UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

LES IMPACTS DE QUATORZE ANS DE COUPE PARTIELLE ET DE COUPE TOTALE SUR LES COMMUNAUTES DE BRYOPHYTES EPYXILIQUES DE LA PESSIERE NOIRE A MOUSSE

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FOURTEEN-YEAR IMPACTS OF PARTIAL AND CLEAR CUT FOREST HARVEST ON EPIXYLIC BRYOPHYTE SPECIES IN BOREAL BLACK SPRUCE –FEATHERMOSS FORESTS.

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SUMMARY

Forest harvest impacts the forest microclimate, existing vegetation, and coarse woody debris abundance. Also, even aged forest management reduce old growth features that supports many forest species. Alteration of these forest attributes during harvest can lead to local species loss. Partial cut harvest has been proposed to reduce the negative impacts associated with forest harvest and encourage the succession of forest structure that supports old growth adapted species. Epixylic bryophytes (that grow on deadwood) are known to be vulnerable to forest harvest due to their sensitivity to microclimate and substrate changes and they have been used as indicator species to assess partial cut efficacy to reduce harvest impacts on forest vegetation. Initial post-harvest studies have indicated the potential of partial cuts to reduce harvest impacts on epixylic bryophytes. However, the long term ability of partial cuts to maintain the epixylic bryophyte community and encourage old growth species assemblages remains uncertain, consequently, there is a need for longer term studies.

This thesis examined partial cut harvest efficacy to maintain residual forest structure that supports epixylic bryophytes and old growth adapted bryophyte species fourteen years after harvest. We resurveyed epixylic bryophytes and their microhabitats in permanent plots established in the boreal black spruce forests of northwestern Quebec, Canada. Specifically, we 1) Examined changes in microhabitat conditions (deadwood characteristics and microclimate) along an unharvested, partial cut and clear cut harvest gradient; 2) Examined the changes in epixylic bryophyte species composition, richness and functional traits resulting from these habitat condition variations; 3) Compared our results to an initial post-harvest study and to a chronosequence of old growth forests. This enabled us to examine species composition and richness changes overtime and the similarity of bryophyte communities in partial cut forests to that of old growth forests.

Partial cut and clear cut stands recorded lower volume of early decay stage CWD and higher volume of advanced decay stage CWD compared to unharvested control stands. Partial cut stands supported richer epixylic bryophyte communities compared to unharvested and clear cut stands. Similar trends were observed in the initial post-harvest study, however, species richness and frequency of occurrence doubled after 9 years the study. Also, epixylic species occurred mostly on coarse woody debris whereas in the initial study most epixylic species occurred on the forest floor. Richness of small-sized species, liverworts, species with rare vegetative and sexual reproduction was higher in unharvested and partial cut stands than in clear cut stands. Additionally, species composition growing on logs in partial cut stands was more similar to that found in old growth forests compared to the initial post-harvest study. Canopy openness, deadwood decay stage and diameter size were the major factors that explained the patterns observed in species richness, composition and functional traits.

In conclusion, partial cut harvest reduced harvest impacts by continuing to provide favorable microhabitat conditions, which supported epixylic bryophytes and/or old growth adapted bryophyte species. Thus, partial cut harvest provides a better option in achieving species and habitat conservation goals than what is been achieved by traditional clear cuts. However, lower volumes of newly recruited coarse woody debris raise concern about long term deadwood delivery potential of partial cut harvests. Deadwood input should therefore be considered in implementation strategies to ensure continual persistence of epixylic bryophytes and deadwood living organisms in general.

Keywords: Epixylic bryophytes, partial cut, coarse woody debris, old growth forest, functional traits.

RÉSUMÉ

La récolte forestière affecte le microclimat de la forêt ainsi que la végétation présente en sous-bois et l'abondance de débris ligneux. Les récoltes effectuées à des intervalles de temps courts et réguliers ont également des impacts sur les vieilles forêts, qui présentent des caractéristiques permettant de soutenir de nombreuses espèces forestières. L'altération de ces attributs de la forêt au cours de la récolte peut également mener, localement, à la perte de certaines espèces. La coupe partielle a été proposée dans l'objectif de réduire les impacts négatifs associés avec la récolte forestière. Cette approche permettrait de favoriser la succession d'une structure forestière pouvant supporter les espèces adaptées aux conditions des forêts matures voire âgées. Les bryophytes épixiliques (qui s'établissent sur le bois mort) sont connues pour être vulnérables à la récolte forestière en raison de leur sensibilité au microclimat et à la modification du substrat. Pour cette raison, ils ont été utilisés comme espèces indicatrices pour évaluer l'efficacité de la coupe partielle à réduire les impacts de la récolte sur la végétation forestière. Des premières études effectuées après récolte ont démontré le potentiel de la coupe partielle à réduire les impacts de la récolte sur les bryophytes épixiliques. Cependant, la capacité de ces coupes partielles à maintenir la communauté de bryophytes épixiliques et l'assemblage d'espèces associées aux vieilles forêts sur le long terme demeure incertain, et par conséquent, cet aspect requiert une étude à plus long terme.

Ce mémoire évalue l'efficacité de la coupe partielle à maintenir la structure de la forêt résiduelle qui supporte les bryophytes épixiliques et les espèces adaptées aux forêts matures quatorze ans après récolte. Nous avons examiné les bryophytes épixiliques et leur microhabitat dans des parcelles permanentes établies en forêt boréale dominée par l'Épinette noire dans le nord-est du Québec (Canada). Plus spécifiquement, nous avons 1) étudié les changements dans les conditions des microhabitats (les caractéristiques du bois mort et du microclimat) dans des parcelles présentant différentes intensités de récolte (non coupées, avec coupe totale et avec coupe partielle); 2) étudié les changements dans la composition, la diversité et les traits fonctionnels d'espèces de bryophytes épixiliques résultant de ces variations dans les conditions de l'habitat; 3) comparé nos résultats avec ceux d'une étude initiale qui avait été effectuée après récolte et une chronoséquence de forêts matures pour évaluer le changement temporel et la similarité des communautés de bryophytes dans les coupes partielles et les vieilles forêts.

Le volume de debris ligneux grossier était plus faible dans la classe de décomposition précoce et plus élevé dans la classe de décomposition avancée dans les peuplements issus des coupes partielle et totale que dans les peuplements témoin. Les coupes partielles supportaient une communauté de bryophytes épixiliques plus riche en comparaison avec les parcelles non coupées et les coupes totales. Des tendances similaires avaient été observées dans l'étude initiale, cependant, la richesse des espèces et la fréquence de leur occurrence a doublé après 9 ans. Aussi, les espèces épixiliques se retrouvaient principalement sur les débris ligneux, alors qu'au cours de l'étude initiale, la plupart des espèces épixiliques se retrouvaient sur le sol forestier. La richesse des espèces de petite taille, des hépatiques et d'espèces avec reproduction végétative ou sexuée rare était supérieure dans les parcelles non coupées et les couples partielles par rapport aux coupes totales. De plus, la composition en espèces s'établissant sur le bois dans les coupes partielles était plus semblable à celle des vieilles forêts en comparaison avec celle de l'étude initiale. L'ouverture de la canopée, le stade de décomposition du bois mort et le diamètre étaient les principaux facteurs expliquant les patrons observés en ce qui a trait à la richesse des espèces étudiées, leur composition et leurs traits fonctionnels.

En conclusion, les coupes partielles réduisent l'impact de la récolte en produisant des conditions de microhabitats favorables, qui permettent de supporter les espèces de bryophytes épixiliques et les espèces adaptées aux forêts matures. Ainsi, la coupe partielle représente une meilleure option pour atteindre les objectifs de conservation des espèces et de leur habitat par rapport à ce qui avait été obtenu dans le passé par les coupes totales. Cependant, l'apport limité de nouvelles sources de débris ligneux représente une préoccupation potentielle de cette approche sur le long terme. L'apport en bois mort à long terme devrait faire l'objet d'un suivi afin d'assurer le maintien des bryophytes et des autres organismes qui dépendent du bois mort en général.

Mots clés : Bryophytes épixiliques, coupe partielle, débris ligneux, vieille forêt, traits fonctionnels.

CHAPTER I

GENERAL INTRODUCTION

1.0 Context

Traditional even aged forest management characterised by short harvest rotations is gradually shaping the composition and structure of the boreal forest (Bergeron and Harvey, 1997, Bergeron et al., 2002). The resulting forest composition and structure have been identified to be outside the range of natural variability (Harvey et al., 2002, McRae et al., 2001, Vaillancourt et al., 2009). This is evident in the decline of key forest habitats (e.g. old growth forests) and their associated species (Berg et al., 1994; Bergeron and Harvey, 1997; Siitonen and Saaristo 2000; Rassi et al., 2001). The negative impact of forest management on biodiversity has generated conservation concerns thus igniting an increasing interest in forest management approaches with reduced effects on biodiversity (Attiwill, 1994). Partial cut harvest has been proposed as a harvest alternative to have a less severe impact on biodiversity and encourage the development of old growth features such as structural diversity, which is currently not accomplished with clear cut harvest (Harvey et al., 2002). This study used epixylic bryophytes as indicator species to examine the impact of partial cut harvest on forest species and their habitat.

1.1 Boreal forest

The boreal forest is one of the largest terrestrial biomes on earth stretching across three continents: Asia, Europe and North America (Burton et al., 2010). It plays a very significant global role by serving as a host for many plants and animal species (Potapov et al., 2008; Burton et al., 2010) and stores more than 35% of the earth's terrestrial carbon stock (Burton et al., 2010). In Canada, 53% of the territory falls within the boreal zone accounting for 12% of the global boreal biome (Burton et al., 2010). The Quebec province of Canada has 70% of its territory falling within the boreal vegetation zone (MRNF, 2008). The boreal forest therefore forms an important resource (economic and social) in Quebec (MFFP, 2015). Unfortunately, increasing human pressure on forest resources is threatening the integrity of the boreal forest and consequently raising a lot of conservation concerns (Bergeron and Fenton, 2012). Forest management practices are therefore being reviewed both at the regional and local levels to address these conservation concerns.

1.2 Old growth habitat conditions

In the past, old growth forests were perceived as ‘over mature’ and ‘senescent’ forests that were less dynamic and less productive (Wirth et al., 2009). Growing ecological knowledge in recent times have unveiled the functional importance of old growth forests thereby igniting new perspectives. Authors like Hunter and Parker, (1993) have argued that forest stands continue to change even at the old growth stage due to gap dynamics (mortality and regeneration), hence old growth stages are not static. Likewise, Söderström, (1988b) stated that old growth structural elements like CWD are dynamic with time due to their decay. Thus, old growth forest has been described as more dynamic than it was previously perceived (Kneeshaw and Gauthier, 2003) and must be considered as part of the continuous forest development process rather than as a single state (Fenton and Bergeron, 2011).

Stand structural components (e.g. tree age, canopy gap size and deadwood characteristics) vary during the successional process in natural forest stands. With increasing time after fire disturbance, tree mortality and secondary natural disturbances (wind throw and insect attacks) create canopy gaps of varying sizes in stands allowing the development of understory cohorts (Franklin et al., 2002; Harvey et al., 2002). Also, a considerable number of snags and CWD of varying sizes and decay classes are created in the successional process (Andersson and Hytteborn, 1991; Hély et al., 2000). The forest stand develops an uneven age and complex internal structure as the late successional cohorts contribute significantly to the stand structure (Bergeron and Harvey; 1997; Jette et al., 2013). At this stage the forest is considered to be in the old growth state (Spies et al., 1988).

The complex structure and compositional diversity that is associated with old growth forests creates a unique understory environment (Bergeron and Harper, 2009), which provides habitat conditions that host different types of forest organisms such as mammals and amphibians (Franklin and Van Pelt, 2004), birds (Drapeau et al., 2003), insects (Work et al., 2004), bryophytes (Fenton and Bergeron, 2008). Maintenance of old growth forests in managed landscapes is thus critical for the conservation of biodiversity (Bergeron and Harvey, 1997).

1.3 Differences between natural disturbance and harvesting disturbance

The boreal forest has been touted as a disturbance adapted biome mainly because of the occurrence of a series of natural disturbances over a long period of time (Bergeron et al., 1999; Harper et al., 2004). Fire, insect attack and wind throw have been identified as the main naturally occurring disturbances in the boreal forest (Bergeron and Harvey, 1997). Previously, these natural disturbances were considered as “wasteful” and “a threat to human progress” (Haeussler and Kneeshaw, 2003). Growing knowledge in recent times have recognized natural disturbances as essential for the functioning of boreal forest ecosystems (Haeussler and Kneeshaw, 2003, Vaillancourt et al., 2009).

Human disturbance has also been recognised as a form of disturbance common to the boreal forest. These disturbances mainly constitute mining, oil and gas exploration, logging, hunting, road construction and hydroelectric developments (Haeussler and Kneeshaw, 2003; Drever et al., 2006). Nevertheless, harvesting has been branded as the dominant human disturbance (World Resources Institute, 2000). Human disturbances, just as natural disturbances, impact boreal forest ecosystems, however, many authors have clearly demonstrated that the impacts of these two disturbances are not the same (McRae et al., 2001; Vaillancourt et al., 2009). This section therefore attempts to review some observed differences between natural disturbances and harvesting disturbances in the documented literature.

One of the main differences observed by many authors hinges on the characteristics of the disturbance (i.e. size, frequency, pattern, and severity of disturbances). Natural disturbances such as fire occur at random intervals where some sites burn frequently, while others remain unburned for a long time (hundreds of years) consequently creating a mosaic landscape consisting of stands of different age classes (Franklin et al., 2002; Harvey et al., 2002). Longer fire intervals have also resulted in the presence of a significant proportion of old growth forest in the Canadian boreal forest landscape (Cyr et al., 2005; Bergeron and Fenton, 2012). Furthermore, burned area size varies from less than a hectare to thousands of hectares (McRae et al., 2001), likewise, fire intensity varies from low-intensity surface burns to high-intensity crown and forest floor burns (McRae et al., 2001). Conversely, harvesting as part of forest management, minimizes natural variability (Pastor et al., 1998) by standardizing variables such as cut block size and harvesting intervals (Haeussler and Kneeshaw, 2003; Vaillancourt et al., 2009). Thus, creating an overabundance of young even-aged stands in the forest landscape (Bergeron and Harvey, 1997). Even at a similar rotation period, Wagner, (1978) has argued that fire and harvesting stand age structure differs. Stand age after fire yields a negative exponential distribution with 37% of stands older than the fire cycle while managed stands generates a uniform stand age distribution, with no or few stands older than the harvesting rotation period (Johnson, 1992).

Natural disturbances leave behind biological legacies such as live and partially killed trees, snags and CWD (McRae et al., 2001; Haeussler and Kneeshaw, 2003). Several authors (McRae et al., 2001; Vaillancourt et al., 2009) have described that these biological legacies act as refugia and habitat for forest organisms; insects, birds, bryophytes, and mammals. In contrast, traditional clear cuts remove all merchantable trees and destroy unmerchantable trees, snags and the forest floor via machine movement leaving very little and altered biological legacies behind (Haeussler and Kneeshaw, 2003; Vaillancourt et al., 2009).

Differences between the impacts of fire and harvesting on the forest floor have also been considered by many studies. Simard et al., (1997) and McRae et al., (2001) point out that fire affects the forest floor by killing understory vegetation and consumes the organic layer resulting in a thin forest floor. Consequently, the removal of the soil organic layer exposes mineral soil that serves as a seed bed for regeneration. Similarly, non-fire disturbances particularly wind throw displaces organic matter via the creation of pits and mounds thereby exposing mineral soil to enhance regeneration (Kneeshaw and Gauthier, 2003). In addition, combustion of vegetation and organic matter releases stored nutrients into the soil thereby stimulating the nutrient cycle (MacLean et al., 1983; Van Cleve et al., 1983; McRae et al., 2001). In contrast, clear cuts disrupt the forest floor through slash deposition and substrate damage (Arseneault et al., 2012). This does not necessarily result in organic matter removal except on skid trails where mineral soils are exposed but also compacted by heavy machine movement (Haeussler and Kneeshaw, 2003). Brais and Camiré, (1998) stated that reduced disturbance of the organic layer and soil during harvesting impairs site productivity by decreasing nutrient availability and regeneration of trees. Again, results from Simard et al., (1997) indicated that soil nitrogen, phosphorous, and calcium, were more abundant after fire than after harvesting.

The impact of forest management and harvesting on biodiversity has generated conservation concerns thus igniting an increasing interest in forest management approaches based on natural dynamics (Attiwill, 1994).

1.4 Ecosystem-based management approach

Ecosystem based forest management is an approach that aims to reduce the disparities between managed forest and natural forest to ensure the maintenance of biodiversity and sustainability of ecosystems (Grenon et al., 2011). It has been suggested that maintaining forest attributes as well as ecosystem functions and processes during forest management will better ensure biodiversity conservation and enhance forest productivity (Attiwill, 1994). Natural disturbance has been recognized as essential to the functioning of boreal forest ecosystems, hence, using natural disturbance as a template for forest management framework is recommended (Haeussler and Kneeshaw, 2003; Vaillancourt et al., 2009).

Ecosystem based forest management is currently widely adopted in Canada as the new phase of forest management (Grenon et al., 2011). Its implementation is built on knowledge of natural disturbance and forest dynamics (Grenon et al., 2011). This begins with first identifying the main ecological issues of a territory, based on the differences observed between the managedforest and a natural forest. The differences are analyzed based on the attributes of the forest ecosystem and according to the habitat needs of species (Attiwill, 1994; Grenon et al., 2011). The second step is to develop silvicultural interventions to resemble natural disturbance dynamics. Finally, an adaptive management practice is developed where the proposed silvicultural interventions are evaluated and new knowledge incorporated into the management practices (Bergeron and Harvey, 1997).

1.4.1 Partial cut harvest

Partial cut harvest is a generic term, which refers to harvesting treatments with varying retention of trees within stands (Harvey et al., 2002; Bose et al., 2015). It has been widely promoted as a key silvicultural technique under the implementation of ecosystem based forest management in the boreal forest (Lieffers et al., 1996; Bose et al., 2013). It has been hypothesized that partial cut harvest can have lower impact on biodiversity and can also recreate plant and animal assemblages consistent within the range of natural variability (Drever et al., 2006). This is explained on the premise that maintaining stand structures consistent with biological legacies after natural disturbance will serve as refugia and habitat for forest species (Attiwill, 1994; Franklin, 1993). Also, residual trees after harvesting create patches of shade that provide favorable microhabitat conditions for forest floor species. In addition, residual stands after partial cut harvest could ensure continual supply of deadwood, encourage the development of old growth structural features and the assemblages of old growth adapted species. Thus, partial cut harvest could balance the loss of deadwood, old growth forests and their associated species (Harvey et al., 2002; Lilja et al., 2005; Fenton and Bergeron, 2008). However, the efficacy of partial cut in creating habitat conditions similar to older forests and consequently accelerating community succession remains uncertain.

Studies on the effects of partial cut harvest on biodiversity are gradually increasing in number. Some preliminary studies examined the effects on partial cut on species such as birds (Vanderwel et al., 2007), small mammals (Moses and Boutin, 2001), insects (Gandhi et al., 2004, Deans et al., 2005, Martikainen et al., 2006), understorey plants (Jalonen and Vanha-Majamaa, 2001, Bradbury, 2004), bryophytes (Fenton et al., 2003, Fenton and Bergeron, 2007, Arseneault et al., 2012), lichens (Coxson et al., 2003, Boudreault et al., 2013) and ectomycorrhizal fungi (Dahlberg et al., 2001, Lazaruk et al., 2005). Ecosystem properties Also, other studies focused on partial cut ability to promote old growth characteristics such as multi-layer canopy (Man et al., 2008) and CWD (Deans et al., 2003, Lilja et al., 2005). Overall, most studies indicated that partial cut promotes the development of old growth characteristics and maintains higher levels of biodiversity compared to clear cut. While early studies have suggested a positive correlation between partial cut and biodiversity conservation, the ability of partial cut to maintain this trend throughout the length of a rotation remains uncertain. Long term studies are needed to assess future trends (Fenton and Bergeron, 2007).

In the boreal black spruce forest of Quebec-Canada, a large project (Réseau des Coupes Partielles en Abitibi) aims to compare the effects of clear cut and partial cut on different forest components. The overall goal is to assess the ability of partial cut to successfully create old growth habitat conditions, which will support a variety of species (Fenton et al., 2013). This current study feeds into the bigger partial cut trial studies.

1.5 Bryophytes on the boreal forest floor

In the boreal forest, bryophytes constitute a significant proportion of the biological diversity (Longton, 1992; Rudolphi, 2007). They form a major component of forest biomass despite their small size and play a very critical role in the boreal forest ecosystem (Rieley et al., 1979; Frego, 2007). Bryophytes play an important role in nutrient recycling (interception, retention, and release). Living bryophytes make use of the trapped nutrients (dissolved nutrients in their capillary spaces) and dead, decaying bryophytes release nutrients to the surrounding plants (Brown and Bates 1990; Turetsky, 2003). Also, decomposing bryophytes serve as humus which enhances soil water and nutrient holding capacity (Weetman, 1968; Frego, 2007). Similarly, cyanobacteria that inhabit bryophyte leaves, contribute to nitrogen production in the forest (DeLuca et al., 2002; Turetsky, 2003). In addition, slow decomposition of bryophytes help build up the organic layer which provides habitat for various micro-organisms and invertebrates, as well as potential seed beds for vascular plants (Glime, 2011). Bryophytes also prevent soil erosion by reducing the direct impact of rain drops on soils (Longton, 1992, Glime, 2011).

Bryophytes are poikilohydric organisms (i.e. organisms that lack specialized structures or mechanisms to regulate uptake and loss of water) hence they absorb water and nutrients through their body surface (Hylander, 2005, Glime, 2011). This makes them very sensitive to changes in their microhabitat conditions particularly moisture content or humidity (Glime, 2011). In addition, bryophytes are sensitive to changes in substrate availability, particularly those species that are restricted to CWD. The dynamic nature of CWD makes its reduction in quantity and quality threatening for the existence of such bryophyte species (Söderström, 1988a). Bryophytes are therefore sensitive to forest harvest which alter forest microclimate and reduces CWD quantity and quality.

1.5.1 Epixylic bryophytes and deadwood

Epixylic species (epi: prefix taken from the Greek that means "on, upon, over, on top, against"; xylic: suffix taken from the Greek that refers to the xylene part of trees) are species that grow on decaying wood (Arseneault et al., 2012). Epixylic bryophytes are therefore bryophytes whose establishment and growth are confined to decaying wood. Epixylic bryophytes require a constantly humid, shady microclimate (Soderstrom, 1987) which is mostly found on CWD as they help regulate moisture conditions on the forest floor (Muhle and LeBlanc, 1975; Arseneault et al., 2012; Haughian and Frego 2017). Also, the elevated position of CWD separates epixylic bryophytes from the continuous mat of larger forest floor bryophyte (Frego, 1996) thereby reducing competition for resources with the larger forest floor species (Rydin, 1997; Arseneault et al., 2012).

During the decomposition of logs, epixylic bryophytes colonise CWD at different times and replace each other successively until the log is totally overgrown by ground vegetation (Andersson and Hytteborn, 1991). This successional change of epixylic bryophytes on CWD mirrors the changes in the physical and chemical properties during decomposition (Ódor and van Hees, 2004). Furthermore, the diameter size of CWD has also been identified to influence the composition of epixylic bryophytes (Andersson and Hytteborn, 1991, Ódor and van Hees, 2004). Large logs (CWD) take a longer time to decompose thus providing epixylic bryophytes ample time to disperse to and colonise the substrate. In contrast, the rapid decomposition of smaller logs does not permit enough time for epixylic bryophyte establishment and colonisation of the substrate (Anger et al., 2005; Arseneault et al., 2012).

In summary, deadwood, particularly CWD at various stages of decay (a characteristic of old growth forest) forms an important component of the forest ecosystem. Their continual supply or input into the forest ecosystem will ensure the survival and maintenance of epixylic bryophytes and biodiversity at large.

1.5.2 Species traits

Biological traits refer to the characteristics or attributes of an organism. Different species differ in biological attributes or traits and this is as a result of adaptations to a range of conditions (Kassen, 2002). The different traits an organism or species exhibits influences the species' ability to establish, grow and reproduce in a habitat (Caners et al., 2013). Species with different traits respond differently to modifications of habitat conditions consequently influencing the species composition in a local habitat (Hewitt et al., 2005; Caners et al., 2013). Also, changes in habitat conditions may affect the persistence of a species in a habitat if the modification in the habitat conditions exceeds the tolerance level of species traits (Chapin et al., 1993; Caners et al., 2013). Biological traits are therefore important indicators of species' persistence and recovery following habitat change or disturbance (Caners et al., 2013).

Bryophyte species exhibit several traits. In the context of this study, emphasis will be placed on bryophyte traits like taxonomic group (liverworts and mosses); size of gametophyte, habitat requirements (substrate), reproduction and dispersal. These traits have been linked to the occurrence of bryophyte species in boreal forests by many studies (Hylander, 2009; Löbel et al., 2009; Caners et al., 2013). For example, smaller species are outcompeted by large species that dominate the forest floor and medium sized species, which are good competitors on specialized substrates. Smaller species therefore colonizes pockets of specialized habitat that are free from these larger species (R.H. Økland et al. 2003, Boudreault et al., 2018). Also, the physiological traits of liverworts make them less tolerant to desiccation and drought compared to mosses (Söderström and Jonsson 1989; Fenton and Frego 2005). Drought and desiccation tolerant species therefore replace shade-loving and desiccation intolerant species during canopy opening after disturbance. In addition, the results of Caners et al., 2013 indicated that species with high moisture requirements were abundant in high canopy retention harvest and less in low canopy retention harvesting. This implies that forest management that is characterized by low or no canopy retention threatens drought-sensitive bryophytes (Söderström, 1988a).

Reproduction and/or dispersal capacities are also considered important traits that influence the reestablishment of species in the forest (Hylander, 2009). In the case of epixylic bryophytes, Söderström, (1987a) described dispersal as an important factor for their distribution and establishment. This is explained by the fact that deadwood, which is the substrate of epixylic bryophytes, diminishes with increasing decomposition (Andersson and Hytteborn, 1991), thereby forcing epixylic bryophytes to continually disperse to new habitats (During 1992; Arseneault et al., 2012). Also, Söderström, (1987b) stated in his studies that many species will be absent in forests with uneven supply of substrate particularly those with limited dispersal ability or those that rarely produce diaspores.

In conclusion, species respond to habitat modification in different ways due to variations in biological traits and this can influence biodiversity in a local habitat. Examining the relations between species' biological traits and their response to changes in habitat conditions can provide insights into the effects of disturbance and species recovery after disturbance (Raunkiaer, 1934; Bates, 1998; Caners et al., 2013).

1.5.3 Effects of harvesting on epixylic bryophytes

Forest management practices as established earlier, alter forest attributes which in turn, affect biodiversity. Traditional harvesting techniques like clear cuts (where all merchantable stems are removed at once) have been identified to have a significant impact on forest vegetation particularly forest floor species. Clear cuts impacts epixylic bryophytes in several ways. These impacts are categorized into direct and indirect impacts.

Direct clear cut impacts involve causing physical damage to already established bryophytes on the forest floor. During harvesting tree limbs and twigs are deposited as slash on the forest floor and bury bryophytes on the forest floor. Also, movement of machinery during harvesting crushes and removes established bryophytes on the forest floor (Fenton et al., 2003, Arseneault et al., 2012).

In contrast, indirect impacts involve the alteration of habitat conditions without damaging the target organism by the physical force of the disturbance agent (Fenton et al., 2003). In this context, canopy removal alters the microclimate of the forest floor without physically damaging bryophytes on the forest floor (Nyland, 1996; Fenton et al., 2003). Canopy removal allows the direct effect of sun rays to hit the forest floor.

Increased temperature combined with the drying effect of wind dries up moist CWD and the forest floor (Andersson and Hytteborn, 1991). Damage to bryophytes occurs immediately or gradually as they react to changes in the habitat conditions (Grime, 1979; Fenton et al., 2003).

Furthermore, clear cut harvest affects the availability and quality of substrate for the establishment and growth of epixylic bryophytes. Removal of all merchantable stems at once during clear cut reduces the amount of deadwood within a forest stand by interrupting the deadwood input cycle (Hély et al., 2000, Arseneault et al., 2012). Existing deadwood on the forest floor are crushed into smaller pieces by moving machinery (Fenton et al., 2003) thereby reducing the amount of bigger CWD which is noted to support the growth and establishment of many epixylic bryophytes.

Leaving residual trees during partial cut attenuates the impacts associated with clear cut by serving as refugia for bryophytes species (Vaillancourt et al., 2009). Also, residual trees after harvesting create patches of shaded floor (Harvey et al., 2002) that provide favorable microhabitat conditions for bryophytes species. Furthermore, residual trees ensure a continual input of deadwood in the stand (Harvey et al., 2002) which allows the reestablishment and colonization of epixylic bryophytes.

1.6 General Objectives

Fourteen years after harvest, this study examines partial cut stands ability to provide more favourable habitat conditions that will support epixylic bryophytes than what is achieved by clear cut stands. Also, if partial cut stands can promote the development of forest structures that supports old growth adapted species.

1.6.1 Specific objectives

1. Examine changes in habitat (substrate availability and microclimate) along an unharvested, partial cut and clear cut gradient.

2. Examine the changes in epixylic bryophyte species composition, richness and functional traits resulting from habitat condition variations along the harvest gradient.

3. Compare the results of each harvesting treatment to a chronosequence of old growth forests and an initial post-harvest study.

1.7 Hypotheses

1. Coarse woody debris (CWD) abundance compared to that of an initial post-harvest study will be maintained in partial cut stands due to continual input from residual stands but will diminish in clear cut stands due to decomposition and lack of continual input. Also, tree growth and regeneration in both partial cut and clear cut stands will create patches of shaded forest floor which will improve moisture conditions compared to conditions found in the initial post-harvest study.

2. Epixylic bryophyte species richness will increase in partial cut but not in clear cut compared to results of the initial post-harvest. This is due to an improvement in habitat conditions (substrate availability and moisture conditions). Partial cut will have a community composition and richness similar to communities of old growth forest stands.

3. In terms of functional traits, liverworts, smaller and specialist species with rare sexual and vegetative reproduction will have higher richness in partial cut stands compared to clear cut stands. Generalist species and species with frequent reproduction will be common along the harvesting gradient.

CHAPTER II

FOURTEEN-YEAR IMPACTS OF PARTIAL AND CLEAR CUT FOREST HARVEST ON EPIXYLIC BRYOPHYTE SPECIES IN BOREAL BLACK SPRUCE –FEATHERMOSS FORESTS

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2.1 Abstract

Partial cut harvest has been hypothesized to have lower impact on forest vegetation and encourage the development of forest structures that support old growth adapted species. Fourteen years after harvest, we used epixylic bryophytes as indicator species to assess partial cut efficacy to attenuate harvest impacts on forest vegetation in the boreal black spruce forest of Quebec. We examined changes in epixylic bryophyte community (composition, richness and functional traits) and their microhabitat (coarse woody debris characteristics and microclimate) in 30 permanent plots along an unharvested, partial cut and clear cut harvest gradient. Also, we compared our results to that of an initial post-harvest study and to a chronosequence of old growth forests to examine species changes over time and the similarity of bryophyte communities in partial cut forests to old growth species assemblages. The results showed that, epixylic species richness and composition were mainly influenced by canopy openness, deadwood decay and diameter size. Partial cut stands recorded richer epixylic community compared to unharvested and clear cut stands. Species richness and frequency of occurrence doubled in partial and clear cut stands over time compared to the initial study. Additionally, conditions in partial cut stands supported drought sensitive and old growth confined species which are threatened by conditions in clear cut stands. In conclusion, partial cut harvest provides a better option in achieving species and habitat conservation goals than clear cut harvest. However, deadwood input should be considered in implementation strategies to ensure continual persistence of epixylic bryophytes and deadwood living organisms in general.

Keywords: Epixylic bryophytes, partial cut, coarse woody debris, old growth forest, functional traits.

2.2 Introduction

Human disturbances, just as natural disturbances, affect the composition and structure of forest ecosystems (Pickett et al. 1989, Johnson and Miyanishi 2007). In the boreal forest, commercial logging characterised by clear cut harvest systems is the prevalent form of human disturbance (Kuuluvainen, 2009). The resulting forest composition and structure of this harvest system have been identified to be outside the range of natural variability for this ecosystem (Harvey et al., 2002, McRae et al., 2001, Vaillancourt et al., 2009). Specifically, at the landscape scale, heterogeneous and un-even aged stands being are replaced by homogeneous and even aged stands (Bergeron and Harvey, 1997; Haeussler and Kneeshaw, 2003; Vaillancourt et al., 2009). Also at the stand scale, clear cut harvest systems eliminate old growth features such as complex internal structures including high deadwood volume. Regenerating stands after clear cut harvest are mainly characterised by simplified internal structure with less deadwood volume (Hély et al., 2000; Bergeron et al., 2002). Modification of these forest attributes both at the stand and landscape scale can lead to species loss and thus clear cut harvest systems poses a potential threat to biodiversity. The negative impact of clear cut harvest systems on biodiversity has generated conservation concerns which have spurred an increasing interest in forest harvest techniques that have reduced effects on biodiversity (Attiwill, 1994).

Partial cut harvest has been hypothesized to have less impact on biodiversity by recreating plant and animal assemblages consistent within the range of natural variability (Drever et al., 2006). This is explained on the premise that, leaving residual stand structures (consistent with biological legacies left after natural disturbance) after harvest will serve as species refugia and enhance species recovery after harvest (Franklin, 1993; Attiwill, 1994; Lindenmayer and Franklin, 2002; Lindenmayer et al., 2006). Furthermore, residual stands after partial cut harvest could ensure a continual supply of deadwood, encourage the development of old growth structural features, and the assemblages of old growth adapted species. Thus, partial cut harvest could mitigate clear cut harvest impacts on deadwood, old growth forests and their associated species (Harvey et al., 2002; Lilja et al., 2005; Fenton and Bergeron, 2008).

Consequently, there have been an accumulating interest in studies on the effects of partial cut harvest on biodiversity. Some studies have examined the effects of partial cut on forest species including small mammals (Moses and Boutin, 2001), birds (Vanderwel et al., 2007), insects (Gandhi et al., 2004;Deans et al., 2005; Martikainen et al., 2006), vascular plants (Jalonen and Vanha-Majamaa, 2001; Bradbury, 2004), bryophytes (Fenton et al., 2003; Fenton and Bergeron, 2007; Arseneault et al., 2012), lichens (Coxson et al., 2003; Boudreault et al., 2013) and fungi (Dahlberg et al., 2001; Lazaruk et al., 2005). Other studies focused on the ability of partial cut harvest to promote old growth characteristics such as a multi-layer canopy (Man et al., 2008) and deadwood characteristics (Deans et al., 2003; Lilja et al., 2005). Overall, most studies indicated that, partial cut harvest promote the development of old growth characteristics and maintains higher levels of biodiversity compared to clear cut harvest. However, these findings are mostly from early post harvest studies which raises questions about future trends. Long term studies have been recommended in order to understand the actual effects of partial cut on biodiversity (Fenton and Bergeron, 2007; Fenton et al., 2013).

Bryophytes dominate the boreal forest floor, forming a major constituent of boreal forest biomass and species diversity (Longton 1992;Rudolphi and Gustafsson, 2011). They play important roles in the boreal forest ecosystem such as influencing the nutrient cycle (Chapin et al. 1987), nitrogen fixation (DeLuca et al. 2007; Gundale et al. 2009), litter decomposition (Uchida et al. 2001), forest floor temperature and moisture regulation (Bonan and Korzuhin 1989; Fenton and Bergeron 2006), provision of habitat for micro-organisms and invertebrates (Gerson 1982; Döbbeler 2002), and seed beds for tree regeneration (Parent et al. 2003). Their poikilohydric nature (i.e. they lack specialized structures to regulate water uptake and loss) make them dependent on habitats with high levels of moisture or humidity. As a consequence, bryophytes are sensitive to forest harvest that alters forest microclimate through canopy removal. In addition, bryophytes are sensitive to changes in substrate availability particularly epixylic bryophytes that are confined to CWD. CWD in its various states of decay is mostly lacking in young even aged managed forests, consequently making epixylic bryophytes vulnerable to local extirpation under forest management (Söderström, 1988a). The sensitivity of epixylic bryophytes to microclimatic change and changes in substrate availability make them good indicator species to assess partial cut effects on bryophytes.

The recovery of bryophyte communities after partial cut harvest have been assessed by many studies (e.g. Fenton and Bergeron, 2007; Arseneault et al., 2012; Caners et al., 2013). In most studies, species composition and richness have been used to explain the impacts of forest harvest on bryophytes. A few studies like Caners et al., (2013) have also used species traits to explain the effects of harvest on bryophyte species. This is based on the notion that species respond to habitat modification in different ways due to variations in traits (e.g. size of shoot, substrate requirement, mode and frequency of reproduction) and this can influence biodiversity in a local habitat (Hewitt et al., 2005; Caners et al., 2013). Examining the relations between species' traits and their response to changes in habitat conditions can provide insight into the effects of disturbance and species recovery after harvest (Bates, 1998; Caners et al., 2013). These studies have shown the ability of partial cut harvest to better conserve bryophyte communities than what is achieved with traditional clear cut harvest. However, most of these findings are results from initial surveys conducted a few years after harvest. Changes in habitat condition resulting from natural processes like tree regeneration, growth and death with increasing time after harvest raises questions on partial cut ability to continually provide favorable habitat conditions for bryophytes in the long term. Longer term studies that seek to revisit already inventoried sites will be crucial in determining the actual effects of partial cut on bryophytes. Also, comparing bryophyte community after partial cut to that of a chronosequence of old growth forest have been recommended in order to asses partial cut ability to encourage old growth species assemblages (Fenton et al., 2013).

Fourteen years after harvest this study resurveyed epixylic bryophytes and their microhabitats in permanent plots established in the boreal black spruce forests of northwestern Quebec, Canada. Specifically, we 1) Examined changes in microhabitat conditions (deadwood characteristics and microclimate) along an unharvested, partial cut and clear cut harvest severity levels ; 2) Examined the changes in epixylic bryophyte species composition, richness and functional traits resulting from these habitat condition variations; 3) Compared our results to that of an initial post-harvest study and to a chronosequence of old growth forests to examine species changes over time and the similarity of bryophyte communities in partial cut forests to that of old growth forest.

We hypothesize that, 1) Coarse woody debris abundance compared to that of initial post-harvest study will be maintained in partial cut stands due to continual input from residual stands but will diminish in clear cut stands due to decomposition and lack of continual input; 2) Epixylic bryophyte species richness will increase in partial cuts but not in clear cuts compared to the results of the initial post-harvest study . This is due to an improvement in habitat conditions (substrate availability and moisture conditions) over time as the forest regenerates after harvest. Consequently, partial cuts will have a community composition and richness similar to communities of old growth forest stands; 3) In terms of functional traits, liverworts, smaller and specialist species with rare sexual and vegetative reproduction will have high richness in partial cuts compared to clear cuts. Generalist species and species with frequent reproduction will be common along the harvesting gradient.

2.3 Materials and methods

2.3.1 Study Area

This study took place in the Clay Belt region of northwestern Quebec (Fig 2.1), which is dominated by black spruce forest (Grondin et al., 1996; Arseneault et al., 2012). This region is prone to paludification as a result of poorly drained clay dominated soil. Fire constitutes the dominant disturbance type in this landscape with a fire cycle of about 398 years since 1920 and an average forest age over 100 years (Bergeron et al., 2004).The study area forms part of an experimental network of sites, the Réseau d'expérimentation des coupes partielles en Abitibi (RECPA). These sites were established to better understand the effect of partial cuts on ecosystem functions, diversity and merchantable timber (Fenton and Bergeron, 2007). Each site in the network consists of one block (each >50 ha) with three treatment types: clear cut (CPRS which preserves advance regeneration by removing all merchantable stems with a minimum DBH of 9 cm and protects most of the soil), partial cut with variable severity (30% to 75%), and an unharvested control (Arseneault et al., 2012). Eighteen permanent plots of 400 m^2 have been established per treatment in each site to monitor post-harvest stand development as well as changes in communities of organisms such as birds, small mammals, hare, lichens, bryophytes, mushrooms and arthropods (Arseneault et al., 2012; Fenton et al., 2013)

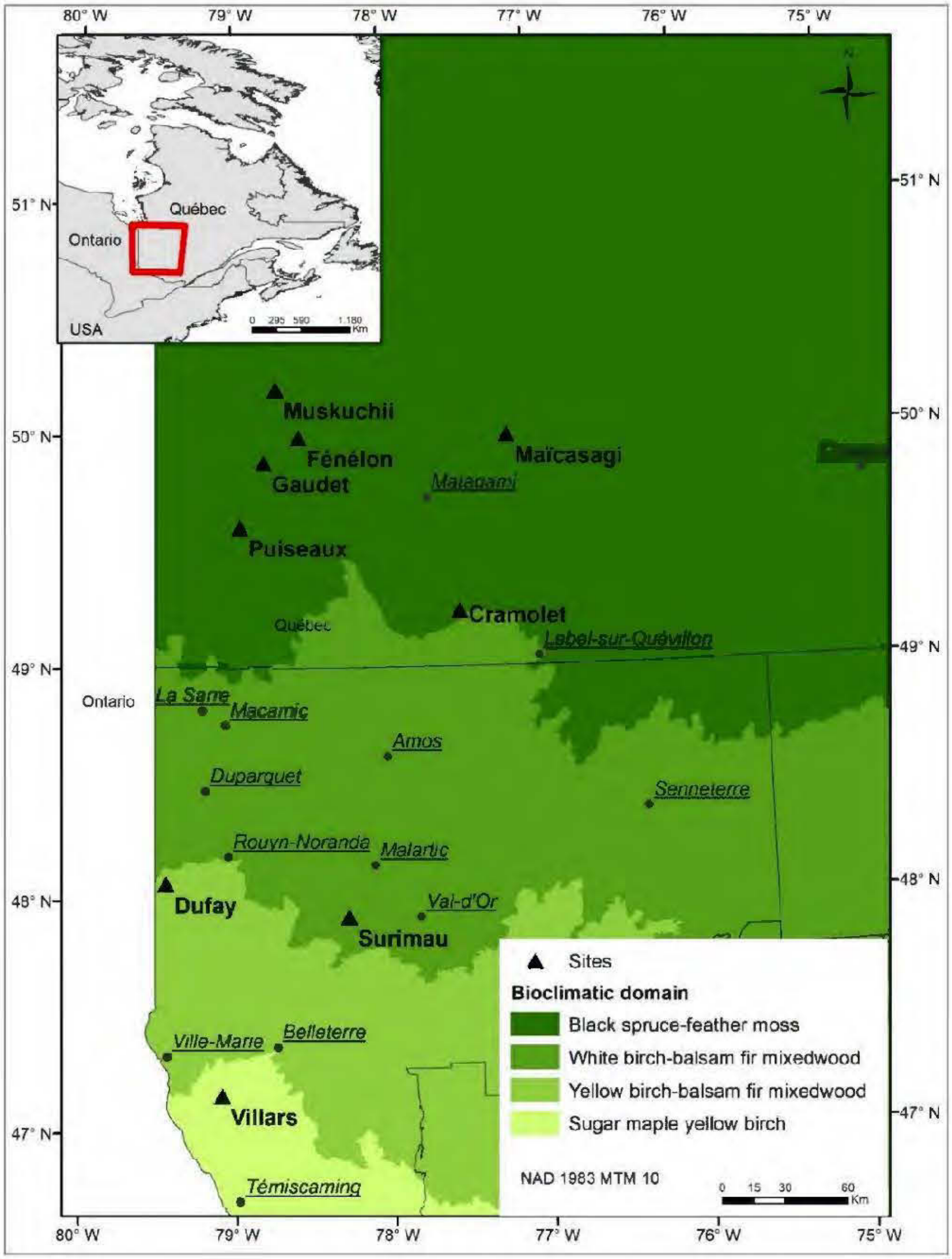

Fig 2.1 Map of the RECPA Network (Réseau des coupes partielles d'Abitibi). Triangles indicate the sites (including one block each of clear cut, partial cut and control), circles indicate cities/towns in the regions of Abitibi-Témiscamingue and Nord-du-Québec. Fenelon and Gaudet were the selected sites for this study.

2.3.2 Plot Selection

Two sites (Gaudet and Fenelon) that were used by the initial post-harvest study were selected based on site accessibility as roads have not been maintained as since harvest. The average age of these sites before harvest was more than 180 years since the last stand-replacing fire. Harvests were carried out in 2003 and 2004, thus this study was conducted 13–14 years (in 2017) after harvest and 5-6 years (in 2009) in the case of the initial post-harvest study. We maintained the same five plots per clear cut and control block used by the initial post-harvest study, except in the control plots in Fenelon because the plots were harvested in the interim. Unaffected Fenelon control plots that were not selected in the 2009 study were used for our study. In the case of partial cut blocks, plot selection for this study was based on plots classified as a silvicultural success, i.e. there is a net growth in residual tree volume ten years after harvest (Leduc, 2013). This is because sites with a high mortality rate of residual trees will show a high decline in merchantable tree volume making them silviculturally unsuccessful hence not recommended for forestry practice. Many partial cut plots in both sites differed from those of the initial post-harvest study because eight out of ten plots didn't qualify using the selection criteria of our study. In total, 30 permanent plots were selected for this study, 10 per harvesting treatment, divided among the two sites.

2.3.3 Microhabitat

We measured substrate (CWD) characteristics and micro-environment variables within each plot (400 m^2). CWD characteristics included CWD abundance, volume, decay class, diameter size and length while micro-environment variables included canopy openness, temperature and relative humidity. In the case of CWD characteristics, a 23m line transect was used to assess the number of pieces of CWD present. On the line transect, the length and the diameter of each piece of CWD were measured at the point of intersection. Also, tree species (where possible) and decay class of the CWD pieces were determined by visual observation. The decay class was categorised from 1 (fresh material) to 5 (well decomposed) based on Hunter Jr, (1990). In each plot, CWD abundance was calculated per count on the line transect (Marshall et al., 2000). CWD volume for each plot was also calculated from the formula:

$$V = (\pi^2/8L)\sum d^2 \qquad [1]$$

where V is volume per unit area, d is CWD diameter at intersection, L is length of transect line (Van Wagner, 1968). We also calculated CWD volume by decay class using the same formula. The first five CWD with a minimum diameter of 9cm on each line transect (Andersson and Hytteborn, 1991a) were subsequently selected from the total inventoried CWD for epixylic bryophyte community sampling. This was to ensure an equal number of sampled CWD in all plots. For each selected CWD, the total length, minimum and maximum diameter, percent of the length directly in contact with the ground, and maximum distance from the ground were measured and recorded. Belts of quadrats were randomly established at three different positions (smaller-end, middle and bigger end of the log) on each selected CWD for bryophyte sampling. At each belt, diameter and decomposition class were evaluated to determine the intrapiece variability of decay class and diameter size.

In terms of canopy openness, unlike the initial post-harvest study which used a densiometer for measurement, the hemispherical photo method was used to measure canopy openness in our case. This was because the hemispherical photo method is less laborious, fast and efficient in measuring various attributes of canopy structure. Hemispherical photos were taken on a cloudy day at the height of CWD using a circular fisheye camera lens at each belt level. Images were then analyzed using Gap Light

Analyzer (GLA Ver. 2.0) to determine canopy openness (Frazer et al., 1999). In addition, microclimate variables (temperature and relative humidity) were measured using HOBO Temperature/Relative Humidity Data Loggers. Due to limited equipment availability, HOBOs were placed in 18 of the 30 permanent plots representing 6 plots per harvest treatment. In each plot, HOBOs were installed close to a randomly selected CWD chosen from the 5 CWD for bryophyte sampling. HOBOs were programmed to measure average temperature and relative humidity values at a 3-hour recording frequency for an entire year in the field. Relative humidity was converted to vapour pressure deficit because it is a more accurate way to express plant water loss from a leaf, which is critical for bryophytes due to their poikilohydric nature. The following formula was used:

$$VPD = (6.1078)\{[17.269T/(273.3 + T)]\}(1 - RH) \qquad [2]$$

where T is temperature in Celsius and RH is relative humidity as a decimal. This formula was adopted from Fenton and Frego; (2005), which was a modified version from (Tanner 1972). Mean temperature and VPD values were calculated for each harvest treatment. Similarly, the daily duration (in hours) and frequency of extreme values recorded were calculated since they have been considered to be biologically important (Fenton and Frego, 2005). In our case, values were considered extreme when they exceeded the 90th percentile mark (i.e., >22.25°C for temperature and >10.61kPa for VPD).

2.3.4 Bryophyte sampling

Bryophytes were sampled on each selected CWD at the belt level. Each belt consisted of three quadrats in systematically placed positions: the top of the CWD (5 cm × 10 cm), the side of the CWD (5 cm × 10 cm), and the ground directly next to the CWD

(10 cm × 10 cm). Larger quadrats were used on the forest floor because of the bulky nature of forest floor species compared to species growing on logs. In addition, this ensured the same amount of sampled surface area on CWD and forest floor (Arseneault et al., 2012). At each belt, the percent cover of bryophytes, as well as the cover of each individual bryophyte species, were evaluated in the quadrats on the top and sides of the CWD. We also checked on the rest of the CWD to sample other species that were not found in the quadrats. Species were identified in the field when possible, all other species were sampled and brought to the laboratory for identification. Nomenclature followed Faubert, (2012-2014).

2.3.5 Species functional traits

Examining the relationships between species' functional traits and their response to changes in habitat conditions can provide insights into the effects and consequences of harvesting on species persistence, recovery and/or diversity patterns. Assessment of species traits in this study were adopted from the methodology of Caners et al.,(2013) and Boudreault et al., (2018). Traits were categorized into broad groups that have been linked to the occurrence of bryophyte species in boreal forests by many studies (Hylander, 2009; Löbel et al., 2009; Caners et al., 2013). First, taxonomic group (liverworts and mosses); second, size of gametophore (small-sized [<40 mm], medium-sized [40–79 mm], and large-sized [≥80 mm]); third, reproduction (main mode of reproduction, frequency of sexual and asexual reproduction); and finally, habitat requirements (substrate). Species' substrate preferences were classified into epixylics, terricolous, generalist and bog species. Epixylic bryophytes were further classified into facultative and obligate epixylics. Facultative epixylics have affinities for other substrates and are less drought sensitive compared to obligate epixylics, which are restricted to deadwood and are very drought sensitive (Schmalholz and Hylander, 2009). Species traits information were obtained from BRYOATT (Hill et al., 2007), in the regional flora literature (e.g., Ley and Crowe, 1999; Paton, 1999; Faubert, 2012-14) and expert advice (laboratory of N.J. Fenton).

2.3.6 Comparison with the initial post-harvest study and a chronosequence of old growth forests

In order to understand the changes in the epixylic community with increasing time after harvesting disturbance, we compared the species data (in terms of richness, composition and frequency of occurrences) of this study with an initial post-harvest study that was carried out 4-5 years after harvest. We also compared our data and the initial post-harvest data from the partial cut blocks to that of a chronosequence of old growth forests in the Clay Belt region of northwestern Quebec. This was to test partial cut ability to advance forest succession to a later stage. These are unharvested and unmanaged forests that have remained unburned for a range of time (50 - >200 years). In the chronosequence, bryophytes were sampled on all available microhabitats in three 50m^2 plots in 44 sites (Chaieb et al., 2015; Barbé et al., 2017). From this, a data set containing only the coarse woody debris microhabitats was compiled. The ages of these forests was determined by dendrochronology and were categorized into age groups (50-100,100-150, 150-200, and >200 years post fire) thus, allowing us to ascertain which age group was most similar to our results.

2.4 Data analysis

Microhabitat variables were compared among treatment types in terms of substrate (CWD) characteristics and microenvironment variables. For CWD characteristics, CWD volume by decay class and total volume per plot were analysed using linear mixed models [LME; R package ‘‘nlme’’ (v. 3.1-131)]. Also, CWD diameter, length and decay class were analysed at the log level using LME models. Additionally, we analysed CWD abundance at the plot level using the Kruskall–Wallis test as data were skewed even after transformation. For microenvironment variables, mean temperature and VPD values, mean extremes values, mean duration and frequencies of extreme values were examined using LME models. In the case of selected CWD for bryophytes sampling, all data measured at the belt level (CWD characteristics, canopy openness) were merged and classified as a single mean measure per CWD. Mean value for canopy openness from the three belts were used. For CWD decomposition class, the decomposition class closest to the mean were used. Canopy openness data were square root transformed and analysed at the log level using models. In all LME models, plots nested within sites were used as random factors. Significant differences between treatments were explored using Tukey HSD (R package ''multcomp'' (v. 1.4-1)) tests for LME models and the dunn test (R package ''dunn.test'' v. 1.3.5) for the Kruskall–Wallis test with significance levels of $p \leq 0.05$.

Epixylic community changes along the harvest gradient were examined in terms of species richness, composition and functional traits. For species richness, species occurring more than once in the three belts of a CWD were considered only once in the total richness. Epixylic species richness data were analysed at the log level using LME. Total richness and frequency of occurrence per log for each trait characteristics for all trait categories (taxonomy, size of gametophore, mode and frequency of reproduction and substrate requirements) were also evaluated using LME and square root transformation was applied where needed.

The association of epixylic bryophyte community to microhabitat variables were evaluated using LME models. Models were developed to assess the relative importance of different habitat variables in explaining species richness. Microhabitat variables were divided in two groups that could influence epixylic communities: substrate characteristics and canopy structure. Substrate characteristics were represented by CWD length, diameter, decay and percent contact with ground. Canopy structure variables influence bryophytes mainly through their effect on factors such as light and microclimate and were represented by canopy openness and harvest treatment type. All environmental variables qualified for the multicollinearity test using variance inflation factor (VIF) and were included in models for analysis. However, not all possible variable combinations were considered. In total, 19 candidate models were developed including a null model and were ranked based on the Akaike's Information Criterion corrected for small sample size (AICc) using the R package AICcmodavg (v. 2.1-1). Model averaging was carried out for top-ranking models with AICc weight <2.0 (Burnham and Anderson, 2003). We then calculated average parameter estimates, and standard errors for top ranking models. R^2 for each variable in the best models was calculated to evaluate their relative contribution in the models. This was achieved using the function r.squaredGLMM of the MuMIn package in r (v.1.42.1). Furthermore, an ordination approach was used to explore epixylic composition in relation to habitat conditions per treatment type. Non-metric multidimensional scaling (NMDS) in CANOCO ver.5 was used for this analysis.

To assess the changes in bryophyte community of each harvesting treatment with increasing time after harvesting disturbance, a comparative analysis was carried out with the data set from an initial post-harvest study (Arseneault et al., 2012). Comparisons were based on species richness, composition and frequency of occurrence at the CWD level. Species data were divided into species growing on logs and species growing on the forest floor. This was to observe changes in the occurrence of epixylic species on CWD and on the forest floor with time, since the majority of epixylic species were reported to be growing on the forest floor during the initial study. A t test (r package) was used to compare epixylic species richness and frequency of occurrence between treatments of the two studies. Non-metric multidimensional scaling (NMDS) of CANOCO ver.5 was also used to explore species composition patterns among treatments of the two studies. Data on species growing on CWD only was used for this analysis.

The ability of partial cuts to advance bryophyte community succession similar to an old growth species composition was assessed by multivariate analysis using ordination techniques. Even though partial cut was the focus for this analysis, all harvest treatment types were included to see their relative patterns in relation to old growth stage. Ordination analysis using Non-metric multidimensional scaling (NMDS) in CANOCO ver.5 was applied for this analysis.

2.5 Results

2.5.1 Effects of harvest treatments on microhabitat

CWD was significantly longer in control stands compared to partial cut stands ($p = 0.0003$) and clear cut stands ($p = 0.0005$) but there was no significant difference between partial cuts and clear cuts. Similar trends were observed in year 5 (2009 post harvest study) except that CWD were shorter in year 14 (2017 post harvest study) compared to year 5 (Table 2.1). In both studies, the mean number of CWD per plot didn't differ among harvest types. However, the mean number of CWD per plot was reduced in year 14 compared to year 5. Mean decay class values in year 14 were significantly higher in partial cut and clear cut stands than in control stands but no significant difference was observed among treatments in year 5. Overall, mean decay class values increased in year 14 compared to year 5. Finally, CWD volume by decay class varied among treatments in year 14, as volumes of decay class 1 and 2 were lower in partial cut and clear cut stands compared to control stands (Fig 2.2 and Table A2). Decay class 1 was totally absent in clear cut stands.

Table 2.1 Mean (±SE) values of coarse woody debris (CWD) characteristics and canopy openness for each treatment between initial post harvest study (2009) and 2017 study

Variables	Year 5 (2009)			Year 14 (2017)		
	Harvest treatment			Harvest treatment		
	Unharvested control	Partial cut	Clear cut	Unharvested control	Partial cut	Clear cut
CWD length (cm)	872.47 ± 44.72a	695.77 ± 45.3b	669.7 ± 43.25b	858.13 ± 47.52a	547.76 ± 39.79b	543.84 ± 37.78b
CWD decay class	2.77 ± 0.14a	2.93 ± 0.12a	2.83 ± 0.13a	3.06 ± 0.15b	3.77 ± 0.14a	3.98 ± 0.10a
Number of CWD per plot	9.2 ± 0.38a	10.34 ± 0.49a	9.6 ± 0.39a	8.2 ± 1.58a	8.9 ± 1.1a	8.6 ± 1.54a
Mean canopy openness (%)	39.51 ± 1.15c	56.64 ± 2.7b	82.39 ± 1.94a	28.78 ± 0.85c	32.98 ± 1.39b	62.17 ± 1.38a

Note: Values are means followed by standard error. Significant differences ($p \leq 0.05$) are indicated by different letters following the ranking (a < b < c). n (CWD characteristics (Year 5)) = 212, n (canopy openness (Year 5)) =146, n (CWD characteristics (Year 14)) = 257 and n (canopy openness (Year 14)) =150.

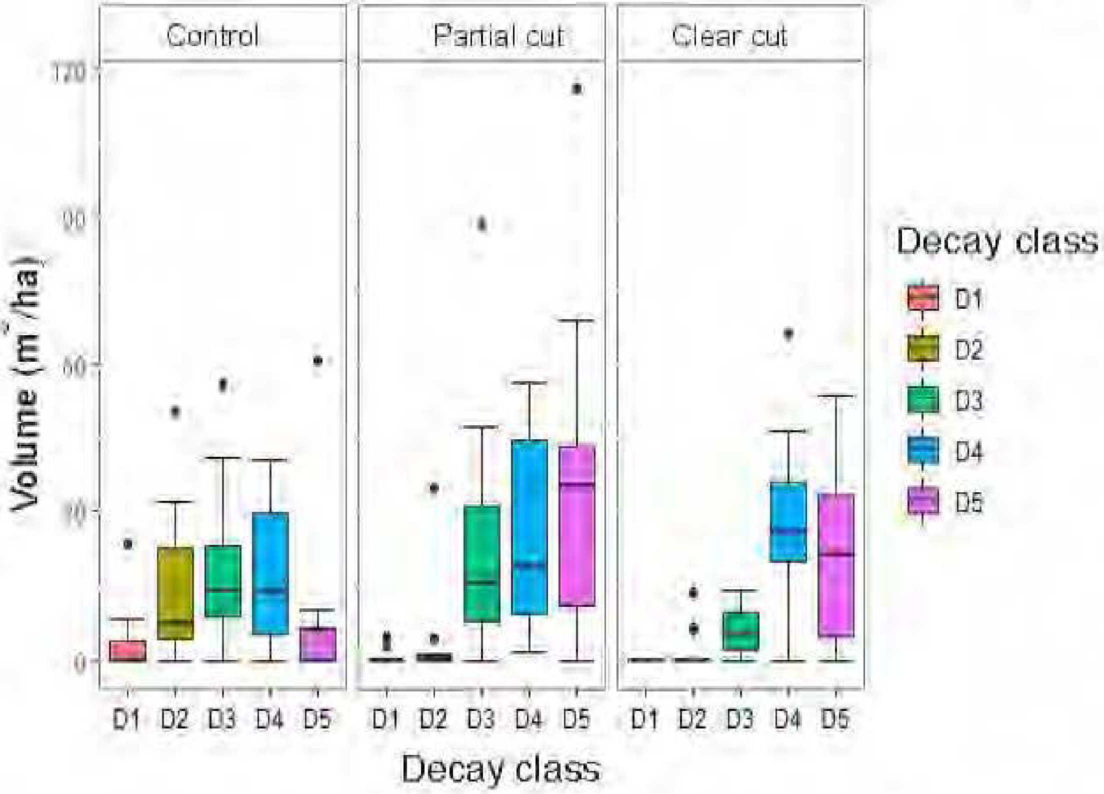

Fig 2.2 Coarse woody debris volume by decay class along a harvest gradient at the plot level (n=30). Control (CT), Partial cut (PC), Clear cut (CC) and Decay class 1 to 5 (Dc1, Dc2, Dc3, Dc4, Dc5).

Canopy openness differed significantly among all treatments with control stands recording the lowest canopy opening, partial cut stands intermediate levels and clear cut stands with the most open canopy (Table 2.1, Fig. A1). A similar trend was observed in year 5 canopy openness even though different methods were used in both studies. Canopy openness values in year 14 were lower compared to year 5. We also observed changes in microclimate variables (vapour pressure deficit (VPD) and temperature) along the harvest gradient. Mean VPD and temperature in clear cut stands differed significantly from partial cut and control stands (Table 2.2). However, no significant differences were observed between control and partial cut stands. Mean extreme VPD values followed a similar pattern as overall mean VPD as mentioned earlier (Table 2.2). Extreme VPD lasted longer and occurred more frequently in clear cut stands compared to partial cut and control stands. Whereas in the case of extreme temperatures, clear cut stands recorded higher mean values compared to partial cut stands but did not differ significantly compared to control stands. Duration in extreme temperatures lasted longer in clear cut stands but no significant difference was observed between partial cut and control stands. Similarly, extreme temperatures occurred more frequently in clear cut stands and was followed by partial cut stands, however, no significant difference were observed among all treatment types.

Table 2.2 Mean (±SE) values of microclimate variables per treatment type

Variable	Unharvested control	Partial cut	Clear cut
Vapour pressure deficit (VPD in KPa)			
Mean	3.050 ± 0.059b	3.105 ± 0.059b	4.229 ± 0.074a
High VPD (KPa)	17.814 ± 0.269b	17.738 ± 0.256b	18.573 ± 0.227a
Duration (hours)	6.705 ± 0.161b	6.898 ± 0.174b	7.797 ± 0.157a
Frequency of occurrence	51.333 ± 5.082b	50 ± 9.702b	73 ± 3.642a
Temperature (°C)			
Mean	10.781 ± 0.090b	10.688 ± 0.088b	11.185 ± 0.096a
High Temperature (°C)	26.095 ±0.109ab	25.825 ± 0.113b	26.249 ± 0.101a
Duration (hours)	7.291 ± 0.215b	7.389 ± 0.220b	8.043 ± 0.204a
Frequency of occurrence	53.167 ± 4.028a	48.167 ± 8.526a	63.167 ± 4.423a

Note: Values are means followed by standard error. Significant differences ($p \leq 0.05$) are indicated by different letters. Analysis are based on daytime measurements between the months of May and October (2017-2018).

2.5.2 Bryophyte communities in different harvest types

2.5.2.1 Species richness

Overall, 59 species were recorded in this study, 28 true mosses, 23 liverworts and 8 sphagna (Table A4). By harvest type, 44 species (20 true mosses, 17 liverworts and 7 sphagna) were found in unharvested control stands, 50 species (25 true mosses, 21 liverworts and 4 sphagna) in partial cut stands, and 39 species (19 true mosses, 13 liverworts and 7 sphagna) in clear cut stands. Out of the total number of species recorded, 3 species were observed only in control stands, 8 only in partial cut stands and 3 only in clear cut stands. In terms of all epixylic species, we recorded 18 species in total including 13 liverworts and 5 true mosses. By harvest type, 12, 17 and 13 epixylic species were found in unharvested control, partial cut and clear cut stands respectively. Four epixylic species were observed only in partial cut stands (*Calypogea neesiana, Chiloscyphus profundus* and *Lophozia longidens*), one in control stands (*Cephaloziella spinigera*) but none were only found in clear cut stands.

Epixylic species richness and total species richness was significantly higher in partial cut stands compared to control and clear cut stands. However, no significant differences were observed between control and clear cut stands (Fig 2.3). Compared to the initial post-harvest study, epixylic species richness was significantly higher in year 14 in partial cut and clear cut stands than in year 5 (Fig 2.3). Also, epixylic species richness and frequency of occurrence, particularly in partial cut and clear cut stands, doubled in year 14 compared to year 5. Overall, total species richness between the two studies didn't differ significantly in control stands however partial cut and clear cut stands were richer in year 14 compared to year 5 (Fig 2.3). In addition, epixylic species occurred mostly on CWD in year 14 compared to year 5 where most epixylic species occurred on the forest floor (Fig 2.4).

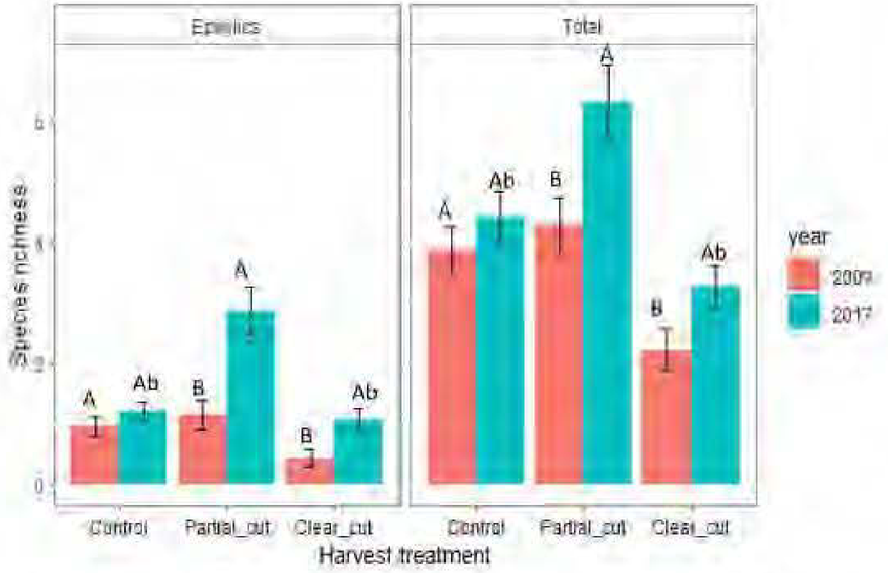

Fig 2.3 Mean species richness per harvest treatment between initial post harvest study (2009) and 2017 study. Significant differences ($p \leq 0.05$) are indicated by different letters following the ranking ($a < b < c$). Different upper case letters indicate significant differences between the same treatment of the two studies; different lower case letters indicate significant differences between all treatments of the same year.

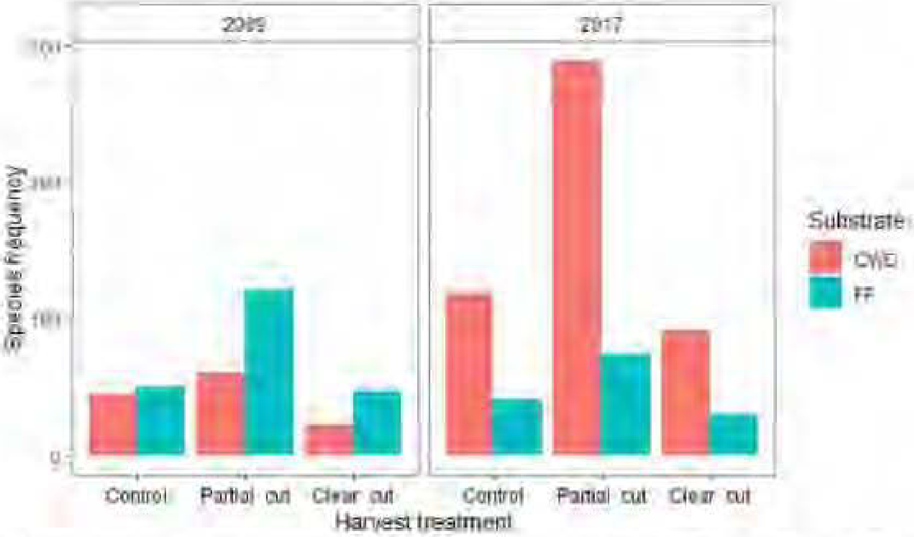

Fig 2.4 Frequency of occurrence of epixylic species on CWD and forest floor (FF) per harvest treatment between 2009 initial post harvest study (year 5) and 2017 study (year 14).

Microhabitat variables that were influenced by forest harvest (Table 2.1) were the drivers of the differences in epixylic richness found among treatments. Akaike model selection (Table A1) indicated that two models were equivalent and model-averaged estimates (Table 2.3) of these models with ΔAICc < 2 found that epixylic richness was influenced by canopy openness, CWD decay class and diameter size. This was also consistent with the Akaike model selection results of the initial post harvest study (year 5). CWD decay class and diameter size positively influenced epixylic richness while on the contrary, canopy openness negatively influenced epixylic richness. Bigger and well decayed CWD supported high epixylic richness whereas more open canopy supported less richness. Also, harvest treatment affected epixylic richness indicating that other variables associated with harvest were important, but they were not accounted for in our models.

Table 2.3 Model-averaged estimates (Est) standard error (SE) and P values (P) of variable epixylic explaining richness

Variables	Est	SE	P
Canopy openness *	-0.022	0.006	0.0006
CWD Decay Class*	0.159	0.071	0.0270
CWD Diameter*	0.048	0.016	0.0035
CWD Ground_contact	0.002	0.003	0.5473
CWD length	0.000	0.000	0.4269
Clear cut	0.439	0.250	0.0938
Partial cut*	0.572	0.143	0.0002
Control	0.330	0.403	0.4192

Note: Variables with significant ($p \leq 0.05$) influence on epixylic richness are indicated by (*) sign.

Year 14 species composition was explored using an NMDS ordination with 59 species and 150 CWD (Fig 2.5). The first axis (EV=0.437) separated species by substrate type with epixylic species (*Anastrophyllum hellerianum, Dicranum fuscescens, Ptilidium pulcherrimum*) on the right, generalist species (*Aulacomnium palustris, Pleurozium schreberi, Ptilidium ciliare*) and terricolous species (*Rhytidiadelphus triquetrus, Dicranum polysetum*) in the center and bog species (*Sphagnum fuscum, S. magellanicum, S. russowii*) on the left of the first axis. The ordination illustrated that control stands were dominated by bog species, partial cut stands by epixylic species and clear cut stands by generalist and terricolous species. The second axis (EV=0.340) separated species along a moisture gradient. Species common in wet areas (*Sphagnum magellanicum, S. russowii*) on the top, moist areas (*Frullania oakesiana, Nowellia curvifolia*) in the center and dry areas below (*Pleurozium schreberi, Ptilidium ciliare*). Control stands dominated wet-condition loving species, partial cut stands moist-condition loving species and clear cut dry-condition loving species. The relationship between microhabitat variables and the species composition pattern was also explored by passively correlating the variables with the plot positions (Fig 2.6). The first axis was correlated with variables related to CWD characteristics (length, decay class and diameter size) and the second axis correlated with canopy openness

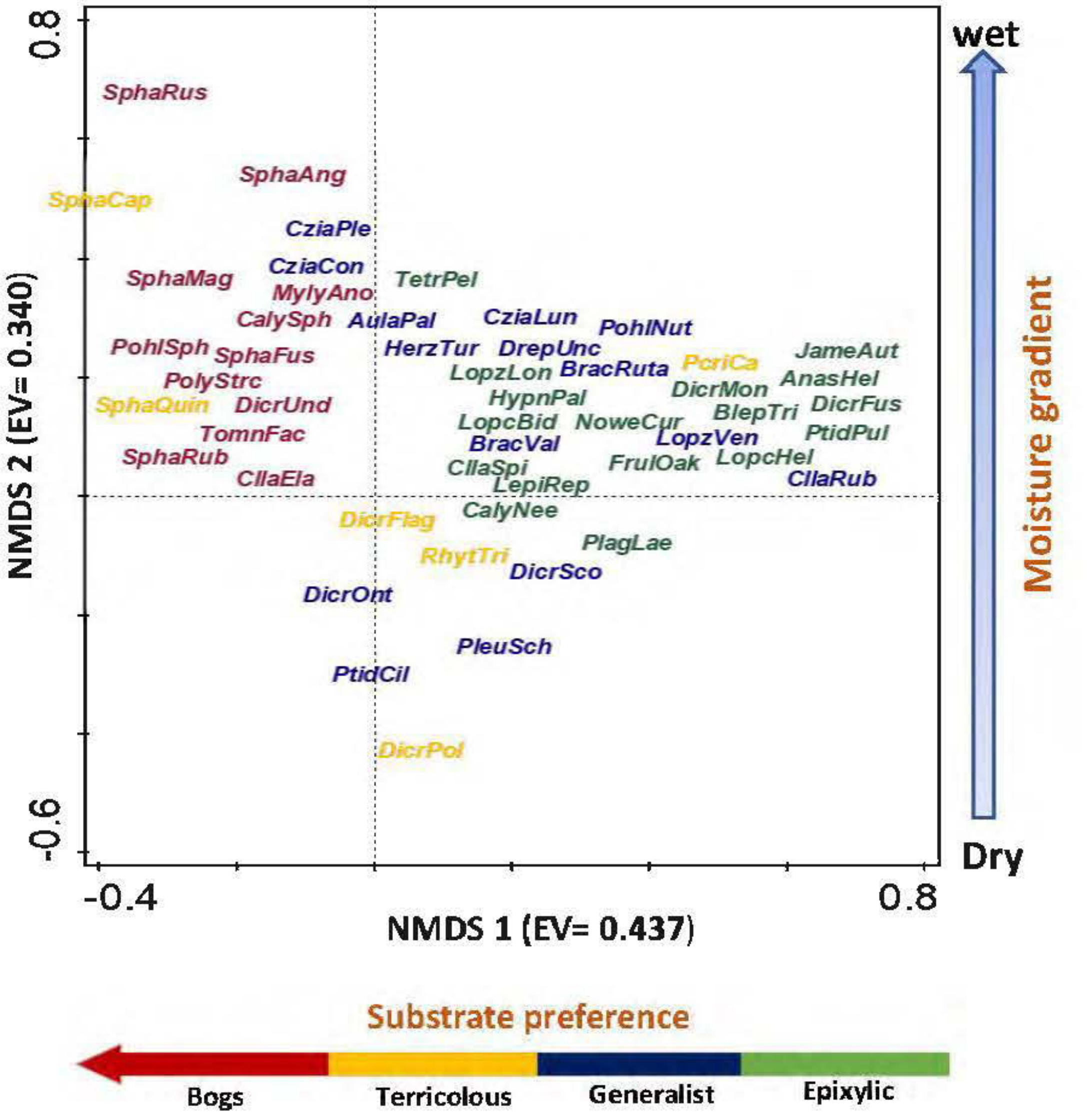

Fig 2.5 NMDS ordination of species assemblages on coarse woody debris in 2017, with eigenvalues (EV) in brackets. Species, n=59. Text colors indicate different substrate types: epixylic species (green), bog species (red), generalist species (blue) and terricolous species (yellow). Some species close to the 0,0 position were deleted to improve clarity of the graph. Stress value 0.161.

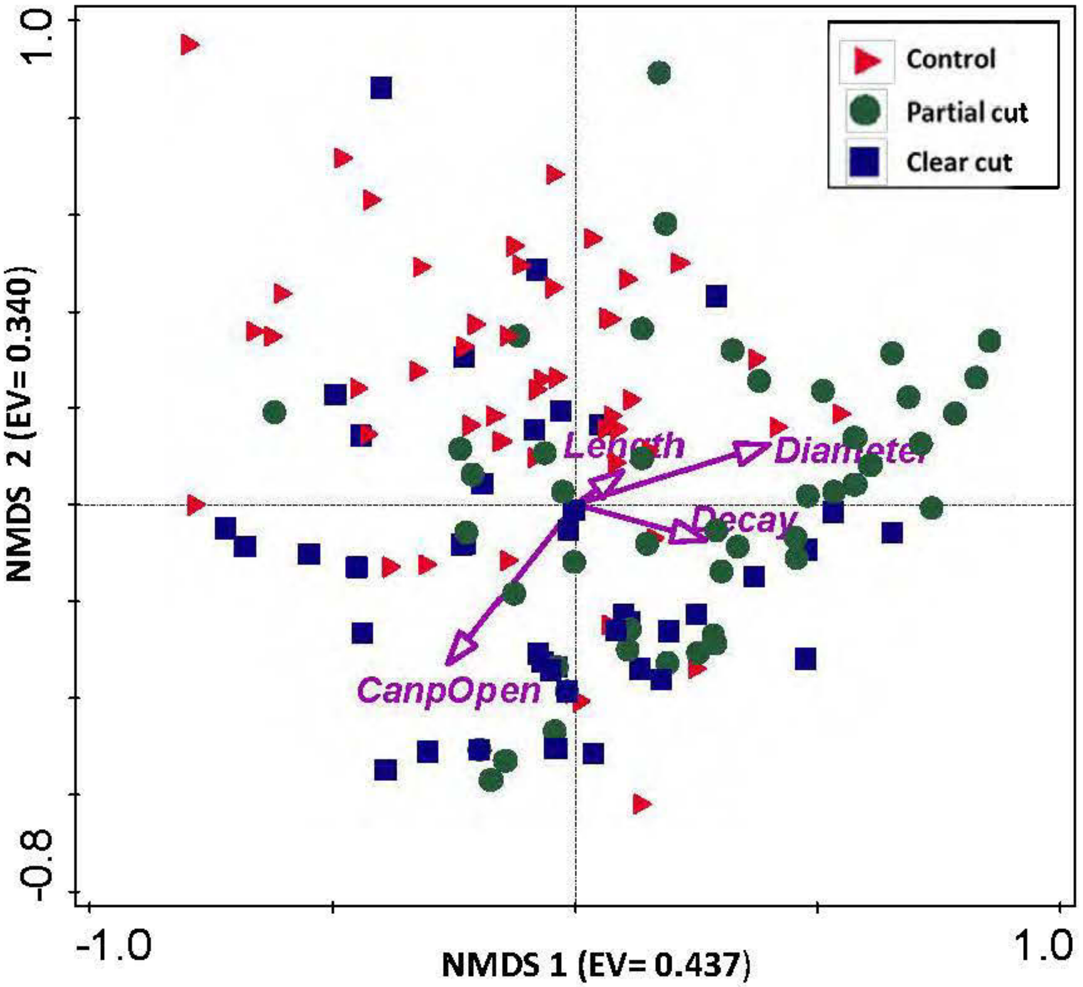

Fig 2.6 NMDS ordination of bryophytes assemblages of species growing on coarse woody debris, with eigenvalues (EV) in brackets. CWD spread based on harvest treatment type, n =150 CWD. Symbols colour indicate; control (blue square), partial cut (green diamond) and clear cut (black circle). Arrows indicate strength of habitat variables relationship with axes and direction of maximum change. Stress value 0.16.

Species composition changes between year 5 and year 14 studies were visualized using NMDS ordination analysis (Fig 2.7). The first axis (EV=0.411) separated species by substrate type with epixylic and generalist species on the left and terricolous, sphagnum and/or bog species on the right. The second axis (EV=0.375) but mainly represented a moisture gradient with species common in moist and wet areas at the top and species common in dry areas below. Differences in species composition patterns between the two studies confirmed the trend observed in species richness (Fig 2.8). Notably, species composition mostly overlapped in the control stands of both studies. Similarly, there were some overlap observed in partial cut stands however species composition in year 14 shifted more towards epixylic species whereas in year 5 species composition pattern spread across ordination space. In the case of clear cut stands, species composition shifted from sphagnum and/or bog species in year 5 to generalist and terricolous species in year 14.

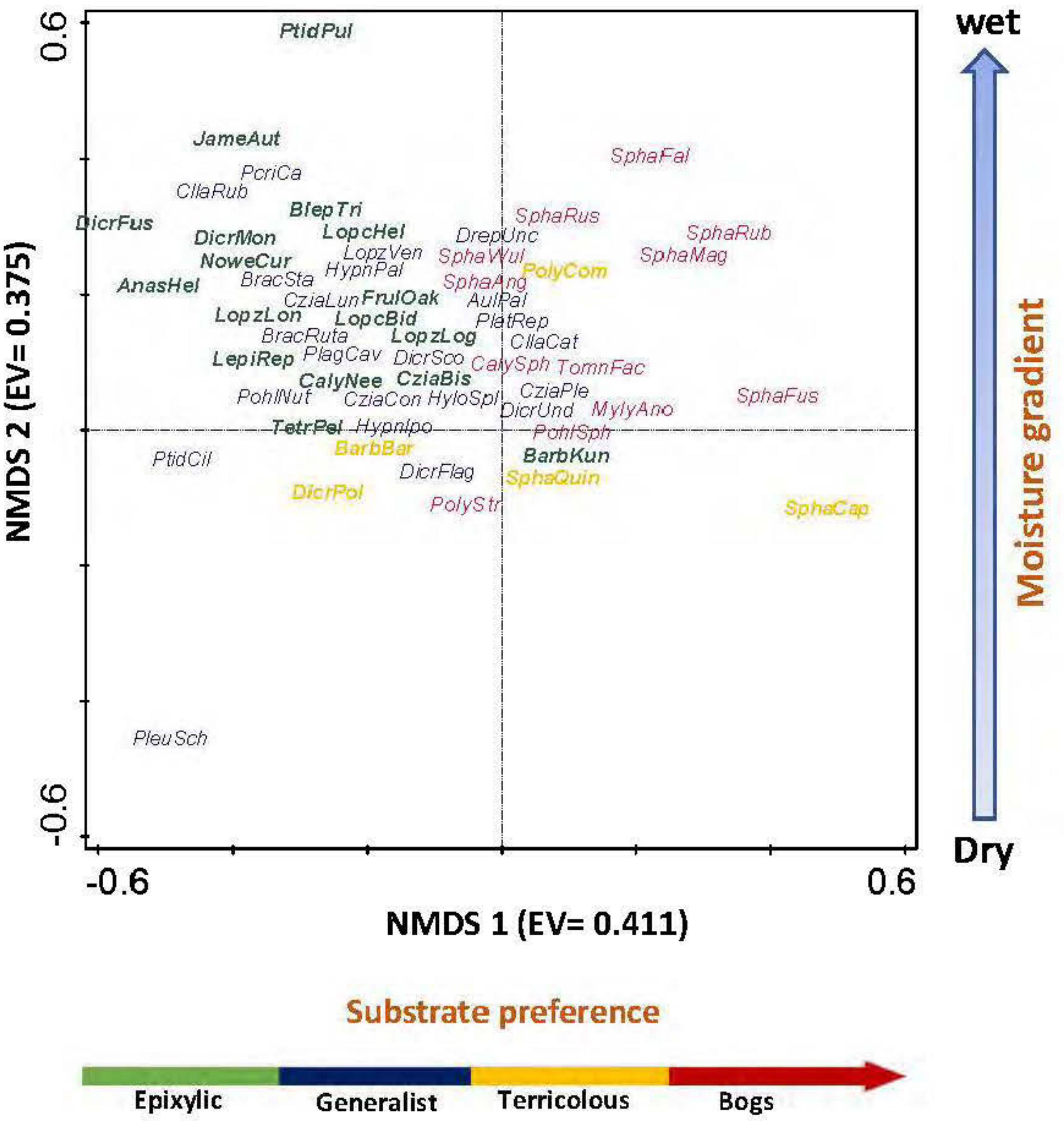

Fig 2.7 NMDS ordination of species assemblages on coarse woody debris in 2009 (n = 63 and 2017 (n = 59 species), with eigenvalues (EV) in brackets. Text colors indicate different substrate types: epixylic species (green), bog species (red), generalist species (blue) and terricolous species (yellow). Some species close to the 0,0 position were deleted to improve clarity of the graph. Stress value = 0.138.

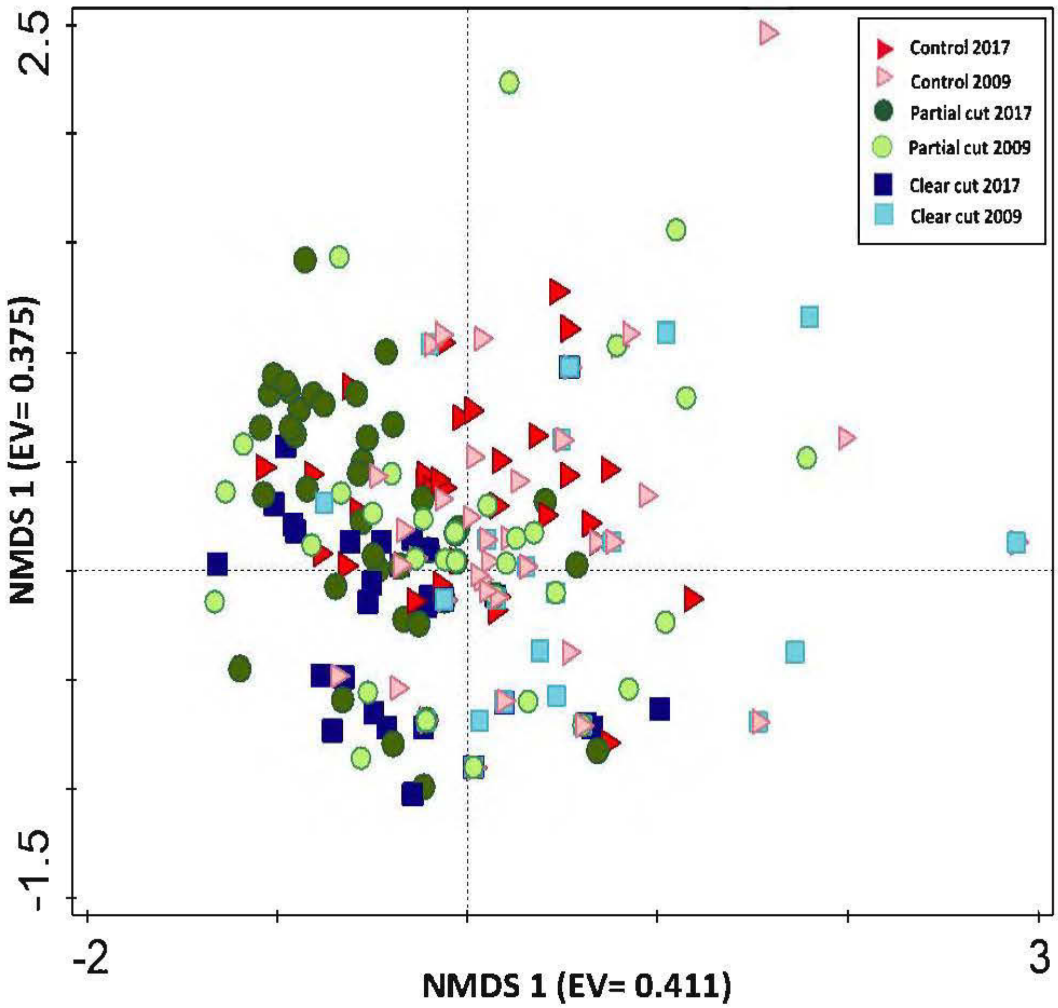

Fig 2.8 NMDS ordination of bryophytes assemblages on coarse woody debris between 2009 initial post harvest study (n= 44 CWD) and 2017 study (n = 50 CWD). Eigenvalues (EV) in brackets and symbols indicate: control 2009 (red right triangle), control 2017 (purple right triangle), partial cut 2009 (yellow circle), partial cut 2017 (blue circle), clear cut 2009 (blue square) and clear cut 2017 (green square). Stress value = 0.138.

In order to assess partial cut ability to encourage old growth species assemblages, a third NMDS analysis was used to visualized CWD species composition in partial cut stands of both studies alongside that of a chronosequence of old growth forests. The chronosequence data did not provide a clear temporal pattern of species composition changes on logs. However, there was a separation between below 100 years versus over 200 years on the horizontal axis but there were not enough young stands to conclude. Species composition in 2009 partial cut were separated from that of old growth forests on the vertical axis. Whereas 2017 partial cut species composition overlapped with that of old growth forest particularly between 100 to 200 years (Fig 2.9).

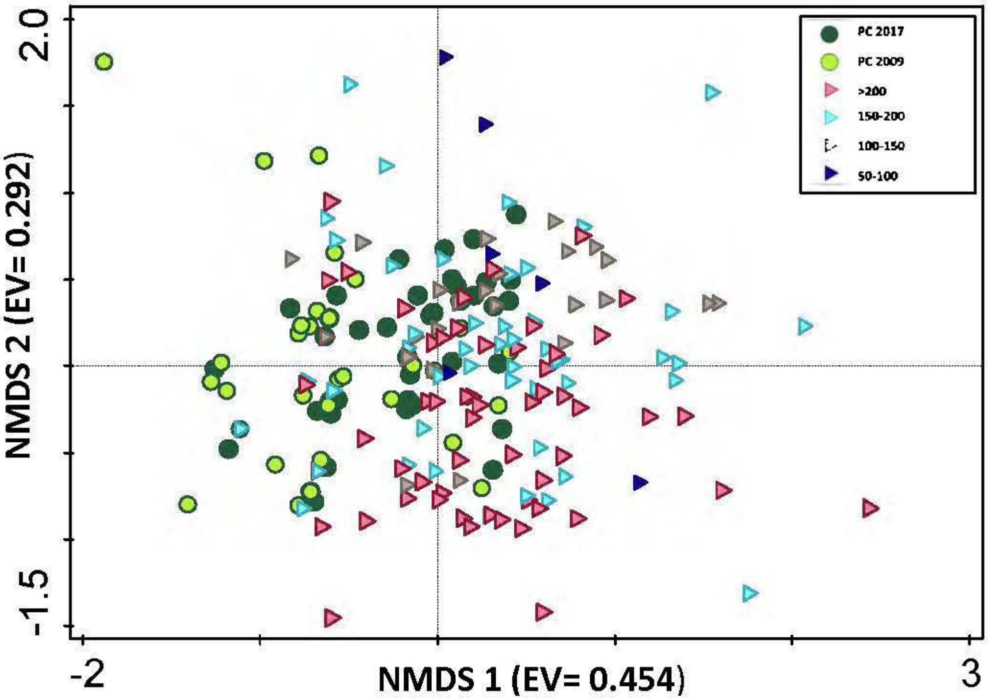

Fig 2.9 NMDS ordination of bryophytes assemblages on coarse woody debris between 2009 initial post harvest study (n= 44 CWD), 2017 study (n = 50 CWD) and a chronosequence of old growth forest (n= 145 CWD). Eigenvalues (EV) in brackets Symbols indicate: partial cut 2017 (green circle), partial cut 2009 (black circle), >200 (purple right triangle), 150-200 (blue right triangle), 100-150 (grey right triangle) and 50-100 (blue right triangle). Stress value = 0.137.

2.5.2.2 Species functional traits

Liverworts, mosses, generalists and terricolous species were richer in control and partial cut stands compared to clear cut stands but did not differ significantly from control stands in the case of liverworts and generalist species (Fig A2). Richness of medium and smaller sized species were higher in partial cut stands than in control and clear cut stands but did not differ significantly from control stands in the case of small sized species (Fig 2.10). In contrast, large sized and bog species were significantly richer in control stands compared to partial cut and clear cut stands. Vegetative, sexual, and vegetative and sexual species richness were higher in partial cut stands than in control and clear cut stands. Control and partial cut stands were richer in species with rare sexual reproduction, however partial cut was not significantly different from clear cut. In the case of species with rare vegetative production, partial cut stands were significantly richer than both control and clear cut stands.

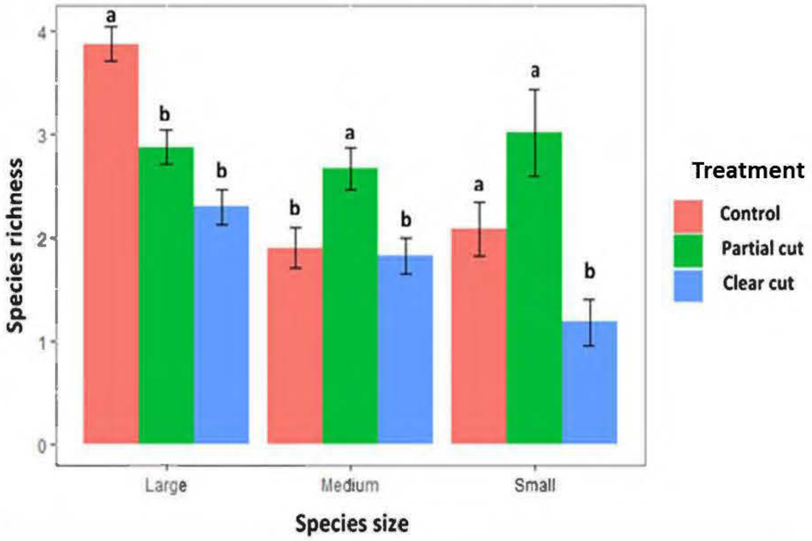

Fig 2.10 Mean species richness according to size of shoot per harvest treatment. n=150 and significant differences ($p \leq 0.05$) are indicated by different letters following the ranking (a < b < c). Size of shoot (small-sized [<40 mm], medium-sized [40–79 mm], and large-sized [≥80 mm]).

2.6 Discussion

The results of this study demonstrated that harvest treatment affected the epixylic bryophyte community by changing microhabitat conditions with increasing time after harvest. Over the time span covered by this study, partial cut continued to provide favorable habitat conditions that maintain higher epixylic richness overtime compared to control and clear cut stands. Also, composition of species growing on logs in partial cut stands were more similar to that found in old growth forests compared to that of the initial post-harvest study. CWD decay class, CWD diameter size and canopy openness were found to be the major factors influencing epixylic species, which was consistent with findings of the initial post harvest study (Arseneault et al., 2012).

In the context of the first hypothesis, our results showed a decrease in CWD abundance in year 14 compared to year 5. This result corroborated with the first hypothesis in the case of clear cut stands but not partial cut stands. Decomposition and lack of continual input of CWD may have accounted for the decrease in CWD abundance in year 14. Lower volumes of early decayed CWD recorded in partial cut and clear cut stands confirmed less input of new CWD into both stands. Lack of bigger trees in regenerating clear cut stands obviously accounted for less CWD input consequently lower volumes of newly recruited CWD. In the case of partial cut stands, lower harvest retention levels (Table A3) indicating less bigger trees, in selected plots may have accounted for lower volumes of newly recruited CWD. Also, lower post harvest tree mortality observed in year 14 partial cut stands compared to year 5 stands (according to year 10 post harvest inventory report by Leduc, 2013) may also explain the higher and lower CWD abundance recorded in year 5 and 14 respectively. Furthermore, canopy openness results corroborated with the first hypothesis as year 14 stands recorded lower canopy openness values compared to year 5. This was due to tree regeneration and growth observed in stands of all treatments.

For the second hypothesis, epixylic species richness increased in both partial cut and clear cut stands in year 14 compared to year 5. This result agreed with the hypothesis in the case of partial cut stands but not clear cut stands. Both partial cut and clear cut stands improved in habitat conditions in terms of substrate availability (due to high volumes of well decayed CWD) and moisture conditions (due to canopy closure resulting from tree regeneration and growth). In terms of substrate characteristics relationship with epixylic richness, our results showed a positive correlation between species richness and CWD decay class and diameter size. Bigger and well decayed CWD supported high epixylic richness as was the case in year 5 studies. Bigger CWD stays longer on forest floor due to slow decomposition, consequently, giving ample time for epixylic species dispersal and colonization (Andersson and Hytteborn, 1991b). Also, bigger CWD physically separates epixylic species from fast growing forest floor species thereby reducing competition (Arseneault et al., 2012). CWD in advance decay stages are generally decorticated with soft and spongy wood which makes them better able to absorb and retain moisture consequently providing moisture for epixylic bryophytes (Rambo, 2001). Thus, high volumes of well decayed CWD recorded in both partial cut and clear cut stands of year 14 partly explains the increase in epixylic richness over time.

Additionally, differences in decay rate associated with diameter size may explain the switch of the occurrence of most epixylic species from smaller woody debris on the forest floor in year 5 to CWD in year 14. Smaller woody debris because of their small size decompose faster and harvested generated pieces were presumed to be at a more advanced decay class compared to the harvest generated CWD in year 5. Consequently, most epixylic species were found on these pieces at that time. The harvest generated smaller woody debris disappeared from the forest floor quickly due to both rapid decomposition and overgrowth by forest floor species such as *Pleurozium scherberi* and *Sphagnum* spp. Considering epixylic bryophyte dispersal limitation as described by Soderstrom, (1987, 1989) and their competitive disadvantage (Söderström, 1988b;

Andersson and Hytteborn, 1991b; Siitonen, 2001; Kumar et al., 2017; Dynesius et al., 2010) with forest floor species, smaller woody debris as a substrate might only favour species with rapid growth and frequent reproduction. In year 14 the harvest generated CWD had advanced in decay stage and with its longer residence time and bigger dispersal target allowed more species to colonise this habitat resulting in both the higher richness of epixylic species and of species with limited reproduction in year 14 compared to year 5. Even though higher volumes of advanced CWD were recorded in both partial cut and clear cut stands, the observed differences in epixylic community between the two harvest types highlights the importance of moisture conditions as reported by Söderström, (1988b) and others.

Canopy openness has both a positive and a negative effect on epixylic bryophytes. Wider canopy opening increases forest floor temperatures and reduces moisture conditions (Fenton and Frego 2005; Hylander et al. 2005; Heithecker and Halpern 2006; Stewart and Mallik 2006). This dries up CWD making them unsuitable substrate for these poikilohydric organisms (Arseneault et al., 2012; Fenton et al., 2013). This is evident in lower epixylic richness observed in clear cut stands in both our study and the initial post-harvest study, as clear cut is associated with wider canopy opening. However wider canopy opening in clear cut stands, favored the abundance of generalist and large-sized species which are noted to be more tolerant to drought and competition as described by other studies (Caners et al., 2013; Boudreault et al., 2018). Contrarily, lower canopy opening is correlated with high epixylic species richness, as found in our study and that of the initial post-harvest study. Lower canopy opening reduces forest floor temperatures and increases moisture conditions thereby creating favorable microclimate for these moisture demanding species. Tree regeneration observed in clear cut stands during field data collection, created patches of shaded floor that improved moisture conditions and consequently created suitable substrates for epixylic species colonisation and establishment. This contributed to the richer epixylic community on CWD in year 14 clear cut stands compared to that of year 5. Despite the increase in epixylic richness in clear cut stands over time, we observed that drought sensitive and old growth indicator species like *Nowellia curvifolia* and *Blepharostoma trichophyllum* (Boudreault et al., 2018) were totally absent in clear cut stands. The absence of these species in clear cut stands agrees with our hypothesis three and Söderström's (1988) assertion that drought sensitive epixylics are the most threatened in managed landscapes.

Furthermore, the matrix of closed and open canopy provided by residual stands and regenerating trees in partial cut stands created a heterogenous microclimate on the forest floor. This heterogenous forest floor microclimate accounted for richer bryophyte community (including epixylic, liverworts and small-sized species), as different species have different moisture requirement due to their functional traits. The presence of richer specialised species in partial cut stands conformed to our hypothesis three. Additionally, the heterogenous microclimate conditions coupled with abundance of advanced decay CWD mimicked the complex habitat conditions observed in old growth forest. This partly explain old growth species assemblages (composition) including the presence of old growth indicator species (*Nowellia curvifolia* and *Blepharostoma trichophyllum*) observed in partial cut stands of our study. This results also confirms our second hypothesis in relation to old growth species assemblages in partial cut stands. However, that was not the case in 2009 as species assemblages on logs fell slightly outside the range of natural variability. This might be attributed to habitat degradation due to high tree mortality after harvest observed in these plots (Arseneault et al., 2012; Leduc, 2013). Whereas in our case, stands in the selected plots experienced less tree mortality and there was a net growth in residual tree volume ten years after harvest (Leduc, 2013).

Considering other factors that also affected epixylic richness, overgrowing of CWD by dominant forest floor species have been described to affect epixylic bryophytes (Söderström, 1988b; Andersson and Hytteborn, 1991b; Siitonen, 2001; Kumar et al., 2017; Dynesius et al., 2010). Fast growing forest floor species gradually grow on and over CWD and out compete epixylic species already established on CWDs (Söderström, 1988a). In our context, *Sphagnum* species that dominated the forest floor of control stands, also dominated the community on advanced decay CWD. *Sphagnum spp* dominance therefore affected epixylic species richness and composition in control stands more than in partial cut and clear cut stands where *Sphagnum spp.* was less dominant on the forest floor. Overgrowing also reduces CWD availability overall as it is buried into the forest floor (Dynesius et al., 2010; Jacobs et al., 2015) before they get into advance decay stage. This was evident in the lower decay class 5 CWD volumes in control stands of our study.

Continual availability of suitable substrates can also affect species richness as Siitonen, (2001) describes for saproxylic species. As a consequence of the dynamic nature of CWD, epixylic bryophytes maintain a colonist life habit as they must colonise new suitable substrates as the old substrate becomes unsuitable because of competition and disappearance (via decay and overgrowth). The number of species that persist at the stand level can therefore be dependent on the availability of suitable substrates within that stand (Siitonen, 2001). Lower volumes of early decay class observed in partial cut and clear cut stands raise concerns of future substrate availability for epixylic bryophytes. In the case of clear cut, regenerating stands with no large trees will not provide a reliable source of CWD for epixylic bryophytes in the future and substrate availability will decrease in the near future due to higher volumes of well decayed CWD. Thus, the increase in epixylic richness observed in clear cut stands in our study might not last but will decline with diminishing suitable substrate availability. Unlike clear cut, residual stands in partial cut provides a potential source of CWD supply even though lower volumes of newly recruited CWD was recorded.

2.7 Conclusion

Our results highlight the fact that, bryophyte richness and composition changes alongside changing habitat conditions with increasing time after harvest. These changes in bryophyte community are driven by species biological traits as they determine their responds and tolerance to the changing habitat conditions. CWD decay class, CWD diameter size and canopy openness were found to be the major habitat factors influencing epixylic bryophyte community. Also, bryophyte shoot size, substrate preference, vegetative and sexual reproduction were found to correlate with species assemblages along the harvest severity gradient. Partial cut continued to provide favorable habitat conditions that maintain high epixylic richness overtime compared to control and clear cut stands. Also, partial cut stands created variable microhabitat conditions that supported vulnerable species such as small-sized species and rare vegetative reproduction species. Additionally, conditions in partial cut stands encouraged old growth species assemblages. Partial cut therefore provides a better option in achieving species and habitat conservation goals than what is been achieved by traditional clear cut. This is consistent with initial reports on partial cut ability to offer an effective strategy for biodiversity conservation compared to traditional clear cuts in managed forest landscapes. However, lower volumes of newly recruited coarse woody debris raise concern about its CWD delivery potential. Unlike clear cut, residual stands in partial cut provides a potential source of continual CWD supply into the forest stand. CWD input should therefore be considered in implementation strategies to ensure continual persistence of epixylic bryophytes and deadwood living organisms in general.

CHAPTER III

GENERAL CONCLUSION

Our results highlighted the effects of harvest treatment on epixylic bryophytes via changing microhabitat conditions overtime. CWD decay class, CWD diameter size and canopy openness were found to be the major factors influencing epixylic species. Also, species traits influenced species response to disturbances along the harvest gradient over time. Bryophyte shoot size, substrate preferences vegetative and sexual reproduction were found to correlate with species assemblages along the harvest gradient. Clear cut stands showed an improvement in habitat conditions which was reflected in high epixylic richness over time, however this trend might not last in the long term due to lack of continuity of future suitable substrates. Consequently, epixylic bryophytes richness in clear cut stands may decline with decreasing amount of suitable substrates. In addition, clear cut stands were mostly composed of disturbance adapted species characterized by frequent reproduction, larger shoot size, drought tolerance and wider substrate preference. On the other hand, partial cut stands continued to maintain high epixylic richness overtime compared to control and clear cut stands. Also, partial cut stands over time developed habitat conditions that encouraged old growth species assemblages. Additionally, partial cut stands created variable habitat conditions that supported small-sized species, rare vegetative reproduction species and narrow substrate preference species. In control stands, onset of paludification which is characterised by accumulating organic matter and *Sphagnum* spp. dominance reduced suitable substrate availability and increased forest floor moisture conditions (rise of water table). Consequently, epixylic species richness and composition as well as species with reduced tolerance to competition and increasing moisture conditions were negatively affected.

Overall, partial cut reduced harvest impacts by continuing to provide favorable microhabitat conditions, which supported epixylic bryophytes and/or old growth adapted species. Thus, in relation to forest management, partial cut harvest presents a better option in achieving species and habitat conservation goals than traditional clear cut harvest. This is therefore consistent with initial reports on partial cut ability to offer an effective strategy for biodiversity conservation compared to traditional clear cuts in managed forest landscapes. However, lower volumes of newly recruited coarse woody debris raises concern about its deadwood delivery potential. Unlike clear cut, residual stands in partial cut provides a potential source of continual deadwood supply into the forest stand. Deadwood input should therefore be considered in implementation strategies to ensure continual persistence of epixylic bryophytes and deadwood living organisms in general. Judging from the effect of paludification on epixylic bryophytes and their substrate, in paludification prone sites, partial cut may not be effective in maintaining high richness overtime since low soil disturbance and canopy opening during harvest may accelerate stand paludification.

APPENDICES

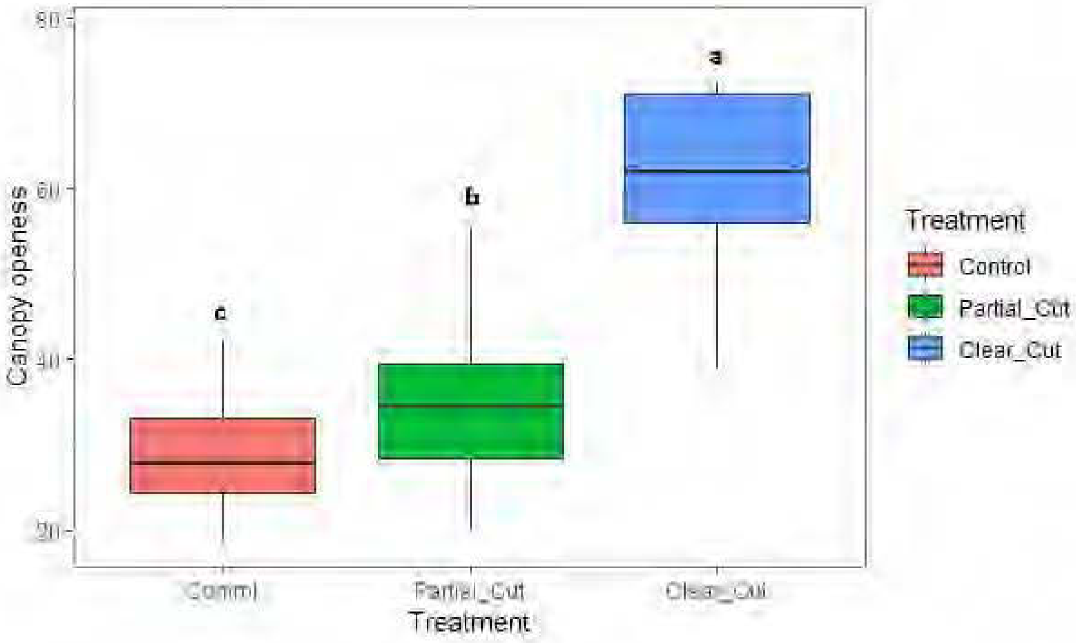

Fig A 1 Mean canopy openness per harvest treatment at the log level (n=150). Significant differences ($p \leq 0.05$) are indicated by different letters.

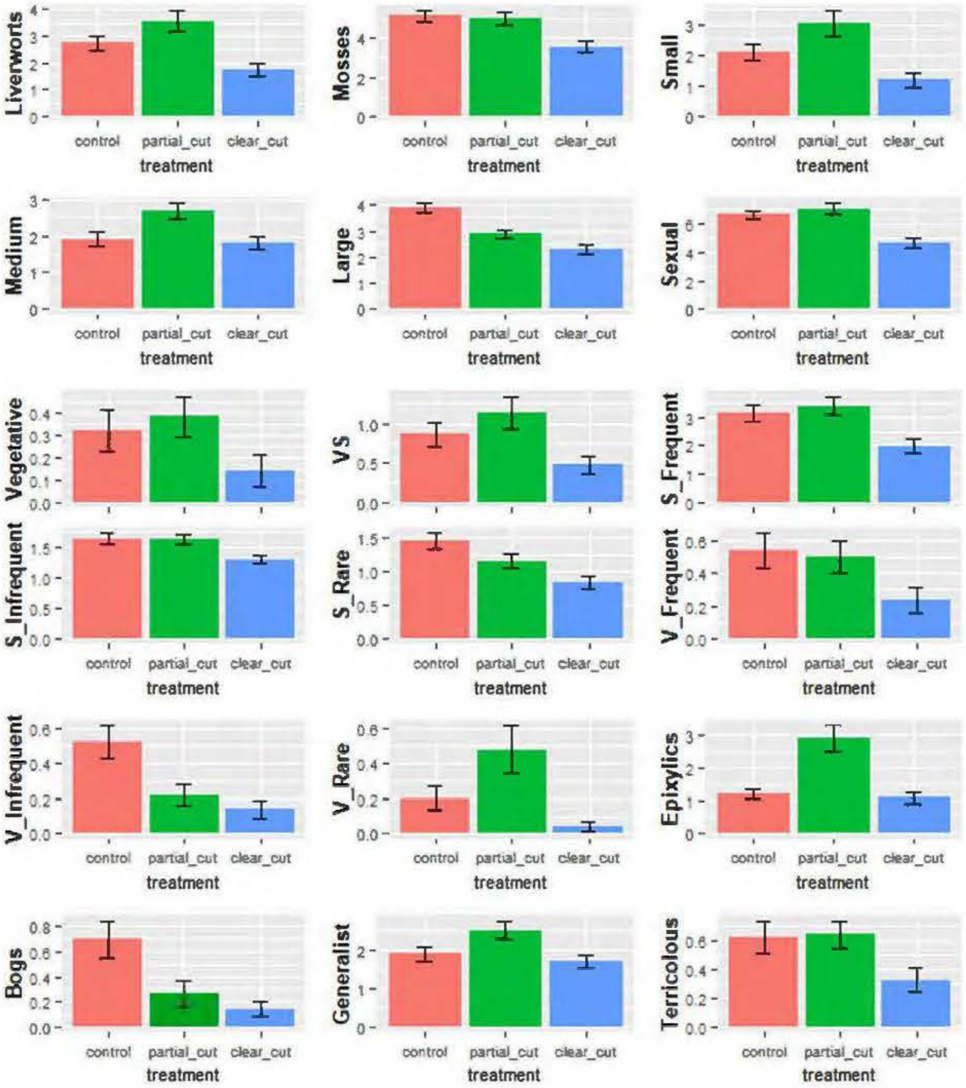

Fig A 2 Richness of mosses, liverworts, small, medium, and large-sized species, sexual species, vegetative species, vegetative and sexual species, species with frequent sexual reproduction, species with infrequent sexual reproduction, species with frequent vegetative reproduction, species with infrequent vegetative reproduction, epixylic species, bogs species, generalist species and terricolous. Significant differences ($p \leq 0.05$) are indicated by different letters ($n = 150$).VS (vegetative and sexual reproduction), S_ Frequent (Frequent sexual reproduction), S_Infrequent (infrequent sexual reproduction), S_Rare (Rare sexual reproduction), V_ Frequent (Frequent vegetative reproduction), V_Infrequent (infrequent vegetative reproduction) and V_Rare (Rare vegetative reproduction).

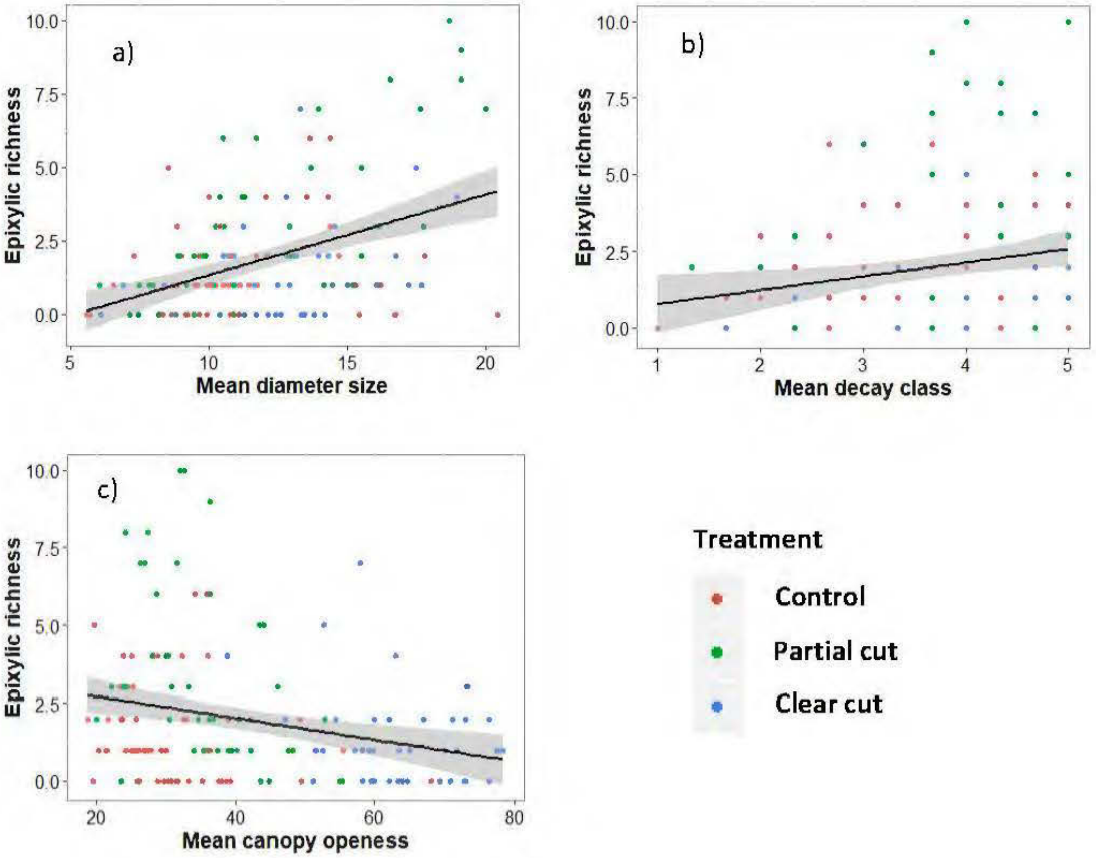

Fig A 3 Epixylic species richness as a function of a) Coarse woody debris (CWD) diameter size, b) CWD decay class and c) canopy openness. Raw data appear as dots, model predictions as the solid line and shaded area represent the 95% confidence of the predictions.

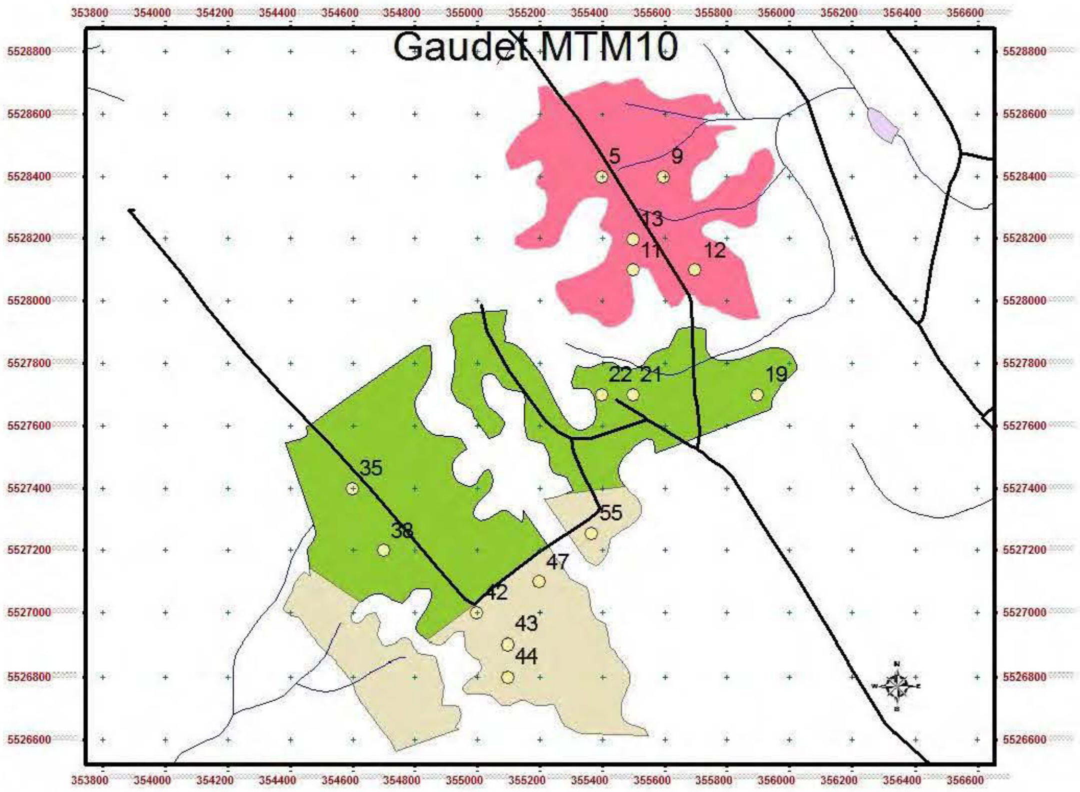

Fig A 4 Site map for Gaudet. Colors indicate blocks of different harvest types: pink (CPRS), green (partial cut) and yellow (unharvested control). Symbols indicate: yellow circles (selected plots) and numbers (plot identification numbers).

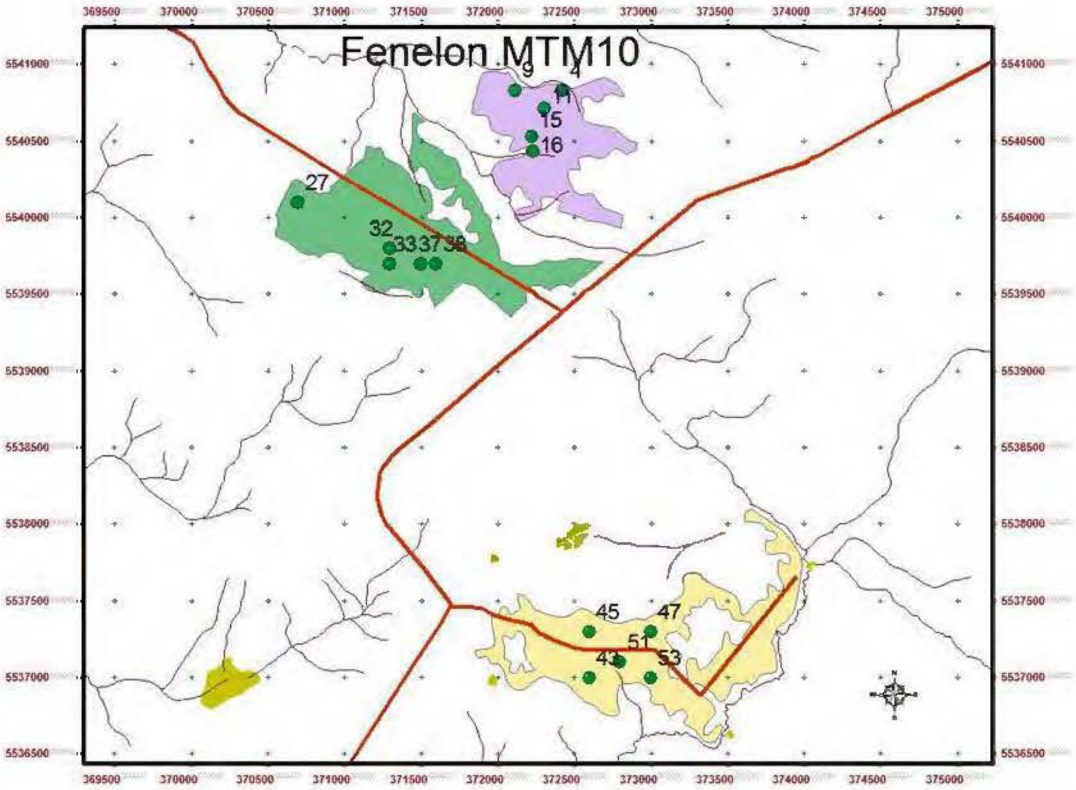

Fig A 5 Site map for Fenelon. Colors indicate blocks of different harvest types: yellow (CPRS), green (partial cut) and purple (unharvested control). Symbols indicate: green circles (selected plots) and numbers (plot identification numbers).

Table A1 Model selection results of variable predicting epixylic richness

Model name	Explanatory variable	K	AICc	ΔAICc	AICcWt
M1	Treatment + canopy openness + diameter + decay class + CWD length + CWD ground contact	11	323.934	0	0.350
M7	Treatment + canopy openness + diameter + decay class	9	324.172	0.237	0.311
M3	Treatment + canopy openness + diameter +decay class + canopy openness* decay class	10	326.208	2.274	0.112
M2	Diameter + decay class + CWD length + CWD ground contact + treatment*canopy openness	13	326.272	2.338	0.109
M8	Treatment + canopy openness + diameter *decay class	10	326.443	2.508	0.100
M4	Canopy openness + diameter + decay class + CWD length + CWD ground contact	9	332.241	8.307	0.006
M5	Treatment + diameter + decay class + CWD length + CWD ground contact	10	332.834	8.899	0.004
M10	Canopy openness + diameter + decay class	7	333.026	9.092	0.003
M9	Decay + treatment + canopy openness	8	334.186	10.252	0.002
M19	Canopy openness + diameter* decay class	8	335.011	11.077	0.001
M11	Treatment + canopy openness	7	341.169	17.234	0.000
M18	Diameter + decay class + CWD length*CWD ground contact	9	341.837	17.903	0.000
M6	Diameter + decay class + CWD length + CWD ground contact	8	342.771	18.837	0.000
M12	Diameter+ decay class	6	343.891	19.956	0.000
M14	Diameter	5	346.372	22.437	0.000
M17	CWD ground contact	5	351.117	27.182	0.000
M13	Canopy openness	5	351.544	27.609	0.000
M15	Decay class	5	354.279	30.345	0.000
M16	CWD length	5	358.298	34.363	0.000
M20	Null model	4	358.456	34.521	0.000

Note: (K) number of parameters, (AICc) Akaike information criterion corrected for small sample size, (ΔAICc) distance from the best model, (AICcWt) Akaike weight and (CWD) coarse woody debris.

Table A2 Model summaries for the effects on harvest treatment on microhabitat variables and species richness

Variables	df	F	P	Test
Coarse woody debris characteristics				
CWD length (cm)	2	11.15	0.0003	lme
CWD decay class	2	9.62	0.0007	Lme (*square root transformation*)
Number of CWD per plot	2	_	0.8596	Kruskal wallis
CWD volume by decay				
Control	4	2.92	0.0309	lme (*square root transformation*)
Partial cut	4	_	0.0089	Kruskal wallis
Clear cut	4	_	0.0015	Kruskal wallis
Micro environment				
Mean canopy openness (%)	2	42.19	<.0001	lme (*square root transformation*)
Temperature	2	7.43	0.0063	lme
VPD	2	7.82	0.0052	lme
Species richness				
Epixylic richness	2	5.25	0.0121	lme
Bogs	2	7.92	0.0021	lme (square root transformation)
Generalist	2	3.97	0.0312	lme (square root transformation)
Terricolous	2	_	0.0024	Kruskal wallis
Total richness	2	5.50	0.0102	lme (square root transformation)

Note: Significant p value (($p \leq 0.05$), F value (F) and degree of freedom (df).

Table A3 Plot environmental characteristics during 2017 inventory and percentage basal area removed during harvest

Plot ID	Site	Treatment	Harvest severity (%)	Number of CWD	CWD Volume	mean CWD diameter (cm)	mean CWD decay class	Mean canopy openness (%)
2	Fenelon	Control	unharvested	8	137.09	17.41	3	38.64
5	Fenelon	Control	unharvested	9	91.17	12.99	2.78	31.87
6	Fenelon	Control	unharvested	3	13.74	9.13	3.33	30.39
7	Fenelon	Control	unharvested	8	34.87	8.90	3.75	30.088
18	Fenelon	Control	unharvested	7	34.93	9.51	2.86	23.06
42	Gaudet	Control	unharvested	5	42.95	12.5	2.40	21.18
43	Gaudet	Control	unharvested	20	149.14	11.35	3.85	35.19
44	Gaudet	Control	unharvested	2	10.95	10.05	3.50	26.59
47	Gaudet	Control	unharvested	9	37.70	8.56	2.67	26.50
55	Gaudet	Control	unharvested	11	79.01	11.045	3.27	24.30
27	Fenelon	Partial cut	85.71	10	132.09	14.50	3.50	28.31
32	Fenelon	Partial cut	78.82	8	105.47	14.66	4.38	30.25
33	Fenelon	Partial cut	78.11	14	155.46	13.64	4.57	30.42
37	Fenelon	Partial cut	69.47	10	143.98	16.09	4.20	29.96
38	Fenelon	Partial cut	79.16	15	189.60	14.10	3.60	29.28
21	Gaudet	Partial cut	70.86	8	42.03	9.64	4	45.95

Table A3 *(continued)*

Plot ID	Site	Treatment	Harvest severity (%)	Number of CWD	CWD Volume	mean CWD diameter (cm)	mean CWD decay class	Mean canopy openness (%)
22	Gaudet	Partial cut	97.06	6	63.38	13.15	4.50	43.66
35	Gaudet	Partial cut	76.23	8	42.02	8.96	3.75	35.08
38	Gaudet	Partial cut	55.08	4	21.73	8.83	2.75	37.99
19	Gaudet	Partial cut	30	6	16.55	6.92	3.33	38.01
43	Fenelon	Clear cut	CPRS	4	17.21	8.03	2.50	65.36
45	Fenelon	Clear cut	CPRS	9	67.07	11.34	4.11	52.83
47	Fenelon	Clear cut	CPRS	12	115.66	12.22	4.17	62.23
51	Fenelon	Clear cut	CPRS	15	69.73	9.13	4.07	62.59
53	Fenelon	Clear cut	CPRS	12	70.36	10.33	4.58	54.75
5	Gaudet	Clear cut	CPRS	7	67.92	12.67	4.57	51.81
9	Gaudet	Clear cut	CPRS	6	37.62	10.48	4.17	71.69
11	Gaudet	Clear cut	CPRS	8	42.60	9.28	4.13	73.90
12	Gaudet	Clear cut	CPRS	6	44.47	11.48	3.67	64.84
13	Gaudet	Clear cut	CPRS	7	50.74	10.60	4.29	61.67

Note: Harvest severity (% basal area harvested), CPRS (harvest which preserves advance regeneration by removing all merchantable stems with a minimum DBH of 9 cm and protect most of the soil), CWD (coarse woody debris).

Table A4 Individual species life strategy (functional traits) and their frequency of occurrence on logs and forest floor at the quadrat level

						Frequency of occurrence					
						Unharvested control		Partial cut		Clear cut	
Species	Size	Mode of reproduction	Frequency of sexual reproduction	Frequency of vegetative reproduction	Substrate	On CWD	On forest floor	On CWD	On forest floor	On CWD	On forest floor
Liverworts											
Anastrophyllum hellerianum	Sm	V	R	A	Ex	1	0	19	4	6	1
Barbilophozia barbata	M	S	F	X	T	1	3	3	3	1	2
Blepharostoma trichophyllum	Sm	S	F	R	Ex	3	2	12	5	0	0
Calypogea neesiana	Sm	V	R	F	Ex	0	0	1	0	0	0
Calypogeia sphagnificola	Sm	V	R	F	B	0	5	1	2	0	0
Cephalozia connivens	Sm	VS	F	R	G	1	1	3	0	0	0
Cephalozia lnnilifolia	Sm	S	F	O	G	9	12	2	2	2	3

Table A4 (*continued*)

						Frequency of occurrence					
						Unharvested control		Partial cut		Clear cut	
Species	Size	Mode of reproduction	Frequency of sexual reproduction	Frequency of vegetative reproduction	Substrate	On CWD	On forest floor	On CWD	On forest floor	On CWD	On forest floor
Cephalozia pleniceps	Sm	S	F	O	G	4	16	2	1	2	1
Cephaloziella ellastica	Sm	VS	F	F	B	0	0	0	0	0	1
Cephalozialla rubella	Sm	VS	F	A	G	2	2	17	7	5	4
Chiloscyphus profundus	Sm	S	A	X	Ex	0	0	10	3	0	0
Cephaloziella spinigera	Sm	VS	F	R	Ex	0	1	0	0	0	0
Frullania oakesiana	Sm	S	A	X	Ex	0	0	3	3	0	0
Jamesoniella autumnalis	Sm	S	A	X	Ex	2	0	29	6	4	2
Lepidozia reptans	Sm	S	A	X	Ex	1	1	0	1	1	1
Lophocolea bidentate	Sm	S	F	X	G	0	0	2	0	0	0

Table A4 (*continued*)

						Frequency of occurrence					
						Unharvested control		Partial cut		Clear cut	
Species	Size	Mode of reproduction	Frequency of sexual reproduction	Frequency of vegetative reproduction	Substrate	On CWD	On forest floor	On CWD	On forest floor	On CWD	On forest floor
Lophozia longidens	Sm	V	R	R	Ex	0	0	1	1	0	0
Lophozia longiflora	Sm	V	A	R	Ex	1	2	2	1	2	2
Lophozia ventricosa	Sm	VS	F	A	G	3	5	3	3	2	3
Mylia anomala	M	V	R	F	B	1	5	1	1	0	1
Nowellia curvifolia	Sm	S	F	R	Ex	1	0	7	0	0	0
Ptilidium ciliare	M	S	R	X	G	58	53	46	55	24	45
Ptilidium pulcherrimum	Sm	S	A	X	Ex	87	18	131	28	43	11
Mosses											
Aulacomnium palnstris	Sm	VS	F	F	G	7	6	1	5	3	1
Brachythecium rutabulum	L	S	A	X	G	0	0	5	9	1	2

Table A4 (*continued*)

						Frequency of occurrence					
						Unharvested control		Partial cut		Clear cut	
Species	Size	Mode of reproduction	Frequency of sexual reproduction	Frequency of vegetative reproduction	Substrate	On CWD	On forest floor	On CWD	On forest floor	On CWD	On forest floor
Brachythecium starkei	L	S	A	X	G	1	1	9	8	1	0
Brachythecium velatinum	Sm	S	A	X	G	0	0	1	1	0	0
Cladopodiella fluitans	Sm	S	R	X	B	0	0	0	0	0	1
Dicranum flagelarie	M	VS	F	F	Ex	0	1	0	1	1	0
Dicranum fuscescens	M	S	F	X	Ex	15	11	41	12	25	11
Dicranum montanum	Sm	VS	F	F	Ex	7	3	21	5	7	1
Dicranum ontariensis	M	S	F	X	G	0	1	3	6	2	3
Dicranum polysetum	L	S	F	X	T	4	19	9	30	13	19
Dicranum scoparium	L	S	O	X	G	1	2	2	2	0	0

Table A4 (*continued*)

						Frequency of occurrence					
						Unharvested control		Partial cut		Clear cut	
Species	Size	Mode of reproduction	Frequency of sexual reproduction	Frequency of vegetative reproduction	Substrate	On CWD	On forest floor	On CWD	On forest floor	On CWD	On forest floor
Dicranum undulatum	M	S	O	X	B	1	0	1	1	0	0
Herzogiella turfacea	Sm	S	A	X	G	2	1	3	0	0	0
Hylocomium splendens	L	S	R	X	G	2	10	4	8	0	2
Hypnum pallescens	M	S	F	X	Ex	0	0	7	0	1	0
Plagiomnium cuspidatum	L	S	F	X	G	0	0	3	2	0	0
Plagiothecium laetum	Sm	S	A	O	Ex	0	0	2	3	1	1
Platygyrium repens	M	V	F	A	G	0	0	1	0	0	0
Pleurozium schreberi	L	S	O	X	G	137	112	158	137	145	126
Pohlia nutans	M	S	A	X	G	2	0	4	2	5	4

Table A4 (*continued*)

						Frequency of occurrence					
						Unharvested control		Partial cut		Clear cut	
Species	Size	Mode of reproduction	Frequency of sexual reproduction	Frequency of vegetative reproduction	Substrate	On CWD	On forest floor	On CWD	On forest floor	On CWD	On forest floor
Pohlia sphagnificola	M	S	F	X	B	1	5	1	4	1	11
Polytrichum commune	L	S	A	X	T	0	1	1	4	0	6
Polytrichum strictum	M	S	F	X	B	0	1	0	0	0	2
Ptilium crista-castrensis	M	S	O	X	T	15	20	43	30	6	11
Rhytidiadelphus triquetrus	L	S	R	X	T	0	0	0	1	0	0
Sanonia uncinata	L	S	F	X	G	1	0	4	2	0	0
Tetraphis pellucida	Sm	VS	O	A	Ex	1	2	2	1	1	0
Tomenthypnum facifolium	L	S	R	X	B	1	2	0	0	0	0

Table A4 (*continued*)

						Frequency of occurrence					
						Unharvested control		Partial cut		Clear cut	
Species	Size	Mode of reproduction	Frequency of sexual reproduction	Frequency of vegetative reproduction	Substrate	On CWD	On forest floor	On CWD	On forest floor	On CWD	On forest floor
Sphagnum											
Sphagnum angustifolia	L	S	F	X	B	16	34	5	6	1	8
Sphagnum capillifolium	L	S	A	X	T	14	39	3	18	2	14
Sphagnum fuscum	L	S	F	X	B	4	14	0	0	1	4
Sphagnum fallax	L	S	O	X	B	0	0	0	0	0	2
Sphagnum magellanicum	L	S	R	X	B	5	11	0	0	0	0
Sphagnum quinquefarium	L	S	O	X	T	5	9	0	0	1	4
Sphagnum rubellum	L	S	R	X	B	8	8	1	1	0	2
Sphagnum russowii	L	S	F	X	B	29	55	8	12	6	11

Note: Size: Sm, small; M, medium; L, large. Mode of reproduction: V, vegetative; VS, vegetative and sexual; S, sexual. Frequency of sexual reproduction: A, abundant; F, frequent; O, occasional; R, rare. Frequency of vegetative reproduction: A, abundant; F, frequent; O, occasional; R, rare; X, inexistent. Substrate: Ex, Epixylic; G, Generalist; T, Terricolous; B, Bogs.

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