scaling (NMDS) was used (MASS package; Venables and Ripley 2002). The most abundant species (consisting of 50 or more individuals) were also plotted onto the NMDS plot to show species associations with treatment. Saproxylic beetle catch rates were first Hellinger transformed to minimize differences in absolute abundance and to allow for comparison of relative abundance. We compared compositional differences in saproxylic beetle assemblages across cutting treatments using PERMANOVA (adonis2; Oksanen et al 2022) with 999 permutations on Hellinger transformed catch rates. All the analyses were done using R (R Core Team 2021).

2.3. Results

2.3.1 Saproxylic Beetles

2.3.1.1. Saproxylic Beetle Abundance

We identified 4,842 saproxylic beetles representing 216 species. Fungivorous beetles were the most abundant feeding guild, with 2,225 individuals representing 103 species. Predators comprised 920 individuals representing 51 species, xylophages 992 individuals in 35 species and decayed wood feeders 497 individuals in 23 species.

Twenty years post-harvest, overall saproxylic beetle abundance did not differ between 1/3 partial cuts and uncut stands (coefficient estimate= -0.154, p=0.229) but was reduced in 2/3 partial cuts (coefficient estimate= -0.444, p=0.001), CPRS treatments (coefficient estimate= -0.578, p<0.001) and CPRS treatments with a burn (coefficient estimate=-0.69; p<0.001) (Figure 1).

Decreases in saproxylic beetles were largely driven by fungivores; however, abundance of fungivores did differ between 1/3 partial cut and uncut stands (coefficient estimate=-0.203, p=0.050) as well as in stands with increasing harvest intensity (Figure 2a). Predator abundance was significantly lower in 2/3 partial cuts than uncut stands (coefficient estimate=-0.546, p=0.020) but was similar in 1/3 partial cuts (coefficient estimate=-0.112, p=0.627) and CPRS cuts without (coefficient estimate=-0.378, p=0.105) and with a burn (coefficient estimate= -0.200, p=0.389) (Figure 2b). Xylophages were unaffected by harvesting (Figure 2c) whereas decayed wood feeders were significantly reduced in 2/3 partial cuts (coefficient estimate=-1.146, p=0.001) (Figure 2d).

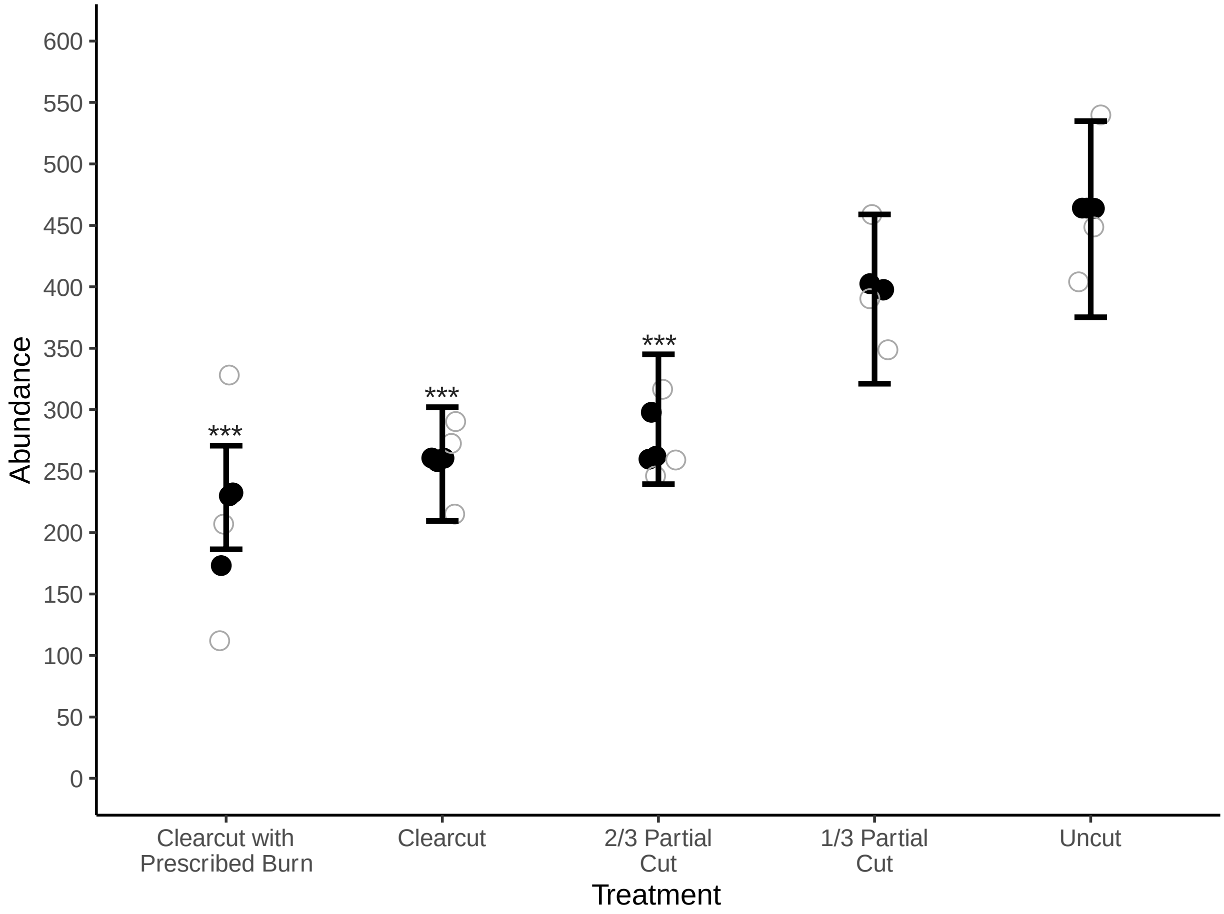

Figure 2.1 Abundance of saproxylic beetles collected in each treatment with 95% confidence intervals. Solid points correspond to model prediction from negative binomial GLM prediction. Open points correspond to observed data. *** indicates a p-value of <0.001 for GLM results.

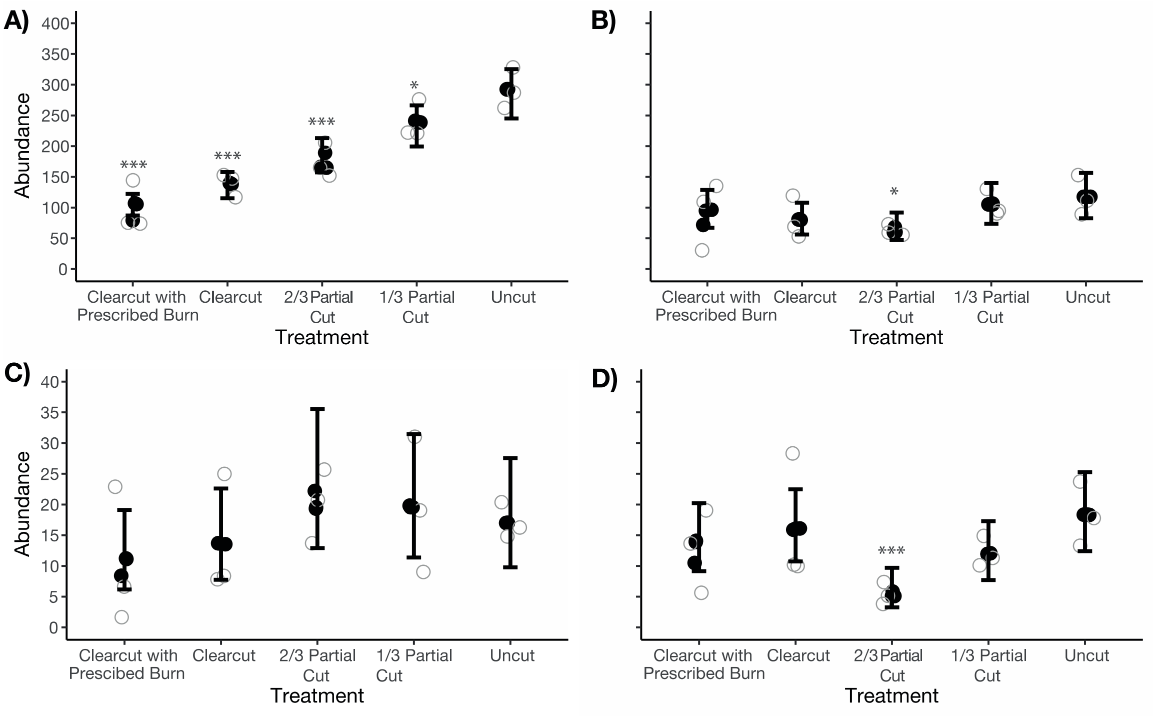

Figure 2.2 Abundance of saproxylic A) fungivores B) predators C) xylophages and D) decayed wood feeders with 95% confidence intervals as modeled by negative binomial GLM (solid points) and observed data (open points). *** indicates a p-value of <0.001, ** a p-value of <0.01 and * a p-value of <0.05 for GLM results.

2.3.1.2 Species Richness of Saproxylic Beetles

One third partial cuts maintained similar species richness with uncut stands and both treatments had about 1.5 times greater richness than either CPRS or CPRS with prescribed burns (Figure 3). Two-third partial cuts had greater richness than clearcuts. Species richness in two-third partial cuts was also generally greater than clearcuts with prescribed burns but 95% confidence intervals did overlap. Species richness estimates for clearcut with prescribed burn, clearcut, 2/3 partial cut, 1/3 partial cut and uncut treatments are 133.37, 132.24, 175.30, 209.08 and 189.14 respectively. Observed species richness for clearcut with prescribed burn, clearcut, 2/3 partial cut, 1/3 partial cut and uncut treatments was 103, 106, 124, 151 and 153 respectively.

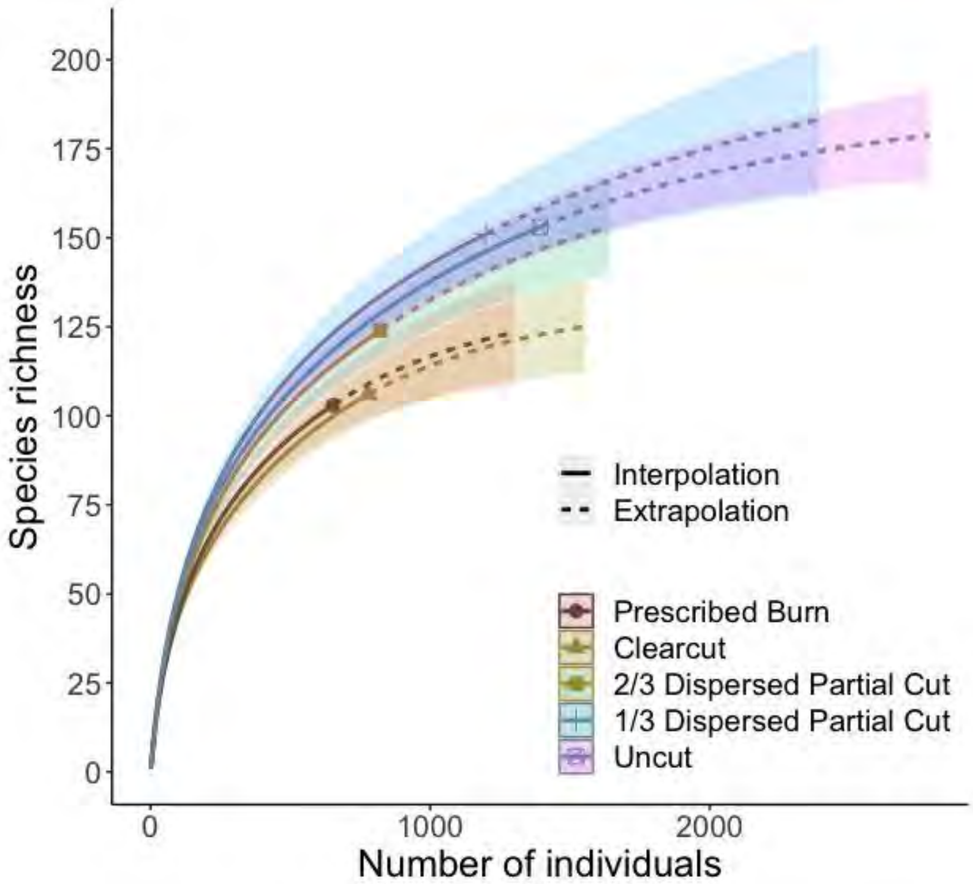

Figure 2.3 Species rarefaction curve with 95% CI showing interpolation and extrapolation of species richness in each treatment based on saproxylic species collected per number of individuals sampled.

2.3.1.3 Saproxylic Beetle Composition

NMDS plotting reveals 1/3 partial cuts had an overall community composition similar to uncut control stands, with 2/3 partial cuts and CPRS treatments differing in composition (Figure 4). CPRS treatments with a burn treatment differed most in composition from uncut stands. Differences in composition between harvest treatment two decades after harvest was statistically significant (PERMANOVA analysis on Hellinger transformed catch rates, $p<0.001$).

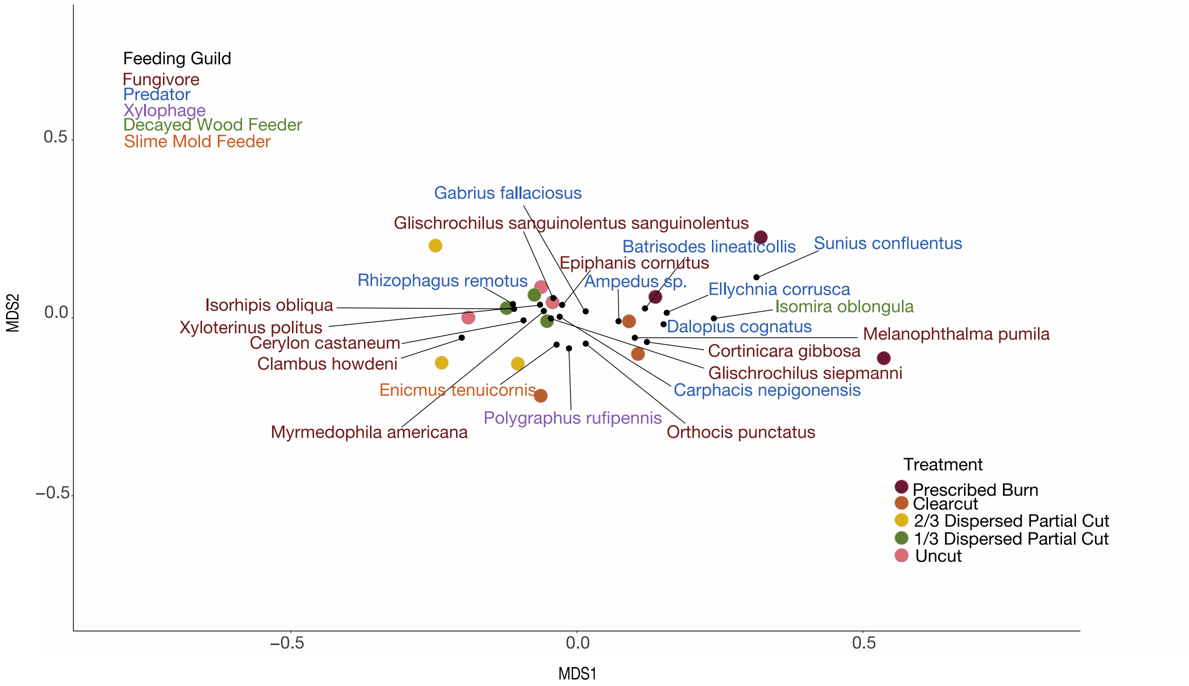

Figure 2.4 NMDS plot showing similarity in saproxylic beetle species community composition between treatments, with abundant (>50 individuals) species. Similarity is relative to distance between points. Points represent three blocks (replicates) per treatment, with three traps pooled into a block for each treatment. Results are generated after 20 iterations with a stress of 0.12.

Plotting our most abundant saproxylic beetles on an NMDS plot revealed that most of our abundant fungivores were associated with uncut stands and 1/3 partial cuts (Figure 4). These fungivores include the ambrosia beetle *Xyloterinus politus* (94 individuals), nitidulids *Glischrochilus sanguinolentus* (Olivier) (69 individuals) and *G. siepmanni* (Brown) (194 individuals), cryptophagid *Myrmedophila americana* (56 individuals) and eucnemids *Epiphanis cornutus* (Eschscholtz) (66 individuals) and *Isorhipis obliqua* (Say) (144 individuals). Three predators were associated with uncut and 1/3 cut stands: *Rhizophagus remotus* (LeConte) (68 individuals) and staphylinids *Carphacis nepigonensis* (Bernhauer) (124 individuals) and *Gabrius fallaciosus* (Horn) (208 individuals). Two fungivores were closely associated with uncut stands: *Cerylon castaneum* (Say) (172 individuals) and *Clambus howdeni* (Endrödy-Younga) (107 individuals). Our most abundant species, latridiids *Melanophthalma pumila* (LeConte) (408 individuals) and *Cortinicara gibbosa* (Herbst) (328 individuals) were more closely associated with clearcuts. Our most abundant decayed wood feeder, *Isomira oblongula* (Casey) (100 individuals) was associated with clearcuts, while our most abundant xylophage, *Polygraphus rufipennis* (Kirby) (94 individuals) was associated with 2/3 partial cuts. *Enicmus tenuicornis* (LeConte), a slime mold feeding latridiid, was also associated with 2/3 partial cuts (112 individuals).

2.3.2. Deadwood Volume

Our GLMs indicated a significant positive effect of overall deadwood volume on overall saproxylic beetle abundance (coefficient estimate= 0.003, p= 0.004; Figure 5), abundance of fungivores (coefficient estimate= 0.004, $p<0.001$) and abundance of xylophages (coefficient estimate= 0.005, p=0.01), but no significant effect of overall deadwood volume on abundance of predators (p=0.639) or decayed wood feeders (p=0.236) was found (Figure 6). Overall mean deadwood volume was highest in uncut stands and while not significantly different from either partial cut, significantly higher than both clearcuts (Table 1). Overall mean deadwood volume was higher in 2/3 partial cuts than in other cutting treatments. When combining volumes of the two freshest decomposition classes (9 and 10), only clearcuts had significantly lower volumes of fresh deadwood (coefficient estimate= -1.667, p= 0.027 for CPRS; CPRS with prescribed burn did not have any deadwood of decomposition class 9 or 10) (Figure 7a). Uncut stands had greater volumes of larger diameter (≥17.6cm) deadwood than treated stands, except for 2/3 cuts stands (coefficient estimate= -0.832; p=0.562) (Figure 7b).

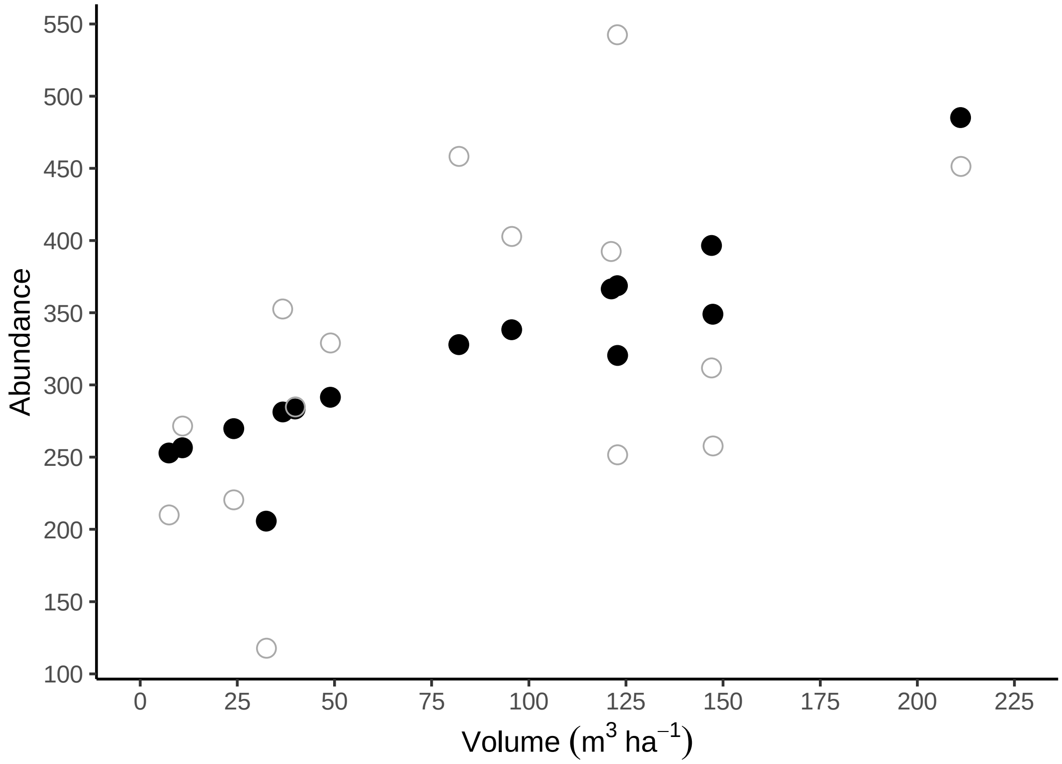

Figure 2.5 Saproxylic beetle abundance relative to overall volume of deadwood as modelled by negative binomial GLM (solid points) and collected data (open points).

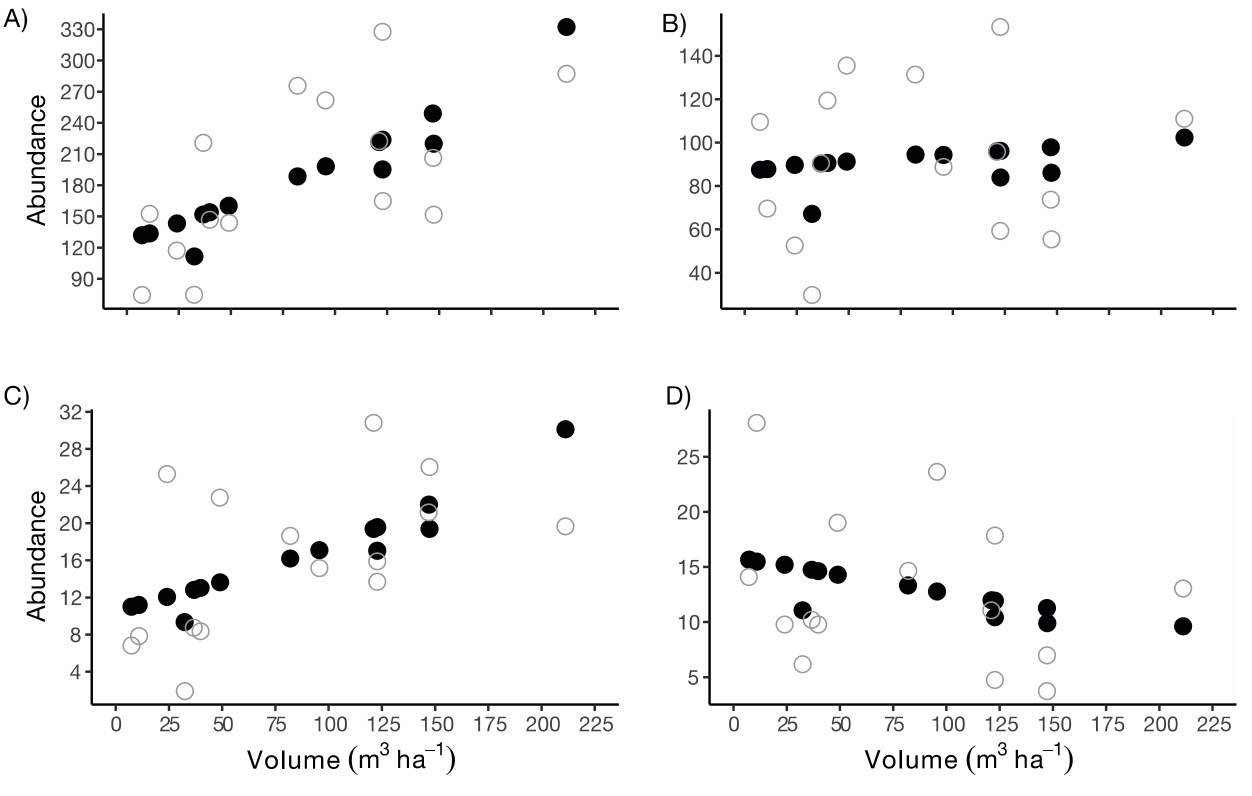

Figure 2.6 Abundance of saproxylic A) fungivores, B) predators, C) xylophages and D) decayed wood feeders plotted against overall deadwood volume (m^3ha^{-1}) as modelled by negative binomial GLM (solid points) and collected data (open points).

Table 1.1 Mean overall deadwood volume (m^3ha^{-1}) with SE for each treatment as well as mean volume for different decomposition and diameter classes. Means are calculated for three blocks containing each treatment.

		Decomposition Class					Diameter Class (cm)				
Treatment	Overall	9	10	11	12	13	<2.5	5	10	15	≥17.6
1/3 Dispersed Partial Cut	79.97± 24.41	4.04±1.37	4.18±2.18	17.73±8.47	17.11±5.29	36.92± 20.63	0.00	11.72±3.52	15.14±4.98	24.63±12.19	28.49±6.44
2/3 Dispersed Partial Cut	139.09± 8.13	3.10± 2.16	10.86±8.46	45.50± 12.63	30.14±2.22	53.10± 20.68	0.00	12.66±3.55	29.28±3.04	39.07±6.55	58.09±7.59
Clearcut	24.94± 8.35	1.12	2.32±1.34	1.83±0.58	6.09±1.60	14.50±8.28	0.00	4.47±1.58	11.57±1.30	8.91±1.89	8.89
Clearcut with Prescribed Burn	29.59± 12.10	0.00	0.00	1.26±0.48	13.74±6.39	14.58±5.27	0.00	4.64±2.82	7.49±2.31	2.32	25.03±0.01
Uncut	143.18± 34.89	9.97± 4.08	7.44±1.97	58.30± 23.60	31.98±9.47	38.82± 11.86	0.08	12.66±3.01	30.47±4.21	23.90±7.50	76.12±29.53

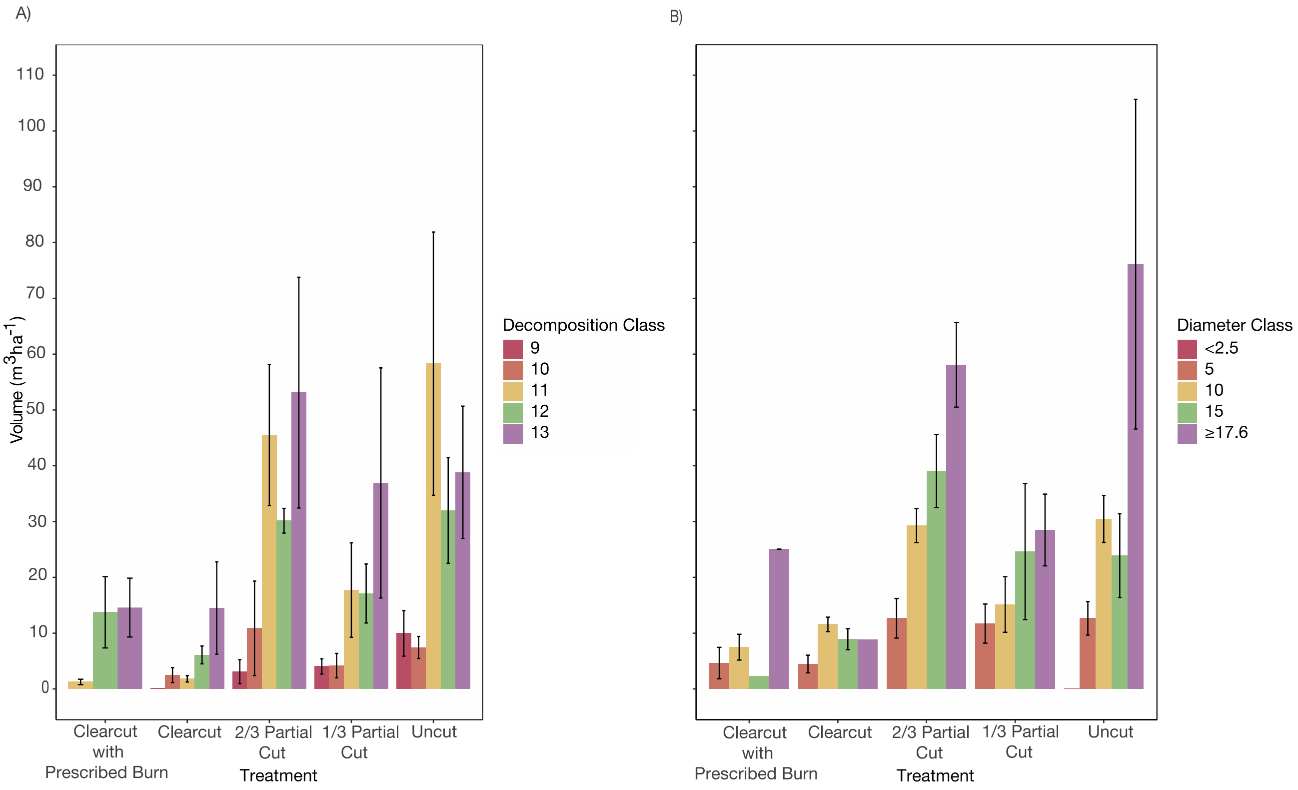

Figure 2.7 Volume of deadwood (m^{3}ha^{-1}) of different decomposition classes (A) (with 9 as the freshest class) in each treatment and of different diameter classes (B). Deadwood volume represents deadwood sampled in three blocks for each treatment according to the triangular transect method by Brais et al (2004).

2.4. Discussion

Partial cutting maintains forest biodiversity mid- to long-term (e.g. Joelsson et al 2017; Pinzon et al 2016; Work et al 2010). As hypothesized, greater intensities of harvesting continued to affect overall saproxylic beetle abundance and composition more than 20 years post-harvest. Two-third cuts may provide only limited benefits for saproxylic beetles but still may be preferable to CPRS treatments in that they promote xylophage abundance and species richness similar to uncut stands. In Canada's boreal forest, even-aged harvesting practices such as CPRS are used almost exclusively (Montoro Girona et al 2023; Fenton et al 2008) and of the experimental cases of partial cutting that exist, similar retention levels to our 2/3 cuts have been ineffective in biodiversity conservation. Consistent with our results, previous research on compositional differences of other non-saproxylic groups of insects suggests increasing harvest intensity increases the difference between harvested stands and uncut stands. For example, in Western Canada, ground-dwelling spider composition in partially cut stands was more similar to uncut stand spider composition 10 years after treatment if retention levels were high (i.e., 75%) (Pinzon et al 2016). Ground beetles required ≥50% retention to maintain composition consistent with uncut stands 5 years after treatment (Work et al 2010). Similar effects of treatment intensity on community composition in our study suggest that after 20 years, while saproxylic beetle communities in 1/3 cuts show recovery, more time is needed for recovery in 2/3 cuts and CPRS treatments.

Significant differences in abundance between high and low intensity cuts should be interpreted with a caveat. Two-third partial cuts had large-diameter, marketable stems harvested using crown thinning, while in 1/3 low intensity partial cuts, small non-vigorous stems were cut through low-thinning (Brais et al 2004). Ideally, to determine whether it is the intensity of harvest affecting long-term saproxylic beetle recovery, both 1/3 and 2/3 cuts would be subject to identical thinning techniques. The SAFE experiment was designed to test whether natural disturbances could be mimicked through various forms of harvest rather than to directly test the effects of intensity of harvest by proportion of trees removed (Bergeron and Harvey 1997). Low thinning used in 1/3 partial cuts was designed to be an analogue of self-thinning in the stem exclusion stage and crown thinning used in 2/3 cuts was to be an analogue of dieback (Harvey and Brais 2007). Nonetheless, scarcity of comparable long-term studies on partial cutting in the boreal forest of North America means the findings of our study may still be regarded as relevant in terms of assessing intensity. Because overall deadwood volume was not significantly different between the 2/3 partial cut and the uncut treatment while overall saproxylic beetle abundance did differ between the two treatments, canopy cover patterns resulting from 1/3 low-thinning cuts two decades earlier could be contributing to beetle abundance patterns more so than deadwood abundance.

Reduced species richness of saproxylic beetles in both CPRS treatments relative to partial cuts or uncut stands was inconsistent with other long-term partial cutting saproxylic studies from Fennoscandia. Joelsson et al (2017) found that species richness for saproxylic beetles did not differ between treatments. A possible reason for discrepancies in our study and those of Joelsson et al (2017) may be attributed to differences in fungi. Fungi can respond rapidly to changes in stand conditions caused by harvesting. Short term (≤1 year after partial cutting) studies on fungal response to partial harvest of 25-30% revealed that basidiomycete species richness declined significantly after harvest (Nordén et al 2008). Norwegian forests with a history of management had a strongly reduced fungal species richness compared with natural forests (Stokland and Larsson 2011). Kebli et al (2011; 2014) found that species richness in saproxylic fungi may be largely attributed to species of deadwood available, suggesting that in our clearcut stands, after two decades, depleted fresh deadwood may lead to loss of saproxylic species preferring fresh deadwood that retains tree species characteristics. Because our study excluded some of the families identified in the work of Joelsson et al (2017), species richness differences between clearcuts and partial cuts may also have diminished if we analysed the same groups.

Abundance of saproxylic beetles decreased with increasing harvest intensity, but overall volume of deadwood did not decrease with increasing harvest, where 2/3 partial cuts had a higher overall deadwood volume than 1/3 cuts. Several reasons may explain why deadwood availability is greater in 2/3 cuts than in 1/3 cuts. More intensive partial cutting may increase windthrow shortly after harvest. Solarik et al found that aspen mortality was approximately 30% 5 years after low-retention (10-20%) partial harvest and approximately 50% after 10 years in the same stands (2011). In our site, this means that two decades after harvest, the elevated volumes of deadwood reflect the higher mortality of retention trees in 2/3 cuts. As well, both fresh (decomposition class 9 and 10) and large diameter deadwood (≥17.6 cm diameter class) was present in stands recovering from 2/3 cuts. The presence of fresh and large diameter deadwood alongside deadwood of other decomposition and diameter classes reflects a diversity of available deadwood in high intensity partial cuts and uncut stands. Diversity of deadwood is known to be important for species diversity, as saproxylic species will often show specificity for deadwood of certain diameter, decomposition, species, etc. (Grove 2002). Although species richness in both our partial cuts was not significantly different from uncut stands, 2/3 cuts did not allow for the recovery of saproxylic beetle abundance. This suggests sufficient deadwood may not be the only, or even most important, factor contributing to saproxylic beetle recovery. Xylophage abundance patterns further allude to this.

Wood borers tend to be more abundant in early decay classes and specialized to specific types of deadwood (Hammond et al 2003), indicating that fresh deadwood or moribund trees are sufficiently available for this group in all treatments, despite our findings that clearcuts do not have deadwood of the freshest decomposition classes. Our most common xylophage, *Polygraphus rufipennis*, primarily attacks wood that is freshly dead (Bowers et al 1996) and was present in all treatments in our study. *P. rufipennis* may be responding to high volumes of fresh deadwood in 2/3 partial cuts as well as environmental cues that may be enhanced in a more highly disturbed site. Interestingly, 2/3 cuts had the highest volumes of highly decomposed deadwood (decomposition class 13) while supporting the lowest abundance of decayed wood feeders. Our most abundant decayed wood feeder, *Isomira oblongula*, was more closely associated with clearcuts than with 2/3 cuts. This strongly suggests that while decayed wood feeders are dependent on advanced decay classes they may also depend on other features such as sun exposure or other environmental factors. Saprophagous species adapted to fire disturbance have been known to prefer open canopy (Rodrigo et al 2008).

Saproxylic saprophagous beetles ingest decaying wood containing fungal biomass (Ulyshen and Šobotník 2018), and may therefore be reacting to fungal diversity patterns. Fungivores may likewise react to a combination of fungal biodiversity patterns and environmental conditions. The association with clearcuts of our most abundant fungivores and most abundant overall saproxylic species, the latridiids *Melanophthalma pumila* and *Cortinicara gibbosa*, suggests that these treatments are supporting a saproxylic community more closely resembling a post-fire community than a recovered one as latridiids have been associated with burned stands (Saint-Germain et al 2004; Boucher et al 2012). Latridiidae have been speculated as likely possessing mycangia in the form of exoskeletal cavities (Grebennikov and Leschen 2010). Thus, the community composition of fungi in clearcuts may also be dominated by species more closely associated with beetle species from clearcuts.

Not only saprophagous and fungivorous saproxylic beetles, but all feeding guilds, may be affected by fungal diversity patterns in deadwood. Fungi are architects of saproxylic communities, as it is often the colonization and conditioning of deadwood by fungi that permits insects to use deadwood (Gimmel and Ferro 2018). Aside from being a food source, fungi may promote higher beetle diversity through the creation of microhabitats known to support more diverse communities, such as tree cavities (Birkemoe et al 2018). Although fungal diversity studies on deadwood can be difficult to complete owing to challenges in fungal identification, Hagge et al (2019) found that functional diversity patterns in saproxylic beetles and fungi mirrored one another across a geographic gradient. Species richness has been found to be positively correlated between saproxylic beetles and fungi (Persiani et al 2010). Beetles reliant on fungi for food would likely show greater correlation in diversity patterns to fungi and in our study, fungivore abundance patterns might be explained by fungal abundance patterns if such a study was also done on fungal communities two decades following harvest.

Community composition patterns of dominant species may suggest inter-guild interactions and response to environmental conditions. The fungivore *Glischrochilus sanguinolentus*, associated with uncut and 1/3 cut stands in our study, has previously been suggested as an old-growth species in hemlock-hardwood forest stands (Zeran et al 2006); thus its prevalence in our 1/3 partial cuts two decades after harvest is an encouraging sign of our 1/3 partial cuts beginning to resemble our uncut stands. Because the fungivores *Cerylon castaneum* and *Clambus howdeni* were more closely associated with uncut stands than 1/3 partial cuts, these may be more sensitive to any intensity of cutting. The fungivores present in higher abundances in uncut and 1/3 cut are likely enabling higher populations of predators specializing on them. *Rhizophagus remotus*, a predator of scolytid beetles, has previously been found in higher abundance when numbers of the ambrosia beetle *Trypodendron retusum* were present (Hammond et al 2001). Members of Tachyporinae, such as those of the genus *Carphacis* are associated with mushrooms such as *Pleurotus ostreatus* (Cline and Leschen 2005). The predator *Carphacis nepigonensis* likewise associated with lower intensities of partial cutting in our study may be benefitting from the increased number of fungivores in these sites.

In the context of saproxylic biodiversity conservation, our findings provide long-term evidence for the benefits of partial cutting as an alternative to clearcutting. Even though 1/3 cuts offer significantly more benefits than 2/3 cuts, they limit how much wood may be harvested and do not yet show recovery of fungivores. These limitations may continue to underscore the importance of reserves in managed forests alongside partial cutting (e.g. Fedrowitz et al 2014). Although our results are long-term in the context of available literature on North American partial cutting for biodiversity conservation, our research does not span the time our stands require to transition between successional stages. Hardwood stands in our study typically last 100 years before transitioning to mixedwood stands (Bergeron and Harvey 1997). Thus sampling of saproxylic beetle communities and deadwood after the passage of subsequent decades can help us better understand what recovery will still occur within the present successional stage, particularly in the context of 2/3 partial cut recovery.

Low intensity 1/3 partial cuts offer a promising compromise between timber extraction and conservation goals. Overall saproxylic beetle abundance and composition recovered in 1/3 partial cuts when compared to uncut stands. Harvest intensity this low will sufficiently reduce profit to require incentives be adopted if partial cutting is used for biological conservation. Forest certification schemes such as those offered by the Forest Stewardship Council (FSC) and the Programme for the Endorsement of Forest Certification Schemes (PEFC) offer certification of forestry activity if guidelines for sustainable forestry are met, encouraging markets who wish to appeal to consumers mindful of conservation to promote practices favouring products produced by certified activity (McDermott et al 2023). Because retention forestry is often socially more accepted than intensive harvest (Lindenmayer et al 2012), if recovery of biodiversity is also supported by low intensity partial cutting, forest certification programs based on recovery of biodiversity following partial cutting may provide enough of an incentive for forest management to adopt, at least in part, some degree of low intensity partial harvest into forestry frameworks.

Author Contributions

Conceptualization: UD, MMG, TTW
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Formal analysis: UD, MMG, TTW
Investigation: UD
Methodology: UD, MMG, TTW
Project administration: MMG, TTW
Resources: MMG, TTW
Supervision: MMG, TTW
Validation: UD, MMG, TTW
Visualization and edition: UD, MMG, TTW
Writing–original draft: UD
Writing–review: UD, MMG, TTW
Funding: MMG, TTW

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Conflict of Interest Statement

The authors declare no conflict of interest.

CHAPTER III

SECOND MANUSCRIPT

Saproxylic beetle communities in mixedwood stands recover two decades after intermediate intensity partial harvests

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Abstract:

Partial cutting, or the retention of living trees and deadwood at time of harvest, may emulate natural disturbances such as windthrow or insect outbreak, promoting recovery. Saproxylic (deadwood-dependent) beetle communities may benefit from the long-term deposition of deadwood as retention trees eventually senesce and fall to the forest floor. We evaluated the response of saproxylic beetle communities 20 years after partial harvest in mixedwood stands. Our research was based on mixedwood stands from the Sylviculture et Aménagement Forestiers Écosystemique (SAFE) project in the Lac Duparquet Teaching and Research Forest (FERLD) in the boreal mixedwood region of Western Quebec, Canada. In 2000-2001, 40% gap cuts, 40% dispersed cuts and clearcuts were replicated across 3 blocks measuring 1-3 ha. In 2021, saproxylic beetles were sampled using IBL flight intercept traps. Deadwood volume was sampled and response of volume to treatment compared to response of beetle abundance to treatment. We caught 3,812 saproxylic beetles from 185 species and observed no significant difference in overall beetle abundance between cutting treatments and unharvested stands. Species richness and community composition did not significantly differ between uncut stands and cutting treatments. Our study suggests most saproxylic beetle groups in mid-seral stage mixedwood stands can recover two decades after 40% partial harvest and in small-scale clearcuts. This excludes xylophages, whose abundance was almost 5 times as great in uncut stands than in clearcuts. For this reason, future studies should consider factors such as study plot size, stand composition and canopy cover alongside deadwood to allow for a more comprehensive understanding of recovery of saproxylic biodiversity under various scales of harvest. Based on our results, intermediate harvest intensity of 40%-50% may aid long-term recovery of saproxylic beetle communities, including xylophage communities, and is a promising silvicultural tool to maintain biodiversity in mixedwood forests.

Keywords: forest recovery, Canadian silviculture, clearcutting, ecosystem-based management, forest succession, long-term anthropogenic effects

3.1 Introduction

Natural and anthropogenic disturbances influence stand structure and composition in forest ecosystems (Bergeron and Fenton 2012; Montoro Girona et al 2016; James et al 2011; Shorohova et al 2023; Aakala et al 2023). Partial cutting retains some living trees and forest elements such as deadwood and canopy cover, presumably emulating natural disturbances of intermediate severity such as windthrow, insect outbreak and gap dynamics (Bergeron et al 1999; Harvey et al 2002). As such, it is a strategy commonly used in natural disturbance-based approaches to forest management (NDBM)(Montoro Girona et al 2023; Gauthier et al 2023). NDBM posits that at each forest successional stage, different cutting techniques can be used to emulate natural disturbance and manipulate the stand into a different successional stage as long as the disturbance regime for the forest is well known (Bergeron and Harvey 1997; Bergeron et al 1999; De Grandpré et al 2018; Kuuluvainen and Grenfell 2012). Presumably, this will allow a forest to recover more closely to recovery following natural disturbances and permit stands to progress through successional stages (Gauthier et al 2008; Ruel et al 2023). For example, in the southeastern Canadian boreal forest, it has been proposed that clearcutting in hardwood stands can “reset” the stand as fire would, partial cutting in mixedwood stands could mimic natural succession, and selection cutting in softwood stands could resemble gap dynamics (Bergeron et al 1999; Harvey et al 2002). In mixedwood stands, while clearcutting will reset a stand to the first stage of succession, partial cutting has been shown to promote conifer regeneration and reduce aspen dominance after 10 years, potentially advancing succession to softwood stands (Prévost et al 2010). In softwood stands, old growth characteristics may be maintained by selection cutting (Ruel and et al 2013), or clearcutting may be used to reset the stand (Harvey et al 2002).

Retention of living trees also ensures that fresh deadwood will continue to be supplied to the forest floor even after deadwood from harvest has decomposed (Montoro Girona et al 2019; Löfroth et al 2023). Maintaining long-term availability of fresh deadwood in managed stands is a particularly important goal, as abundant deadwood volume is characteristic of unmanaged mature forest stands (Kuuluvainen and Laiho 2004; Rouvinen et al 2002) and if we are to maintain biodiversity consistent with unmanaged stands, appropriate deadwood profiles may enable this. Saproxylic insects comprise a large proportion of saproxylic forest species; in northern Europe, where forest biodiversity is best known, 20-30% of forest insects are saproxylic (Ulyshen and Šobotník 2018). Saproxylic beetles are the most well-studied, with 65% of families having at least one saproxylic species (Gimmel and Ferro 2018). Saproxylic beetle communities will be distinct according to deadwood decomposition stage and other deadwood characteristics (Bouget et al 2012; Hjältén et al 2007; Hjältén et al 2010; Hjältén et al 2012; Hjältén et al 2023). Thus, saproxylic beetle communities should also follow a successional cycle as the deadwood composition changes throughout forest successional stages (Crites and Dale 1998).

For many forest organisms, achieving conservation targets is dependent on retention level (Montoro Girona et al 2023). For non-saproxylic biodiversity, studies have shown that if retention is sufficient, recovery is observed even short- to mid-term following harvest. Retention of ≥50% was necessary to maintain carabid composition consistent with uncut stands 5 years after cutting (Work et al 2010). Retention of 75% of trees maintained litter-dwelling spider composition more consistent with uncut stands after 10 years than if less was retained (Pinzon et al 2016). Because retention levels and time needed for recovery have varied depending on the arthropods studied, conservation frameworks will need to consider what factors associated with retention are driving recovery for various groups and whether these factors overlap for different groups. Successional stage has previously been shown to affect recovery of biodiversity, with spider and carabid assemblages differing from uncut stands more when cutting occurs in later seral stages (i.e. mixedwood and softwood stands) (Pinzon et al 2016; Work et al 2010). Finally, spatial pattern of silvicultural treatments in a stand are able to influence growth of residual trees (Montoro Girona et al 2017), regeneration (Montoro Girona et al 2018) and may influence biodiversity patterns. Gap cuts may have more severe effects on biodiversity though reducing connectivity between the cut area and surrounding forest. Klimaszewski et al (2008) found that when using gap cuts, increasing the size of a gap was associated with rove beetle composition increasingly different from uncut stands and a decreased catch rate.

Cutting techniques that maintain retention and future deposition of deadwood necessarily will reduce the volume of wood that can be recovered at harvest. Furthermore, if retention is low, retained trees may be lost relatively quickly after cutting. Retained trees are vulnerable to mortality from windthrow (Scott and Mitchell 2005). Less trees retained also mean that should a severe disturbance such as fire affect the cut site, all remaining trees may be lost (Heikkala et al 2014). In Canadian forests, clearcutting is predominantly used as an even-aged harvesting technique (Montoro Girona et al 2018; Fenton et al 2008). If retention of trees is too low to expect benefits for biodiversity, but necessary retention for biodiversity conservation too economically unrealistic, forest management may altogether choose to completely harvest all trees in a stand and preserve unmanaged stands for biodiversity. Unmanaged stands designated for biodiversity preservation are already promoted as a complementary strategy alongside any proposed cutting practices, even those within a NDBM framework (Nordén et al 2008; Burton et al 2006). Some research suggests dividing forests into thirds: one for conservation, one for multiple use forestry and one for intensive timber production (Burton et al 2006). If we evaluate silvicultural practices that allow for timber yield while promoting the recovery of biodiversity, we can develop a framework to harvest in a manner that allows for a compromise between extracting natural resources and enabling recovery of biodiversity.

We aimed to compare saproxylic beetle communities in mixedwood stands of Canada's eastern boreal mixedwood forest that have been treated to 40% partial cutting in an aggregated cut and dispersed cut over two decades ago. We predicted that 40% gap cuts would have beetle assemblages different from 40% dispersed cuts, be less species rich and have a lower abundance of saproxylic beetles. Because we are working with an intermediate cutting intensity, we also expected both 40% cuts to be of lower species richness, abundance and of different composition than uncut control stands, thus not yet showing recovery, but to be higher in species richness and abundance than clearcut stands albeit also of different composition. We hoped to use our findings to evaluate whether silvicultural practices such as these may be used as a tool to maintain biodiversity in the boreal forest.

3.2 Methods

3.2.1 Study Site

Our study was located in the mixedwood stands of the Lac Duparquet Teaching and Research Forest (FERLD) in the Abitibi-Témiscamingue region of Québec (48°86'N-48°32'N, 79°19'W-79°30'W)(Brais et al 2004), occuring in the mixedwood zone of the boreal shield (Harvey and Brais 2007) and in the balsam fir-white birch bioclimatic domain (Larochelle et al 2018). The region has a continental climate, receiving a mean annual precipitation of 890mm and temperature of 0.7°C (Brais et al 2013). The soil is characterized by clay deposits originating from Lake Barlow-Ojibway (Veillette 1994). Mixedwood stands of this site consist of mature aspen stands with an understorey of balsam fir (*Abies balsamea* L.), black spruce (*Picea mariana* Mill.), and white spruce (*Picea* glauca Moench), and are of 1910 fire origin.

3.2.2 Experimental Design

The mixedwood stands in which our study was located is part of the SAFE experiment, with mixedwood stands designated SAFE 3. SAFE is a French acronym for "sylviculture et aménagement forestiers écosystemique", or "sylviculture and ecosystem forest management". In 2000-2001, harvesting treatments were replicated across 3 blocks measuring 1-3 ha in a randomized complete block design. Treatments in the mixedwood cohort of SAFE consisted of 40% aggregated cuts and 40% dispersed cuts, in a basal area harvest of stems >9cm dbh (Brais et al 2013). A clearcut (Coupe avec Protection de la Régénération et des Sols, or CPRS) was also completed, in which all stems ≥9cm diameter at breast height (DBH) were removed but advanced regeneration was left in place (Ruel et al 2013). Dispersed cuts used single tree selection throughout the plot, while aggregated gap cuts consisted of the removal of grouped stem islands ~400m^2. Stands with no cutting treatments were designated as controls.

3.2.3 Data Compilation and Measurements

Each experimental treatment within each block contained 5 circular plots measuring 400m^2. We collected insects from 3 of the 5 plots in each experimental treatment. We sampled saproxylic beetles continuously between May 25 and August 28 in 2021 using IBL intercept traps (Polish IBL2-traps, CHEMIPAN, Warszawa, Poland). IBL traps were emptied regularly at approximately 3-week intervals. Traps were installed on May 25 2021 with collection and reset dates of June 24, July 15-17, August 5 and August 28. Propylene glycol was used as a preservative in collection bottles and refilled at each collection.

3.2.3.1 Beetle Sampling and Identification

All beetles caught were categorized as saproxylic or non-saproxylic according to literature on species biology. Major groups of saproxylic beetles were identified to species using American Beetles I (Arnett and Thomas 2000) and American Beetles II (Arnett et al 2002) and by comparing them with specimens from the Réné Martineau Insectarium at the Laurentian Forestry Centre (Natural Resources Canada). Families or subfamilies whose identification was difficult to reliably achieve within the limits of our resources were excluded from our analyses and these include: Cryptophagidae, (except for *Antherophagus suturalis* (Mäklin), *Caenoscelis subdeplanata* (Brisout de Barneville), *Henoticus serratus* (Gyllenhal) and *Henotiderus centromaculatus*) (Reitter), Leiodidae, Epuraeinae (Nitidulidae)(except for *Epuraea flavomaculata*

(Mäklin)), Ptiliidae, Aleocharinae (Staphylinidae), Pselaphinae (Staphylinidae) (except for *Batrisodes lineaticollis* (Aubé)), Scaphiidinae (Staphylinidae) and Scydmaeninae (Staphylinidae).

3.2.3.2 Deadwood Volume

Deadwood sampling was done in May-August 2019, using the line-intercept method (Van Wagner 1968). The triangular transect protocol (Brais et al 2004) was used in which a triangle of 30m sides was set up in each treatment site. Diameter and decomposition class of deadwood overlapping the transects forming the triangle was recorded. Decomposition classes were assigned between classes 9 and 13, with 13 being the most decomposed class. Daniels et al (1997) was used for criteria to assign deadwood decomposition class and Van Wagner's formula (1968) to estimate deadwood volume, which consists of the following:

$$(V = \left(\frac{\pi^2}{8L}\right) \Sigma d^2$$

where V is volume, L is length of sample line, and d is piece diameter at intersection.

3.2.4 Statistical Analysis

Overall saproxylic beetle abundance, abundance of specific feeding guilds (fungivores, xylophages, predators, decayed wood feeders and slime mold feeders) were compared between treatments using generalized linear models (GLMs) generated by the MASS package in R (Venables and Ripley 2002). Feeding guilds such as parasitoids and phytophages were included in overall saproxylic beetle analysis, but not analyzed independently as a group owing to low relative abundance. A negative binomial distribution was used to account for overdispersion (O'Hara and Kotze 2010) when comparing abundances between treatments for overall saproxylic beetles and different feeding guilds. Models were validated using likelihood ratio chi-squared tests. Traps from each block and treatment combination were pooled and abundance data was offset by trapping days when performing GLMs to account for slight differences in collection periods for each trap owing to inclement weather or trap disturbance. GLMs were also used to determine whether overall deadwood volume significantly had a significant effect on overall saproxylic beetle abundance and abundance of different feeding guilds. To generate species richness estimates, rarefaction curves were created using the package iNEXT (Hsieh et al 2020). Confidence intervals of 95% were plotted for interpolated and extrapolated curves to determine significant difference between species richness in different treatments 20 years after harvest. Nonmetric multidimensional scaling (NMDS) was used to generate a plot showing community composition similarity between treatments by positions of treatment sites relative to one another (MASS package; Venables and Ripley 2002). Catch rates were first Hellinger transformed to account for prominence of abundant species over rarely occurring species (Legendre and Gallagher 2001). PERMANOVA tests using adonis2 (vegan package; Oksanen et al 2022) were run to determine whether the effect of treatment on communities was significant using 999 permutations and cutting treatment as fixed effect. All the analyses were carried out using R (R Core Team 2021).

3.3 Results

3.3.1 Saproxylic Beetles

3.3.1.1 Saproxylic Beetle Abundance

We identified 3,812 saproxylic beetles belonging to 185 species. Over half of these (61%), or 2 329 individuals, were classified as fungivores, representing 90 species. Predators comprised 21% of saproxylic beetles caught, with 793 individuals within 40 species. Xylophages made up 11% with 427 individuals in 25 species. Less than 5% of our total saproxylic beetle abundance was represented by decayed wood feeders, (117 individuals in 20 species) and slime mold feeders (117 individuals in 8 species). Additionally, we caught 8 individuals of the parasitoid *Pelecotoma flavipes* (Melsheimer) (Coleoptera: Ripiphoridae) and 21 individuals of the phytophage *Athous rufifrons* (Coleoptera: Elateridae) (Randall).

Twenty years post-harvest, abundance of saproxylic beetles did not significantly differ between uncut stands and 40% gap cuts (GLM coefficient estimate=-0.298, p=0.240) or 40% dispersed partial cuts (GLM coefficient estimate=-0.247, p=0.331) nor between uncut stands and clearcuts (GLM coefficient estimate=-0.203, p=0.424) (Figure 3.1). With the exception of xylophages, abundance of feeding guilds did not differ between uncut stands and 40% cutting treatments or clearcuts. Nearly 5 times more xylophages were collected in uncut stands than in clearcuts (GLM coefficient estimate=-1.542, p=0.002) (Figure 3.2C); however, 25% of this abundance was represented by *Dryocoetes caryi* from one of the three control blocks. For less abundant saproxylic feeding guilds, we caught 7 individuals of *Pelectoma flavipes* (parasitoid) in 40% gap cuts and 1 individual in uncut stands; we caught 4 individuals of *Athous rufifrons* (phytophage) in clearcut stands, 3 in gap cuts, 10 in dispersed cuts and 4 in uncut stands.

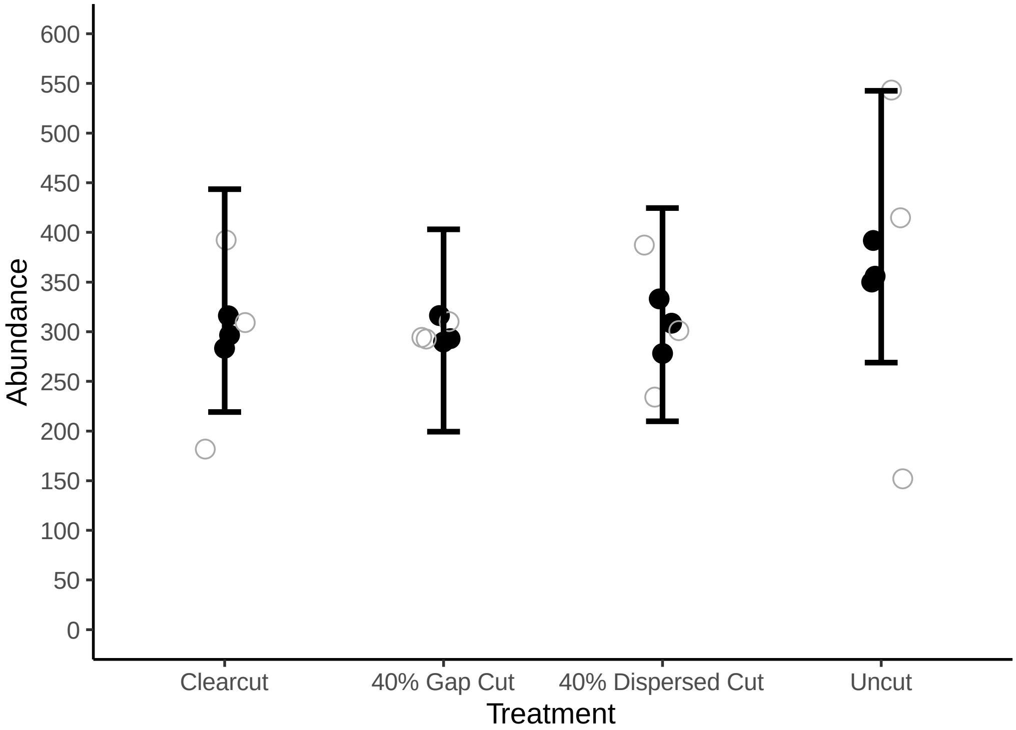

Figure 3.1 Overall saproxylic beetle abundance in clearcut, 40% cut (gap and dispersed) and uncut stands as modelled by negative binomial GLM (solid points) and collected data (open points). Open points represent three blocks (replicates) per treatment, with three traps pooled into a block for each treatment.

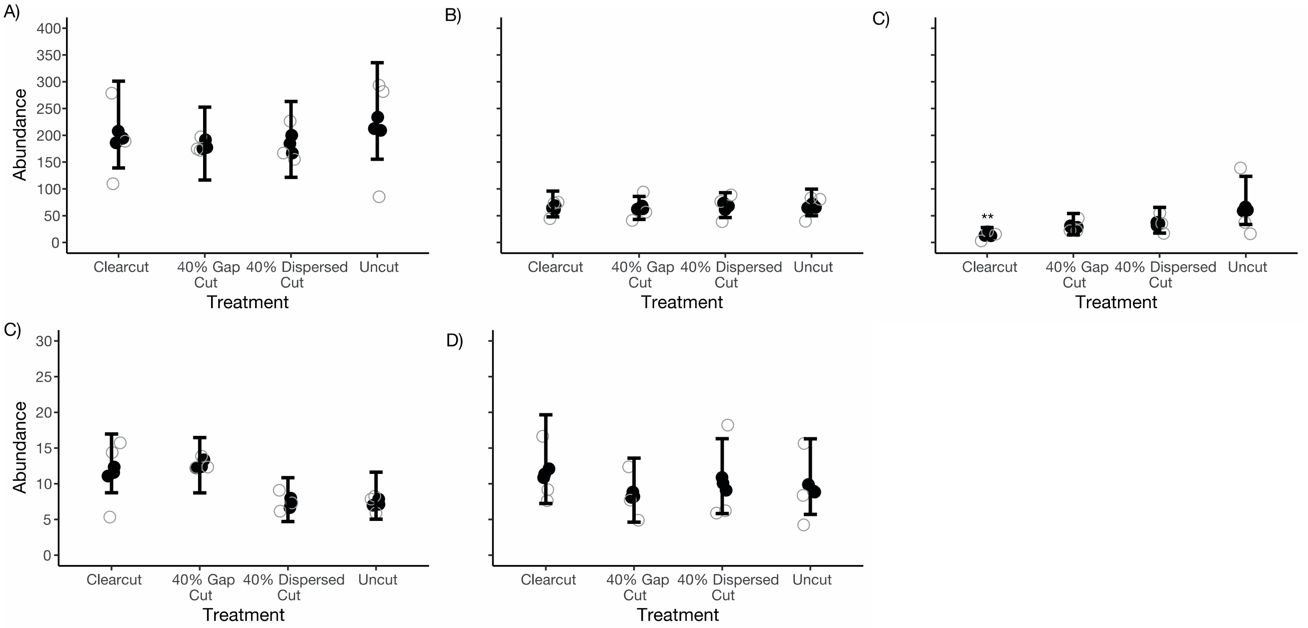

Figure 3.2 Abundance of saproxylic A) fungivores B) predators C) xylophages D) decayed wood feeders and E) slime mold feeders as modelled by negative binomial GLM (solid points) and collected data (open points). Open points represent three blocks (replicates) per treatment, with three traps pooled into a block for each treatment. ** indicates a p-value of <0.01.

3.3.1.2 Species Richness of Saproxylic Beetles

The confidence intervals of the rarefaction curve generated for uncut stands overlap with those of every other treatment. This suggests 20 years after partial harvest and clearcutting, there is no significant difference between species richness in uncut stands and any of the cutting treatments (Figure 3.3). However, 40% gap cut confidence intervals do not overlap with clearcut confidence intervals and just barely with 40% dispersed cut confidence intervals, signifying a higher species richness by ~53 species in gap cuts than clearcuts and dispersed cuts. Species richness estimates were highest for gap cuts (189.88) and lowest for dispersed cuts (136.98). Observed species richness was highest in gap cuts (133) and lowest in clearcuts (111).

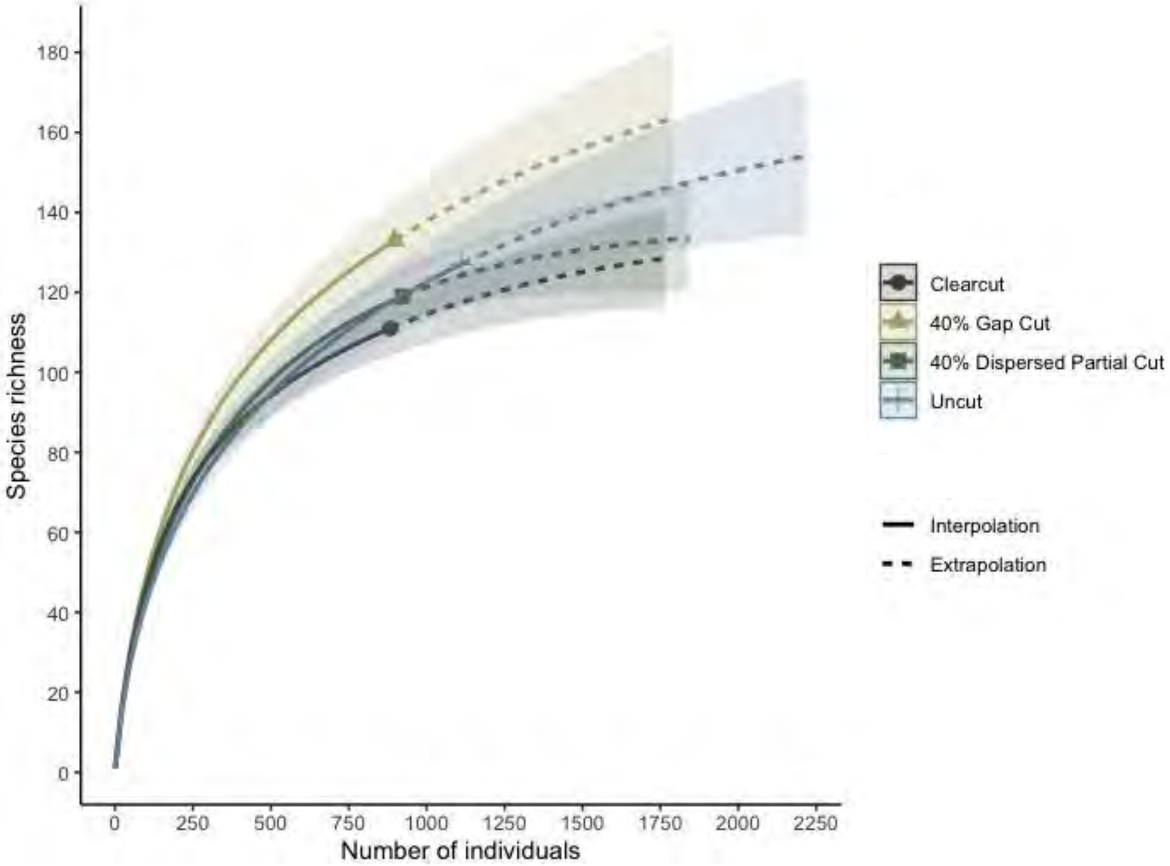

Figure 3.3 Species rarefaction curve with 95% CI showing interpolation and extrapolation of species richness in each treatment based on saproxylic species collected per number of individuals sampled.

3.3.1.3 Saproxylic Beetle Composition

Examining abundant species on our NMDS plot, we found that the scolytid xylophage *Dryocoetes caryi* (Hopkins) (127 individuals) was collected mostly from one uncut stand (107 individuals) (Figure 3.4). Our most common xylophage, scolytid

Polygraphus rufipennis (Kirby) (203 individuals), was more closely associated with uncut stands and 40% dispersed partial cuts.

The nitidulid fungivore *Glischrochilus sanguinolentus* (Olivier) was associated most closely with uncut stands (73 individuals). Erotylid fungivore *Triplax dissimulator* (Crotch) (65 individuals) was less common in 40% dispersed cuts than other treatments. Our most abundant species, *Clambus howdeni* (Endrödy-Younga), with 504 individuals caught, did not have an obvious association with a particular treatment.

PERMANOVA analysis showed no significant effect of treatment on overall saproxylic beetle community composition two decades after harvest (P value of 0.07). Plotting community differences using NMDS reveals that community composition in uncut stands tended to differ most from clearcuts. Overall however, treatments were similar to each other in terms of community composition (Figure 3.4).

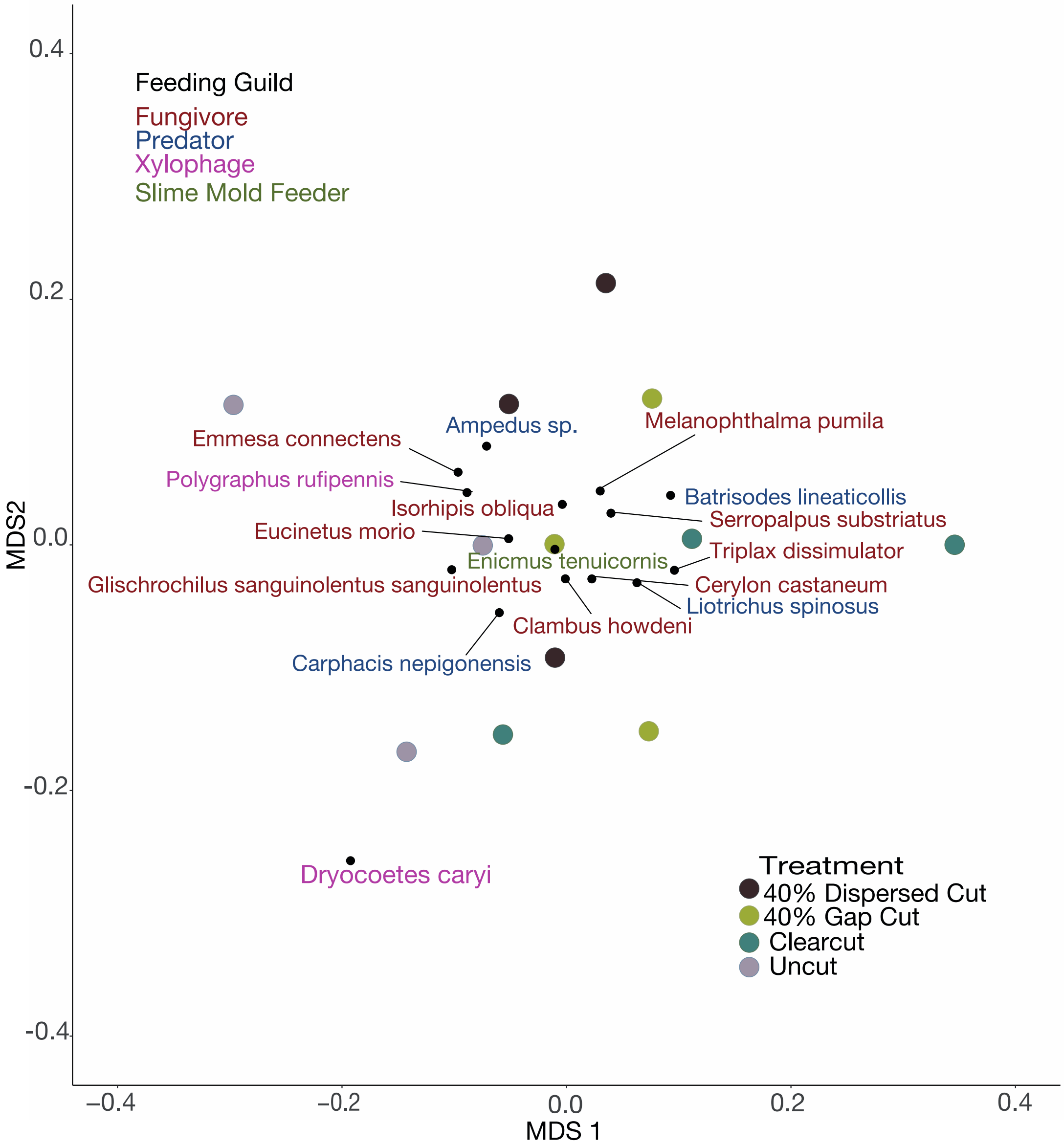

Figure 3.4 NMDS plot showing similarity in saproxylic beetle species community composition between treatments, with abundant (>50 individuals) species. Similarity is relative to distance between points. Points represent three blocks (replicates) per treatment, with three traps pooled into a block for each treatment. Results are generated after 20 iterations with a stress of 0.16.

3.3.2 Deadwood Volume

Uncut stands had low volumes of deadwood of the freshest decomposition class (class 9), but 4 times as much deadwood of intermediate decomposition (class 11) as clearcuts (Table 2). Large diameter deadwood was abundant in all treatments, ranging from a mean of 39.99 m^3ha^{-1} in clearcut stands to 46.63 m^3ha^{-1} in gap cuts. Although xylophage abundance did significantly differ between uncut stands and clearcut stands, this was not true also true for fresh deadwood. When a GLM analysis was done to determine whether volume of fresher deadwood (decomposition classes 9-11) was positively related with xylophage abundance, no such relation was found (P value of 0.94).

Our GLM analysis indicated no significant effect of overall deadwood volume on overall saproxylic beetle abundance (P value of 0.72) or abundance of any of our analyzed feeding guilds (P value of 0.75 for fungivores, 0.92 for predators, 0.60 for xylophages, 0.79 for decayed wood feeders and 0.72 for slime mold feeders). Although overall mean deadwood volume was highest in uncut stands (Table 2), linear regression models generated from square root transformed data revealed no significant difference between overall volume in uncut stands and all treated stands, as was the case with patterns of overall saproxylic beetle abundance and abundance of most feeding guilds.

Table 2.1 Mean overall deadwood volume (m^3ha^{-1}) with SE for each treatment as well as mean volume and SE for different decomposition and diameter classes. Means are calculated for three blocks containing each treatment.

		Decomposition Class					**Diameter Class (cm)**			
	Overall	**9**	**10**	**11**	**12**	**13**	**5**	**10**	**15**	**≥17.6**
40% Dispersed Cut	118.86±15.22	9.98±2.83	14.97±7.25	33.29±6.12	28.27±10.06	35.67±1.72	9.73±1.20	20.35±6.48	46.19±3.85	42.59±17.41
40% Gap Cut	125.76±29.60	4.01±1.91	11.12±4.21	38.41±17.90	43.78±10.01	29.78±2.64	12.16±3.12	29.95±8.00	37.02±3.78	46.63±30.29
Clearcut	102.23±37.57	8.82±7.98	8.11±7.77	16.45±10.33	34.80±11.57	39.69±5.48	16.98±7.59	17.24±5.73	28.03±13.47	39.99±16.05
Uncut	142.33±39.31	0.90±0.28	15.81±7.99	67.87±23.26	37.31±8.53	20.74±2.01	18.84±1.92	31.40±6.57	45.75±11.84	46.34±28.82

3.4 Discussion

Twenty years post-harvest, we detected few differences in overall saproxylic beetle abundance and composition between control stands and cutting treatments, or in the abundance of major feeding guilds such as fungivores and predators between control stands and cutting treatments. Limited differences between treatments suggests that impacts of clearcutting and partial cutting do not persist beyond two decades post-harvest when cutting is done within the parameters of our study, that is, 40% gap or dispersed partial cutting or clearcutting 1-3 ha. This extends our knowledge of the timeline of recovery after partial harvest that other studies have been developing with forest organisms other than saproxylic insects. Five years post-harvest in mixedwood stands, epiphytes had significantly reduced species richness and abundance at 50% retention, as well as significantly different community composition than in uncut stands (Caners et al 2010). For spider populations in the same study site, for 10 years after harvest, species assemblages in mixedwood stands tended to differ from those in uncut control stands more with decreasing retention (Pinzon et al 2016). Carabids required ≥50% retention in mixedwood stands to maintain composition similar to uncut stands (Work et al 2010).

For some taxa, short- and mid-term studies have suggested that if retention is high enough, partial cutting benefits the recovery of biodiversity (Caners et al 2010; Pinzon et al 2016; Work et al 2010). Tree removal of 40% is an intermediate intensity partial cut and studies have found that just slightly higher intensities may negatively affect various communities at least in the initial years following harvest.

Species richness between cut and uncut stands is consistent with the findings of Joelsson et al (2017) who also found that species richness did not differ between sites that had been selectively felled 2-15 years ago and uncut control stands. Additionally, a global meta-analysis by Mori and Kitagawa (2014) concluded that arthropod species richness does not differ between primary forests and forests with retention. Interestingly, our clearcuts did not have a significantly different species richness than our uncut stands, although they did have lower species richness than our gap cuts. The gap cut creates a new, distinct environment and because our gaps were only 400m^2, edge effects may be prominent at these sites, increasing species richness and creating an ecotone (Wiens 1976). Harper and Macdonald (2002) found that 16 years after clearcutting, edge canopy was more heterogenous than interior forest. In our study, species heterogeneity could be a response to canopy heterogeneity at the edges of our gap cut.

Species richness can be higher for both plant and animal communities following disturbance as the new conditions can create an ideal environment for species adapted to fire (Toivanen and Kotiaho 2010), increased volumes of deadwood (Franc and Götmark 2008) and sudden opening of the canopy (Burke et al 2008); however, increased species richness is not necessarily a desirable outcome of partial harvest, as species adapted to post-disturbance environments are often of low concern with regards to conservation (Franc and Götmark 2008). Because we did not observe species composition in our clearcuts characteristic of sites following an intense disturbance such as fire (dominance of pyrophilous or open-canopy loving species), our findings suggest recovery twenty years later to the state of uncut stands.

Recovery times for biodiversity may vary among successional cohorts. For example, response of epigaeic arthropods to partial cutting have been more severe and long-lasting in later seral stages (Work et al 2010; Pinzon et al 2016). This may not be the case for saproxylic insects in our study. In our study on hardwood stands (SAFE 1 manuscript), we observed reduced saproxylic abundance with increased harvest intensity in earlier seral stages dominated by a deciduous canopy of trembling aspen. In our hardwood stands, we also observed overall volume of deadwood had a positive effect on saproxylic beetle abundance. This may suggest that as a stand matures, the effect of deadwood on insects decreases or is mediated by other effects. Seibold et al (2016), working in sunny and shaded mature closed canopy sites and clearings in south eastern Germany, observed that canopy openness strongly mediated the effects of deadwood addition on arthropods, increasing or decreasing abundance of different groups based on ecological preferences. Although Seibold's work is on epigeal rather than saproxylic arthropods, based on our results, saproxylic beetles may also be responding more strongly to variables such as canopy openness the older a stand becomes. Working in the same mixedwood stands we used, Noulhaguet et al (2023) found that 20 years after cutting, stem density per ha in both gap and dispersed cuts had regenerated to a similar degree and to a greater extent than in uncut stands. This implies that gap cuts and dispersed cuts, as well as clearcuts measuring 1-3ha, may have a comparable canopy openness after 20 years and this may be what saproxylic beetles respond to in mixedwood stands more strongly than deadwood availability.

Similar community composition for saproxylic beetles between treatments suggests that from a saproxylic biodiversity perspective, clearcuts did not "reset" succession in the long-term, nor partial cutting advance succession to coniferous stands, as similar community composition suggests similar stand composition between treatments. If natural disturbance were indeed emulated, we would expect that community composition of saproxylic beetles would differ to reflect different successional stages as promoted by cuts of varying intensities. Partial cutting has been shown to promote conifer regeneration 10 years after cutting by Prévost et al (2010), suggesting that it may be used as a tool to advance succession. However, Noualhaguet et al (2023), found that in SAFE mixedwood stands, partial cutting did not promote regeneration to coniferous stands but rather maintained a 50-50 ratio of hardwood to coniferous tree species. Noualhaguet furthermore observed that although clearcuts reset mixedwood stands in terms of returning them to an earlier seral stage, clearcutting in hardwood stands resulted in different stand composition 20 years post-harvest than clearcutting in mixedwood stands, with more conifers in regenerated mixedwood stands. The findings of Noualhaguet as well as our own suggest that silviculture struggles to emulate natural disturbance.

Overall saproxylic community composition did not prominently differ between uncut stands and cutting treatments on our NMDS plots, a result that contrasts with the community compositional changes we observed 20 years after cutting in our previous study on the hardwood stands of SAFE. For example, *Glischrochilus sanguinolentus* was associated with low intensity 1/3 partial cut stands from our previous study of partial harvest in hardwood stands of SAFE (SAFE 1manuscript). This species has previously been suggested as an old-growth species in hemlock-hardwood forests by Zeran et al (2006), who found when working in the St. Lawrence forest region, southeastern Ontario, that 73% of individuals were collected from old-growth stands, as opposed to managed stands. Although the largest abundance of this species (22 individuals) was collected from one block of our uncut stands, this number was not significantly higher than abundances in other treatments. Zeran et al elaborate that the majority of *G. sanguinolentus* individuals in their study were caught using trunk-window trapping, and that the species may have been more likely to be caught this way owing its association with the bracket fungi that traps were placed near. While uncut stands may be more likely to harbor resources such as bracket fungi preferred by *G. sanguinolentus*, as discussed earlier, the canopy closure of cut stands after two decades may mean the species is able to take advantage of connectivity between stands.

Triplax dissimulator, also a fungivore, was present in all our treatments but less common in 40% dispersed cuts. This species was previously found by Bouchard and Hébert (2021) to be negatively associated with coniferous stands (>60% basal area in *Abies balsamea* and *Picea mariana*). Noulhaguet et al found that 20 years after cutting in our mixedwood site, balsam fir continued to dominate stands with composition of 54% after clearcutting, 59% after gap cuts, 73% after dispersed cutting and 94% in the control (2023). Because Bouchard and Hébert also found *T. dissimulator* was negatively associated with warmer climates, this may suggest that the species reacts to climate alongside stand composition and underscores the point previously made that saproxylic species may react not primarily to deadwood availability or to other isolated factors, but deadwood availability alongside other factors. With regards to another of our fungivores, *Clambus howdeni*, Majka and Langor (2009) reported that 89% of specimens recorded from Nova Scotia were collected in coniferous forests and that in some studies, the species seemed to prefer old growth stands (Chandler 1991; Bishop 2009). Because this was our most abundant species, our collection of this fungivore suggests that mixedwood forests also may support relatively high abundances of the species.

Fungivores contributed heavily to the overall pattern in saproxylic beetle abundance. This observation was also made in our study on hardwood stands in the SAFE experiment (SAFE 1 manuscript). Kebli et al (2014) inventoried fungal communities by installing wood blocks on site and found no differences in community composition between treatments 6-9 years after cutting treatments at SAFE. This raises two possibilities to consider with regards to the fungivorous beetles we sampled. The first is that if saproxylic fungivorous communities are mainly driven by saproxylic fungal communities, recovery of saproxylic beetle communities in mixedwood stands of SAFE may have occurred even earlier than the two decades after which we did our sampling (<6 years according to the recovery of saproxylic fungi found by Kebli et al 2014). The second is that fungivorous saproxylic beetles, although dependent on fungi as a food source, may not be reacting primarily to fungal diversity patterns or be reacting to a combination of fungal community patterns and other factors such as those previously discussed (i.e. canopy cover, connectivity).

Xylophage abundance patterns suggest that although there is a benefit to 40% partial cuts over clearcuts for this feeding guild, there is no evidence to support the use of a dispersed cut over a gap cut. In our study, we did not observe a relationship between deadwood volume and saproxylic beetle abundance, nor between xylophages and volume of fresher deadwood. One of our most abundant xylophages, *Dryocoetes caryi*, has been described as a rare bark beetle breeding in weakened spruce (Bright 1976); however, the species was collected mainly from one block of our uncut treatment, and this may simply be an indication of the species migrating to the site to exploit weakened spruce that has become available. Noualhaguet et al reported availability of spruce in uncut mixedwood stands 20 years post-harvest (2023). The dispersal range of many bark beetles is greater than the size of our cuts (Jones et al 2019) and the relatively small scale of our gap cuts (~400m^2) may contribute to why stands with dispersed cuts and gaps cuts did not differ in xylophage as well as overall saproxylic beetle abundance in our study. Working in deciduous and coniferous stands of Québec’s boreal forest, Bouchard and Hébert (2021) found that few species were significantly associated with exclusively older stands and also speculated that proximity of treatments to one another may have allowed for recolonization from neighbouring stands. However, small treatment size would then not account for why clearcuts still had a lower xylophage abundance than uncut control stands 20 years post-harvest.

Prochàzka and Schlaghamerský (2019) found that canopy openness had a significant effect on obligate saproxylic beetles, which would include xylophages. Sun exposure can have a significantly positive effect on saproxylic beetle densities and richness as canopy openness can promote diversity in microhabitat (Edelmann et al 2022; Bouget et al 2013; Lindhe et al 2005). In the study of Noualhaguet et al (2023), we see that basal area in clearcut stands remains much lower than in all other treatments. Although not reliable in every situation (McIntosh et al 2012; Bentley 1996), basal area has sometimes been used to estimate canopy cover (Buckley et al 1999; Mitchell and Popovich 1997) and if basal area is lower in clearcut stands, we may expect canopy openness to be higher. Greater richness and abundance of scolytinae has been sampled from understorey versus canopy traps (Ulyshen and Hanula 2007; Flaherty et al 2019; Dodds 2013; Marchioro et al 2020). Because our two most abundant xylophages were the scolytines *Dryocoetes caryi* and *Polygraphus rufipennis*, a significantly lower abundance of xylophages in clearcuts is a surprising result and may be owing to the previously mentioned aggregation of *D. caryi* individuals at a single site to exploit the suddenly available resource of moribund spruce.

For saproxylic beetle communities in our study, there appears to be little long-term consequence of moderate intensity partial cutting when done on a small scale. Furthermore, small-scale clearcuts also show recovery in terms of overall saproxylic beetle abundance, richness and community composition, suggesting that at least for some saproxylic communities, even intense harvesting can have the expectation of recovery. Nonetheless, not all taxa may recover after clearcutting, such as the xylophages in our study. Based on previous studies with partial cutting intensities close to ours, 40% dispersed or gap partial cuts may be recommended as an alternative to clearcutting when exercising caution around how clearcuts may impede recovery for taxa not yet studied. Previously retention levels as high as ≥50% for ground beetles

(Work et al 2010) or 75% for spiders (Pinzon et al 2016) were necessary to maintain community composition similar to uncut stands. These studies were 5 and 10 years post-harvest respectively, in contrast to our two decades after harvest, so recovery for these taxa may be possible in a longer term, small cut scale study like ours. If moderate or even high intensity partial harvesting occurs at small-enough scale, recovery of saproxylic beetle communities is possible.

NDBM has evolved to anticipate challenges in biodiversity conservation by modelling based on what has already been observed and adapting silviculture to mitigate damage (Achim et al 2022). Because NDBM is a holistic approach to managing forests which takes into consideration how cutting affects tree recovery and in turn the recovery of fungi, insects and other organisms, we need to understand how different components of the cutting approach interact with one another and affect recovery (Moussaoui et al 2020; Kim et al 2021). Our work contributes to the body of knowledge concerning how forest biodiversity reacts to NDBM in hopes of continuing to develop better silvicultural frameworks. We have seen the importance of using stand characteristics prior to harvest to assess how recovery in the stand may be proceed (Noualhaguet et al 2023; Moussaoui et al 2020; Raymond et al 2023). NDBM must furthermore anticipate what factors may exacerbate cutting disturbance in the future, such as climate change or repeated harvesting (Montoro Girona et al 2023; D’Amato et al 2023). In Fennoscandia, intensive harvesting practices since the 1950s have resulted in very even-aged forests of uniform composition (Gustafsson et al 2010; Koivula and Vanha-Majamaa 2020; Kouki et al 2010). Deadwood in managed Fennoscandian forests is estimated at 2-10m^{3}ha^{-1} and in old-growth at 60-90m^{3}ha^{-1}, signifying a 90-98% reduction of deadwood owing to forest management (Siitonen 2001). Average overall deadwood in our stands in significantly higher than Fennoscandian stands, with even our clearcuts having an overall deadwood volume only 28% lower than in uncut stands.

Our clearcuts were done on mixedwood stands of 1910 fire origin, introducing a novel intensive cutting disturbance into the stand. The state of deadwood in Fennoscandia may therefore serve as a warning to repetitive intensive harvest, as successive cuts in our clearcut sites may not continue to allow for the recovery seen after our first cut.

Author Contributions

Conceptualization: UD, MMG, TTW
Data curation: UD, TTW
Formal analysis: UD, MMG, TTW
Investigation: UD
Methodology: UD, MMG, TTW
Project administration: MMG, TTW
Resources: MMG, TTW
Supervision: MMG, TTW
Validation: UD, MMG, TTW
Visualization and edition: UD, MMG, TTW
Writing–original draft: UD
Writing–review: UD, MMG, TTW
Funding: MMG, TTW

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Conflict of Interest Statement

The authors declare no conflict of interest.

CHAPTER IV

GENERAL CONCLUSION

4.1 Scientific Contribution and Perspective

Forest management is increasingly concerned not only with resource extraction, but harvest that promotes eventual recovery of biodiversity and natural forest structure (Gauthier et al 2023; Kuuluvainen et al 2021). Partial cutting has previously been suggested as a promising alternative to clearcutting, albeit with the limitation that most of what we know with regards to biodiversity and stand response in North American forests is based on short- to mid-term studies (Work et al 2010; Lee et al 2018; Pinzon et al 2016; Bose et al 2013; Moussaoui et al 2020; Thorpe and Thomas 2007). The findings presented in this project contribute to knowledge of what recovery looks like for saproxylic beetle biodiversity two decades after harvest. Our results from hardwood and mixedwood stands of the eastern boreal forest in Québec revealed that partial cutting promotes saproxylic beetle recovery long-term while allowing for some timber yield. Understanding diversity patterns after anthropogenic disturbances is complex and factors influencing recovery remain unknown.

4.2 Drivers of Beetle Diversity

Physical stand characteristics such as canopy cover, microclimate temperature, and ground plant cover may influence saproxylic beetle communities either by affecting the deadwood profile of a stand or directly by being an environmental variable just as important, or more so, than deadwood. Seibold et al (2016) found that canopy openness strongly mediated the response of non-saproxylic epigeal arthropods such as arachnids and springtails to deadwood. Lettenmaier et al (2022) found that sunny forest stands harboured greater saproxylic beetle diversity than shaded stands owing to microclimatic temperature differences in deadwood in both types of stands. Although herbaceous plant increases on the forest floor following cutting are likely to have a stronger impact on herbivorous fauna than saproxylic, Franc and Götmark found that there were some similarities between the response of herbivorous and saproxylic beetles to partial cutting (2008). Because herbivores may attract saproxylic predators, or some beetles may have herbivorous and saproxylic life stages (i.e. Cerambycidae (Linsley 1961)), herbaceous plant cover following partial cutting may have some effect on saproxylic beetle communities. Particularly in mixedwood stands where we did not observe an effect of deadwood on saproxylic beetle abundance, it is likely other factors may be acting in tandem with deadwood availability or as a main direct effect.

An observation made in both hardwood and mixedwood stands was that fungivores were the dominant feeding guild collected in our samples and thus the main drivers of overall saproxylic beetle abundance patterns. This underscores the importance of better understanding how saproxylic fungal communities respond to partial harvest long-term as saproxylic fungi play a major role in structuring overall saproxylic communities (Gimmel and Ferro 2018). Eight years after cutting in SAFE 1, Kebli et al (2012) analyzed fungal diversity on logs of various sizes and decay classes, noting that size and decomposition class of logs affected fungal diversity and that cutting treatment affected log diameter in stands. A long-term study in SAFE sites on biodiversity of saproxylic fungi would complement our study well as missing links between effects of cutting treatment, deadwood availability, fungal diversity and beetle diversity may become more apparent.

4.3 Forest Management Implications

Because long-term recovery of saproxylic beetle communities was apparent in both hardwood and mixedwood stands of our research forest, partial cutting as an alternative to clearcutting for recovery of saproxylic biodiversity is recommended. Nonetheless, the level of intensity must be low enough to allow for the recovery of biodiversity belonging to different taxa. Many feeding guilds analyzed in our work showed recovery after twenty years even in clearcuts and only fungivores in hardwood stands and xylophages in mixedwood stands had abundances significantly lower in clearcuts than uncut control stands. Thus if some recovery for saproxylic beetles is possible in even clearcuts, the question becomes of what intensity should we harvest to reach a compromise between resource extraction and biodiversity conservation?

Mid- and long-term research suggests much biodiversity and physical stand characteristics do not recover decades after a clearcut, but not all long-term effects of a clearcut are negative for biodiversity. Kischuk et al (2015) found that clearcutting increased soil nutrients a decade after cutting. Much biodiversity benefits from the increased canopy openness, and species richness can increase following a clearcut (Paillet et al 2010; Edelmann et al 2022; Bouget et al 2013; Lindhe et al 2005). However, a persistent elevated species richness does not align with conservation goals of recovery to a species richness and community that would be observed in natural stands. Although saproxylic beetle communities in our hardwood stands did not show recovery after a clearcut in terms of species richness, abundance or community composition, communities in our mixedwood sites showed recovery and resemblance to uncut stands. Based on our study and previous work, if we are to incorporate partial harvest into forest management and use it alongside clearcutting, parameters should be defined to allow for usage of both techniques in an appropriate context.

Partial harvest and the use of clearcutting should be structured on a framework of retention and scale known to promote recovery. Clearcuts with retention of elements necessary for recovery of biodiversity may promote recovery. Martikainen (2001) found that retention of living and dead aspen trees in clearcuts supported the presence of even threatened saproxylic beetles and concluded that for aspen-associated species, clearcuts may be tolerated if at least some trees are retained. In Québec, the CPRS method of clearcutting aims to minimize effects on soil organic layers during removal of the canopy and is furthermore usually done in winter to reduce soil disturbance (Simard et al 2008). In our mixedwood stands, this approach appears to enable recovery of saproxylic beetles; in our hardwood stands, this was not the case. Noualhaguet et al (2023) found that clearcutting mixedwood stands did not reset them so that in 20 years they might resemble the hardwood stands that had also been clearcut. Thus, while the CPRS approach appears to allow saproxylic beetle recovery in mixedwood stands, the same approach in hardwood stands does not support recovery of saproxylic beetles as the two stands differ in tree composition. Scale of CPRS may also have contributed to why recovery was observed in mixedwood stands.

Compared to previous studies on the effects of clearcutting on recovery of biodiversity, our clearcuts were relatively small. Work done at the Ecosystem Management Emulating Natural Disturbance (EMEND) site used treatment blocks of 10 ha (Work et al 2010; Pinzon et al 2016; Lee et al 2017). In the EMEND studies, clearcuts of this size did not promote recovery of biodiversity 2-10 years after cutting. Miller et al (2007) found research plots with harvest gaps of 0.15ha with 10-30% of basal area retention supported lower numbers of Araneae and Collembola than closed canopy plots 8-9 years after harvest. Because these studies are shorter-term than ours, it is possible that even larger clearcuts may show recovery in some fauna after cutting when more years have elapsed, as was the case in our mixedwood stands. However, because in our hardwood stands overall saproxylic beetles and some feeding guilds did not recover, more should be known about recovery after large-scale clearcuts before management decisions using them are made.

4.4 Future Research

Some of our most unexpected findings concern the relationship between deadwood and saproxylic beetles. In hardwood stands, overall deadwood volume was positively related with overall saproxylic beetle abundance, abundance of fungivores and abundance of xylophages. This is not surprising as although the definition of saproxylic may be broad, fungivores and xylophages are groups especially dependent on deadwood since their diet consists of fungi growing on deadwood or fresh dying or dead wood itself (Andersson et al 2015; Vodka et al 2009). For this reason, it was surprising to find that in our mixedwood stands, no such relations were found between deadwood and overall saproxylic beetle abundance or abundance of any feeding guilds. Even when we compared overall volume of only our three freshest decomposition classes against abundance of xylophages, we found no relation. Xylophage abundance did not recover in clearcuts 20 years after harvest, meaning a variable besides deadwood may be more influential on recovery, even for saproxylic biodiversity.

Two decades post-harvest is a relatively long-term study when compared with existing North American literature on the effects of partial harvest on biodiversity. However, this length of time is short relative to the successional cycle of our study forest. Similar studies to this one completed years after ours would be useful to continue to monitor change over time, especially in stands that have not yet shown recovery. Because the partial cutting treatments do not appear to emulate natural disturbance in the SAFE site based on our community composition results and the findings of Noulhaguet et al

(2023), a long-term understanding of stand progression in terms of both tree composition and biodiversity may help us to learn how to create silvicultural practices that could allow us to develop more a more effective NDBM framework. Similar studies to ours on different groups of animals would also allow us to understand if the recovery patterns we see in beetles are present in biodiversity as a whole.

4.5 Conclusion

In conclusion, we recommend that appropriate mitigation measures be applied already existing cutting practices to allow for recovery of biodiversity. These include provision of appropriate retention, of deadwood or living trees, selection of appropriate treatment size to allow for recovery, accounting for variables that will be affected by harvest, such as canopy cover, and considering seral stage of stand. Implementation of these will require that we continue to study different groups of biodiversity and their reaction and recovery to the variables presented.

Because harmful effects of clearcutting were observed in our hardwood stands and lacking in our mixedwood stands, clearcutting is not recommended without mitigation measures, primarily because a) many studies have documented the negative, persistent effects of clearcutting (e.g. Berg et al 1994; Pawson et al 2006; Keenan and Kimmins 1993; Montoro Girona et al 2023) and b) the recovery observed in our clearcut mixedwood stands was in the context of very specific parameters as part of an experimental design. Because commercial clearcuts are usually of a much larger scale than our experimental 1-3 ha blocks (McRae et al 2001), our findings from mixedwood stands should not be applied to clearcuts in general. Rather, our findings suggesting the benefits of partial cuts should be used to further develop studies that help to determine which factors long-term contribute to recovery of saproxylic biodiversity.

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