UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

IMPACTS DE L'AMÉNAGEMENT FORESTIER ÉCOSYSTÉMIQUE EN FORÊT BORÉALE MIXTE : STRUCTURE, COMPOSITION, RÉGÉNÉRATION ET BIODIVERSITÉ

THÈSE

PRÉSENTÉE

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A toute ma famille, les plus vieux comme les
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AVANT-PROPOS

Cette thèse est présentée sous la forme de trois articles scientifiques correspondant aux chapitres 2, 3 et 4 complétés par une introduction et une conclusion générale (chapitres 1 et 5, respectivement). Le chapitre 2 a été accepté avec corrections majeures par le Canadian Journal of Forest Research. Le chapitre 3 a été publié dans le journal Forest Ecology and Management. Le chapitre 4 est en finition pour soumission.

Les trois principaux articles scientifiques (chapitres 2, 3 et 4) ont été réalisés avec la contribution essentielle de chacun de leurs auteurs. Je me trouve principale auteure de ces articles étant donné mon implication majeure, comprenant la prise, l'exploration et l'analyse des données mais chacun a été développé avec la collaboration essentielle des co-auteurs. Mes superviseurs, la Dre Nicole J. Fenton et le Dr Timothy T. Work occupent respectivement la dernière et la première position de co-auteurs dans tous ces articles. Tous deux ont activement contribué à leur élaboration, dans la conception des études, l'acquisition des données, l’interprétation des résultats et la révision des manuscrits. Maxence Soubeyrand a participé de manière significative à l'élaboration des chapitres 2 et 3, y compris les analyses statistiques ainsi que des révisions critiques et constructives du manuscrit. Tous les chapitres analysent les effets d’une variété de traitements sylvicoles sur différents aspects des peuplements forestiers. Les deux premiers articles portent essentiellement sur le dispositif SAFE (Sylviculture et Aménagement Forestier Ecosystémique) au Québec. Grâce aux études de Suzanne Brais et Brian Harvey réalisées il y a 20 ans, nous avons pu ajouter une dimension temporelle au chapitre 2, portant sur la structure et composition des peuplements. Le chapitre 3 se concentre sur les bryophytes. Le chapitre 4 se concentre sur la réponse fonctionnelle de la végétation de sous-bois. Grâce à la collaboration du Dr Ellen MacDonald et du Dr Charles Nock de l’Université de l’Alberta à Edmonton, nous avons pu comparer les effets des coupes sur deux dispositifs expérimentaux au Canada, SAFE au Québec et EMEND (Ecosystem Management Emulating Natural Disturbance) en Alberta. Avec la collaboration du Dr Isabelle Aubin, du Service canadien des forêts, nous avons pu enrichir notre jeu de données.

Chapitre 1. Introduction générale

Chapitre 2. Noualhaguet, M., Work, T. T., Soubeyrand, M., and Fenton, N. J. (2023). Twenty-year recovery of managed stand, in structure and composition, in boreal mixedwood stands of northwestern Quebec. *Canadian journal of forest research, 53*(2).

Chapitre 3. Noualhaguet, M., Work, T. T., Soubeyrand, M. et Fenton, N. J. (2023). Bryophyte community response 320 years after forest management in boreal mixedwood forest. *Forest Ecology and Management*, *531*, 120804.

Chapitre 4. Noualhaguet, M., Work, T. T., Nock, C., Macdonald, E., Aubin' I. and Fenton, N. J. Functional responses of understory plant to natural disturbance-based management in eastern and western Canada. Submitted to *Ecological Applications*.

Chapitre 5. Conclusion générale

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AFE : Aménagement forestier écosystémique

CP, PC : Coupe partielle (partial cut)

CT, CC : Coupe totale (clearcut)

DHP : diamètre à hauteur de poitrine

EMEND : Ecosystem Management Emulating Natural Disturbance

FERLD : Forêt d’enseignement et de recherche du lac Duparquet

LDMC : teneur en matière sèche foliaire (leaf dry matter content)

LNC : contenu en azote foliaire (leaf nitrogen content)

LPC : contenu en phosphore foliaire (leaf phosphorus content)

NDBM : Natural Disturbance Based Management

SAFE : Sylviculture et aménagement forestier écosystémique

SLA : surface foliaire spécifique (specific leaf area)

TOPIC: Traits of plants in Canada

RÉSUMÉ

Aujourd’hui l’aménagement forestier écosystémique (AFE) est préconisé pour implanter un aménagement durable des forêts grâce à une gamme d’approches qui visent à maintenir des écosystèmes sains et résilients en reproduisant la diversité des structures et des compositions forestières observées après perturbations naturelles. Tandis que les coupes totales, longtemps pratiquées au Québec, réinitialisent la régénération, favorisant la présence des jeunes peuplements, les coupes partielles permettent de maintenir des peuplements mixtes et résineux ainsi que des attributs de vieilles forêts. Dans cette perspective, elles constituent un complément intéressant aux coupes totales pour maintenir la diversité des structures et compositions des peuplements à l’échelle du paysage. Toutefois, l’AFE reste plutôt récent et seuls des suivis pérennes permettraient d’évaluer son efficacité à maintenir la biodiversité et la productivité forestière sur le moyen et long termes. Il est donc nécessaire de continuer les recherches afin d’évaluer les impacts des pratiques sylvicoles sur des échelles plus large. C’est dans cet objectif global que s’inscrit cette thèse par l’étude de la régénération des écosystèmes forestiers à divers stades de développement en réponse à différents traitements sylvicoles. Pour réaliser cela, nous évaluons les effets de diverses méthodes de récolte, appliquées à différents stades de développement, sur différents éléments des peuplements. Dans le chapitre 2, nous étudions les effets des coupes sur la structure, composition et régénération arbustives ainsi que sur les apports de bois morts, dans le chapitre 3, les effets sur la richesse en bryophytes et dans le chapitre 4, les effets sur la diversité fonctionnelle des communautés végétales de sous-bois.

Au Canada, la mise en œuvre de dispositifs expérimentaux basés sur le modèle conceptuel de l’AFE permet d’évaluer les impacts à long terme de différentes intensités de coupe sur la productivité et la biodiversité forestière. En 1998, deux grands

dispositifs, Sylviculture en Aménagement Forestier Écosystémique (SAFE), à l'Est au Québec, et Ecosystem Management Emulating Natural Disturbance (EMEND), à l'Ouest en Alberta, ont été mis en place. Différents traitements sylvicoles ont été planifiés et répliqués, dans les trois types de peuplements communs dans les séquences de succession des forêts boréales mixtes qui sont les peuplements dominés par les feuillus, les mixtes et dominés par les résineux.

D'un point de vue de la productivité, au sein du projet SAFE, les suivis juste après coupes et 20 ans plus tard montrent que les coupes plus intensives entraînent des différences plus importantes et pérennes avec les peuplements évoluant naturellement. Ces différences se manifestent en terme (1) de régénération, avec une densité de gaules supérieure après coupes intensives, en particulier de gaules de peupliers faux-trembles ; (2) de structure et de composition, avec une surface terrière des arbres commerciaux réduite après coupes, en particulier pour les espèces de conifères ; (3) et en apport de bois mort, avec une infériorité du bois mort sur pied mais une supériorité de bois mort au sol après coupes. Nos résultats montrent que les PC permettent le maintien de peuplements à structure et composition mixtes, constituant un complément intéressant aux CC, qui réinitialisent la régénération des peuplements. Cependant, les PC n'ont pas permis de faire transitionner les peuplements vers des stades plus avancés avec une exploitation moins intensive ou vers des stades plus précoces avec une exploitation plus intensive. Avec les PC, nous avons essentiellement eu un impact initial, retardant ou stoppant l'évolution des peuplements, qui se dissipe avec le temps et plus rapidement avec lorsque la récolte fut moins intensive.

D'un point de vue de la conservation de la biodiversité, l'inventaire des bryophytes réalisé 20 ans après coupes au sein du projet SAFE souligne la façon dont l'intensité de la récolte et le type de peuplement forestier interagissent pour affecter les bryophytes. Concernant l'intensité de récolte, nous retrouvons une présence récurrente de nombreuses espèces forestières généralistes et communes dans tous les niveaux de récolte et types de peuplements. Cependant, des espèces spécialistes, principalement composant le groupe des hépatiques, diffèrent davantage entre les peuplements non coupés et les peuplements coupés totalement qu'entre les peuplements non coupés et les peuplements coupés partiellement. Concernant le type de peuplement, les espèces de bryophytes des peuplements dominés par les feuillus témoignent d'une tolérance supérieure aux fluctuations des conditions environnementales comparativement aux espèces des peuplements mixtes. Ces différences seraient influencées par la composition arbustive de la canopée, avec les conifères qui amortissent d'avantage les variations climatiques que les feuillus, rendant les communautés de bryophytes plus sensibles à la structure du peuplement lorsque celui-ci compte des conifères. Cependant, pour les espèces des peuplements dominés par les conifères, toutes étaient communes aux peuplements feuillus et mixtes, ce qui pourrait être lié à des épidémies antérieures de tordeuse des bourgeons de l'épinette.

Par la suite, le suivi de la végétation vasculaire de sous-bois, à la fois en termes de changement de composition fonctionnelle (en utilisant les valeurs moyennes des traits de la communauté) et de variation de la valeur des traits (variabilité intra spécifique des traits) nous permet de comparer les effets des coupes effectuées dans l'Est, avec le projet SAFE, à celles effectuées dans l'Ouest du Canada, avec le projet EMEND. 20 ans après coupes, les communautés dans les peuplements de feuillus différait selon les projets SAFE et EMEND, mais pas selon le type de traitement, tandis que dans les peuplements mixtes, les communautés différaient à la fois selon les projets et les traitements. Cependant, nous n'avons pas observé de différences significatives en richesse taxonomique ou fonctionnelles entre les communautés des peuplements coupés et les communautés des peuplements évoluant naturellement. En revanche, à l'échelle des espèces, des différences dans la variation des traits morphologiques entre les différents traitements ont été observées. Chaque espèce a été caractérisée par une réponse fonctionnelle différente après les coupes, montrant la réaction individuelle spécifique de l'espèce à la variation environnementale. Ces résultats ont montré le potentiel de l’AFE pour maintenir la diversité des communautés fonctionnelles du sous-étage s'il est appliqué et contrôlé avec soin. Plus encore, ils soulignent l'importance relative d'examiner la variabilité intraspécifique des communautés végétales lorsque nous cherchons à explorer les effets de conditions environnementales contrastées résultant de perturbations locales telles que l'exploitation forestière. Cela a des implications pour le plan d'échantillonnage et la sélection des traits pour des études à petite et grande échelles.

L’ensemble de nos résultats témoigne du potentiel de l’AFE pour réaliser une gestion durable des peuplements. Nous montrons que la combinaison de coupes partielles et de coupes totales pratiquées en proportions équivalentes sur les peuplements permet de maintenir une gamme de peuplements à structure et composition mixtes et que d’un point du vue fonctionnel, l'impact des coupes sur le sous-étage peut ne plus être observable 20 ans plus tard, qu’elles soient menées à l’Est ou à l’Ouest. Cependant, la préservation de peuplements naturels est essentielle pour conserver de nombreuses espèces qui sont sensibles à tout degré de récolte, comme certaines espèces de bryophytes. Les avantages des forêts ont de multiples facettes et ne doivent pas être limités à une division binaire entre la production de bois et tous les autres services écosystémiques. Les compromis et les interactions sont complexes, dépendent du contexte et sont susceptibles de changer en fonction des priorités sociétales et de l'évolution des conditions écologiques. Ainsi, malgré la confirmation du potentiel de l’AFE de maintenir un plus large éventail de services écosystémiques que les seules pratiques forestières intensives, nous ne pouvons pas conclure que nous parvenons à imiter toute la complexité des peuplements générés par les régimes de perturbation naturelle. Pour avoir une évaluation plus complète dans un contexte de gestion durable des forêts, il faudrait réaliser des études supplémentaires focalisées sur davantage d’aspects économique, de conservation et de services écosystémiques. Un des grands avantages des dispositifs expérimentaux SAFE et EMEND est l’existence de parcelles permanentes d’échantillonnage qui garantit le suivi des peuplements dans le temps et

le développement des recherches futures. De plus, ils se trouvent dans des domaines bioclimatiques très importants pour la productivité et conservation forestière au Canada. Ainsi, les recherches déjà menées et celles de ce doctorat contribuent donc directement à l'industrie du bois.

Mots clés : aménagement forestier écosystémique, conservation, forêt boréale mixte, coupe partielle, coupe totale, bryophytes, végétation de sous-bois, traits fonctionnels, variabilité intraspécifique des traits

ABSTRACT

Natural disturbance-based forest management (NDBM) is currently proposed as a way to implement sustainable forest management through a range of approaches that aim to maintain healthy and resilient ecosystems by reproducing the diversity of forest structures and compositions observed after natural disturbances. While clearcuts, long practiced in Quebec, resets regeneration, favoring the presence of young stands, partial cuts allow the maintenance of mixed and coniferous stands as well as some old-growth attributes. That is why they are an interesting complement to clearcuts to maintain the diversity of stand structures and compositions at the landscape scale. However, NDBM is a relatively recent concept and only long term monitoring of experimental systems can measure its effectiveness in maintaining biodiversity and forest productivity over the medium and long term. It is therefore required to carry out research to evaluate the impacts of silvicultural practices on larger spatial and temporal scales. It is within this overall objective that this thesis studied the regeneration of forest ecosystems at various stages of development in response to different silvicultural treatments. To do so, we quantified the effects of various harvesting methods, applied at different developmental stages, on different stand components. In Chapter 2, we studied the effects of harvesting on structure, composition, and regeneration of trees and deadwood inflows. In Chapter 3, we focused on the effects on bryophyte richness and in Chapter 4, the effects on functional diversity of understory plant communities.

In Canada, the implementation of experimental systems based on the conceptual model of the NDBM makes it possible to evaluate the long-term impacts of different cutting intensities on forest productivity and biodiversity. In 1998, two large-scale projects, Sylviculture et Aménagement Forestier Écosystémique (SAFE) in eastern Quebec and Ecosystem Management Emulating Natural Disturbance (EMEND) in western Alberta,

were established. Various silvicultural treatments were planned and duplicated in hardwood, mixedwood and coniferous dominated stands. Those three stands are common in the successional sequence of boreal mixedwood forest.

In terms of productivity, in the SAFE project, monitoring immediately after harvesting and 20 years later showed that intensive harvesting results in larger and long-term differences when compared with naturally evolving stands. These differences were visible in terms of (1) regeneration, with a higher density of saplings after intensive cuts, particularly trembling aspen saplings; (2) structure and composition, with a reduced basal area of commercial trees after cuts, particularly for coniferous species; (3) and dead wood supply, with less standing dead wood but more ground dead wood after cuts. Our results showed that PC maintained stands with mixed structure and composition, providing an attractive complement to CCs, which reset stand regeneration. However, PC did not transition stands to later stages of succession with less intensive PC or to earlier stages with more intensive PC. With PC, we essentially had an initial impact, delaying or stopping the stand evolution, which dissipates over time. This dissipation was more rapid with less intensive harvesting.

In terms of conservation, the bryophyte inventory in SAFE, 20 years post-harvest, highlighted how harvest intensity and stand type interact to affect bryophytes. Regarding the harvest intensity, we found a recurring presence of many generalist and common forest species across all harvest levels and stand types. However, specialist species, mainly composing the liverwort group, differed more between uncut and clearcut stands than between uncut and partially cut stands. Regarding the stand type, bryophyte species in hardwood-dominated stands showed greater tolerance to changes of environmental conditions than species in mixedwood stands. These differences were thought to be influenced by the tree composition of the canopy, with conifers buffering seasonal climatic variations more than hardwoods species, making bryophyte communities more sensitive to stand structure when canopy is perturbed. However, for species in conifer-dominated stands were all common to both hardwood and mixed stands, which may be related to previous spruce budworm outbreaks.

Subsequently, we did monitor the functional composition (using mean community trait values) and change in trait value (intraspecific trait variability) of understory vascular vegetation. It allowed us to compare the effects of harvest in eastern Canada (SAFE Project) with those in western Canada (EMEND project). 20 years post-harvest, communities in hardwood stands differed between SAFE and EMEND experiments, but not between treatments, while in mixedwood stands, communities differed between both, experiments, and treatments. However, we did not observe significative differences in taxonomic or functional richness between communities in harvested stands and communities in naturally evolving stands. On the other hand, at the species level, differences in morphological trait variation between treatments were observed. Each species was characterized by a different functional response after harvesting, showing the individual species-specific response to environmental variation. These results demonstrated the potential of NDBM to maintain the diversity of understory functional communities if carefully applied and controlled. Ultimately, they highlighted the relative importance of examining intraspecific variability in plant communities when we search to explore the effects of contrasting environmental conditions resulting from local disturbances such as harvest. This has impacts for sampling design and trait selection for both small- and large-scale studies.

All our results demonstrated the potential of AFE to achieve sustainable stand management. We showed that a combination of partial and full cuts could maintain a range of stands with mixed structure and composition. It also showed that the impact of cuts on the understory might no longer be observed 20 years later, whether they were done in the east or west. However, the preservation of natural stands is essential to maintain many species that are sensitive to any degree of harvesting, such as certain bryophyte species. The benefits of forests are multifaceted and should not be limited to

a binary division between timber production and all other ecosystem services. Trade-offs and interactions are complex, context dependent, and subject to change in response to societal priorities and changing ecological conditions. Thus, despite the potential of NDBM to maintain a wider range of ecosystem services than intensive forestry practices alone, we cannot conclude that we are successfully mimicking the full complexity of stands generated by natural disturbance regimes. A more complete assessment in the context of sustainable forest management would require additional studies focusing on more economic, conservation and ecosystem service aspects. A major advantage of the SAFE and EMEND projects is the existence of permanent sample plots, which ensures the monitoring of stands over time and the development of future research. In addition, they are in bioclimatic areas that are very important for forest productivity and conservation in Canada. Thus, the research already conducted, and this PhD contribute to the wood industry.

Keywords : natural disturbance-based management, conservation, boreal mixed stands, partial cuts, clearcuts, bryophyte communities, understory vegetation, functional traits, intraspecific trait variability

CHAPITRE 1

INTRODUCTION

1.1 Contexte

Partout dans le monde, les écosystèmes forestiers sont des espaces de vie où des milliers d'espèces interagissent entre elles et avec le milieu physique (Whittaker, 1962). Lieu de subsistance jusqu'au XVIIIème siècle, puis apport commercial à partir du XIXème siècle, la forêt sert depuis de longues années à l'Homme qui puise dans ses ressources (Drushka, 2003; Singer, 2015). Au début des années 1990, une prise de conscience émerge face à la « crise » de la biodiversité causée principalement par l'urbanisation et l'exploitation du territoire qui causent des pertes d'habitats pour une grande variété d'espèces animales et végétales (Agnoletti et Anderson, 2000; Andren, 1994; Ehrlich et Wilson, 1991; Rouget et Schmitt, 2018). Vient s'ajouter à cela, l'émergence de la notion de développement durable lors du sommet de la Terre de Rio en 1992, qui met l'accent sur l'importance de tenir compte des valeurs environnementales dans tous les domaines d'activité économique. Ainsi en 1995, le Conseil canadien des ministres des forêts adopte des critères de développement durable des forêts qui incitent les provinces à modifier leurs politiques et réglementations forestières dans le sens de la gestion durable (Gouvernement du Canada, 1996; Gouvernement du Québec, 1994). Entrée en vigueur le 1er avril 2013, la Loi sur l'aménagement durable du territoire forestier (Gouvernement du Québec, 2015) encadre la gestion des forêts publiques afin de mieux respecter les préoccupations changeantes de la société vis-à-vis de l'environnement. Quels que soient les besoins et les intérêts des usagers de la forêt, celle-ci n'est plus perçue uniquement comme un réservoir de matière ligneuse (Kimmins, 2004).

La gestion du milieu forestier aujourd'hui fait face à de nombreux défis, notamment la multiplicité et la diversité des usagers qui nécessitent de prendre en compte la demande de chacun pour de nouvelles utilisations des ressources forestières mais aussi les attentes en matière de durabilité des écosystèmes (Bouchard, 2008; Cyr *et al.*, 2009; Johnson *et al.*, 1996; Schwartz *et al.*, 2000). Aujourd'hui l'aménagement forestier écosystémique (AFE) est préconisé comme l'approche à utiliser pour implanter un aménagement durable des forêts. Cette réflexion a engendré des changements dans le concept de la gestion traditionnelle des forêts, centrée sur les activités visant la planification, l'exploitation, les perturbations naturelles et la protection des forêts. La gestion écosystémique est une approche de la foresterie qui vise à combler le fossé entre les forêts naturelles et les forêts gérées de manière à préserver l'intégrité écologique et la biodiversité des écosystèmes. C'est dans cette perspective qu'a été créé le concept d'aménagement forestier écosystémique (AFE). L'AFE c'est,

> « une approche d'aménagement qui vise à maintenir des écosystèmes sains et résilients en misant sur une diminution des écarts entre les paysages naturels et ceux qui sont aménagés afin d'assurer, à long terme, le maintien des multiples fonctions de l'écosystème et, par conséquent, de conserver les bénéfices sociaux et économiques que l'on en retire » (Gauthier *et al.*, 2009)

La mise en place de l'AFE requiert un plan d'aménagement qui exige une habileté à évaluer et prédire la composition forestière future mais pour cela il est nécessaire de bien comprendre le fonctionnement naturel des paysages et des peuplements forestiers (Taylor *et al.*, 2009). Pouvoir projeter les conditions forestières qui suivront les actions d'aménagement à travers les multiples échelles temporelles et spatiales est capital, car les changements compositionnels sont liés aux enjeux de productivité forestière, de séquestration du carbone et de conservation de la biodiversité (Taylor *et al.*, 2009). La connaissance de la dynamique forestière et des processus qui la gouvernent ouvre la porte à la « manipulation » des peuplements. L'application des coupes pouvant donner des structures et des compositions s'apparentant à celles qui caractérisent les peuplements à différents moments de la succession naturelle et ainsi équilibrer la mosaïque de structure d'âge et de composition des peuplements à l'échelle du paysage par rapport aux variabilités historiques (Bergeron, 2000; Harvey *et al.*, 2002). Ainsi, l'AFE requiert une compréhension du fonctionnement passé, présent et futur des écosystèmes naturels (Natural Disturbance Based Management (NDBM) (Bergeron et Harvey, 1997; Kuuluvainen, 2002).

1.2 Dynamique en forêt

La dynamique d'un peuplement forestier s'évalue en observant les changements de structure (abondance relative de différentes classes d'âges) et de composition (espèces arbustives) d'un peuplement au cours du temps. Les perturbations naturelles sont des processus écologiques intrinsèques aux écosystèmes forestiers, notamment en forêt boréale (Lefort *et al.*, 2002; McCarthy, 2001; Morin, 1994), où elles constituent le moteur de la dynamique forestière et façonnent la variété des habitats observés à l'échelle des paysages et des peuplements.

1.2.1 Les perturbations naturelles

Les perturbations sévissent à différentes échelles (arbres, peuplements, paysage, biome) et degrés (gravité, intensité, fréquence, taille) (McCarthy, 2001). Selon l'âge et l'état du peuplement où elles surviennent, la gravité et la taille qui les caractérisent, leur durée et leur fréquence, les perturbations affectent plus ou moins la structure et la composition des peuplements (Chen et Popadiouk, 2002; Gauthier *et al*., 2009; Hart et Chen, 2008).

Le feu est considéré comme une perturbation majeure en forêt boréale. Là où ils passent, ils entrainent une réduction de l'épaisseur de la matière organique, une exposition du sol minéral et une élimination de la compétition arbustive (Miyanishi et Johnson, 2002; Nguyen-Xuan *et al.*, 2000). Par l'ouverture de la canopée ainsi que par la combustion de la couverture morte et des débris ligneux, le feu favorise également l'augmentation des températures du sol (Swift Jr *et al.*, 1993) ainsi qu'une augmentation du pH suite à un relargage rapide de bases échangeables par les cendres (Simard *et al.*, 2001; Ulery *et al.*, 1993). Ces nouvelles conditions stimuleraient l'activité microbienne, la décomposition et la minéralisation (Prieto-Fernandez *et al.*, 1993) et entraîneraient ainsi une remise en circulation accrue des nutriments immobilisés dans la matière organique (Neff *et al.*, 2005; Wells, 1979).

Les épidémies d'insectes, plus lentes et spécifiques, chaque insecte défoliateur a ses hôtes de prédilection, sont des perturbations dites secondaires (Chen et Popadiouk, 2002; Kneeshaw *et al.*, 2011). On compte deux espèces principales d'insectes défoliateurs en forêt boréale à l'est du Canada. La tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* Clemens) s'en prend principalement au sapin baumier (*Abies balsamea* (L.) Mill) et, dans une moindre mesure, aux épinettes blanches (*Picea glauca* [Moench] Voss) et noires (*Picea mariana* [Mill.] B.S.P). La livrée des forêts (*Malacosoma disstria* Hübner) s'en prend principalement au peuplier faux-tremble (*Populus tremuloides* Michx) et au bouleau à papier (*Betula papyrifera* March) (Moulinier *et al.*, 2011; Simpson et Coy, 1999). Dans les régions où elles sévissent, les épidémies vont influencer la mosaïque forestière, dans laquelle les espèces non hôtes des défoliateurs et moins vulnérables vont se maintenir (Kneeshaw et Bergeron, 1999). Plus l'épidémie sera sévère et longue, plus la mortalité des arbres va augmenter. Les arbres défoliés continuent significativement de mourir durant les dix années qui suivent la fin de l'épidémie, créant des trouées au niveau de la canopée (Chen et Popadiouk, 2002).

La combinaison de ces perturbations naturelles, feux et épidémies, influencent la dynamique de succession et de régénération (de Römer *et al.*, 2007). Cette dynamique évoque le passage d'un état à un autre, soit d'une structure et composition à une autre qui peut être représentée par un assemblage d'espèces végétales. Cette dynamique a été schématisée en 3 stades, appelés cohortes dans les travaux de Bergeron *et al.* (1999) portant sur la forêt boréale mixte de l'Ouest du Québec, Canada. Ces trois stades représentent des états de référence cibles en AFE (Villard et Jonsson, 2009).

1.2.2 Concept des trois cohortes

Le concept de cohorte renvoie à la composition et la structure des peuplements. Les cohortes représentent la proportion relative de chaque espèces arbustives dans les peuplements, aux différents stades de développement à la suite d'un feu (Bergeron *et al.*, 2002).

En forêt boréale mixte, après un feu sévère, les peupliers faux-tremble avec leurs drageons, les bouleaux à papier avec leurs rejets de souches et la dissémination des semences puis les pins gris (*Pinus banksiana* Lamb.) et les épinettes noires avec leurs banques de graines en cônes sérotineux et semi-sérotineux (Greene *et al.*, 1999) vont coloniser en premier les aires brûlées (Zasada, 1992). En fonction de la composition du peuplement avant la perturbation, ces espèces pionnières viennent s'installer rapidement et atteignent rapidement la canopée grâce à leurs attributs autécologiques. C'est le début de la succession, le stade de première cohorte. Sur les sites "mixtes" (environ 50% feuillus et 50% résineux), les feuillus intolérants à l'ombre seront les premiers à dominer la canopée (Harvey *et al.*, 2002) grâce à leur mode de reproduction végétatif et à leur croissance rapide (Finér *et al.*, 1997; Légaré *et al.*, 2005). Épinettes blanches, noires, et sapins baumiers sont souvent établies au même moment que les arbres qui forment la première cohorte et peuvent également arriver en début de succession. Cependant, leur taux de croissance plus lent et leur capacité de tolérance à l'ombre leur permettent de se maintenir plus longtemps dans le sous-étage (Bergeron, 2000; Harvey *et al.*, 2002). Elles viendront s'établir dans la canopée lors de la formation de trouées crées principalement par la compétition inter-espèces pour les ressources (Greene et Johnson, 1999; Messier *et al.*, 1999). Les arbres qui vont décéder, laissent la place à d'autres individus déjà établis en sous-étage, qui vont atteindre la canopée par la suite. C'est la phase d'auto éclaircie du peuplement où il y a une stratification verticale du couvert forestier. Nous sommes alors au stade de deuxième cohorte, mi succession, dont la canopée est composée d'un mélange d'arbres « pionniers » et d'espèces tolérantes à l'ombre qui entrent dans la canopée, soit un mélange d'espèces feuillues et résineuses. Le stade de fin de succession de troisième cohorte est atteint lorsque la structure est dominée par des espèces tolérantes à l'ombre comme l'épinette noire ou blanche, le sapin baumier et le thuya occidental (*Thuya occidentalis* L.). Il restera une proportion très faible d'espèces intolérantes à l'ombre établis après feu (Bergeron, 2000; Chen et Popadiouk, 2002). C'est un peuplement de structure inéquienne et irrégulière composé principalement de résineux, où les espèces pionnières peuvent s'installer tardivement dans des trouées de grandes tailles.

Les perturbations naturelles comme les feux, les épidémies et les chablis (arbres brisés ou arrachés) font transiter les peuplements d'une cohorte à une autre. Les feux, en tant que perturbation majeure, ramènent les peuplements au stade de cohorte 1 et servent ainsi de marqueur de datation d'un peuplement, puisque l'âge d'une forêt est défini selon le temps depuis le dernier feu (Bergeron *et al.*, 2002). Les épidémies d'insectes, chablis, maintiendraient et voire accéléreraient la dynamique de succession des peuplements. Peu importe la sévérité de la perturbation, des éléments résiduels appelés legs biologiques seront maintenus à l’échelle du paysage et du peuplement (Bergeron *et al.*, 2017b; Johnstone *et al.*, 2016).

1.2.3 Legs biologiques

Les legs biologiques peuvent être des processus biotiques, des gradients biogéochimiques ou encore des organismes vivants et morts (Bergeron *et al.*, 2017b; Perry *et al.*, 2008). Parmi ces legs, les proportions d’arbres vivant et mort constituent des legs biologiques importants associés à la capacité de régénération des écosystèmes après perturbations. Le bois mort est souvent associé aux forêts anciennes, qui peuvent être défini comme des peuplements influencés principalement par la dynamique des trouées, avec une mortalité des arbres causée par des perturbations secondaires (McGee, 2018; Wirth *et al.*, 2009). On s'attend généralement à ce que les forêts anciennes soient les écosystèmes forestiers définis par la plus grande abondance et diversité de bois mort comparées aux forêts plus jeunes (Martin *et al.*, 2018; Paillet *et al.*, 2015). Pour cette raison, les forêts anciennes sont souvent considérées comme des modèles à imiter pour promouvoir le caractère naturel et la conservation de la biodiversité dans les peuplements gérés (Bauhus *et al.*, 2009; Keeton *et al.*, 2018).

Les arbres résiduels vivants permettent une bonne régénération entre les peuplements pré et post perturbation en apportant des semences et de l’ombre pour les futurs peuplements (Franklin *et al.*, 1997). De plus, ils créent des conditions propices au déplacement et au maintien de plusieurs espèces animales et végétales et permettront un recrutement de bois mort dans le futur (Imbeau et Desrochers, 2002; Kruys et Jonsson, 1999; Nappi *et al.*, 2004). Des arbres sénescents, en passant par les chicots pour finir avec le bois mort au sol bien décomposés, ces legs constituent des microhabitats essentiels pour certaines espèces, qui pendant au moins une partie de leur cycle de vie, vont les utiliser pour se développer, se nourrir, s'abriter ou se reproduire

(Larrieu *et al.*, 2018). Sur pied, parmi les plus connus et les plus étudiés, on retrouve les pics, une espèce dite excavatrice qui nichent dans les cavités (Drapeau *et al.*, 2009). Au sol, ils favorisent l'établissement de certaines espèces végétales comme l'épinette blanche et le thuya occidental (Simard *et al.*, 2003). Connues pour leurs graines de petites tailles, ces espèces sont particulièrement dépendantes des débris ligneux qui constituent des microsites d'établissements viables (Iijima *et al.*, 2007; Iijima *et al.*, 2006). Premièrement, ils constituent un environnement plus sécuritaire et plus propice à la pénétration des racines dans la mesure où les semis se trouvent surélevés par rapport au sol où la compétition est importante (Beach et Halpern, 2001) et où la couche de feuilles mortes constitue une barrière à l'enracinement (Iijima *et al.*, 2007). Ensuite, ils favorisent l'établissement d'une couche de mousses qui va limiter l'évaporation de l'eau et donc maintenir un milieu dont l'humidité est plus stable, et favoriser l'adhérence des semis (Iijima *et al.*, 2006).

Plusieurs facteurs déterministes et stochastiques influencent donc le recrutement, la croissance et la mortalité des espèces végétales qui mènent aux changements de structure et de composition des peuplements au fil du temps soit la dynamique des peuplements. La possibilité d'installation d'un individu dépend donc de l'environnement mais également de son adaptation à cet environnement, de son autécologie.

1.3 Composition des peuplements

L'autécologie est définie par les traits fonctionnels qui sont des attributs morphologiques, physiologiques et phénologiques qui déterminent la réponse fonctionnelle d'un organisme à un filtre environnemental donné déterminant ainsi l'assemblage des communautés dans un peuplement (Reich *et al.*, 2003)

1.3.1 Processus d’assemblage des peuplements en forêt boréale mixte

D’après HilleRisLambers *et al.* (2012), on pourrait schématiser l’établissement des organismes ainsi. Au départ il y aurait un stock paysager composé d’organismes adaptés aux conditions environnementales présentes y compris les modalités de compétition (Tilman, 1990). Ces organismes doivent passer à travers des filtres biotiques et abiotiques, qui représentent des conséquences écologiques de la sélection naturelle, pour s’installer dans les communautés locales (Figure 1.1).

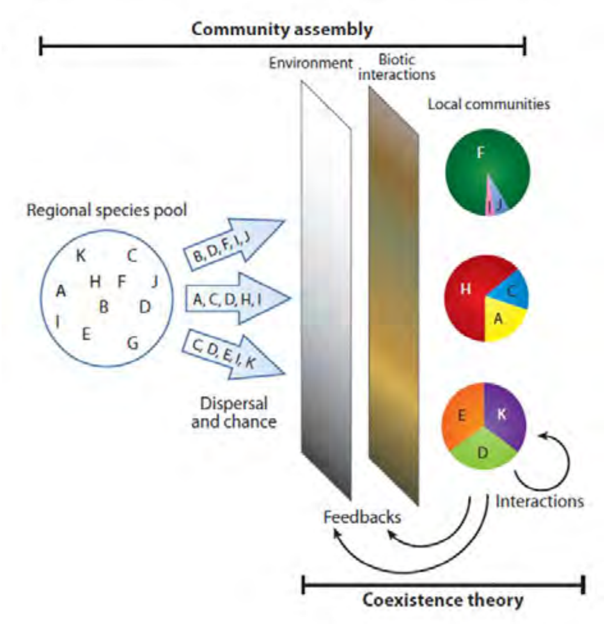

Figure 1.1 Schéma conceptuel des processus d’assemblage. Tiré de HilleRisLambers *et al.* (2012).

Ce processus de sélection dépend des caractéristiques climatiques, topographiques et édaphiques du paysage et des organismes (Levine et Murrell, 2003). La possibilité d’installation, de maintien et de reproduction d’un individu dans des conditions données dépend alors des valeurs spécifiques de traits fonctionnels de l’individu, de ses attributs. Seuls des individus présentant certaines combinaisons d’attributs pourront être présents à un site particulier. En d’autres termes, la sélection détermine quelles caractéristiques, ou valeurs de traits, seront favorables ou non à un site (Shipley, 2010). Par exemple, le mode de reproduction d’une espèce arbustive après un feu, ou sa tolérance à l’ombre permettront d’établir une population viable dans un site perturbé (Kneeshaw *et al.*, 2011).

L'écologie basée sur les traits offre une approche alternative pour étudier la structure d'occupation de niche dans un espace fonctionnel (Li *et al.*, 2018). Le regroupement des espèces par traits fonctionnels permet de réunir les espèces ayant un tel trait pouvant réagir de telle façon et selon les mêmes mécanismes face aux changements au sein d’un écosystème. En outre, l’étude de la diversité des traits fonctionnels aide à mieux comprendre comment les espèces et les communautés sont susceptibles de réagir face à une perturbation qui modifie les conditions d'habitats (lumière, nutriments, micro météorologie, microtopographie, compétiteurs) (Aubin *et al.*, 2013).

1.3.2 Stratégie fonctionnelle des plantes vasculaires

Beaucoup d’études scientifiques dans la zone boréale se sont concentrées sur les grands organismes, tels que les arbres et les vertébrés, cependant il y a un intérêt grandissant concernant la végétation de sous-bois qui influence les propriétés de l’écosystème, à la fois en surface (régénération et productivité des arbres forestiers) et dans le sol (processus de décomposition, cycle des éléments nutritifs) (Nilsson et Wardle, 2005).

Les perturbations intenses entrainant le remplacement des peuplements, comme les feux de forêt, induisent généralement des changements de composition importants dans les communautés végétales du sous-bois, principalement liés à la mortalité directe ou à des modifications importantes des conditions de l'habitat qui vont favoriser différents attributs fonctionnels (Fenton et Frego, 2005; Schmalholz *et al.*, 2011). Le remplacement des arbres au cours de la succession influence des processus tels que la luminosité, la température, l'humidité de l'air et du sol et l'apport en éléments nutritifs lors des précipitations et de la chute des feuilles (Salemaa *et al.*, 2019; Tonteri *et al.*, 2016). Ces changements semblent être les principaux filtres ayant un impact sur la composition de la végétation du sous-bois (Lecomte *et al.*, 2006; Porté *et al.*, 2004).

Les premières synthèses sur les changements dans les caractéristiques morphologiques et physiologiques des espèces végétales, le long des gradients nutritifs, sont que les espèces qui se développent sur les habitats riches en nutriments ont tendance à croître rapidement, avec une capture rapide des ressources et un renouvellement rapide des organes conduisant à une mauvaise conservation interne des ressources, tandis que l'inverse est vrai pour les espèces des habitats pauvres en nutriments (Lavorel et Garnier, 2002). D'un point de vue fonctionnel, cela se traduit par une abondance d'individus avec une surface foliaire spécifique élevée, une courte durée de vie des feuilles et des concentrations foliaires en azote et phosphore élevées sur les sites riches avec une plus grande disponibilité en eau et/ou en nutriments. De plus ces espèces ont généralement une densité plus faible du tissu de la tige qui leur permet de fournir des nutriments et de l'eau efficacement à une grande surface foliaire totale (Chave *et al.*, 2009). Ces caractéristiques favorisent et permettent une stratégie de croissance et d'acquisition de ressources rapide dans les sols à fertilité élevée où la compétition est importante mais également entrainent une durée de vie plus courte. C'est la stratégie dite « acquisitive » (Aerts et Chapin, 1999). En forêt boréale, les espèces arbustives feuillues, telles que *Betula papyrifera*, *Populus* spp, et de sous-bois comme, *Impatiens capensis Meerb*. et *Rubus pubescens*, possèdent ces caractéristiques d'acquisition (TOPIC database, Traits of Plants in Canada).

La sélection dans les habitats pauvres en nutriments ne repose pas nécessairement sur une capacité compétitive élevée pour les nutriments et un taux de croissance élevé, mais plutôt sur des traits qui réduisent les pertes de nutriments : une plus grande longévité des organes, en particulier les feuilles, de faibles concentrations en nutriments dans les tissus, une efficacité élevée d'absorption des nutriments, des tiges à haute densité tissulaire. Cette stratégie est dite « conservative ». En forêt boréale, les espèces d'arbres résineux, telles que *Pinus banksiana* ou *Picea* spp. et de sous-bois comme *Cornus canadensis* et *Mitella nuda* possèdent ces caractéristiques de conservation (TOPIC database, Traits of Plants in Canada).

La végétation de sous-bois est la strate forestière composée de toutes les plantes vasculaires inférieures ou égales à 1 mètre de hauteur (Gilliam, 2014) mais aussi des plantes invasculaires (Bisbee *et al.*, 2001). Parmi les plantes invasculaires, les bryophytes sont de plus en plus reconnus comme des éléments clés de la biodiversité et de la fonction des écosystèmes que ce soit en terme de succession écologique, de formation des sols et plus largement des cycles biogéochimiques et de la régulation du climat (Lindo *et al.*, 2013).

1.3.3 La végétation invasculaire

Le terme Bryophyte s.l. regroupe trois phylums de plantes terrestres thalloïdes, sans système racinaire et vasculaire pour le transport des nutriments : les Anthocerophyta (anthocérotes), les Marchantiophyta (hépatiques) et les Bryophyta s.s. (mousses et sphaignes) (Glime, 2013). Elles occupent une part conséquente de la biodiversité totale dans le monde avec environ 25 000 espèces recensées jusqu'à présent (Li et Chang, 2021). Ces espèces influencent fortement les cycles biogéochimiques et la régulation du climat par l'incorporation de l'azote et du phosphore dans la biosphère (Porada *et al.*, 2014), le stockage de carbone (Turetsky *et al.*, 2010) et leur capacité d'absorption de l'eau (Belnap et Lange, 2001; Porada *et al.*, 2018). Elles augmentent également la stabilité des sols en créant une couche protectrice et isolante qui empêche l'érosion et régule la température et l'humidité (Belnap et Lange, 2001).

Les bryophytes influencent mais sont également influencées par les conditions environnementales. Leur nature poïkilohydriques et l'absence de système racinaire les rendent dépendantes de l'eau à toutes les phases de leur cycle phénologique (Frahm, 2007). Cependant, on les retrouve dans tous les écosystèmes et sur tous les substrats. Ainsi, les espèces de milieux désertiques ou vivant sur des substrats soumis à la dessiccation (rochers, branches), peuvent maintenir un métabolisme quasi normal même en conditions sous-optimales ou évitent le stress hydrique en entrant en dormance (Takezawa, 2018). Ajoutée à l'humidité, la température est également un facteur de première importance pour les bryophytes puisqu'elle régule des mécanismes tels que la photosynthèse et la libération des spores (Vanderpoorten et Goffinet, 2009).

Les bryophytes ont développé différentes stratégies pour s'établir, se développer et se reproduire dans un environnement. On retrouve les espèces colonisatrices qui allouent une grande part de leur énergie à la reproduction, particulièrement sexuée et évitent les stress sévères par entrée en dormance des propagules (During, 1979). Ce sont des espèces souvent pionnières qui peuvent supporter des variations microclimatiques plus importantes et occuper des microhabitats plus variés (*Pleurozium schreberii* Willd. Ex Brid., *Pohlia nutans* Hedw. Lindb.). Elles sont qualifiées de « généralistes » (Frahm, 2007). D'autres espèces sont en revanche plus « délicates » et contraintes à un nombre restreint de microclimats et microhabitats, on parle d'espèces « spécialistes » (Frahm, 2007). C'est le cas de nombreuses hépatiques inféodées aux bois morts, épixyliques (*Frullania oakesiana Aust.*, *Nowelia curvifolia* Dicks.). Ces espèces sont plus sensibles aux modifications de l'habitat et plus généralement liées à des conditions micro environnementales plus stables telles que retrouvées dans les forêts matures et non perturbées (During, 1992; Ewald, 2000).

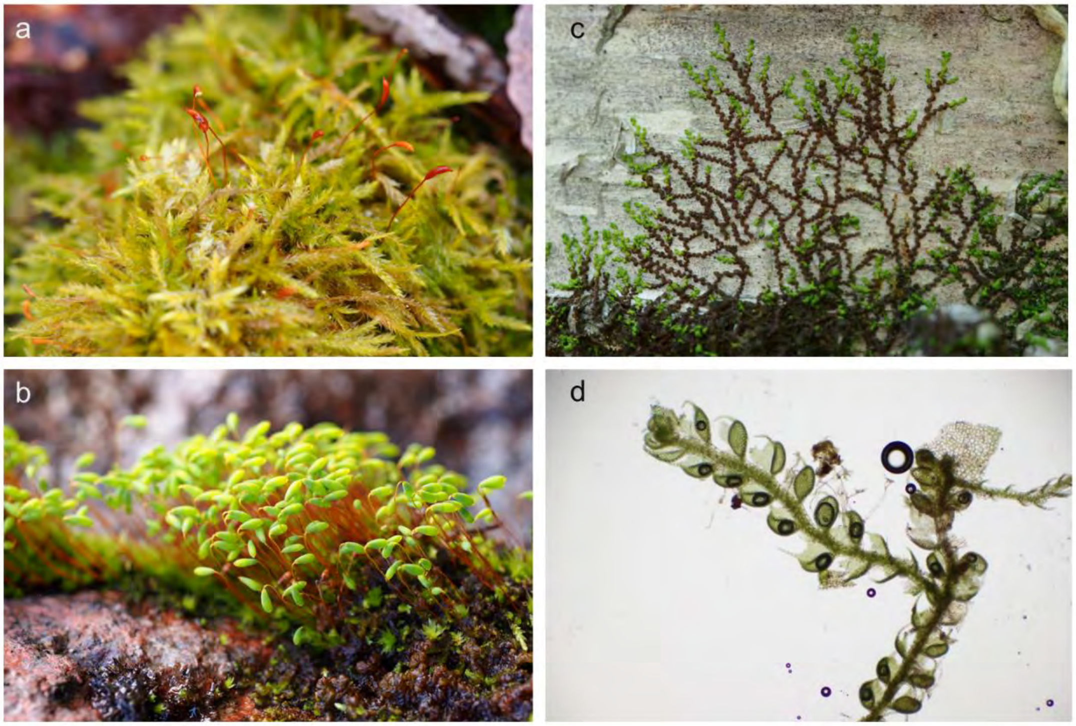

Figure 1.2 a. Pleurozium schreberi, b. Pohlia nutans c. Frullania oakesiana d. Nowelia curvifolia.

Les relations entre les bryophytes et les conditions environnementales en font de parfaites espèces bioindicatrices de la qualité de l'habitat (Czerepko *et al.*, 2021; Frego, 2007). Ainsi, le suivi de ces petits et discrets organismes, longtemps restés dans l’ombre des grands arbres, nous permet d’avoir une vision multi-échelle des impacts de l’aménagement forestier écosystémique.

1.4 Aménagement forestier écosystémique

Il y a actuellement un consensus voulant qu'un régime d'aménagement forestier s'inspire du spectre de variabilité (intervalle de temps, taille, sévérité) produit par un régime de perturbation pour minimiser les impacts de nos interventions sur les écosystèmes (Gauthier *et al.*, 2009; Haeussler et Kneeshaw, 2003; McRae *et al.*, 2001). Les perturbations naturelles représentent ainsi le « filtre brut » sur lequel on devrait s'appuyer pour répondre au grand enjeu de l'AFE, soit la simplification des structures et compositions internes des peuplements (Gauthier et al., 2009).

1.4.1 Les principes de l'aménagement

Grâce à une gamme d'approches et de traitements sylvicoles qui reproduisent la diversité des structures et des compositions forestières observées après perturbations naturelles, la biodiversité, les fonctions écosystémiques et la productivité de la forêt devraient être préservées (Gauthier *et al.*, 2009). Dans ce sens, les coupes totales (CT) qui consistent à retirer l'ensemble des arbres de dimensions marchandes (plus de 9,0 cm de diamètre à hauteur de poitrine) d'un peuplement, visent à ramener les peuplements à une structure équienne/ régulière que l'on retrouve généralement après une perturbation intense comme le feu (Larouche *et al.*, 2013). Pendant longtemps et encore aujourd'hui, elles ont été et sont réalisées dans des forêts naturelles vierges matures et âgées, influençant de manière conséquente les processus de succession et modifiant ainsi l'évolution naturelle des peuplements (Barrette *et al.*, 2022).

Si les CT sont considérées comme analogues des feux, les coupes partielles (CP) sont pratiquées pour se rapprocher des effets des épidémies d'insectes et de la succession naturelle. Définies comme toute pratique prélevant seulement une partie des arbres d’un peuplement, les CP sont utilisées afin de favoriser des éléments associés à la résilience forestière, par exemple une structure irrégulière ainsi que le maintien de legs biologiques tels que le bois mort (Bose *et al.*, 2014; Fenton *et al.*, 2008). Les CP regroupent plusieurs types de coupes, telles que l'éclaircie commerciale, la coupe progressive (régulière ou irrégulière), la coupe de rétention et les coupes de jardinage (Larouche *et al.*, 2013). Celles-ci ont toutes des objectifs différents et sont pratiquées à des stades de développement qui peuvent différer.

En forêt boréale mixte, des études préliminaires portant sur les effets des CP sur la structure et la composition des forêts montrent que des CP à rétention élevée parviennent à maintenir des peuplements dont la structure est semblable à celle de peuplements matures (Brais *et al.*, 2013; Graham-Sauvé *et al.*, 2013). Les arbres qui demeurent sur pied après la coupe et les jeunes arbres tolérants à l’ombre qui entament leur croissance forment ensemble une forêt dont la structure est irrégulière (Bouchard, 2008). Ces mêmes études, montrent également que des coupes de rétention peuvent être utilisées soit pour retarder ou devancer la succession (Bose *et al.*, 2015a). Une éclaircie commerciale appliquée sans contraintes opérationnelles (i.e. récolte de 45% de la surface terrière dans toutes les classes de diamètre de tiges commerciales) aurait le potentiel d’ « accélérer » la succession en créant au travers de la canopée des trouées à la manière de celles observées dans les vieilles forêts, favorisant le recrutement à la fois d’espèce tolérantes (sapin baumier) et intolérantes (peuplier faux tremble) à l’ombre (Bose *et al.*, 2015a). Inversement, une éclaircie par le haut (i.e. récolte d’environ 60% de la surface terrière) permettrait de retarder le développement d’un peuplement en favorisant de manière disproportionnée le recrutement et la croissance d’espèces intolérantes à l’ombre (Bose *et al.*, 2015a). De plus, il a été observé que des niveaux de récolte élevés peuvent initialement permettre une augmentation du taux de croissance des arbres en raison de l’augmentation de la disponibilité des ressources d’habitats (lumière, eau et nutriments) (Brais *et al.*, 2004; Lapointe *et al.*, 2006).

Dans cette perspective, les traitements de CP, dans l'ensemble de leur gamme de variabilité, constituent un complément intéressant aux CT en permettant de maintenir des peuplements mixtes et résineux ainsi que des attributs de vieilles forêts tandis que les CT réinitient la régénération des peuplements (Bergeron et Harvey, 1997; Prévost *et al.*, 2003). L'utilisation d'une gamme d'approches et de traitements sylvicoles variés à l'échelle du paysage permettra de reproduire la variété des structures et des compositions forestières observées après les perturbations naturelles afin de préserver la biodiversité, les fonctions écosystémiques et la productivité forestière (Gauthier *et al.*, 2009). Ces principes constituent des intentions sylvicoles établies dans le sens de l'AFE.

1.4.2 Effets des récoltes

Les opérations sylvicoles (récolte, préparation de terrain, plantation) sont des perturbations mécaniques dont la nature est différente des perturbations naturelles (chimiques, biologiques, physiques). Les effets des deux types de perturbations seront différents même si le régime peut être semblable (Bergeron *et al.*, 2017a; Brais *et al.*, 2013; Roberts, 2007; Simard *et al.*, 2001). Les effets de récolte sur la productivité d'un site peuvent être influencés par de multiples facteurs comme le type de récolte (arbre entier, tiges, CT, CP), les espèces récoltées (autécologie), les taux d'altération (préparation de terrain, chemins) et fertilité du sol (texture, épaisseur de la matière organique). Globalement le dégagement du couvert végétal entraine une augmentation de la disponibilité en azote et des taux de minéralisation qui sont attribués à l'apport de matière organique fraîche, au mélange du sol minéral et forestier et à l'augmentation des températures et de l'humidité (Keenan et Kimmins, 1993). Les coupes, comme les perturbations peuvent produire un pool d'éléments nutritifs minéralisés à durée et intensité variables (Ilisson et Chen, 2009). Le feu en réduisant la masse de matière organique dans le sol forestier, génère une impulsion d'éléments nutritifs disponibles tandis que les CT en augmentant la masse de matière organique au sol, produisent une impulsion d'éléments nutritifs grâce à la minéralisation. La végétation en régénération est exposée à de plus grandes concentrations d'éléments nutritifs disponibles dans les sites brûlés que dans les peuplements de CT mais la masse totale d'éléments nutritifs plus élevée suite aux coupes pourraient avoir une meilleure capacité que les peuplements brûlés à fournir des nutriments pour soutenir la productivité sur le long terme (Simard *et al.*, 2001). Ces perturbations indirectes (modification du microclimat) mais également directes (création des sentiers de récolte, passage des machines) causées par les récoltes affectent la composition et la diversité des plantes de sous-bois (Hart et Chen, 2008; Roberts, 2004, 2007).

De nombreuses études, évaluant les effets de l'intensité des récoltes sur la diversité des espèces du sous-bois, ne montrent pas de réduction à court terme de la richesse spécifique après une intervention sylvicole (Battles *et al.*, 2001; Graae et Heskjær, 1997; Nagaike *et al.*, 1999; Roberts et Gilliam, 1995). Après CT, l'ouverture du peuplement et le dégagement du sol permettent à de nouvelles espèces (majoritairement de stratégie « acquisitive ») de venir s'établir, entrainant une plus grande richesse (Battles *et al.*, 2001; Duguid et Ashton, 2013). Les perturbations modérées crées par les CP maintiennent une proportion d'espèces de sous-bois limitant ainsi l'établissement de nouvelles espèces en raison d'une compétition supérieure pour les ressources (luminosité, nutriments du sol). Les espèces qui parviennent à s'établir sont typiques de peuplements de stades de succession avancés (Battles *et al.*, 2001).

Une différence entre les traitements est observée en termes de traits caractéristiques des espèces qui y sont retrouvées (Berger *et al.*, 2004; Haeussler *et al.*, 2002; Harrington et Edwards, 1999). Plus une récolte va affecter le sol du site, CT, plus des espèces de types « envahissantes » (facilité de dispersion des graines) et « évasives » (banques de graines enfouies dans le sol qui vont se retrouver en surface) vont être présentes (Berger *et al.*, 2004; Haeussler *et al.*, 2002; Rowe, 1983). Inversement, les coupes de rétention élevée, pratiquées afin de favoriser des éléments associés à la résilience des peuplements aux perturbations, comme le maintien de legs biologiques tels que le bois mort (Bouchard, 2008) sont plus profitables pour des plantes de type « ultérieures » (établissement tardif par dispersion des graines) (Brais *et al.*, 2013; Rowe, 1983) et les bryophytes épixyles (Boudreault *et al.*, 2000; Kruys et Jonsson, 1999). Par conséquent, moins le sol est perturbé et moins les espèces envahissantes ont d'espace pour s'établir, ce qui réduit leur diversité et leur recouvrement.

1.4.3 Les projets de recherche SAFE et EMEND

Une grande partie de nos connaissances des effets initiaux de l'AFE en forêt boréale mixte du Canada vient des projets de recherche SAFE (Sylviculture et Aménagement Forestier Écosystémique) et EMEND (Ecosystem Management Emulating Natural Disturbance). Le premier se situe à l'Ouest du Québec, dans la Forêt d'enseignement et de recherche du Lac Duparquet en Abitibi-Témiscamingue (Brais *et al.*, 2004; Brais *et al.*, 2013) et le second au Nord de l'Alberta (Sidders et Luchkow, 1998) (Figure 4.1). Ces projets constituent des expériences à grande échelle programmées spécifiquement pour évaluer les impacts à long terme des différents traitements de coupe sur la biodiversité, les fonctions écosystémiques et la productivité forestière. Ils regroupent des séries d'études expérimentales permettant de tester les objectifs de l'AFE. Ainsi, différents traitements sylvicoles ont été répliqués et planifiés, dans les 3 types de cohortes de succession, pour tester un système d'aménagement basé sur la dynamique forestière naturelle de la forêt boréale mixte (Figure 1.3, Figure 1.4).

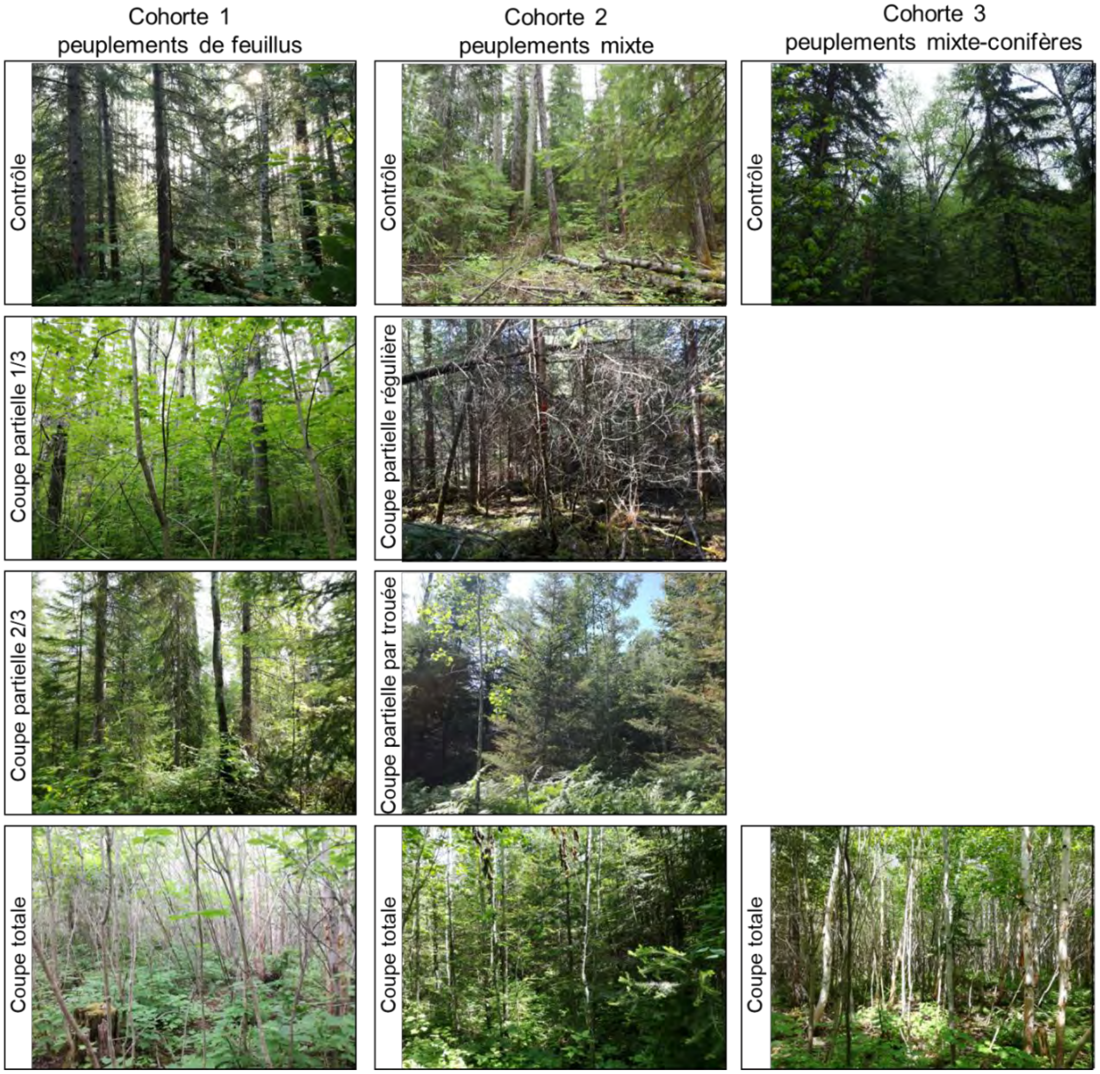

Figure 1.3 Visualisation des peuplements, 20 ans après la mise en place du projet SAFE dans les trois types de peuplements de cohortes 1, 2 et 3 en fonction des différentes intensités de récolte.

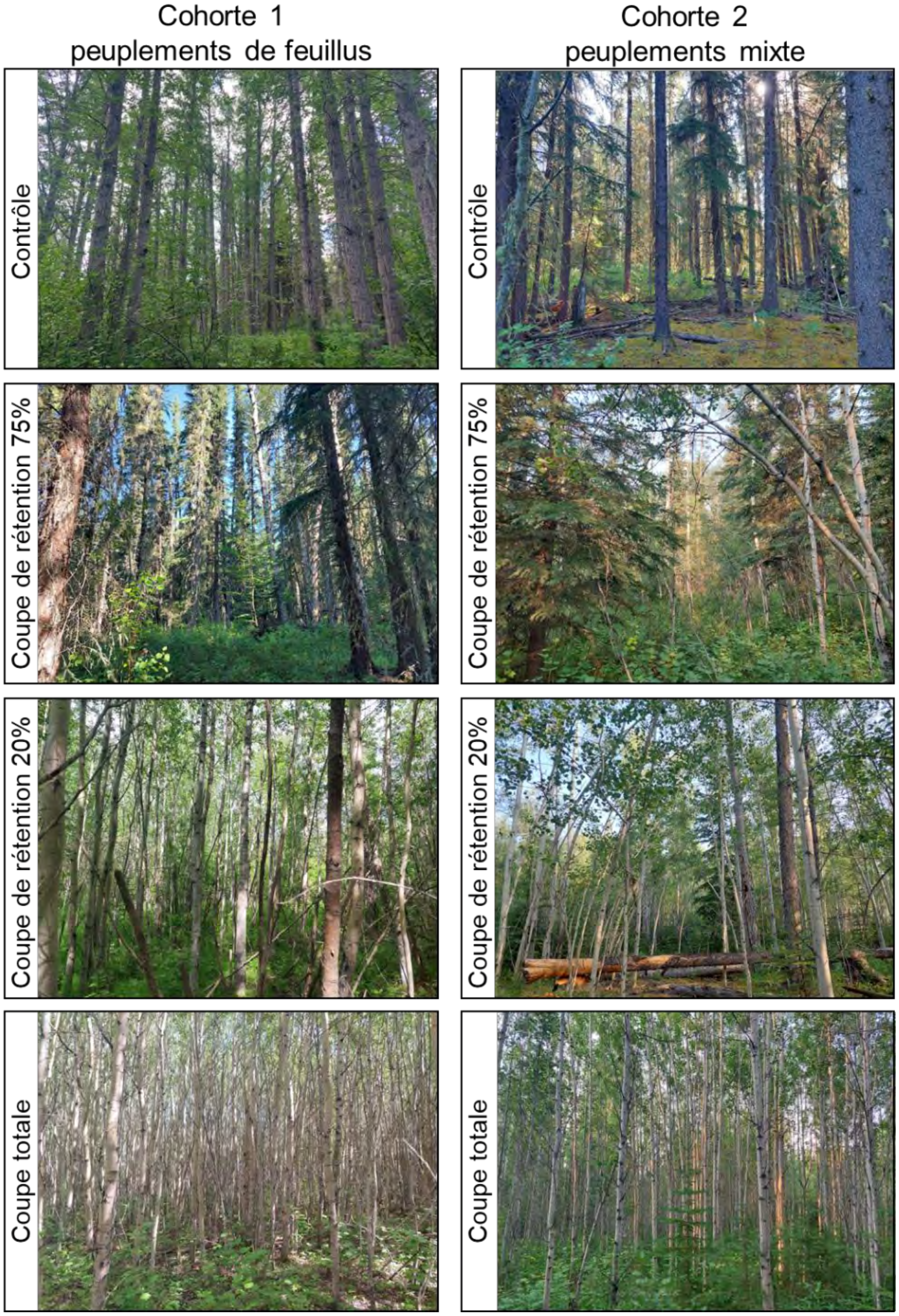

Figure 1.4 Visualisation des peuplements, 20 ans après la mise en place du projet EMEND dans les deux types de peuplements de cohortes 1 et 2 en fonction des différentes intensités de récolte.

Initié en 1998, les projets ont permis d'accumuler une quantité importante de connaissance sur les effets de la récolte sur la biodiversité végétales et d'arthropodes (Brais *et al.*, 2004; Craig et Macdonald, 2009; Jacobs et al., 2007b; Webb *et al.*, 2008), la dynamique du bois mort, la décomposition de la litière (Jacobs *et al.*, 2007a; Strukelj *et al.*, 2012), les flux de nutriments (Belleau *et al.*, 2006; Frey *et al.*, 2003a; Lapointe *et al.*, 2006) et la productivité et dynamique des forêts (Bose *et al.*, 2014; Bose *et al.*, 2015a; Brais *et al.*, 2004; Gradowski *et al.*, 2010; Solarik *et al.*, 2012) et a contribué à l'élaboration de recommandations aux gestionnaires responsables de la mise en place de l'AFE au Canada. En reprenant une partie de ces données et en les complétant par des suivis 20 ans après coupe, nous continuons les recherches afin d'évaluer les impacts des pratiques sylvicoles sur des échelles de temps plus longues.

1.5 Objectifs

Les méthodes utilisées aujourd'hui en sylviculture sont plutôt bonnes pour contrôler la composition ou la structure d'un peuplement, mais la difficulté est de maintenir la mosaïque de ces peuplements (variété de composition, structure et âge) à l'échelle du paysage (échelle d'aménagement) proche d'un paysage naturel. Ceci est le but de l'AFE qui vise à réduire les écarts entre les paysages aménagés et les paysages naturels en termes de variété de composition, de structure et d'âge. Pour cela il est nécessaire d'avoir des données sur l'ensemble des éléments qui vont influencer les peuplements.

Grâce au suivi des parcelles du projet SAFE, environ 20 ans après l'application initiale des coupes, nous possédons une longue série temporelle de données portant sur l'aménagement écosystémique en forêt boréale à l'échelle des peuplements. Soit des données d'inventaires forestiers de l'arbre au semis (espèces, diamètres), de bois morts (stades de décomposition, diamètre) et de température et humidité du sol. Une meilleure compréhension des répercussions des coupes sur la dynamique naturelle d'un peuplement après feu permettra aux professionnels de la forêt de développer de meilleures politiques et procédures destinées à réduire certains des impacts négatifs de l’aménagement forestier sur l’intégrité de l’écosystème. Nous pourrons de plus visualiser l’évolution de la régénération des peuplements pour ainsi déterminer si les CP permettent, à moyen terme, le maintien, la récupération ou l’accélération des attributs des peuplements boréaux mixtes. Ainsi nous pourrons émettre des lignes directrices aux responsables d’aménagements forestiers pour l’amélioration des pratiques sylvicoles au regard de l’utilisation des coupes en forêt boréale mixte.

L’objectif général de cette thèse est donc de tester si nous parvenons à reproduire la diversité des structures et des compositions forestières observées après perturbations naturelles grâce à une gamme de traitements sylvicoles. Soit, si les intentions sylvicoles établies dans le sens de l’AFE s’appliquent dans le temps suite à différents traitements en forêt boréale mixte. Cet objectif répond aux besoins de maintien de la productivité forestière mais aussi de conservation de la biodiversité. Nous avons examiné, 20 ans après coupes, les effets de l'intensité croissante de récolte des arbres sur la structure, la composition et la régénération des peuplements en termes d'arbres vivants, de bois mort, de richesse en bryophytes et de la diversité fonctionnelle des plantes de sous-bois.

Dans chaque chapitre nous cherchons à :

- Chapitre 2 : Examiner les effets au cours du temps, de l'intensité croissante de l'enlèvement des tiges sur la structure, la composition et la régénération des peuplements en termes d'arbres vivants mais aussi de bois mort, dans les trois types de cohortes 1, 2 et 3. D’après des études antérieures, les ressources libérées lors des récoltes (nutriments, lumière) sont attribuées à la croissance des arbres résiduels. Dans le cas d’une intensité de prélèvement forte (CT), les ressources bénéficieront majoritairement aux espèces qui étaient présentes avant l’application des traitements grâce aux capacités de reproduction des espèces (drageonnement), la persistance d’une banque de graines ou encore la présence d’individus matures à proximité du site (Brais et al., 2004). Dans le cas d’une intensité de prélèvement modérée (CP), les ressources bénéficieront majoritairement à la croissance des arbres résiduels et à la croissance des arbres établis en sous-bois (conifères). Nous nous attendions donc à ce que le taux d'intensité de la récolte génère un gradient de réponse linéaire. Plus la coupe est intense, plus nous observerons de différences qui seront maintenues dans le temps entre les peuplements coupés et les peuplements évoluant naturellement. De plus, nous nous attendions à ce que 20 ans représentent un délai suffisant pour observer un effet de vieillissement des peuplements suite aux CP, se traduisant par une augmentation de la complexité structurale et de la diversité des espèces végétales. Les peuplements de début et de milieu de succession où des CP ont été appliqués seront comparables aux peuplements naturels témoins de milieu de succession et de fin de succession, respectivement.

- Chapitre 3. Examiner les effets, 20 ans après coupes, de l'intensité croissante de l'enlèvement des tiges sur les communautés de bryophytes dans les trois types de cohortes 1, 2 et 3. Plus précisément, nous cherchions à regarder si l'intensité de la récolte, dépendamment de la cohorte où elle a été pratiquée, influence les communautés de bryophytes, 20 ans après coupes en supposant que les CP favorisent d’avantage les espèces de bryophytes « sensibles ». De plus, nous cherchions à savoir quels facteurs environnementaux sont les moteurs de la richesse des communautés de bryophytes. 20 ans après CT, des différences de structure, composition et conditions micro environnementales (lumière, température et humidité du sol) des peuplements devraient encore se maintenir avec les peuplements évoluant naturellement ce qui impacteraient les communautés de bryophytes. Nous nous attendions à retrouver moins d’espèces sensibles, comme le groupe des hépatiques après les coupes plus intenses. 20 ans après CP, dans la mesure où les modifications des conditions microclimatiques sont limitées, et où des legs biologiques sont conservés (arbres sur pied, bois morts), les communautés de bryophytes devraient se maintenir par rapport aux peuplements non récoltés. De plus, les traitements de récolte réalisés dans les peuplements plus anciens, devraient avoir des effets plus importants sur les communautés de bryophytes que dans les jeunes forêts. Cela serait dû à une plus grande stabilité des conditions micro-environnementales dans les peuplements plus anciens et la présence de communautés de bryophyte plus sensibles qui devraient donc se remettre plus lentement des perturbations comparativement aux communautés pionnières et colonisatrices retrouvées dans les jeunes peuplements. Les facteurs environnementaux tels que la structure et composition des peuplements, abondance de bois morts, température et humidité du sol qui sont directement et indirectement impactés par les coupes, devraient encore influencer les communautés, 20 ans après récolte.

- Chapitre 4 : Examiner les effets, 20 ans après coupes, de l'intensité croissante de l'enlèvement des tiges, sur la diversité fonctionnelle de la végétation de sous-bois dans des peuplements de cohortes 1 et 2, situés à l'Ouest et l'Est du Canada. Plus précisément nous cherchions à regarder à l'échelle de la communauté et à l'échelle de l'individu si l'intensité de la récolte, dépendamment de la cohorte où elle a été pratiquée et du site influence la fonctionnalité de la végétation. Au niveau de la communauté, nous nous attendions à ce que les récoltes plus intenses, par l'ouverture du couvert, favoriseraient des traits d'acquisition (par exemple, intolérance à l'ombre, croissance rapide, LDMC faible, SLA élevé, LNC, LPC) et entraineraient une augmentation de la richesse en espèces et de la diversité fonctionnelle par rapport aux peuplements témoins. De plus, nous nous attendions à ce que les différences entre les peuplements récoltés et les peuplements témoins seraient plus prononcées à l'est qu'à l'ouest où le climat est plus sec, le cycle des feux plus court et le sol plus riche, et en particulier dans les forêts mixtes plus anciennes et stables. Au niveau de l'individu, nous nous attendions à ce que chaque espèce ajusterait la valeur de ses traits pour obtenir une meilleure condition physique à la suite de la récolte, ce qui se traduirait par des individus ayant un LDMC plus faible et un SLA, un LNC et un LPC plus élevés après la récolte par rapport aux peuplements témoins non récoltés. De plus, la variabilité intraspécifique mesurée au sein d'une espèce, pourrait révéler davantage de différences fonctionnelles entre les intensités de récolte que la variabilité mesurée à l’échelle de la communauté (Kichenin et al., 2013 ; Kumordzi et al., 2019).

CHAPITRE 2

TWENTY-YEAR RECOVERY OF MANAGED STAND, IN STRUCTURE AND COMPOSITION, IN BOREAL MIXEDWOOD STANDS OF NORTHWESTERN QUEBEC

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2.1 Abstract

The Natural Disturbance Based Management (NDBM) aims to maintain specific structural and compositional attributes of natural forests in managed stands. Operationally, NDBM relies on diversifying and adapting silvicultural practices, including partial harvesting (PC), to expand the range of options beyond that of simply clearcuts (CC). Established in 1998, the SAFE (Sylviculture et Aménagement Forestier Écosystémique) project evaluates this potential in hardwood, mixedwood and coniferous stands in northwestern Québec, Canada. Our results confirmed a part of the NDBM objectives were attained i.e., PC allowed the maintenance of stands with mixed structure and composition, constituting an interesting complement to CC, which reset stand regeneration. However, PC did not accelerate the transition of stands to later stages with less intensive harvesting or to earlier stages with more intensive harvesting. We essentially had an initial impact, delaying or stopping the stands evolution which dissipates over time and more quickly with less intensive harvesting. Furthermore, our results did not support the ability of PC to enhance the development of old-growth attributes like deadwood. Despite the 20-year horizon of this study further field surveys will be required in the future to better understand the impact of different silvicultural treatments on forest productivity and biodiversity preservation throughout a forest rotation.

2.2 Résumé

L’Aménagement forestier écosystémique (AFE) vise à maintenir les structures et composition des peuplements des forêts naturelles dans les peuplements aménagés. Sur le plan opérationnel, l’AFE repose sur la diversification et l'adaptation des pratiques sylvicoles, comprenant la coupe partielle (PC), afin de multiplier les options au-delà de la pratique intense de la coupe totale (CC). Établi en 1998, le projet SAFE (Sylviculture et Aménagement Forestière Écosystémique) évalue son potentiel dans des peuplements de feuillus, mélangés et de conifères dans le nord-ouest du Québec, Canada. Nos résultats ont confirmé une partie des objectifs du NDBM, c'est-à-dire que les PC permettent de maintenir des peuplements à structure et composition mixtes, constituant un complément intéressant aux CC, qui réinitialisent la régénération des peuplements. Cependant, les PC n'ont pas permis d'accélérer la transition des peuplements vers des stades plus avancés avec une récolte moins intensive ou vers des stades plus précoces avec une récolte plus intensive. Nous avons essentiellement eu un impact initial, retardant ou stoppant l'évolution des peuplements qui se dissipe avec le temps, et de manière plus rapide lorsque la récolte est moins intensive. De plus, nos résultats n'ont pas confirmé la capacité des PC à améliorer le développement des attributs des forêts anciennes, comme le bois mort. Malgré l'horizon de 20 ans de cette étude, d'autres études de terrain seront nécessaires à l'avenir pour mieux comprendre l'impact des différents traitements sylvicoles sur la productivité de la forêt et la préservation de la biodiversité tout au long de la révolution forestière.

2.3 Introduction

Natural Ecosystem Based Management (NDBM) has been widely advocated as a means to maintain healthy and resilient forest ecosystems by reducing differences between natural and managed landscapes throughout North America (Franklin, 1997). Operationally, NDBM relies on varying silvicultural treatments to better reflect different aspects of natural forest dynamics (Gauthier *et al*., 2009), which are often shaped by a range of natural disturbances (Chen and Popadiouk, 2002). In boreal forests, natural disturbances drive forest dynamics and shape the variety of habitats observed at the landscape and stand scales (Chen and Popadiouk, 2002). Fire, considered as the primary disturbance, opens the canopy, reduces organic matter thickness, and exposes mineral soil, resulting in young stands with increased nutrient supply and a diminution of shrub competition (Bergeron *et al.*, 1999; Neff *et al.*, 2005).). Unlike fires, slower and more specific, insect epidemics, considered as secondary disturbances, affect specific species. Each defoliator insect has its preferred hosts, acting differently and at different stages of stand development. The longer and more severe the epidemic, the greater the mortality of host species, favoring the development of non-host species (Chen and Popadiouk, 2002; Moulinier *et al.*, 2011). Intense sylvicultural treatments such as clearcuts (CC) can be used to favor the regeneration of stands, serving as a partial surrogate for stands regenerating by fire (Chen and Popadiouk, 2002; Nguyen-Xuan *et al.*, 2000). In contrast, less intense silvicultural treatments like partial cuts (PC) can be used to emulate insect outbreaks, windfall, or natural mortality processes. For example, the “stem exclusion phase” where many stems die due to competition for resources or the “canopy transition phase” where dominant and codominant trees senesce and die may both be emulated through the use of partial cuts For example, depending on stand age, vertical structure, and species present, PC prescriptions could emulated the “stem exclusion phase” where many stems die due to competition for resources or the “canopy transition phase” where dominant and codominant trees senesce and die (Chen and Popadiouk, 2002). Thus, stands resulting from PC conserve irregular stand’s structure and biological legacies such as live trees and deadwood. These elements are essential for the maintenance of biodiversity and forest productivity (Bose et al., 2015a; Drapeau et al., 2009; Martin et al., 2021). However, the long-term capacity of partial cuts prescriptions to push stands either forward or backward along a successional sequence has yet to be demonstrated.

In boreal mixedwood forests, preliminary studies following stand evolution a few years after harvest (0 to 12 years), suggested that PC can be used to delay or advance the transitions through successive stages depending on the harvesting intensity applied (Bose *et al.*, 2015a; Brais *et al.*, 2013). Low harvesting intensity (i.e. harvesting about

45% of the basal area) would accelerate succession by creating gaps in the canopy similar to those created by senescence in old growth forests. This would promote the growth and the establishment of both shade tolerant (balsam fir, *Abies balsamea* (L.) Mill., white spruce, *Picea glauca* [Moench] Voss, and black spruce, *Picea mariana* [Mill.] B.S.P.) and shade intolerant (trembling aspen, *Populus tremuloides* Michx., and paper birch, *Betula papyrifera* March) tree species (Bose *et al.*, 2015a). In contrast, high harvesting intensity (i.e. harvesting about 60% of the basal area) would delay stand development and generally favor growth and recruitment of shade intolerant species (Bose *et al.*, 2015a). PC across their range of intensity variability are an interesting complement to CC to maintain mixed-structure stands and old-growth attributes such as biological legacies, while CC resets stand regeneration. The use of diverse silvicultural treatments at the landscape scale would allow the reproduction of the variety of stand structures and compositions observed after natural disturbances allowing for the maintenance of biodiversity, ecosystem functions and forest productivity. These principles are silvicultural intentions established in the sense of NDBM. However, NDBM is still rather new and only long-term monitoring would allow to evaluate its effectiveness to maximize forest production while minimizing impacts on the forest. A thorough knowledge of the overall effects of practices will serve as a basis for forest managers to develop the best strategies of harvesting.

In boreal mixedwood stands on mesic sites, we observe a general transition through three successive stages. First, the hardwood stands, dominated by shade intolerant and pioneer tree species such as trembling aspen. Then, the mixedwood stands composed of both shade tolerant coniferous species such as balsam fir and spruces and shade intolerant hardwood species. And at the end of the successional sequence, the coniferous dominated stands composed of mainly shade tolerant species however some shade intolerant species such as trembling aspen and paper birch can establish in the gaps formed by the senescence of trees (Bergeron *et al.*, 1999; Bergeron *et al.*, 2002). In NDBM, different combinations of silvicultural treatments could be used in concert to maintain the stand structural and compositional variability observed in natural forests. Ultimately, which silvicultural strategies will be effective at maintaining the structure and composition of natural stands as well as maintaining forest biodiversity and productivity must be verified through long-term monitoring. This study examined the effects of different harvest intensities (stem removal of 33%, 40%, 66% and 100%) on stands structure, composition, regeneration, and deadwood legacies in the three successional stages of boreal mixedwood forest. Specifically, we tested 1.) if PC and CC can be used to delay, maintain or advance the transitions through successive stages over 20 years 2.) if PC can maintain more biological legacies than CC over 20 years. We hypothesized that (1) PC of lower intensity will advance the transition of stands through successional stages. That is, low intensity PC realized in the hardwood or mixedwood stands, will result in stands with a similar structure and composition to the unharvested mixedwood or coniferous stands respectively, over 20 years. In contrast, PC of higher intensity will maintain the stands in the same stage that it was before harvest. That is, high intensity PC realized in the hardwood or mixedwood stands, will result in stands with a similar structure and composition to the unharvested stands of the same stage, over 20 years. In contrast, CC will delay the transitions of stands by resetting their regeneration. That is CC practiced in hardwood, mixedwood or coniferous stands should have similar structure and regeneration, over 20 years. (2) We also hypothesized that increasing harvesting intensity will have increasing and more persistent impacts over time on biological legacies and, the impact of harvests will be greater in more advance successional stages that are more sensitive. This will be seen with greater differences between CC and unmanaged stands than between PC and unmanaged stands, from the same successional stage, in term of live and dead trees, over the 20 years.

2.4 Materials and method

2.4.1 Study area

The study was conducted in the Lake Duparquet Research and Teaching Forest (LDRTF) in the Abitibi region of northwestern Quebec (48°30’N, 79°20’O). This region is characterized by glaciolacustrine clay deposits left by proglacial Lake Ojibway (Vincent and Hardy, 1977). The soil texture is that of heavy clay (>75% clay) and the forest floor is a thin mor 2–7 cm thick (Canadian Agricultural Services Coordinating Committee, 1998). The climate is continental with an average annual temperature of 1°C and annual precipitation of 989 mm with 30% falling in the form of snow (Mont Brun weather station, average over the last 25 years) (Environnement Canada, 2019).

The LDRTF is situated in the mixedwood zone of the boreal shield, in the bioclimatic domain of the balsam fir-white birch forest. Forests of the region are characterized by a mixed composition of boreal conifers and shade intolerant broad-leaved species. Trembling aspen, paper birch, and jack pine (*Pinus banksiana* Lamb.) are common early successional species. Balsam fir is the dominant species in late-successional forests on mesic sites, and is associated with white spruce, black spruce (*Picea mariana* [Mill.] B.S.P.) and eastern white-cedar (Bergeron *et al.*, 1999). The LDTRF is composed of a variety of stands resulting from multiple fires and insect outbreaks (Bergeron and Harvey, 1997; Bergeron *et al.*, 1995; Morin *et al.*, 1993)..

2.4.2 Experimental design

The SAFE project (French acronym for “Sylviculture et Aménagement Forestier Ecosystémique”) is a series of silvicultural experiments replicated across the three successional stages that was put in place between 1998 and 2001. The initial intolerant deciduous dominated stand is composed of aspen-dominated stands originating from a fire in 1923. The mixedwood stand is composed of stands originating from a fire in 1910 and contains roughly equal proportions of deciduous and conifers in the overstory. The conifer-dominated stand is composed of stands originating from a fire in 1760 (Bergeron and Dansereau, 1993). Multiple spruce budworm outbreaks have affected the stands, and the last one that occurred between 1970 and 1987 was considered to be severe (Bergeron *et al.*, 1995; Morin *et al.*, 1993). These successional stages represent three different stand types with different structures and species compositions that developed over time following stand-replacing wildfire (98, 111 and 260 years since the last fire) (Figure 2.1).

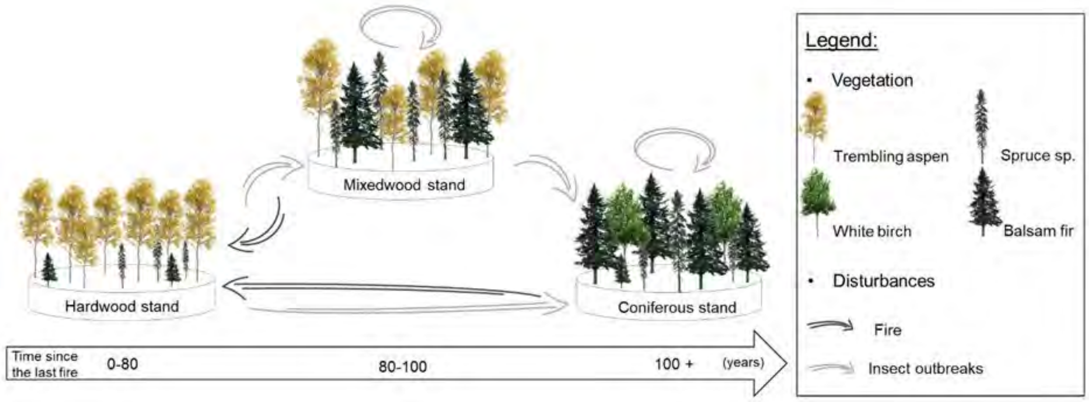

Figure 2.1 Classic dynamics of white birch-fir stands on mesic sites in Canada’s boreal mixedwood forest illustrating the main three successional stages (Bergeron and Harvey, 1997). The main stages of forest structure and composition and the effects of primary natural disturbances such as fire and secondary disturbances such as insect outbreaks are indicated.

In each stand, three replicated blocks comprising harvesting treatments and an uncut control stand were put in place in a randomized complete block design. The number and type of harvesting treatments differed between the three successional stages to achieve management objectives described in Bergeron and Harvey (1997) and Brais *et al*. (2004) (Figure 2.2). In hardwood dominated stands, harvesting treatments included clearcuts (CC); 1/3 partial cuts (PC1/3), where approximately 33% of the total basal area was removed; 2/3 partial cuts (PC2/3), where approximately 66% of the total basal area was removed; and uncut stands as controls. For both partial cutting treatments, stems were removed throughout the stand. Stands in the 1/3 regular removal treatment were low thinned as non-vigorous stems were removed. Stands in the 2/3 removal treatment were crown thinned with larger and vigorous stems preferentially selected for retention. In mixedwood stands, harvesting treatments included clearcuts (CC), two partial cutting treatments where 40% of stems were removed either throughout the stand (PCreg) or in concentrated gaps of approximately 400 m^2 (PCgap), and uncut control stands (Figure 2.2). In coniferous stands, harvesting treatments included only clearcuts and uncut control stands (Figure 2.2). Each replicate treatment was applied over an area ranging from 1 to 2.5 ha. Harvesting was done manually during the winter to limit damage to the forest floor in the years 1998 for treatments in hardwood stands, 1999 for treatments in coniferous stands and 2000 for treatments in mixedwood stands. Before harvesting, 5 permanent 400m^2 plots (radius = 11.28m) were established in each experimental unit, resulting in 60 plots in hardwood stands, 60 plots in mixedwood stands, and 30 plots in coniferous stands for a total of 150 plots.

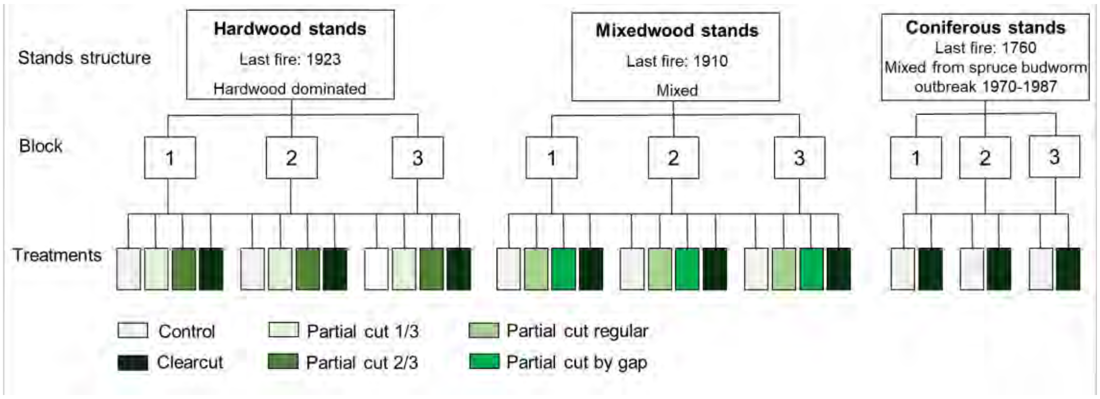

Figure 2.2 Experimental treatments applied in the SAFE project, in each of the three successional stages.

2.4.3 Inventory design

2.4.3.1 Forest inventory

In each 400 m^2 monitoring plot, DBH of commercial stems (diameter at breast height (DBH) > 9 cm) was measured on trembling aspen, paper birch, balsam fir and spruce (black and white spruce) trees. In addition, DBH of all saplings of commercial species (DBH from 2 to 9.0 cm) were measured in one quarter of each plot. Inventories were completed the summer following harvest (1999 hardwood stands, 2000 coniferous stands, 2001 mixedwood stands, time = initially) (Brais *et al.*, 2004) and approximately 20 years post-harvest in 2019. All stems with a DBH smaller than 40 cm were then reclassified into 2cm DBH classes. Above 40 cm, stems were grouped in a unique 40+ cm diameter class. We used changes in tree DBH as well as the distribution of stem diameters to characterize changes in stand structure and composition and changes in sapling density to characterize regeneration.

2.4.3.2 Deadwood inventory

Deadwood inventories were realized at the same time as forest inventory, the summer following harvest (Brais *et al.*, 2004) and approximately 20 years post-harvest in 2019. Volume of downed deadwood (diameter > 5 cm) (m3/ha) was calculated with the line intercept method (Van Wagner, 1982) using three 30 m transect lines for each block of each treatment. Along transects, the frequency of downed deadwood pieces intercepting the transect was recorded by species. Diameter was measured and a decay class was attributed to each piece (1 to 5, see (Daniels *et al.*, 1997)). Decay classes 1 to 3 refer to downed deadwood that are not well decayed and classes 4 and 5 to well decayed downed deadwood. In all plots, inventories for standing deadwood snags were completed at the same time as the living stem inventories. We only included snags with a diameter superior to 5 cm and a height superior to 2 meters (Daniels *et al.*, 1997). The diameter of each snag was measured.

2.4.4 Statistical analyses

To examine the impact of harvesting on structure, regeneration, and standing and downed deadwood we compared five environmental variables between harvest treatments within each three stands at the beginning of the experiment and 20 years post-harvest: live tree basal area (structure, DBH > 9 cm), density of saplings (regeneration, DBH from 2 to 9.0 cm), snag basal area (DBH > 9 cm), and fresh and old downed deadwood volume (diameter > 5cm). We analyzed the interaction between treatment, successional stages, and time on the five environmental variables with generalized linear mixed models (GLMM). Because the same stands were measured twice and are not independent, we used successional stage x block x treatment combinations as a random effect in our models. Square root and log transformations were applied for the multiple tests when normality and homogeneity of variances were not respected. Tukey post-hoc tests have been performed to examine differences between harvest treatments in each successional stage.

To examine the impact of harvesting on composition, we compared the abundance of all live stems, from 2 to + 40cm DBH, between harvest treatments within each cohort at the beginning of the experiment and 20 years post-harvest. The abundance of each of the four commercial species was determined by diameter classes, treatments, successional stages and time. The abundance of each four species was not high enough in each of the 18 diameter classes to perform statistical comparative analyses.

All analyses were conducted with R software (version 4.0.3, R core Team 2020). General linear mixed models and Tukey post-hoc tests were respectively analyzed with Lme4 and emmeans packages. In all statistical tests, a *p* value ≤ 0.05 was considered significant.

2.5 Results

2.5.1 Changes in sapling density and tree basal area after 20 years

Initially after harvesting, sapling density per hectare was similar (mean of 416 ± 210 saplings/ha) in all treatments and successional stages (Figure 2.3 A). In hardwood stands, 20 years post-harvest, sapling density increased to 12,093 ± 3574 saplings/ha in clearcuts, 5980 ± 1583 saplings/ha in PC2/3 and 2233 ± 1298 saplings/ha in PC1/3. This translates to an approximate 30-fold increase compared to the initial density for CC, a 15-fold increase in PC2/3 and a 5-fold increase in PC1/3. Sapling density in control was roughly doubled (952 ± 434 saplings/ha) after 20 years. In mixedwood stands, 20 years after harvesting, regardless of the whether stem removal was dispersed throughout the stand or concentrated in gaps, regeneration density was high. Sapling density per hectare between the three types of cuts (clearcut and PCreg and PCgap) was similar with a mean of 11,042 ± 2224 saplings/ha, which represents a 26-fold increase over 20 years. In control stands, increases in sapling density were significant but less than what was found in harvested stands (from 1126 ± 641 saplings/ha to 5633 ± 1867 in 20 years). In coniferous stands, the regeneration after CC (5385 ± 3368 saplings/ha) was approximately 10 times lower compared to the regeneration in clearcuts in hardwood and mixedwood stands.

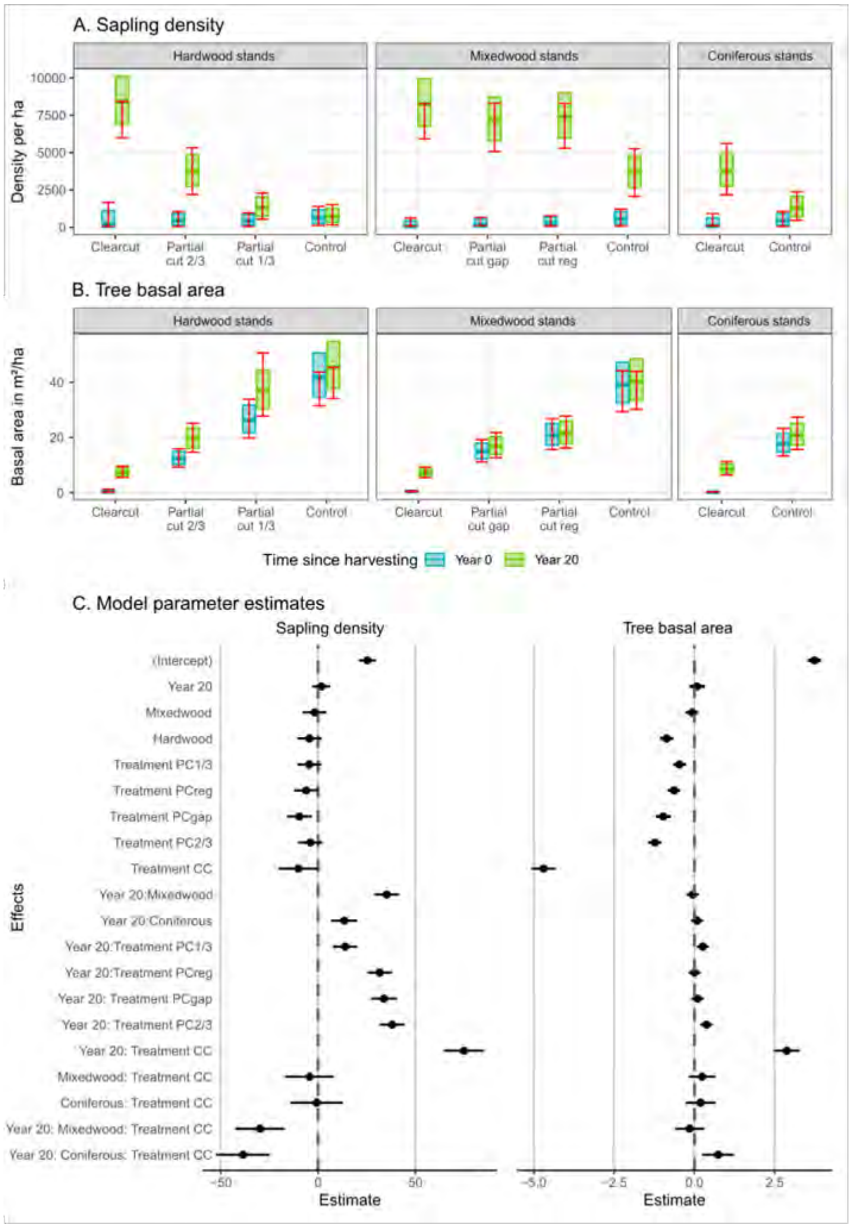

Figure 2.3 Results of the generalized linear mixed models for basal area of all stems over time for A sapling density and B commercial tree basal area and C the model parameter estimates with standard errors. In panels A and B blue and green rectangles represent confidence intervals for the mean values at year 0 and year 20 respectively. Red bars represent comparisons based on a Tukey test. Crossing bars on the response variable axis indicate that the means are not significantly different (at a threshold α=0,05). In panel C standard errors that do not intersect the 0 estimate are statistically significant.

Tree basal area did not decrease in any treatment over the twenty-year period (Figure 2.3 B). Clearcutting effectively homogenized differences in basal area across the three successional stages 20 years post-harvest. Immediately after clearcutting, basal area was reduced to 0.5 ± 0.3m^2/ha in all stages and twenty-years later basal area in all stages increased to 8.7 ± 3.9 m^2/ha. Twenty-years following partial cutting (PC), increases in basal area were greater in hardwood stands than in mixedwood dominated stands. Within hardwood stands, basal area increased significantly from 26.9 ± 6.1 m^2/ha to 38.2 ± 9.9 m^2/ha in PC1/3 (Figure 3B, Figure 3C). PC1/3 basal area was and remained similar to basal area in control over the 20-year period. More intense removal in the PC 2/3 resulted in smaller but significant increases in basal area with time (Figure 2.3 B, Figure 2.3 C). PC1/3 basal area was and remained similar to basal area in control over the 20-year period. More intense removal in the PC 2/3 resulted in smaller but significant increases in basal area with time (12.8 ± 3.5 m^2/ha to 19.9 ± 4.0 m^2/ha; Figure 3B, Figure 3C). In mixedwood stands, the average basal area remained similar between both pCreg and pCgap over time, showing a mean of 22.0 ± 6.0 m^2/ha and a mean of 17.6 ± 7.6 m^2/ha, respectively. These were significantly lower than that found in control stands (i.e., 41.0 ± 9.3 m^2/ha) over time (Figure 2.3 B).

2.5.2 Evolution in stem diameter distribution over 20 years

As expected, immediately following harvest, in the three successional stages, stem density in all diameter classes was higher in the control stands (Figure 2.4). As expected, within a successional stage, lower harvesting intensity resulted in stem diameter distributions that were more similar to control stands. With time, the significant increase in saplings added a positive skew and a J-shape to the stem diameter distribution. Consequently, twenty years post-harvest, the maximum density of stems shifted, in most successional stages and harvesting intensities, towards smaller diameters classes (4 to 8cm).

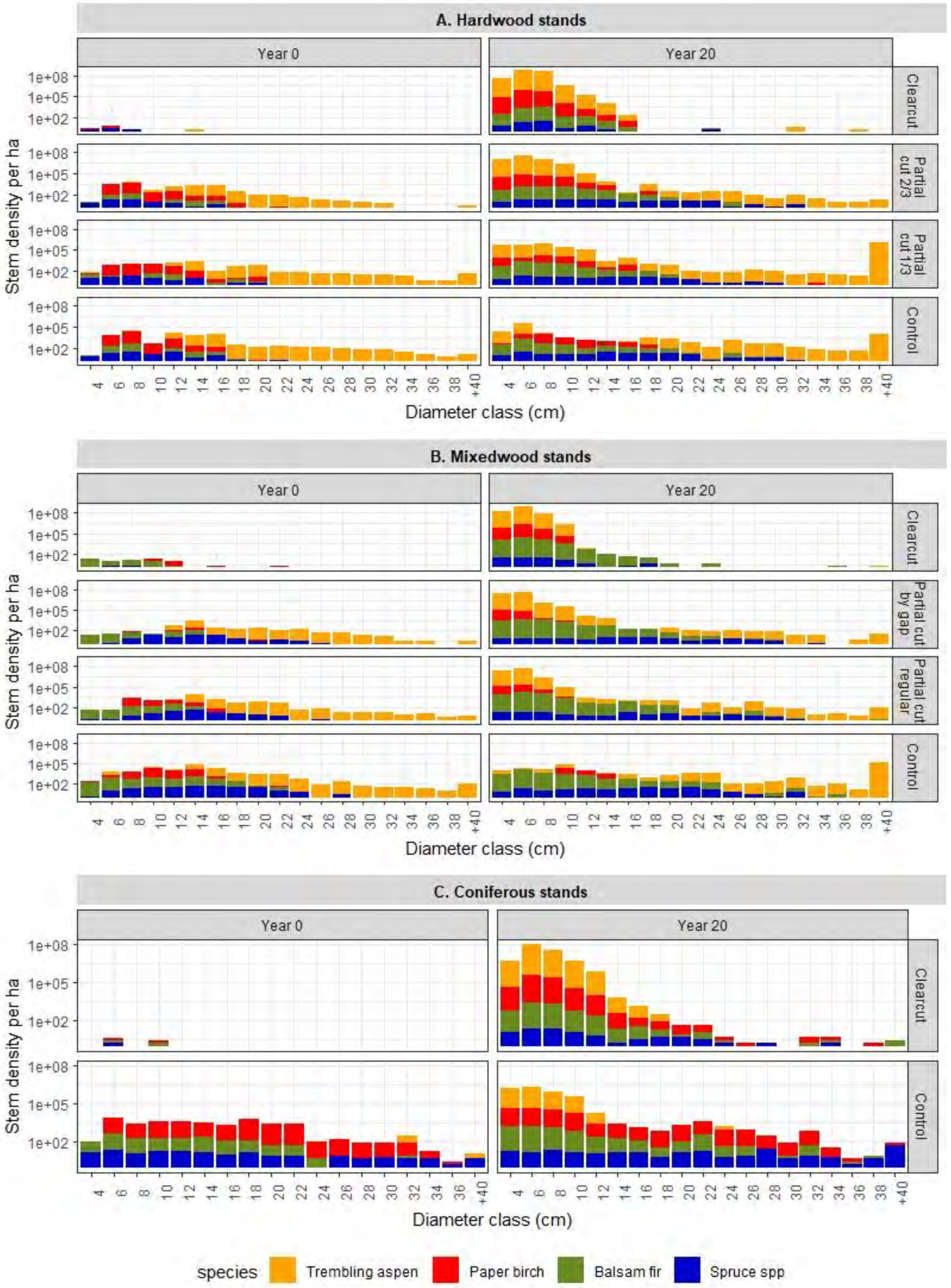

Figure 2.4 Diameter distribution of live stems per hectare, immediately and 20 years following harvest at different intensities in stands from hardwood, mixedwood and coniferous stands. Each color represents a different commercial tree species.

Immediately after harvest in hardwood stands, sapling composition (4-8cm DHP) was dominated by paper birch and spruce in all treatments (Figure 2.4). In the diameter classes 10-20 cm, aspen dominated all treatments composing 100% of stand after CC, 53% after PC2/3, 45% after PC1/3 and 57% after control. The other species, birch, fir, and spruce were equally distributed in terms of abundance. For larger trees (superior to 20cm DBH), in PC and control, aspen dominated the stands with an average proportion of 94%. Twenty years later, saplings were mostly composed by trembling aspen and balsam fir after P2/3 (74% and 14%, respectively), PC1/3 (44% and 40%, respectively) and control (44% and 36%). After CC, trembling aspen and paper birch saplings were mostly present (61% and 24%, respectively).

In mixedwood stands, year 0, saplings were dominated by balsam fir (around 70% in all treatments) and few spruce were present in the 6 and 8 cm diameter classes in all treatments (Figure 2.4). In PC and control stands, few paper birch were also present in the 8cm diameter class. In the diameter classes 10-20 cm, balsam fir were also dominant with paper birch in CC stands (58% and 42% respectively). Paper birch was a minor component in PC and control stands where trembling aspen, balsam fir and spruce dominated. In diameter classes superior to 20 cm DBH, trembling aspen dominated PC and control stands (85%). 20 years later, saplings were still mostly composed of balsam fir in all treatments (54% after CC, 59% after PCgap, 73% after PCreg and 94% after control). In CC and both PC types, trembling aspen was the second most frequent species in saplings (36% after CC, 37% after PCgap and 21% after PCreg). Its abundance was inversely proportional to size class in all harvested stands. In diameter classes 10-20 cm, balsam fir stayed dominant in all treatments composing 78% of stand stems after CC, 63% after PCgap, 73% after PCreg and 55% after control. After CC and PCgap, trembling aspen was the second most frequent species, composing 13% of stand after CC, and 22% after PCgap. After PCreg, trembling aspen and paper birch were the second most frequent species composing each 12% of the stand. After control, spruce was the second mostly present species, composing 28% of the stand. In higher diameter classes, even if trembling aspen stayed dominant in all stands, coniferous species, balsam fir in harvested stands and spruce in the control stands, were also found.

In coniferous stands, immediately after harvest, spruce, fir and birch saplings made up the composition of the CC and control stands (37%, 32% and 31% respectively) (Figure 2.4). In the 10-20cm diameter classes, CC was composed of half birch and half fir. No aspen was present in CC or the control stands. Larger trees were only found in control stands, where the four commercial species were present with a dominance of hardwood (49% birch and 12% aspen). Twenty years later, in diameter classes 4-20 cm, spruce, fir and birch were still found but aspen dominated in both CC (63%) and control (59%) stands. In the diameter classes superior to 20 cm DBH, half coniferous and half hardwood species were found in both CC and control stands.

2.5.3 Evolution in deadwood structure over 20 years

In hardwood dominated stands, immediately after harvesting, snag basal area was similar in PC and control stands (Figure 2.5). 20 years later, the average snag basal area in PC2/3 decreased (4.8 ± 2.2 m^2/ha to 3.8 ± 2.0 m^2/ha) and increased in PC1/3 (2.6 ± 1.4 m^2/ha to 4.0 ± 2.7 m^2/ha; Figure 2.5, Figure 2.6). In CC stands, while no snags had been inventoried immediately after the cuts, the basal are increased to 0.17 ± 0.06 m^2/ha twenty years later but, this value stayed significantly lower than in all other treatments. In terms of fresh downed deadwood, the pattern was reversed for the harvested stands. In 20 years, we observed a 98% decrease in fresh downed deadwood volume after CC and a 50% decrease after PC1/3. After PC2/3, the volume doubled (Figure 2.5). However, only clearcut stands were significantly different from control strands at both times (Figure 2.5, Figure 2.6). For old downed deadwood, we only observed a significant decrease in volume in clearcut stands (13% decrease) compared to control.

After PC2/3, the volume of old downed deadwood was lower immediately after harvest, it increased four-fold after 20 years to volumes similar to that found in the control stands. After PC1/3 and control, the volume increased slightly (from 44.8 ± 40.6 m^3/ha to 55.4 ± 29.0 m^3/ha; Figure 2.5, Figure 2.6).

In mixedwood stands, for all treatments, the average snag basal area remained similar over time with a slight decrease for the three harvested stands and a slight increase for the control stands (Figure 2.5, Figure 2.6). Only CC stands had a significantly lower snag basal area than control stands, at both times. The mean volume of fresh downed deadwood remained similar between all treatments over time with a slight decrease after clearcut and a slight increase after both PC and in control stands (Figure 2.5, Figure 2.6). The mean volume of old deadwood was similar between all treatments at both times (Figure 2.5, Figure 2.6). After all treatments it increased over time and significantly for PCgap. It doubled in the clearcut, increased sixfold for PCgap, fourfold in PCreg and tripled in control.

In coniferous stands, just after clearcut, no snag was inventoried and 20 years later we observed a few snags (0.8 ± 1.2 m^2/ha) but significantly less than found in the control stands (3.4 ± 2.0 m^2/ha) (Figure 2.5, Figure 2.6). For downed deadwood, fresh and old, there was a significant decrease after clearcut, but the decrease was more important for the fresh deadwood (divided by 51) than for the old deadwood (divided by 5) (Figure 2.5, Figure 2.6). If the volumes were significantly higher than control stands year 0, they became similar at year 20.

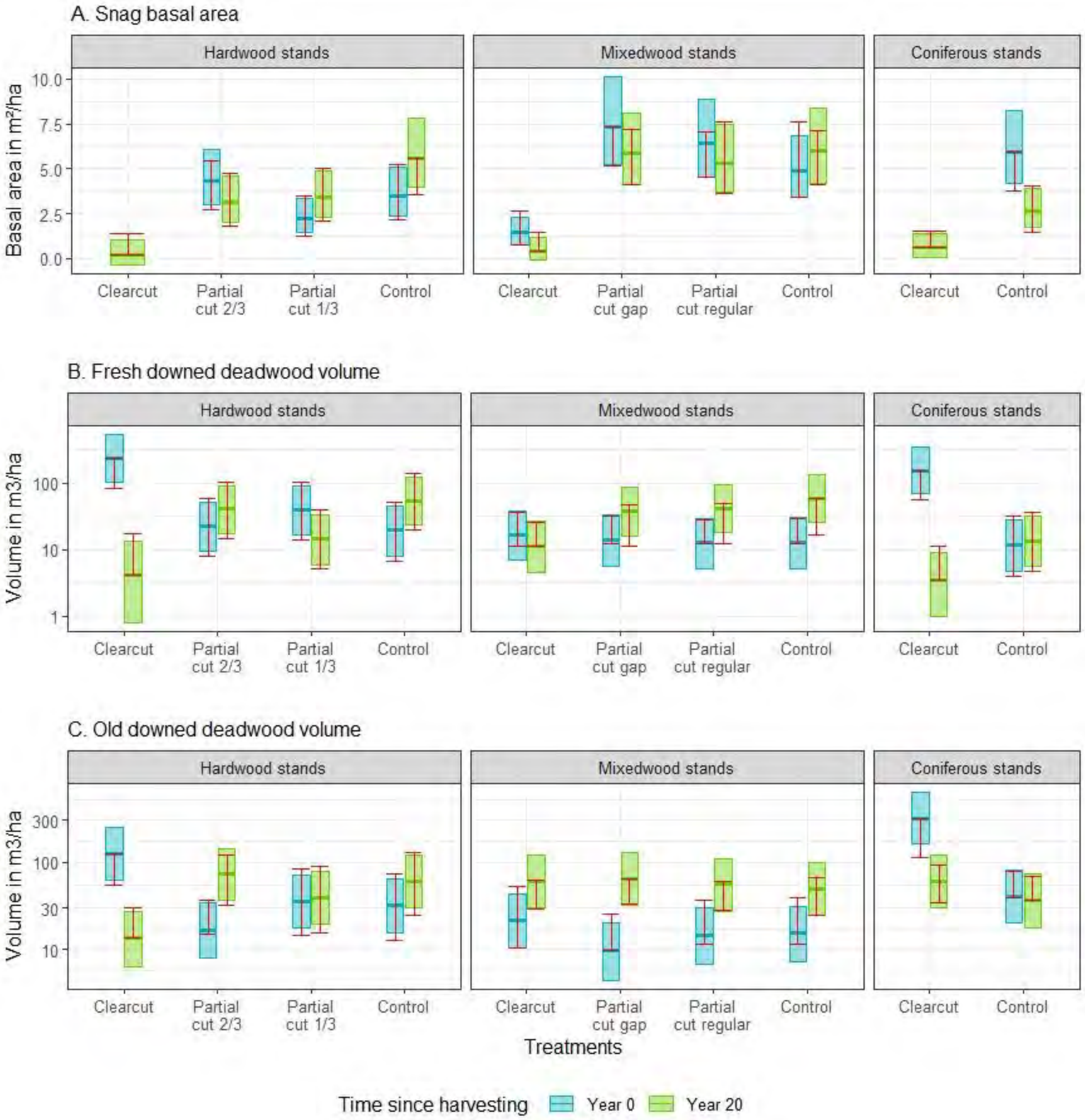

Figure 2.5 Results of the generalized linear mixed models for standing and downed fresh and old deadwood over time. A Snags basal area, B Fresh downed deadwood, and C Old downed deadwood. Note the log10 scale on the y axis in panel B. Blue and green rectangles represent confidence intervals for the mean values. Blue represents the data for year 0, and green represents the data 20 years after harvesting. Red bars represent comparisons based on a Tukey test. Crossing bars on the response variable axis indicate that the means are not significantly different (at a threshold α=0,05).

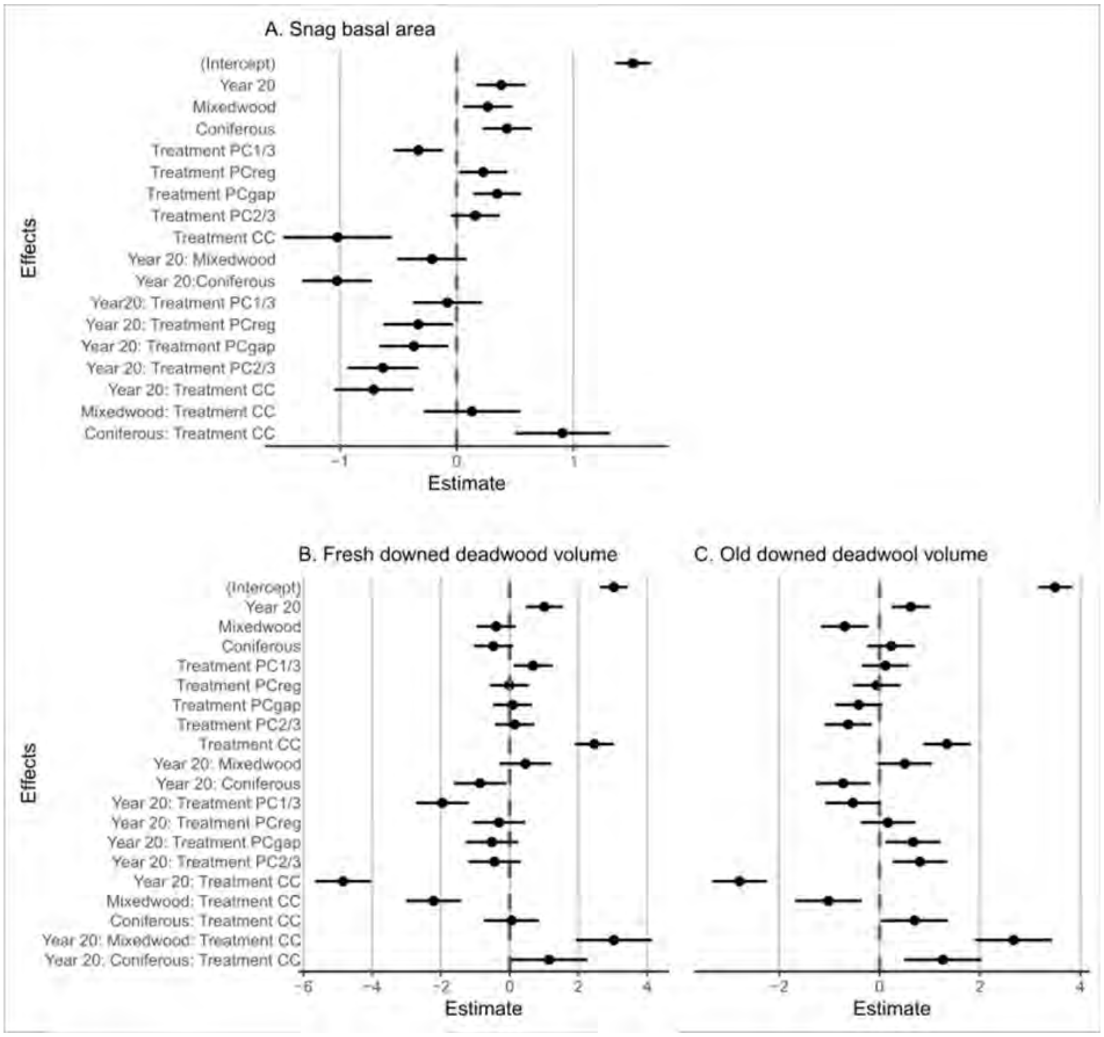

Figure 2.6 The generalized linear mixed model parameter estimates with standard errors. In panel A. Snag basal area, B. Fresh downed deadwood, and C. Old downed deadwood. Standard errors that do not intersect the 0 estimate are statistically significant.

2.6 Discussion

2.6.1 Potential of Ecosystem-based Management to delay, maintain or advance the transitions through successional stages

2.6.1.1 Dynamics in hardwood stands after partial harvesting

In the hardwood dominated stands, the sapling density increased by a factor of 3 for every 1/3 of overstory removed, in the 20 years following the harvesting. With an increase in cut intensity, the density of aspen increases while that of fir decreases over time. Gradowski *et al.* (2010) observed the same pattern in Western Canada in the same three successional stages- a reduced regeneration of aspen when a portion of the original stand was retained. Leaving residual mature aspen stems maintains some supply of auxin to the root system, which prevents suckering (DesRochers and Lieffers, 2001). In addition, aspen is a shade intolerant species, and its regeneration is negatively affected by shade and therefore by canopy retention (Frey *et al.*, 2003a; Man *et al.*, 2008). Thus maintaining 77% of the stems with the PC1/3 limited aspen suckering, resulting in decreased stem mortality and increased growth of pre-harvested established trees, over 20 years. However, between less intense PC (PC1/3) and control stands, regeneration and commercial tree basal area rates remained similar, over the 20 years. These results showed that PC1/3 only had negligible effects on stand structure, and thus, less intensive removal did not allow to accelerate the stand transition through successive cohort but rather maintained it in its original state.

In more intense PC, the density of aspen saplings was sufficient to establish a new aspen dominated stand or to conserve the aspen composition of an existing stand. The regeneration rates were significantly higher and commercial tree basal area were significantly lower than those found in the control stands, over the 20 years. These results showed that more intensive partial removal did not maintain the stand in its original state but set the stand back to an anterior to the pre-harvest stage and thus delayed the transition through successive cohorts. Even if the focus in conservation is often on old growth forests, aspen dominated stands are an important part of the boreal landscape, housing a specific biodiversity of vascular plants species (De Grandpre *et al.*, 2003), mosses, lichens (Boudreault *et al.*, 2000) and birds (Drapeau *et al.*, 2000). If aspen regeneration is an objective to maintain hardwood stands, more intensive cuts may be suggested. Conversely, less intensive cuts may be an effective strategy to minimize aspen regeneration in favor of coniferous species.

2.6.1.2 Dynamics in mixedwood stands after partial harvesting

In mixedwood stands, the two PC types had the same harvesting intensity (40% of the basal area) but differed in spatial configuration. Regardless of the harvesting configuration applied, we observed a strong regeneration of 11,042 ± 2224 saplings/ha, with a strong increase of trembling aspen saplings, significantly superior to that observed in control stands. This contradicts some studies that found that large open areas are needed to obtain significant regeneration of aspen (Landhäusser *et al.*, 2019; Rogers *et al.*, 2014), while here harvesting 40% of the total basal area was enough to stimulate regeneration. In these mixedwood stands, balsam fir saplings were more abundant than trembling aspen saplings in all harvest intensities, however fir abundance decreased, and aspen abundance increased along a gradient of PCreg, PCgap, CC. It is likely that the area of both small and large gaps has increased, partly due to windthrow, resulting in the observed higher densities of intolerant hardwood stems than those of the control stands in both partial harvests. In contrast, the presence of more fir than aspen saplings, suggests a “legacy” phenomenon of the original stand composition. Compared to the aspen dominant stands, the fewer aspen stems and consequently the sparser bud bank resulted in lower potential sucker production (Gradowski *et al.*, 2010) as has been found in other studies conducted in mixedwood stands (Bose *et al.*, 2015a; Maleki *et al.*, 2020b).

The two PC harvests slowed down the stand level growth rate and seemed to have stopped it over time as both PC harvest types resulted in a significantly inferior tree basal area than that found in control stands. Thus, they did not meet the objective of NDBM of advancing the transition of stands towards the next successional stage (coniferous stands) (Bergeron and Harvey, 1997; Gauthier *et al*., 2009). However, they maintained a 50-50 proportion of hardwood and coniferous tree species. Bose *et al.* (2015b), with a spatially explicit stand dynamics model SORTIE-ND, simulated over 100 years the development of the same stands after logging. They showed that, by favoring a continuous recruitment of trembling aspen as well as tolerant conifers, all gap treatments, and 80% dispersed harvesting created more complex stand structures in both stand types (Bose *et al.*, 2015b). Our field-based results observed after 20 years support these modelled trends in structure and composition. Thus, both partial cut types, regular and dispersed, have the potential to maintain a mixed stand structure over hundreds of years.

2.6.1.3 Dynamics after clearcuts

Twenty years after CC, the three successional stages had similar commercial tree basal areas meaning no matter in what type of stand the harvests were carried out, aspen dominated, mixed or conifer dominated stands, there is about 8 m^2/ha of commercial trees established after 20 years. Furthermore, this implies that an equal number of young trees established after harvest have reached 10 cm in DBH after 20 years in all successional stages. However, if we compared 20 years after harvest the regeneration in the three successional stages, there was a very limited density of saplings in coniferous stands compared to hardwood and mixedwood stands (half as much). This limited regeneration shows the limits of applying CC in old forests. In 2000, the low frequency of aspen (2% of plots) found in control stands in coniferous stands probably explains the significantly smaller aspen sapling density found 20 years after CC (Gradowski *et al.*, 2010). Despite this, a higher regeneration of hardwood species compared to coniferous species was observed. The limited conifer recruitment and growth may be due to the strong competition for resources with hardwoods but also with shade-tolerant woody shrubs, such as *Acer spicatum* Lamb., which vigorously occupies openings after harvesting. We did not consider these non-commercial species in our study, but we know that they limit the establishment of seedlings just after cuts (Brais *et al.*, 2004). Often, they are pioneer species that benefit from the openings in the canopy to multiply, preventing the establishment of commercial tree seedlings. Thus, CC practiced in mixedwood and coniferous stands did not completely "reset" the development of the stands, because we did not find a structure and composition similar to clearcuts stands in hardwood stands. It has limited the establishment of conifers and should continue to do so at least 80 years (Maleki *et al.*, 2020b).

2.6.2 Potential of Ecosystem-based Management to enhance the development of old-growth attributes in mature even-aged stands

In hardwood dominated stands, Bose *et al.* (2014) observed that 12% of total stems died three years after PC2/3, compared to 1% three years after PC1/3. The higher tree mortality after more intensive PC was translated into higher snag density than in PC1/3 and controls stands. In the PC2/3, after 20 years, , snag basal area decreased and downed deadwood volume increased, the reverse of what was observed after PC1/3. Solarik *et al.* (2012) observed in hardwood, mixed and coniferous stands of Western Canada that residual aspen mortality was highest after more intense cuts (90 and 80% of BA harvesting) and that five years after harvest, most of the dead trees remained standing as snags (87%) but at ten years after harvest approximately 40% of the dead trees had fallen. If the snag development continues to decrease over time it might be a problem for species associated with this habitat in hardwood forests, like bryophytes, lichens (Crites and Dale, 1998) and birds (Drapeau *et al.*, 2009). The increases in downed deadwood deposition after PC2/3 might be due to windthrow (Lavoie *et al.*, 2012; Mascarúa López *et al.*, 2006), causing snag density to decrease. Thus, retention time of snags is relatively short as much of the potential deadwood reaches the ground within 20 years and probably even earlier. After PC1/3, the decreases in downed deadwood deposition over time suggest that the deadwood delivery system provided by retention can be slow or delayed. This can be a constraint for the biodiversity associated with this type of habitat like bryophytes, insects, or mammals (Caners *et al.*, 2013a; Fauteux *et al.*, 2012; Saint-Germain *et al.*, 2006).

In mixedwood dominated stands, the diminution of snag basal area across time is reflected in the increased volume of fresh downed deadwood. This increased supply of fresh deadwood is expected to decay at a slower rate than in hardwood dominated stands, with decay times estimated at fifty years for hardwoods and eighty years for conifers, which should offset the loss of snags for a few decades (Brais *et al.*, 2006). The increase in old downed deadwood, particularly in PCgap, allows the conservation of the different deadwood structures in the stand and thus the biodiversity associated with it (Cole *et al.*, 2008).

In coniferous stands, in the first few years after CC, high volumes of fresh downed deadwood has been documented in similar stand types in managed and natural settings (Heikkala *et al.*, 2014; Moussaoui *et al.*, 2016). Mortality, in the first years after disturbance, may occur because of competition for resources or gaps generated by the harvest which create wind inlets, increasing the risk of windthrow (Lavoie *et al.*, 2012; Mascarúa López *et al.*, 2006). In our case, the fact that we found high volumes of fresh downed deadwood may be related to the absence of inventoried snags. Snags were probably present in the pre-harvest stands, but they must have been weakened by the harvesting which create wind entries, and thus fallen on the ground. The volume of downed deadwood strongly decreased over time in contrast to the snag basal area which increased. This growth is a good sign that in the future, deadwood will be available on the ground, which is necessary to conserve old-growth attributes in mature stands (Martin *et al.*, 2018).

2.6.3 Combining natural and anthropic disturbances

The continuous recruitment of young trembling aspen in mixed and coniferous stands could come from the spruce budworm outbreak that occurred in the region between 1971-1985 (Campbell *et al.*, 2008; Morin *et al.*, 1993). Maleki *et al.*, (2020b) found that the effect of spruce budworm epidemics on stand development, might be visible for at least 100 years after the event. Stand replacement dynamics following disturbances depended upon the composition of the disturbed stands and site conditions, for instance, seed sources or seed bed limitations (Bergeron, 2000; Colford-Gilks *et al.*, 2012). Insect outbreaks can increase the regeneration of hardwood species if conifer regeneration is not sufficient (Bergeron *et al.*, 2014). The epidemic impacted the regeneration but also probably the vitality of residual coniferous trees, particularly in the oldest stands. Normally, in natural stands of this age we were expecting to find a majority of large diameter coniferous trees (Bergeron, 2000; Campbell *et al.*, 2008; Chavardès *et al.*, 2021; Chen and Popadiouk, 2002). In our case, stands were dominated by two to four times more saplings than larger trees, dominated by shade intolerant birch and shade tolerant spruce. This result suggests that in the future, if hardwood species persist and grow with the coniferous species, we would have more of a mixed stand than a coniferous dominated stand. The conversion of conifer-dominated stands to mixedwood stands by spruce budworm outbreaks that favor the recruitment of shade-intolerant tree species, such as trembling aspen and white birch was also observed by Chen and Taylor (2012) and Kneeshaw and Bergeron (1998). This effect would be accelerated with the combination of CC and would be perceptible for at least 100 years of post-disturbance succession (Maleki *et al.*, 2020b). Our study confirms the importance of taking the site natural disturbance post history into account in harvesting planification.

2.7 Conclusions

The principal aim of this study was to identify if silvicultural objectives established in NDBM were reached following different harvest intensities practiced in three different stand types representing the three successional stages, in the boreal mixedwood forest. The residual tree layer in the PC1/3 of hardwood dominated stands clearly retains much of the closed, relatively intact structure of the control stands. Like Brais *et al.*, (2004) suggested, the moment of final harvest should be determined by stand health. PC1/3 may be used to prolong final harvest in stands of nonclonal species by reducing inter-stem competition and removing the most suppressed trees. In contrast PC2/3 has slowed the stand development by disproportionately favoring the recruitment and growth of shade-intolerant species such as trembling aspen. This cut can be used to conserve hardwood-dominated stands until the saplings in clearcuts grow. These effects are somewhat similar to those of regular and gap cuts in mixedwood stands, slowing down the development but also maintaining the stand in its original structure.

Our observations confirmed the assumptions of many others that (1) the more intense the harvest, the longer it takes for the stand to return to its reference state, (2) post-harvest stand structure and composition depends on several factors including spatial patterns of harvest and retention rate, and (3) post-harvest stand successional dynamics may be influenced by pre-harvest natural disturbances such as spruce budworm outbreaks (Bose *et al.*, 2015a; Bose *et al.*, 2015b; Brais *et al.*, 2013). Our study confirmed that this silvicultural approach fulfills a part of the NDBM objectives i.e., PC allowed the maintenance of stands with mixed structure and composition, constituting an interesting complement to CC, which reset stand regeneration. However, it did not support the ability of PC to enhance the development of old-growth attributes in mature even-aged stands which could imply future biodiversity losses and thus deserves a more important temporal follow-up. Furthermore, partial harvest did not progress younger stands to earlier stages with more intensive harvesting, or even advance stands to later stages with less intensive harvesting. We essentially had an initial impact that seemed to dissipate over time.

2.8 Acknowledgements

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CHAPITRE 3

BRYOPHYTE COMMUNITIES’ RESPONSE, 20 YEARS AFTER FOREST MANAGEMENT IN BOREAL MIXED FOREST

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3.1 Abstract

Sustainable forest management relies on a diversity of harvesting practices to conserve the variety of stand structures and compositions found in natural forests. Extensive use of clearcuts can homogenize stand structure by removing all the canopy, damage forest soils and destroy older downed woody debris already present within stands. In contrast partial cuts maintain some standing overstory and conserve certain biological legacies like large live trees as well as standing and downed dead wood, and thus should better conserve biodiversity. However, given the large number of species potentially affected by harvest operations, balancing harvesting intensity and conservation of biodiversity requires a clear understanding of habitat requirements of resident organisms and species conservation post-harvest. We examined the impacts of increasing intensities of stem removal (33%, 40%, 66% and 100%) 20 years after harvest on bryophyte communities in three stand types common in the succession sequences of Eastern boreal mixedwood forests that were dominated by trembling aspen, mixedwood and conifers. While many generalist and common forest species were shared among all harvesting levels and forest types, more specialized species like liverworts differed strongly between uncut and clearcut stands and less between uncut and partial cut stands. Bryophyte species in hardwood dominated stands tolerated more fluctuations in environmental conditions than species in mixed stands. We were unable to find habitat specialists typically associated with coniferous stands and may be related to prior outbreaks of spruce budworm that occurred 30 years ago. Our results highlight how harvest intensity and forest stand type interact to affect bryophytes and how intact stands may be required to conserve many species that are sensitive to any degree of harvesting.

3.2 Resumé

La gestion durable des forêts repose sur l’utilisation d’une diversité de pratique de récolte afin de conserver la variété de structures et de compositions des peuplements que l'on trouve dans les forêts naturelles. L'utilisation intensive des coupes totales homogénéise la structure des peuplements en retirant l’ensemble de la canopée, endommageant les sols forestiers et détruisant le bois mort plus ancien déjà présents dans les peuplements. En revanche, les coupes partielles maintiennent une partie de l'étage dominant et conservent certains héritages biologiques tels que les grands arbres vivants ainsi que le bois mort sur pied et abattu, et devraient donc mieux préserver la biodiversité. Cependant, étant donné le grand nombre d'espèces potentiellement affectées par les pratiques de récolte, l'équilibre entre l'intensité de la récolte et la conservation de la biodiversité nécessite une compréhension claire des besoins en habitat des organismes résidents et de la conservation des espèces après la récolte. Nous avons examiné les impacts d'intensités croissantes d'enlèvement des tiges (33%, 40%, 66% et 100%), 20 ans après récolte, sur les communautés de bryophytes dans trois types de peuplements communs dans les séquences de succession des forêts boréales mixtes de l'Est qui étaient dominées par les feuillus, mixtes et les conifères. Alors que de nombreuses espèces forestières généralistes et communes étaient partagées entre tous les niveaux de récolte et tous les types de forêts, les espèces plus spécialisées comme les hépatiques différaient fortement entre les peuplements non coupés et issus de coupes totales et moins entre les peuplements non coupés et issus de coupes partielles. Les espèces bryophytes des peuplements dominés par les feuillus toléraient davantage les fluctuations des conditions environnementales que les espèces des peuplements mixtes. Nous n'avons pas trouvé d’espèce spécialiste des peuplements de conifères, ce qui pourrait être lié à des épidémies antérieures de tordeuse des bourgeons de l'épinette survenues il y a 30 ans. Nos résultats soulignent la façon dont l'intensité de la récolte et le type de peuplement forestier interagissent pour affecter les bryophytes

et comment des peuplements intacts peuvent être nécessaires pour conserver de nombreuses espèces qui sont sensibles à tout degré de récolte.

3.3 Introduction

Despite a growing consensus that forest management aiming to conserve biodiversity should be based on the spectrum of disturbance variability (time interval, size, severity) produced by natural regimes (Gauthier *et al.*, 2009; Kuuluvainen, 2002; Puettmann *et al.*, 2012), clearcutting remains the dominant harvesting approach in boreal forests (Boucher *et al.*, 2021; Kuuluvainen and Gauthier, 2018). These intensive cuts produce complex impacts on species assemblages, including bryophyte communities (Caners *et al.*, 2013b; Paquette *et al.*, 2016). Bryophytes are a fundamental boreal ecosystem component in terms of richness and function (Fenton *et al.*, 2015; Holland‐Moritz *et al.*, 2018; Rudolphi and Gustafsson, 2011; Turetsky *et al.*, 2012). They are implicated in water filtration, carbon sequestration, and soil thermoregulation and they also provide important habitats for cyanobacteria, invertebrates, and seedlings of vascular plants (Fenton *et al.*, 2015; Holland‐Moritz *et al.*, 2018; Rudolphi and Gustafsson, 2011; Turetsky *et al.*, 2012). Given the functional roles of bryophytes in forest ecosystems, a change in bryophyte community in response to disturbances like clearcuts could have repercussions on the overall boreal system.

Clearcutting removes all merchantable stems from the canopy and can damage the forest floor as well as future inputs of downed woody debris. Clearcutting also simplifies and eliminates old growth forest structure, and stands are established that would otherwise be initiated by natural disturbances such as fire (Bergeron *et al.*, 2002; Nguyen-Xuan *et al.*, 2000). In contrast, partial cuts can attenuate many of these problems by reducing impacts on forest soils and by conserving biological legacies such as live standing and deadwood (Gustafsson *et al.*, 2012; Maleki *et al.*, 2020a). Thus, partial cuts are thought to maintain elements of existing stand structure and in some cases even to accelerate the development of structure similar to that of mature stands that are affected by insect outbreaks, disease and senescence (Brais *et al.*, 2013; Gauthier *et al.*, 2009).

The term "bryophyte" groups three phyla of terrestrial plants: the Marchantiophytes (liverworts), the Bryophytes senso stricto (mosses including the genera sphagnum) and the Anthocerotophytes (hornworts) which can be differentiated by their morphological and physiological characteristics but also by their habitat requirements (Boudreault *et al.*, 2000; Lõhmus *et al.*, 2006). For example, many liverwort species are restricted to deadwood (Ewald, 2000) and while some species are associated with well-decomposed coniferous deadwood, such as *Cephalozia lunulifolia* (Dumort.) and *Tritomaria exsectiformis* (Breidl. Schiffn), others such as *Chiloscyphus pallescens* (Ehrh. Ex Hoffm.) are associated with well decomposed hardwood deadwood (Caners *et al.*, 2013a). In addition, bryophytes are poikilohydric, they can gain and lose water rapidly and have no control over water loss compared to vascular plants. This means that changes in microclimate like a decrease in humidity generated by canopy removal will negatively impact their diversity (Chen *et al.*, 1999; Heithecker and Halpern, 2006). These unique physiological and habitat requirements make them very sensitive to forestry operations and thus well suited to study the consequences of forest harvesting on biodiversity (Caners *et al.*, 2013b; Paquette *et al.*, 2016).

Consequently, studies have examined the direct effects of harvesting on bryophyte biodiversity. Clear cuts can have direct negative impacts on biodiversity, particularly epixylic bryophytes (deadwood-living bryophytes), as these species require a constant supply of decaying wood, and a humid and shady microclimate (Cole *et al.*, 2008; Hofmeister *et al.*, 2015). Partial cuts, in contrast, are believed to have less impact than clearcuts as the residual stands promote the development of old growth forests structural features by ensuring a continual supply of deadwood and the presence of later successional species (Caners *et al.*, 2013a; Kuuluvainen *et al.*, 2019).

Boreal mixedwood stands can be characterized by the successive dominance of intolerant hardwood, mixed and softwood stands (Bergeron *et al.*, 2000; Bergeron *et al.*, 2002) and offer a diversity of valuable habitats for bryophytes (Barbier *et al.*, 2008). For example, variation in deciduous tree foliage results in seasonal changes in temperature, humidity, irradiance, and wind in the understory (Barbier *et al.*, 2008). In contrast, the constant and relatively dense overstory of coniferous stands, which retain their needles all the year, buffers seasonal variations of regional climate on the understory (Barbé *et al.*, 2020). Thus, bryophyte species in predominantly hardwood stands must be able to tolerate more fluctuating seasonal conditions than species in mixed stands, which must be able to tolerate more fluctuating conditions than species in coniferous stands.

This study examined the effects of increasing stem removal (33%, 40%, 66% and 100%) on bryophyte communities in three successional cohorts of boreal mixedwood forests. Specifically, we tested: 1) whether harvest intensity influenced bryophyte communities, 20 years post-harvest; 2) whether partial harvesting promotes old-growth forest bryophyte assemblages; and 3) which environmental factors are drivers for bryophyte communities' richness? We hypothesized that (1) harvesting treatments in the oldest forests (cohorts 2 and 3) will have greater effects on bryophyte communities than in young forests (cohort 1). Twenty years after harvesting, we anticipated greater differences between control and harvested in the oldest stands where bryophyte communities should reform more slowly from disturbance. We also hypothesized that (2) the more intense the cut, the longer it would take to recover habitat conditions similar to the control stands and thus to observe bryophyte communities similar to the communities in the respective control stands. Finally we expected (3) that across all cohorts, that more specialist species, such as those dependent on specific microhabitats, would be better maintained in less intense harvests (Király *et al.*, 2013; Rambo, 2001).

3.4 Materials and methods

3.4.1 Study area

Our study area was located in the Lake Duparquet Research and Teaching Forest (LDRTF) in the Abitibi region of northwestern Quebec, Canada (48°30'N, 79°20'O). The region is situated in the mixedwood zone of the boreal forest, in the balsam fir-white birch (*Abies balsamea* (L.) Mill and *Betula papyrifera* Marsh) bioclimatic domain. The territory of the LDRTF is located on glaciolacustrine clay deposits left by proglacial Lake Ojibway (Vincent and Hardy, 1977). Soil texture is characterized by heavy clay (>75% clay) and the forest floor is a thin mor of 2–7 cm. The climate is continental with an average annual temperature of 1°C and annual precipitation of about 989 mm with 30% in the form of snow (Mont Brun weather station, average over the last 25 years) (Environnement Canada, 2019).

3.4.2 Experimental design and treatments

The SAFE project (french acronym for "sylviculture et aménagement forestier écosystémique" or ecosystem management and sylviculture) was established between 1998 and 2001. SAFE consists of a series of silvicultural experiments carried out in three stand types corresponding to three cohorts that typify post-fire succession in this region. Cohort 1 stands were aspen dominated stands (*Populus tremuloides* Michx.) of fire origin dating from 1923. Cohort 2 stands were mixed stands principally composed of aspen, balsam fir, and white and black spruce (*Picea glauca* [Moench] Voss and

Picea mariana [Mill.] B.S.P.) of fire origin dating from 1910. Cohort 3 stands were mixed stands with balsam fir, spruce and paper birch (*B. papyrifera*) that experienced a partial disturbance from the spruce budworm outbreak (*Choristoneura fumiferiana Clem.*, Lepidoptera: Tortricidae, 1970-1987), in fire origin stands dating to 1760 (Bergeron and Dansereau, 1993; Morin, 1994) (Figure 3.1).

In stands from cohort 1, one no-harvest (control), one clear cut treatment (CC) and two partial cut (PC) treatments were carried out. One-third cuts (PC1/3), removing about 33% of the total basal area, and two-third cuts (PC2/3), removing about 66% of the total basal area were applied. The first cut consisted of a thinning from below where non-vigorous stems were removed and the second cut was essentially thinned from above with larger, vigorous stems preferentially selected. For stands from cohort 2, one control, one CC and two types of PC cuts where 40% of the stems were harvested were made: one cut with regular harvest, i.e. all trees were removed in 5 m-wide hauling trails, and approximately 25% of stems were harvested to a depth of 6 to 7 m in the adjacent strips (PCreg), and one cut with harvest by gaps of approximately 400 m^2 in area (PCgap) (Figure 3.1). In stands from cohort 3, one control and one CC were applied. Experimental units ranged from 1 to 2.5 ha in size and were applied in a complete block design with three replications of each treatment. Harvesting was done without heavy machinery in all treatments. Before harvesting, in each experimental unit, 5 circular permanent plots of 400m^2 (radius = 11.28m) were established to follow the stand structure and composition over time for a total of 150 plots, 60 plots in each stand of cohorts 1 and 2, and 30 in stands of cohort 3.

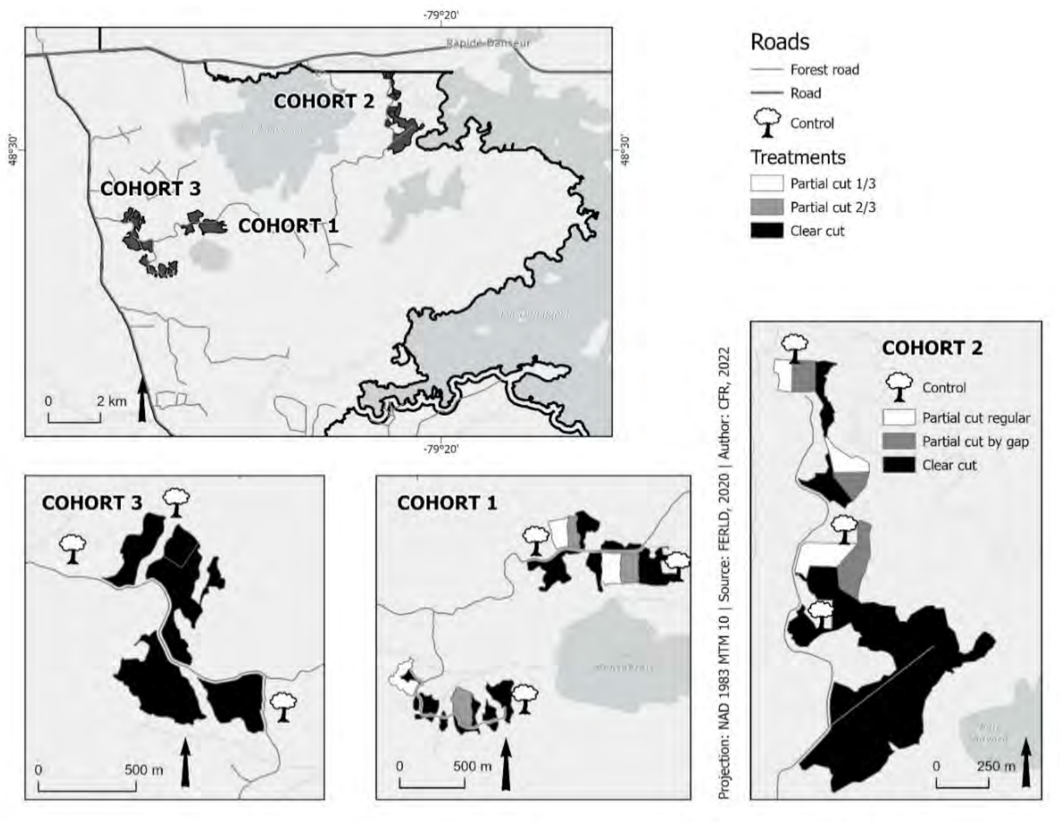

Figure 3.1 Experimental treatments of the three phases of the SAFE project. Source: http://safe.uqat.ca/default.htm.

3.4.3 Sampling design

3.4.3.1 Stand structure and downed deadwood

In each permanent 400m² plot, all live stems greater than 9.1 cm in diameter at breast height (DBH) were identified and measured to determine tree density by species (Annexe B). Total hardwood and coniferous basal area in each plot represent the "stand" descriptor variables in the models. In each permanent plot, we also count all stumps and standing deadwood, snags, where bryophytes were present. We estimated volume of downed deadwood (for logs with a diameter > 5 cm) using the line-intercept method (Van Wagner, 1982). One triangle with 30 m sides was sampled in each block of each treatment and deadwood frequency was recorded by diameter and by decomposition class based on Daniels *et al.* (1997). Coarse deadwood was divided into two large decomposition classes: fresh and well decomposed (fresh_dw = classes 1 to 3, old_dw= classes 4 to 5) and summed over all diameter classes. Stump abundance, snag abundance, fresh deadwood volume, and old deadwood volume represent the "microhabitat" variables in the models.

3.4.3.2 Environmental conditions

Weather micro-stations (WatchDog 1525 Micro station) with soil moisture and temperature probes (SM 100 soil moisture sensor and SMEC 300 soil moisture / EC / temperature) were placed 10 cm deep in the soil. We selected randomly and placed stations in three of the five permanent 400m² plots in each treatment, per block, per cohort, for a total of 90 stations. Temperature and air humidity measurements were taken every hour, during a growing season (June 1st to the end of September in 2020) (Annexe B). We took the 2 extremes of temperatures, minimum and maximum, at each plot to then make an average minimum and maximum per treatment per cohort, over a growing season. Average minimum and maximum soil temperature and moisture content represent the climate variables in the models.

3.4.3.3 Bryophyte communities

We used the transect method for the bryophyte inventory (Kerns *et al.*, 2002). From the center of each permanent plot, we traced a 11.28 meter long (radius of the permanent plot) and 1 meter wide transect, oriented north to south. Across the entire transect, we collected bryophytes by microhabitat. The types of microhabitats were trees bases (<2m from the ground), snags, fresh deadwood, old deadwood, stumps, and mineral soil. All the sampled bryophyte specimens were placed in individual marked paper bags to be identified in the laboratory. Taxonomy is based on Faubert (2012, 2013, 2014).

species have a good dispersal capacity and few ecological requirements to establish a colony. Therefore, they often have a large distribution range and are found in a variety of habitats. Specialist species are closely associated with specific microhabitats (the smallest subunit of forest habitat like pieces of deadwood, rocks), with narrow ecological requirements and reduced dispersal abilities (During, 1992; Johansson *et al.*, 2012).

3.4.4 Data analyses

3.4.4.1 Response of bryophyte communities to treatments, as a function of cohorts

We evaluated the pattern of overall community composition by species lifeform across cohorts and treatment types with principal coordinate analysis (PCoA; (Borcard *et al.*, 2018)) based on Bray-Curtis dissimilarity. Negative eigenvalues, obtained from PCoA axis were corrected by the Cailliez correction (Gower and Legendre, 1986). Caillez correction consists of adding a constant to the dissimilarity matrix to get two null eigenvalues and the others positive in PCoA. We performed a priori tests of treatment and cohort effects on community pattern using distance-based tests of multivariate differences between treatment types (10 predefined groups) using multiple response permutation tests (PERMANOVA), with 9999 permutations (Anderson, 2014). These analyses PCoA and PERMANOVA were then repeated for each cohort separately. To visualize species found and share by treatment of each cohort we made Venn diagrams (Gao *et al.*, 2021).

We compared bryophyte richness between treatments within each cohort. Bryophyte richness was expressed as the average number of species per plot per treatment type in each cohort and are examined for all bryophyte species combined (total species richness) and for each bryophyte life form (average richness of liverworts, acrocarpous and pleurocarpous mosses). To determine the response of species richness to treatments, we first ran model selection to identify the best random effects model, associated with the nested sampling structure. The model with only block effect, excluding the plot had the lowest AICc. Then generalized linear mixed models (Poisson family) with random block effects were used to evaluate the differences in specific richness between treatments as a function of cohort (Annexe A). Post hoc tests based on Tukey were performed to examine the differences among pairs of treatments.

3.4.4.2 Relationship between life form and environmental conditions in the cohorts

To investigate the effect of environmental variables on bryophyte communities, represented by the richness of each life form in each cohort, we performed multimodel selection based on eight candidate models that included a null model, individual and combined models of the environmental variables and the bryophyte richness for each life form in each cohort (Tableau 3.1). We used generalized linear mixed models with the Poisson family. The responses to treatments and environmental conditions of acrocarpous, pleurocarpous and liverworts communities were examined cohort by cohort. Environmental conditions were represented by stand structure (hardwood and coniferous species densities), microhabitats (abundance of stumps and snags, volume of fresh and old deadwood on the ground) and climate (mean minimum and mean maximum soil temperature and moisture content over a growing season).

Tableau 3.1 Models tested for multimodel selection procedure for each life form and each cohort.

Model	Variables considered
Null model	1
Each class of variable separately	
Climate	min_temp + max_temp + min_soil_moist + max_soil_moist
Stand	hardwood + coniferous
Microhabitats	stumps + snags + fresh_dw + old_dw
Combined models	
Climate + Stand	min_temp + max_temp + min_soil_moist + max_soil_moist + hardwood + coniferous
Climate + Microhabitats	min_temp + max_temp + min_soil_moist + max_soil_moist + stumps + snags + fresh_dw + old_dw
Stand + Microhabitats	hardwood + coniferous + stumps + snags + fresh_dw + old_dw
Global model	
Complete	min_temp + max_temp + min_soil_moist + max_soil_moist + hardwood + coniferous + stumps + snags + fresh_dw + old_dw

Candidate models were ranked based on the Akaike information criterion corrected for small sample size (AICc, (Burnham and Anderson, 2002)). Models with the lowest AICc were considered the best compromise of parsimony and explanatory power. Several models can be selected, we have chosen to keep the models that had a delta AICc < 2. In this case, evidence-ratio tests were performed to compare their respective explanatory weight. Subsequently, based on the previous models, the effect of each explanatory variable of the best model(s) was examined and it was determined that variables with 95% confidence intervals excluding 0 had a significant effect on community composition.

All analyses were conducted with R software (version 4.0.3, R core Team 2020). Lme4 and emmeans packages were used for general linear models and post-hoc tests. PCoA and PERMANOVA were conducted with the vegan package (version 2.3.0; (Therneau, 2004)). AICc were computed with the aiccmodavg package (version 2.1.1, (Mazerolle, 2017)). In all statistical tests, a P value ≤ 0.05 is considered significant.

3.5 Results

3.5.1 Bryophyte community: composition across cohorts

We identified a total of 69 species of bryophytes, 25% of which can be considered rare in the dataset (≤ 5 occurrences, $< 0.1\%$ of the total observations) (Figure 3.2, Annexe C). 19 species of all those identified were found in all treatments in the 3 cohorts. Four of these species were acrocarpous, ten were pleurocarpous and five were liverworts. Bryophyte composition varied by cohort (PERMANOVA results, pseudo-F = 5.233, $R^2 = 0.15467$, p = $1\ e^{-04}$***) but community differences among treatments within a cohort were more limited. There was a gradient from hardwood dominated stands, cohort 1, to mixedwood stands, cohort 2, along the first axis (variance explained: 10.16%) with clearly separated ellipses (Figure 3.2). The coniferous stands, cohort 3 was primarily explained by the second axis (variance explained: 6.70 %) (Figure 3.2). Many forest generalist species were shared among the three forest types, including 78% of acrocarpous species (e.g. *Dicranum montanum* Hedw*.*, *Dicranum polysetum* Sw*.*, *Plagiomnium cuspidatum* Hedw.) and 68% of pleurocarpous (*Brachythecium campestre* Műll.Hal*.*, *Callicladium haldanianum* Grev*.*, *Sanionia uncinata* Hedw.) (Figure 3.2, Annexe C). However, only 35% of the liverworts were found in all three cohorts, such as common species like *Chiloscyphus profundus* Nees*, Ptilidium ciliare* L. and *Ptilidium pulcherrimum* Weber. This lowest similarity among cohorts in the liverwort group is reflected by the presence of species unique to a given treatment. *Aneura pinguis* L.*, Barbilophozia attenuata* Mart.*, Bazzania trilobata* L.*,* and *Geocalyx graveolens* Schrad., were only found in cohort 1 in the PC or in the control (Figure 3.2, Annexe C). *Frullania inflata* G.*, Homalia trichomanoides* Hedw.*, Jamesoniella autumnalis* DC.*, Radula complanate* L. were only found in the PC or in the control from cohort 2. No species were unique to cohort 3 which had only two treatments, control and clearcut.

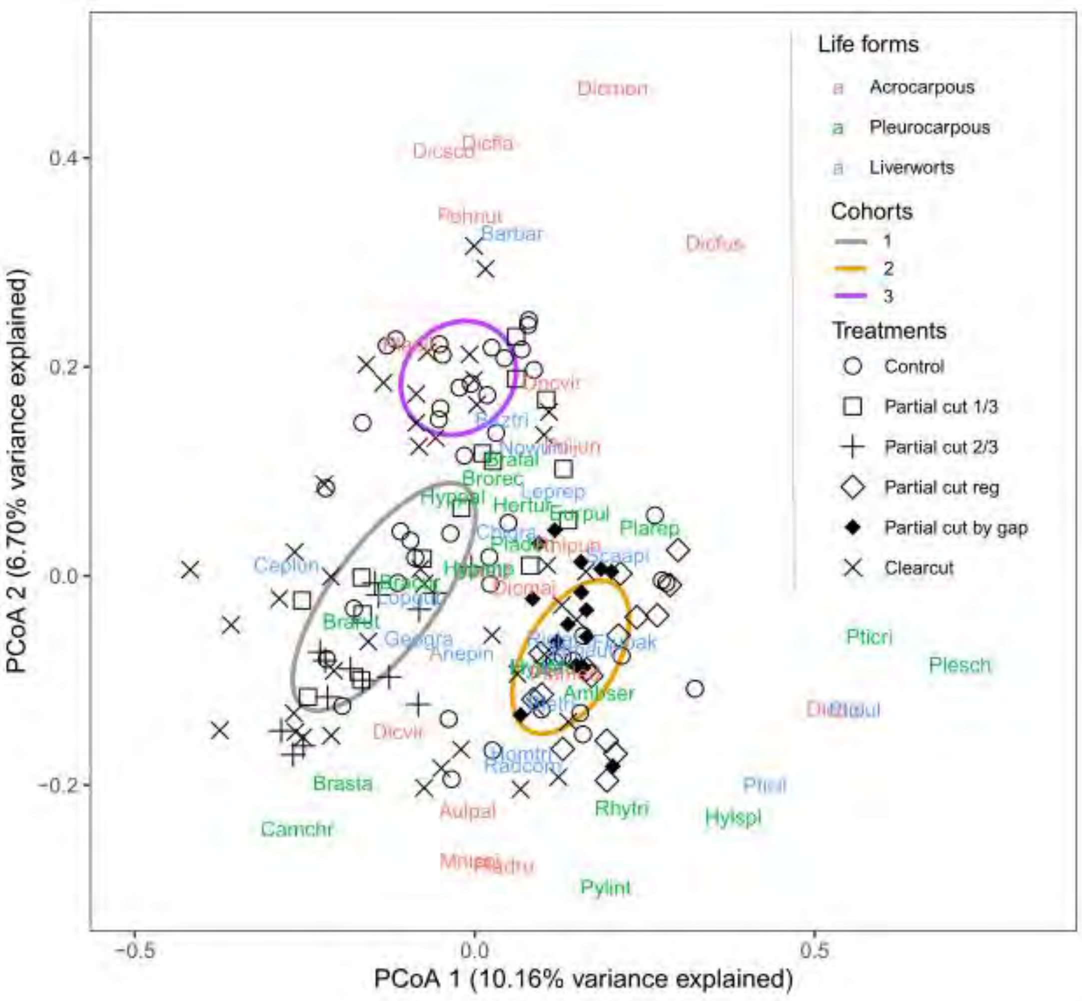

Figure 3.2 Principal coordinates analysis (PCoA) based on the abundance of species, in function of life form, in each plot represented by a treatment (harvesting type) and a cohort (stand age at the time cuts were made). Acrocarpous species are represented by red, pleurocarpous species by green, and liverworts by blue. The ellipses regroup the most common species in each cohort. Each treatment is represented by a different.

When performing PCoA on each cohort separately, a gradient from control to CC, via PC stands seemed to be mostly explained by the second axis (7.37% in cohort 1, 8.32% in cohort 2, and 9.19% in cohort 3). However, differences between treatments are not visible (Figure 3.3) suggesting that very few species are unique to one treatment. With PERMANOVA analyses, differences between communities were found in cohort 1 (F

= 2.5941, $R^2 = 0.12201$, p = $1\ e^{-04}$***) and cohort 2 (F = 2.5086, $R^2 = 0.11847$, p = $1\ e^{-04}$***). In cohort 3, there was no difference between the two treatments applied, CC and control (F = 1.3963, $R^2 = 0.04917$, p = 0.1541).

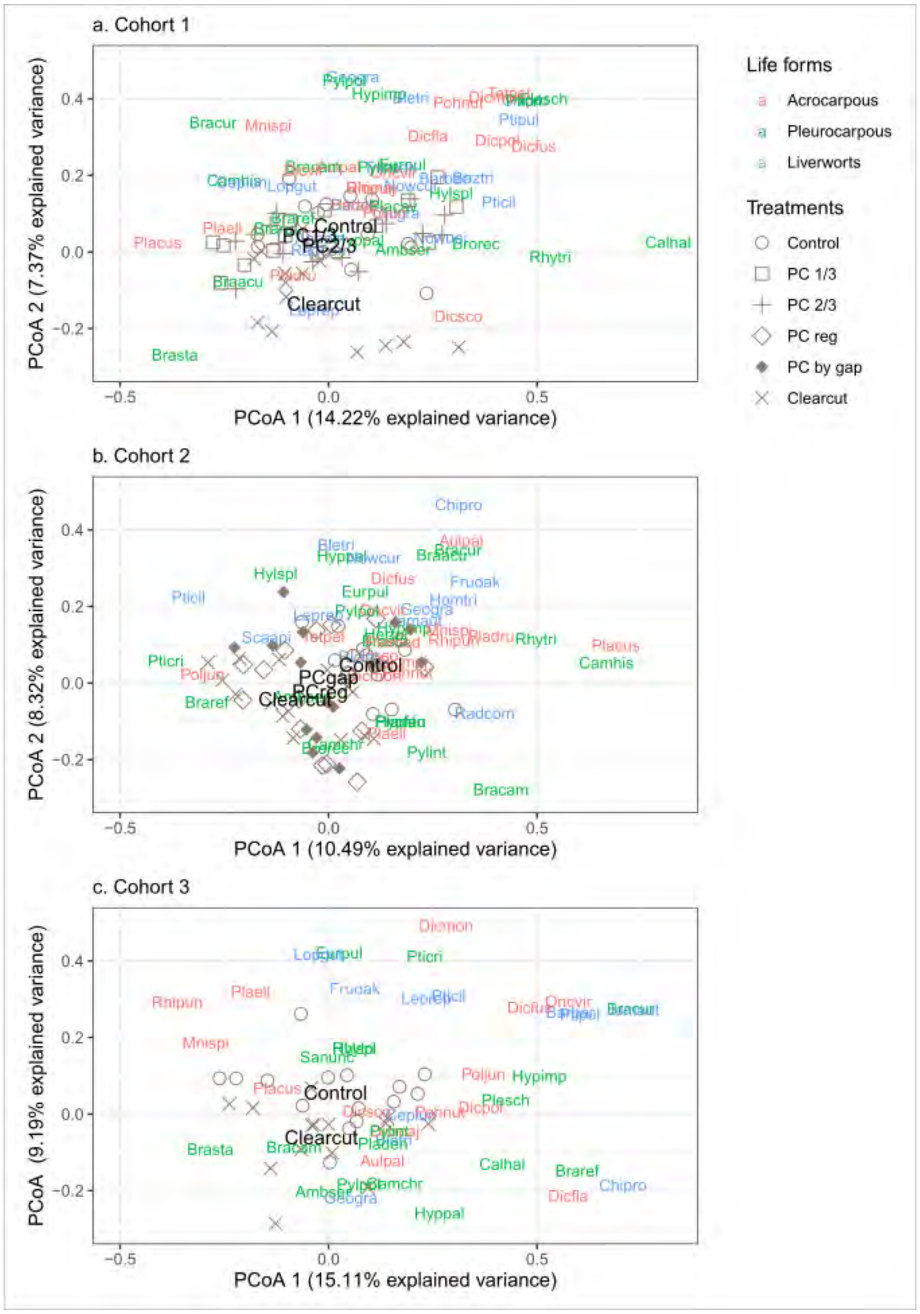

Figure 3.3 Principal coordinates analyses (PCoA) for each cohort/stand age (a. Cohort 1, b. Cohort 2, c. Cohort 3), based on the abundance of species, in function of life forms, in each treatment (harvesting type). The centroid of the plots for a same treatment is represented by the treatment name in the PCoA. PC is for partial cut. See Annexe C for more details on the species in each cohort.

In cohort 1, 54.1% of the total species found (61 species) were present in all treatments (Figure 3.4). There were very few species unique to a given treatment (11 species). Two unique species were found in the most intensive harvesting stands (PC2/3 and CC) and three and four species were found in control and PC1/3, respectively. Most of these species were acrocarpous in control stands and all species unique to PC were liverworts. In PC1/3 were *Hedwigia ciliate* Hedw., *Barbilophozia attenuata* Mart., *Nowellia curvifolia* Dicks.Mitt. and *Radula complanate* L.Dumort. and in PC2/3 were *Aneura pinguis* L.Dumort and *Chiloscyphus graveolens* Schrad. (Figure 3.3, Annexe C). In cohort 2, 52.7% of the total species found (55 species) were present in all treatments (Figure 3.4). Two generalist species were unique to CC stands, one acrocarpous (*Polytrichum juniperinum* Hedw.) and one pleurocarpous (*Brotherella recurvans* Michx.) (Figure 3.3, Annexe C). The unique species in PCgap was a liverwort, *Scapania apiculata* Spruce. Ten species were unique to control stands: four acrocarpous species, three pleurocarpous species, and three liverworts (Figure 3.4, Annexe C). In cohort 3, 79.2% of all the species found (48 species) were found in control and CC stands (Figure 3.3). The eight species unique to control stands were primarily pleurocarpous (4 species) and then liverworts (3 species) and finally acrocarpous (1 species) (Figure 3.3, Annexe C). The two species unique to the CC stands were pleurocarpous (*Amblystegium serpens* Hedw.Schimp. and *Pylaisia polyantha* Hedw.Schimp.).

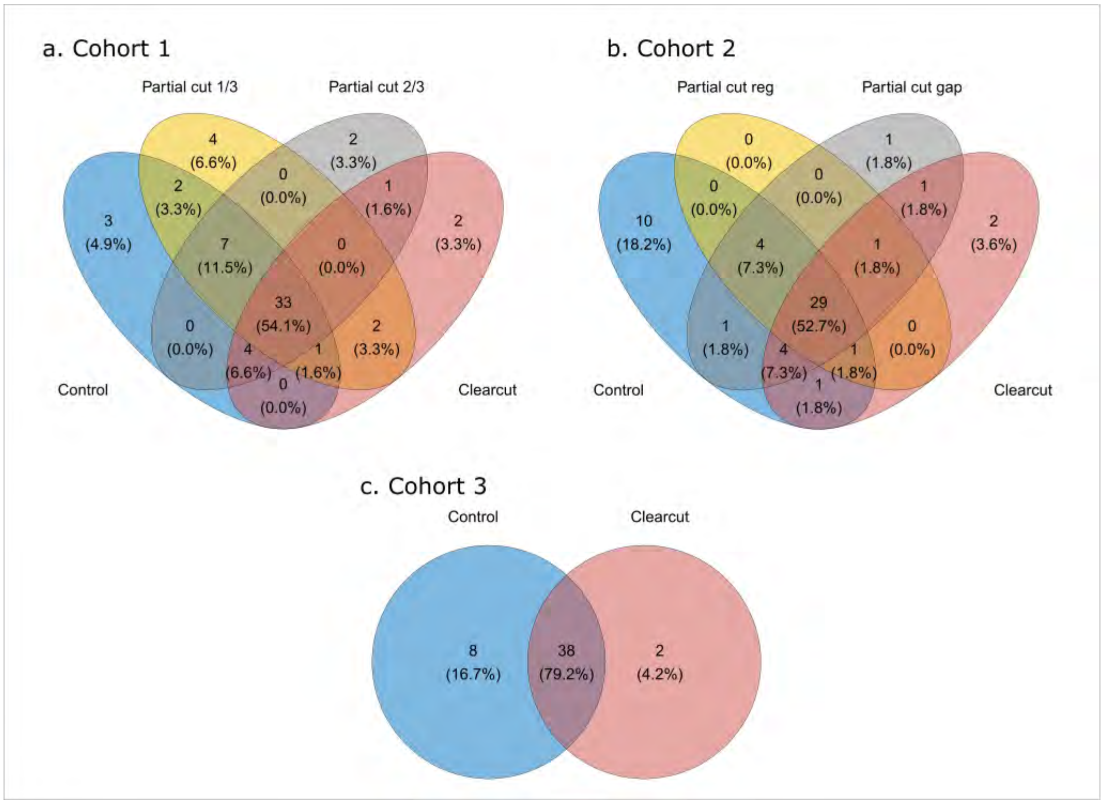

Figure 3.4 Venn diagram of all species found in each treatment of each cohort, a. Cohort 1, b. Cohort 2, c. Cohort 3. Numbers in overlapping areas indicate the number of species found in more than one treatment. See Annexe C for more details on the unique species in each section.

3.5.2 Bryophyte community: differences between treatment as a function of cohort?

The response of bryophyte species richness to harvesting treatment varied by cohort and by life form. The random effect block had a variance of 0.00065 ± 0.04 meaning that it may be considered uniform (Annexe A). In cohort 1, total bryophyte richness was lower in CC stands than in control and partial cuts (Figure 3.5). These differences were driven primarily by the loss of pleurocarpous species in the CC stands. No differences were observed for acrocarpous species richness among treatments. For liverworts, PC2/3 stands had higher richness than the other treatments. In cohort 2, total bryophyte richness declined significantly in PC regular and CC stands relative to uncut stands. This trend is particularly visible for the liverworts. Control and PC gap stands had higher liverwort richness than in PC regular and CC stands. While overall bryophyte richness did not change in cohort 3 between treatments, fewer liverworts were observed in CC than in control stands (Figure 3.5).

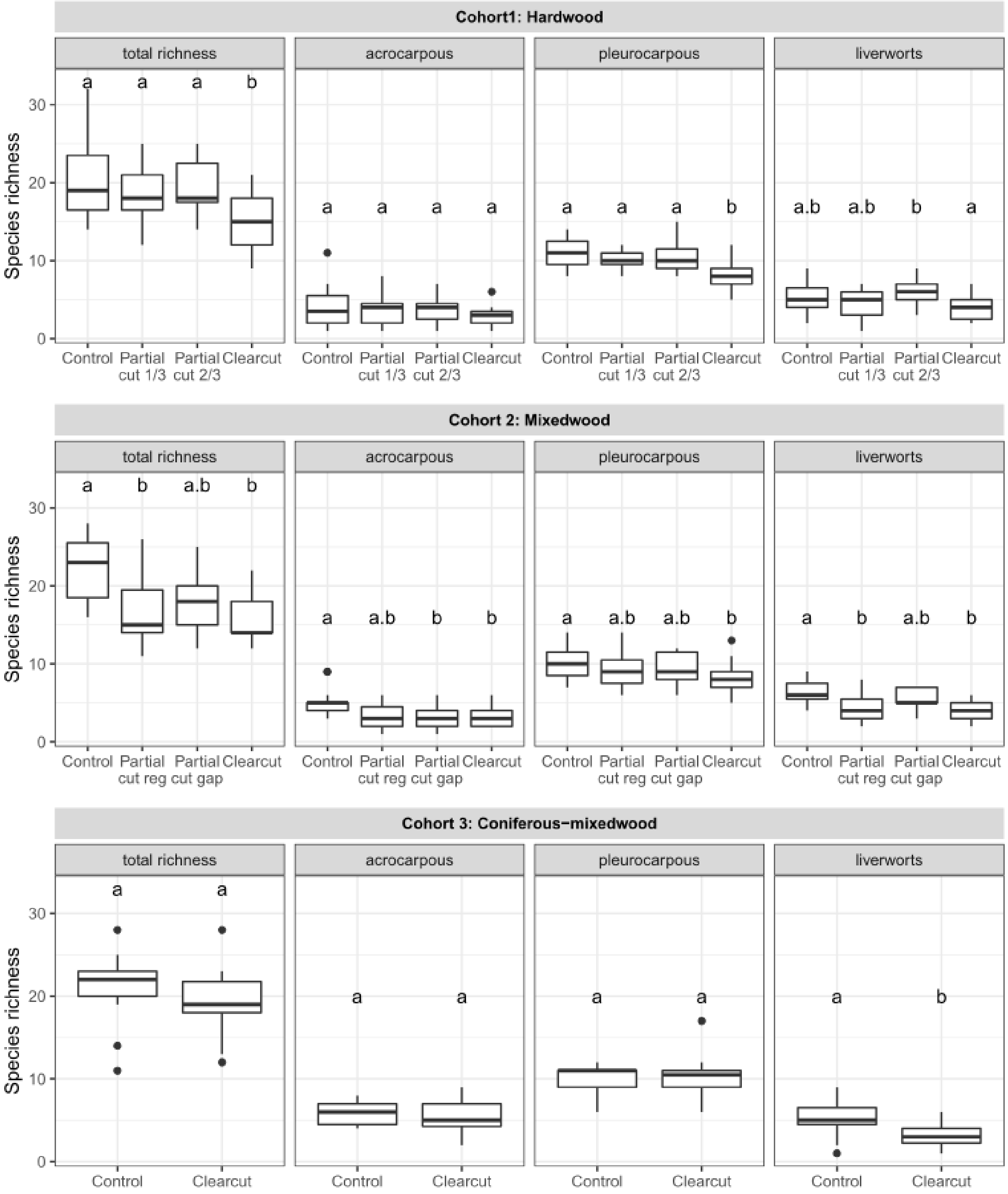

Figure 3.5 Mean specific richness per transect presented by total species richness and bryophyte life forms for the three cohorts. Richness is compared between treatments of the same cohort. Statistical significant difference as determined by Tukey tests is indicated by letters. Different letters indicate a significant difference by panel.

3.5.3 Relationships between life form and environmental conditions in the cohorts

For acrocarpous and liverworts species, variables related to the microhabitat and to stand composition had the greatest influence in the three cohorts (Tableau 3.2), indicating the presence of specialized species associated with living or dead trees. In the case of acrocarpous species, the presence of epiphytic species like *Dicranum flagellare* Hedw., *Mnium spinulosum* Bruch & Schimp. or *Plagiomnium drummondii* Bruch & Schimp or epixylic species like *Aulacomnium palustre* Hedw. Schwägr., *Oncophorus virens* Hedw. Brid. or *Tetraphis pellucida* Hedw. (Hill *et al.*, 2007), in the three cohorts, might explain the influence of the microhabitat and stand models. In the case of liverworts, most of species found in the three cohorts are associated with microhabitats and especially deadwood like *Chiloscyphus profundus*, *Jamesoniella autumnalis* or *Ptilidium pulcherrimum*, the three most frequent species. For pleurocarpous species, the best model was the Null model for the three forest types, suggesting that the richness of this life form maybe related to other ecological variables that were not measured in this study. Most of the species found are considered epigeic (*Brachythecium campestre*, *Pleurozium schreberi* Willd. Ex Brid., *Ptilium crista-castrensis* Hedw. De Not.) so probably related to soil conditions, which must be other than temperature or humidity measured in this study or other more stochastic variables such as those related to dispersion.

Tableau 3.2 Results of the multimodel selection of Poisson mixed models describing the effect of the environment on bryophyte life form richness in the communities per cohort/forest type. See Figure 6 for more details on the variable effects for each life form in each cohort.

Cohort: forest type	Life form	Model name	K	AICc	ΔAICc	AICcwt	Evidence ratio
Cohort 1: aspen dominated stands	Acrocarpous	Microhabitat	5	241.96	0.00	0.47	2.37
		Stand + Microhabitat	7	243.69	1.73	0.20	
	Pleurocarpous	Null	1	275.34	0.00	0.77	
	Liverworts	Stand	3	249.58	0.00	0.44	2.14
		Microhabitat	5	251.10	1.52	0.21	
		Null	1	251.37	1.80	0.18	
Cohort 2: mixed stands	Acrocarpous	Stand	3	233.13	0.00	0.48	2.24
		Null	1	234.74	1.61	0.21	
		Microhabitat	5	235.11	1.98	0.18	
	Pleurocarpous	Null	1	276.88	0.00	0.92	
	Liverworts	Stand	3	241.67	0.00	0.50	2.7
		Climate	5	243.65	1.98	0.19	
Cohort 3: coniferous mixedwood	Acrocarpous	Null	1	121.44	0.00	0.69	2.38
		Stand	3	123.17	1.73	0.29	
	Pleurocarpous	Null	1	134.56	0.00	0.85	
	Liverworts	Null	1	123.19	0.00	0.51	1.43
		Stand	3	123.91	0.72	0.36	

Notes: Only the first three best models are presented. Number of parameters (K), second order Akaike information criterion (AICc), distance from the best model (ΔAICc), Akaike weight (AICcwt), and value of the evidence ratio between the best model and the second model.

Taken separately, most environmental variables had little effect on the richness of bryophyte lifeforms (Figure 3.6). However, in cohort 1, acrocarpous species richness decreased significantly with increasing volumes of downed fresh wood. In cohort 2, pleurocarpous species richness decreased significantly with increasing volumes of older downed wood.

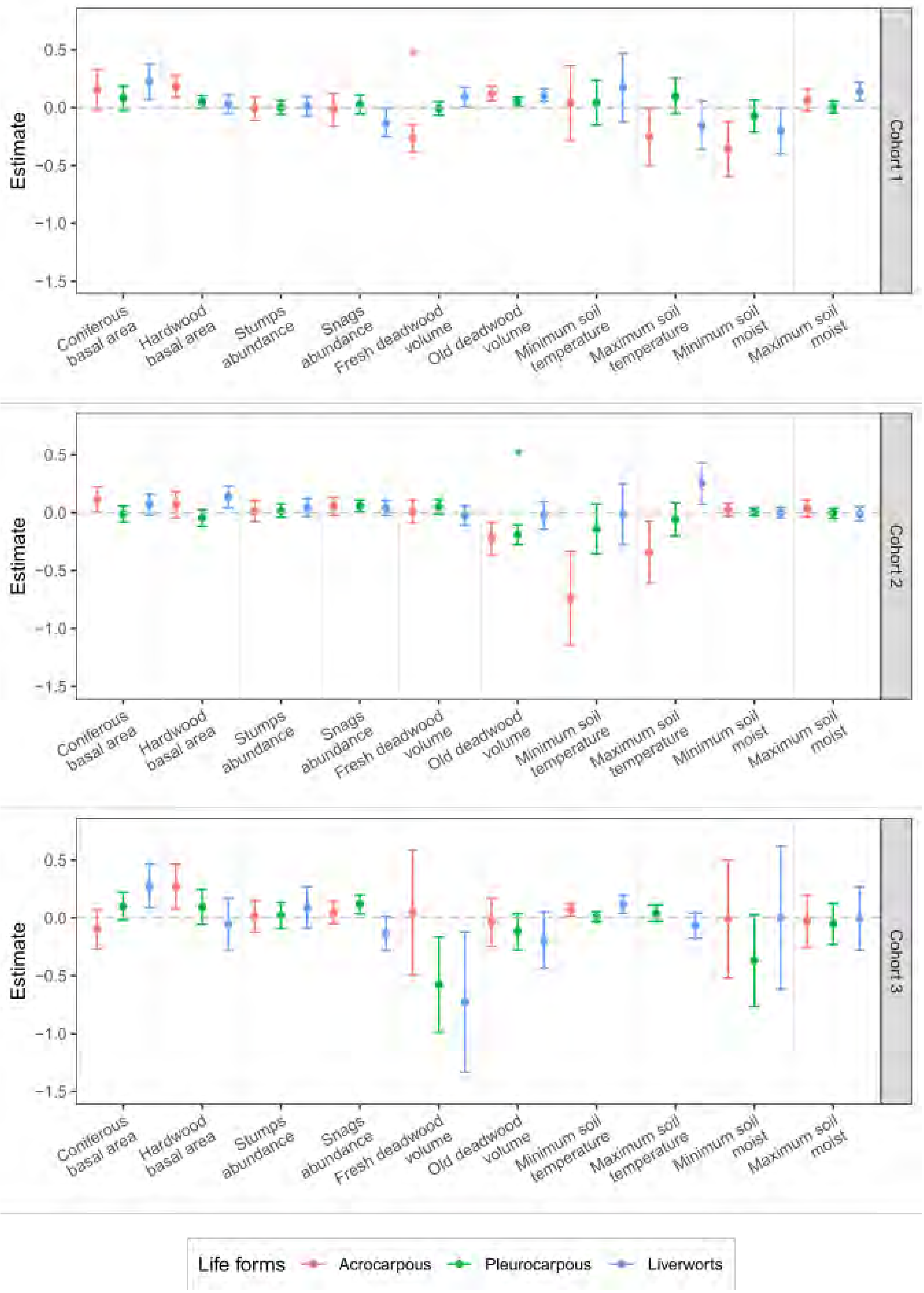

Figure 3.6 The influence of environmental variables on bryophyte abundance per life form based on Generalized linear mixed models (Poisson family). Statistical significance is indicated by an asterisk, * indicate a p-value < 0.05.

3.6 Discussion

3.6.1 Influence of cohort phases in community response to treatments

Bryophyte responses to harvest intensities differed among the three cohort types. In cohort 1, regardless the intensity of partial cut, total bryophyte and life form richness was similar to that found in the stands evolving naturally (controls), showing the resilience of the communities. In contrast, 20 years after clear cut the bryophytes richness was lower compared to the control stands, especially for the pleurocarpous and liverwort species. In deciduous forests composed primarily by trembling aspen, birch spp. and black alder (*Alnus glutinosa*) of Latvia, Madžule *et al.* (2012) showed that non-intensive management (selective cuts) for a period up to 90 years can result in a high biological value hardwood forest. They found that epixylic bryophyte richness was significantly higher in these less managed stands compared to intensive managed stands (clearcuts), which may be explained by the greater temporal continuity of dead wood supply in the latter. In our sites, the snag inflow in clearcuts was significantly lower than in control stands and there was less fresh and old downed deadwood amounts, which can explain the differences found in bryophyte richness between treatments (Noualhaguet *et al.,* 2023c). Species associated with deadwood like the acrocarpous species *Hypnum imponens* and *Pylaisia intricata* or the liverworts *Bazzania trilobata* and *Frullania oakesiana* (Hill *et al.*, 2007) were found in control and less intensive treatments but not in clearcuts stands. In contrast, by looking on the total bryophyte species richness, like us, Madžule *et al.* (2012), did not find significant differences between intensive and non-intensive managed stands.

In cohort 2, regardless of the harvest level, there was a loss in bryophyte richness; acrocarpous species decreased after partial cut by gap and liverworts decreased after partial cut regular. In cohort 3, while total richness was similar between clearcut and control stands, differences were found for the liverworts. Caners *et al.* (2013a) studied the bryophyte assemblage structure after partial harvesting in western boreal forests in Canada, dominated by varying amounts of broadleaf (*Populus tremuloides* Michx. and *Populus balsamifera* L.) and coniferous (*Picea glauca* [Moench] Voss) canopy cover. They also noted a decrease in richness of liverworts 5–6 years after partial harvest in mixed and coniferous stands attributed to a reduction in tree retention. In their study the same species as in our study, *Blepharostoma trichophyllum*, *Cephalozia lunulifolia* and *Lepidozia reptans,* were less frequent with the increasing harvest intensity. Moreover in their study the group of mosses *sensus stricto* did not differ in richness between retention levels, suggesting that they were not as sensitive to changes in local habitat conditions as liverworts (Caners *et al.*, 2013a). We again found the same species, such as the acrocarpous species *Dicranum fuscescens* and *Plagiomnium cuspidatum* or the pleurocarpous species *Brachythecium campestre* and *Sanionia uncinata,* which were present at high frequency in all types of treatments. Our similar results indicate that these different bryophyte life forms respond similarly to harvesting in eastern and western Canada in mixed boreal stands.

3.6.2 Role of environmental conditions in determining species and community response

Bryophyte richness in deciduous stands was less impacted after treatment than in mixed stands. This completes the study of Barbé *et al.* (2020) conducted in mixed and coniferous forests. They showed that the bryophyte community in mixed forests were more tolerant to changes in environmental conditions than the community in coniferous forests. Here, we showed that the community in hardwood stands are even more tolerant than the community in mixedwood stands following partial cuts. The greater tolerance of these communities could be due to a greater tolerance to changing environmental conditions. In fact, young stands were mostly composed of trembling aspen (*Populus tremuloides* Michx.). This deciduous species loses its foliage every winter creating seasonal fluctuations in temperature, humidity, irradiance, and wind in the understory (Barbier *et al.*, 2008). In contrast, the constant and relatively dense overstory of coniferous stands, which retain their needles all year, mitigate seasonal variations of regional climate in the understory (Barbé *et al.*, 2020). In our study, the maximum and minimum soil temperature and soil moisture varied significantly in only the cohort 2 stands but not in cohorts 1 and 3 stands. These variables were not found significant, but they could be biologically, influencing the richness of the different life forms. Thus, bryophytes would have been primarily affected by the intensity of harvesting, correlated with the density of hardwoods and conifers in the canopy. Bryophyte species in predominantly hardwood stands were able to tolerate greater fluctuations in seasonal conditions than species in mixed stands which might be able to tolerate more fluctuating conditions than species in coniferous stands.

In cohort 3, we observed no differences between bryophytes in clearcuts and uncut stands 20 years post-harvest and nearly all bryophyte species in these stands were also found in Cohorts 1 and 2. A previous epidemic of spruce budworm that occurred between 1970 and 1987 (Morin, 1994) may have had lasting impacts on bryophytes that obscured differences generated by harvesting. In the absence of spruce budworm outbreaks, conifer species strongly influence light, temperature and humidity in the understory which in turn can favor bryophyte communities that are rich in specialized species, particularly liverworts and small species (Bergeron and Fenton, 2012; Paquette *et al.*, 2016). However, during spruce budworm outbreaks, the defoliation of coniferous species, leaves space and light in the understory that often favors the reestablishment of hardwood species. After the end of the epidemic, defoliated trees continue to die for decades, allowing hardwood species to reach the canopy (Chen and Popadiouk, 2002). Hardwood dominated or mixed overstories necessarily impart more seasonal changes in the understory when leaves are lost during fall and winter. Increased light and wind can reduce soil forest moisture and alter bryophyte composition (Barbier *et al.*, 2008).

We could therefore assume that the bryophyte communities present before the cuts were already habituated to fluctuating seasonal environmental conditions, such as the communities present in mixed, or hardwood stands. The influence of the canopy composition was directly reflected by the results of the multimodel selection. The Stand model, represented by the total basal area of hardwood and coniferous tree species, was among the best models explaining the acrocarpous species and liverwort richness in the three cohorts.

Pleurocarpous species were the most abundant in all treatments in all stand types, but no environmental conditions explained pleurocarpous species richness probably because most of the species found are known to be forest generalists, with broad ecological requirements and distribution ranges that indicate good dispersal abilities (Barbé *et al.*, 2020; During, 1992). In aspen stands dominant species were *Brachythecium campestre* and *Callicladium haldanianum* and in mixed stands, cohorts 2 and 3, feather mosses, mainly *Pleurozium schreberi* and *Ptilium crista-castrensis* were dominant (Paquette *et al.*, 2016). These species, considered as good colonizing and perennial species, inhibit the establishment of other species.

3.6.3 Response of liverworts to harvesting

Liverworts are known to be more specialist species, closely associated with one or a few well-defined microhabitats, with narrow ecological requirements and reduced dispersal abilities (Caners *et al.*, 2013a; Johansson *et al.*, 2012). In our study, liverwort species richness was primarily explained by stands variables (hardwood and coniferous basal area). The liverwort community richness differed from control stands when cuts were intense (i.e., CC) in cohorts 2 and 3 or when cuts were regularly spaced (i.e., PC regular) in mixedwood stands from cohort 2. The regular partial cut is when all types of stems are harvested in a uniform manner to imitate/accelerate the self-thinning phenomenon, during which some intermediate individuals in competition for resource capture will die (Brais *et al.*, 2013; Chen and Popadiouk, 2002). Practiced in mixedwood stands, thinning cuts “release” balsam fir and thus accelerates natural succession by homogenizing the proportion of trembling aspen and fir found (Prévost and Gauthier, 2012). In our study sites, even though we observed a homogenization between deciduous and coniferous species after this regular partial cut, the abundance of trees was significantly lower than in unharvested stands (Noualhaguet *et al.*, 2023c). This might explain the significantly lower presence of liverwort species, in particular epiphytic species, which grow on the trunk of trees. In control and regular partial cut stands, 14 species of liverworts were found, nine were in both treatments and four were uniquely found in control stands. Of these, three were associated with trees: *Frullania inflata*, *Homalia trichomanoides*, and *Radula complanata.* In contrast, the thinning cut in cohort 1 stands, had no impact on liverwort communities 20 years later, probably because stands conserved and recovered structures, compositions, and attributes of control stands (Noualhaguet *et al.*, 2023c). This suggests that in addition to the overall level of retention, the distribution of standing residual trees within harvested blocks is also an important factor to maintain communities of species that we find in uncut stands. Similar responses have been reported elsewhere for bryophytes (Caners *et al.*, 2013a), seedling regeneration (Bose *et al.*, 2015a), and ground beetle communities (Brais *et al.*, 2013).

In cohort 1, liverwort species richness was secondly explained by microhabitat variables (deadwood volume, stumps, snags), which was consistent with the tight relationship of this group with its substrate (Caners *et al.*, 2013a; Johansson *et al.*, 2012). Liverworts commonly grow as epixylics on decayed wood in boreal forests and are sensitive to canopy removal (Arseneault *et al.*, 2012; Fenton *et al.*, 2003). Deadwood dynamics are often the focus of restoration and species conservation efforts (Harvey and Brais, 2007; Vanha-Majamaa *et al.*, 2007). The elevated, convex surface of this substrate may lose moisture quickly after harvest (Hylander, 2005). Any degree of partial harvesting in mixed and coniferous stands results in a significant reduction in soil moisture compared to intact forest (Caners, 2010) and a loss of species associated with decaying wood (Arseneault *et al.*, 2012; Caners *et al.*, 2013a). Therefore, value of deadwood as a habitat for bryophytes is diminished after harvesting.

3.7 Conclusion: implications for species conservation and forest management

These observations underscore the importance of harvest configuration and intensity, but also the condition of the post-harvested stands, structure, and composition, for the maintenance of bryophytes in managed forests. If the conservation efforts typically focus on older forests, we showed in this study the diversity of species associated with young forests and thus the importance to also consider these stands in management and conservation plans. Overall, harvesting intensity led to reduced bryophyte richness, hardwood forests showed less response to harvesting than did mixedwood or conifer forests, and alternative forest management practices, like partial cuts, can have a considerable influence on bryophyte assemblages. The threshold of harvesting intensity, to preserve species associated with mature forest, seems to be at a maximum of 33% of basal area. After 20 years, we observed a good recolonization of generalist and common forest species shared among all harvesting levels and forest types. However, these larger species could inhibit the establishment of other species. To counteract this effect, the addition of live or dead wood trunks, substrates suspended above ground level, create relatively protected habitats from competition by perennial feathermosses, and thus promote new species establishment (Arseneault et al., 2012). By letting the stands evolve completely naturally during these 20 years, like a passive conservation, it seems that the initial deadwood inflow created by harvesting developed and allowed the presence of rare and more specialized species like liverworts. Many attributes of wood influence the quality of habitat that it provides to epixylic species:

water content, texture, abundance, decomposition class and position relative to the forest floor. Thus, passive conservation can be problematic if there is no new inflow of deadwood which can stop the diversity of these bryophytes' microhabitats. It was estimated that passive conservation of a harvested stand can allow it to reach an adequate biological value in a period of 45 to 90 years (Madžule *et al.*, 2012). If we want to accelerate the processus of recolonisation of species, active restoration which creates a continuous supply of dead wood combined with passive conservation, like already suggested in other countries in the boreal zone (Berglund *et al.*, 2011; Lilja-Rothsten *et al.*, 2008), are prescribed in the boreal mixedwood forest.

CHAPITRE 4

FUNCTIONAL RESPONSES OF UNDERSTORY PLANTS TO NATURAL DISTURBANCE-BASED MANAGEMENT IN EASTERN AND WESTERN CANADA

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4.1 Abstract

Natural Disturbance Based Management (NDBM) is hypothesized to maintain managed forest ecosystem integrity by reducing differences between natural and managed forests. The effectiveness of this approach is commonly assessed by quantifying differences in species composition or diversity for a variety of biota. Monitoring often includes understory vegetation because of its broad importance to nutrient cycling, forest regeneration, and wildlife. Despite progress on understanding responses of plant communities to forest harvesting, most of these studies have been conducted at local scale. A trait-based approach allow to obtain greater comparability among sites, improving our understanding of similarities and differences in responses to disturbance by communities with distinct species assemblages. We sought to better understand the long-term influence of retention harvesting in two distinct regions of the Canadian boreal forest. We utilized two large experimental tests of NDBM: Sylviculture en Aménagement Forestier Ecosystémique (SAFE) and Ecosystem Management Emulating Natural Disturbance (EMEND), located in the eastern and western regions of the Canadian boreal, respectively. Both experiments were designed to test the effects of canopy retention levels on biodiversity including understory plant communities. EMEND and SAFE have distinct tree communities, while sharing some ubiquitous species, with distinct soils and climate. We examined functional composition (using community trait mean values) and variation in trait values (intraspecific trait variability (ITV)) for five common species. The impacts of harvesting on understory community taxonomic richness, functional diversity, and functional traits were limited 20 years post-harvest. In terms of ITV, leaf morphological traits varied between retention levels within each experiment, depending on the species identity. The five species studied were characterized by different functional responses to retention, showing species-specific reactions to environmental variation. These results showed the potential of NDBM to maintain understory communities.

Furthermore, they highlight the importance of intraspecific variability in plant communities for understanding responses to forest harvesting and the relevance to choose traits appropriate to study the species response' at the environment.

4.2 Résumé

La gestion basée sur les perturbations naturelles (NDBM) permettrait de maintenir l'intégrité écologique des écosystèmes forestiers gérés en réduisant les différences entre les forêts naturelles et les forêts gérées. L'efficacité de cette approche est généralement évaluée en quantifiant les différences dans la composition ou la diversité des espèces pour une variété de biotes. Les suivis portent souvent sur la végétation du sous-bois en raison de son importance dans le cycle des nutriments, la régénération des forêts et ressources pour la faune. Malgré les progrès réalisés dans la compréhension des réponses des communautés végétales à l'exploitation forestière, la plupart des études ont été menées à l'échelle locale. Une approche basée sur les traits permet d'obtenir une plus grande comparabilité entre les sites, améliorant ainsi notre compréhension des similitudes et des différences dans les réponses des communautés aux perturbations. Nous avons cherché à mieux comprendre l'influence à long terme de la récolte par rétention dans deux régions distinctes de la forêt boréale canadienne. Nous avons utilisé deux grands tests expérimentaux du NDBM : Sylviculture en Aménagement Forestier Ecosystémique (SAFE) et Ecosystem Management Emulating Natural Disturbance (EMEND), situés respectivement dans les régions est et ouest de la forêt boréale canadienne. Les deux expériences ont été conçues pour tester les effets des niveaux de rétention de la canopée sur la biodiversité, y compris sur les communautés végétales du sous-bois. SAFE et EMEND ont des communautés d'arbres distinctes avec des sols et des climats différents, tout en partageant certaines espèces omniprésentes. Nous avons examiné la composition fonctionnelle (en utilisant les valeurs moyennes des traits de la communauté) et la variation des valeurs des traits (variabilité intraspécifique des traits (ITV)) pour cinq espèces communes. Les impacts de la récolte sur la richesse taxonomique, la diversité fonctionnelle et les traits fonctionnels de la communauté du sous-étage étaient limités après 20 ans. En termes d'ITV, les traits morphologiques foliaires ont varié entre les niveaux de rétention au sein de chaque expérience, en fonction de l'identité de l'espèce. Les cinq espèces étudiées se sont caractérisées par des réponses fonctionnelles différentes à la rétention, montrant des réactions spécifiques aux espèces aux variations environnementales. Ces résultats ont montré le potentiel du NDBM pour maintenir les communautés du sous-étage. En outre, ils soulignent l'importance de la variabilité intraspécifique dans les communautés végétales pour comprendre les réactions à l'exploitation forestière et la pertinence de choisir des traits appropriés pour étudier la réaction de l'espèce à l'environnement.

4.3 Introduction

In the boreal forest of Canada, conventional forestry practices such as clearcutting prioritize efficient timber production. While clearcutting achieves the objective of efficient timber production, it simplifies forest structure and composition at multiple scales, which reduces habitat and species diversity (Gustafsson *et al.*, 2012; Venier *et al.*, 2014). Increasingly, a broader set of priorities is emphasized, including sustaining forest biodiversity. The use of the Natural Disturbance Based Management (NDBM) approach has been promoted as a method to retain the range of variability found in natural ecosystems (Bergeron and Harvey, 1997; Kuuluvainen, 2002). Operationally, NDBM relies on a variety of silvicultural approaches, including those that retain both live and dead trees at the stand scale to maintain forest complexity at the landscape scale, constituting a sustainable alternative to traditional clearcutting practices often applied in boreal forests (Gauthier *et al*., 2009; Kuuluvainen, 2002; Puettmann *et al.*, 2012).

In North American boreal mixed forests, natural and anthropogenic disturbances drive forest dynamics and shape the variety of habitats observed at the landscape and stand scales (Chen and Popadiouk, 2002; Venier *et al.*, 2014). Timber harvesting leads to a series of changes in ecosystem properties, including increased light availability, soil moisture and available nutrients (Aerts and Chapin, 1999; Haeussler *et al.*, 2002; Weiher and Keddy, 1995). Harvesting also creates colonization opportunities by liberating space and increasing resource availability. Following harvest, species richness often increases (Dodson *et al*., 2008; Wei *et al*., 2019; Wienk *et al*., 2004) due in part to establishment of species with an "acquisitive" ability (fast-growing, shade intolerant species, short life span) (Aerts and Chapin, 1999; Haeussler *et al.*, 2002; Weiher and Keddy, 1995). Through time as plant communities develops the availability of light, soil nutrients, and moisture decline, and plant species with more "conservative" ability (low-growing, shade tolerant species, long life span) become more dominant (Aerts and Chapin, 1999; Cornwell and Ackerly, 2009; Weiher and Keddy, 1995).

Quantifying how species composition or diversity differs between unmanaged *versus* harvested forests has been a key measure of the effects of forest management. Understory plants play an important role in maintaining biodiversity, carbon stocks and soil nutrient cycling (Gilliam, 2007; Zhou *et al.*, 2018) and are also important indicators of forest site quality (Wei *et al.*, 2020). The study of plant functional traits offers a means to effectively characterize and compare, in a standardized way, plant performance and fitness across large environmental gradients where similarity in species composition, and thus direct comparisons of performance, may be limited (Garnier *et al.*, 2016; Violle *et al.*, 2012).

Environmental filtering not only selects local species from a larger regional species pool, but also selects individuals within species, represented by the intraspecific trait variability (ITV) (Kichenin *et al.*, 2013; Kumordzi *et al.*, 2019; Violle *et al.*, 2012). It is well known that leaf morphological traits, such as specific leaf area (SLA, the ratio of water-saturated leaf area to leaf dry mass) and leaf dry matter content (LDMC, the ratio of leaf dry mass to water-saturated fresh mass), and leaf chemical traits, such as leaf nitrogen and phosphorus concentrations (LNC, LPC), respond plastically to the light environment in which a leaf grows (Boiffin *et al.*, 2015; Thiffault *et al.*, 2007). Based on the leaf economic spectrum (Wright *et al.*, 2004), canopy removal is expected to lead to increased abundance of individual plants with high SLA, LNC and LPC and lower LDMC. Over time as canopy closure increases and understory light availability declines, individuals with lower SLA, LNC and LPC and high LDMC will establish (Aerts and Chapin, 1999; Haeussler *et al.*, 2002; Weiher and Keddy, 1995). However, this is not necessarily the case and substantial differences of ITV among species suppose the influence of random processes (Bolnick *et al*., 2011; Joner *et al*., 2012; Moran *et al*., 2016).

The boreal mixedwood forest region in Canada forms a wide belt encompassing a large proportion of the boreal forest distributed over 5,200 km longitudinally. This region is characterized by a complex diversity of forest structure and composition strongly influenced by an east-to-west gradient in climate, edaphic conditions and disturbance regimes (Baldwin *et al.*, 2019). The eastern portion of the mixedwood region is generally characterized by wetter conditions, and lower size and frequency of fires compared to the west (Bergeron and Fenton, 2012; Fulton, 1989; Hare and Thomas, 1979). These differences strongly influence forest vegetation composition, structure, dynamics, and functional traits (Brassard *et al.*, 2008; Crispo *et al.*, 2021; Johnstone *et al.*, 2010; McIntire *et al.*, 2005). Within-stand temporal variability in conditions is nested within larger scale climatic gradients of precipitation and temperature (Baldwin *et al.*, 2019; Chen and Popadiouk, 2002). Following harvest, stand structure and composition often evolves over time from young hardwood stands with relatively bright understory conditions, and lower moisture, then passing through a mixture phase, and then to older coniferous stands with relatively moist and shady understory conditions (Chen and Popadiouk, 2002). However, there are differences in post-harvest forest development across the region; for example, Bartels *et al*. (2016) showed that stand recovery after harvesting was longer in the eastern Boreal Shield ecozone (32.9 years), which is characterized by mostly clay deposits, than in the western Boreal Plains ecozone (14.1 years), which is characterized by rich mineral deposits. In the Boreal Shield ecozone, Barbé *et al*. (2020) and Noualhaguet *et al*. (2023b) showed that the bryophyte community in hardwood stands, which would be better adapted to seasonal climate variation, is more tolerant to changes in environmental conditions than is the community in mixedwood stands, which is again more tolerant than the community in coniferous stands. Some understory vascular plant species are well adapted to the full range of these environmental variations and are present across a vast geographical extent and have broad ecological range (Hart and Chen, 2006; Kumordzi *et al*., 2019). ITV could help to understand this ecological breadth and also their ability to maintain themselves in varying environmental conditions at local scales.

Evidence-based forest management requires testing of ideas and concepts, and experimentation is one method of assessing whether forest ecosystems respond to retention levels in the ways we predict. In 1998, two large-scale experiments, Sylviculture en Aménagement Forestier Ecosystémique (SAFE) and Ecosystem Management Emulating Natural Disturbance (EMEND), based in Eastern and Western Canada respectively, were established to assess the feasibility of NDBM silvicultural practices via a series of experimental retention harvesting treatments (Brais *et al.*, 2004; Spence *et al.*, 1999). Here, we report on the functional responses of the understory forest plant community, 20 years post-retention, in these two experiments. We employ a trait-based approach that allows us to determine if the disturbance levels lead to similar effects on communities in the two regions with contrasting environmental conditions; i.e. changes in community mean trait values or ITV. This trait-based approach allows for comparisons between areas with similar functioning but differing regional species pools. Our first objective was to compare community species richness and functional responses among retention levels and between experiments. We hypothesized that: i) traits favoured by harvest will be those reflecting an acquisitive strategy (e.g., shade intolerant, fast growth, low LDMC, high SLA, LNC, LPC); ii) species richness and functional diversity will increase after harvest compared to control stands; and iii) differences between harvest and control stands will be more pronounced in the east than in the west, and especially in the older mixedwood forests. Secondly, we sought to compare ITV in the different retention levels within each experiment (trait frequency, variation and means). We hypothesized that: i) each species would adjust their trait values to obtain a better fitness following the treatment, and that this will be expressed by individuals with lower LDMC and higher SLA, LNC, LPC after harvesting compared to unharvested control stands; and ii) that ITV, measured within a species, might reveal more functional differences between retention levels than the community patterns in functional diversity or traits (Kichenin *et al.*, 2013; Kumordzi *et al.*, 2019). This will be reflected by more differentiation among individuals from lower retention levels than from control.

4.4 Materials and methods

4.4.1 Study area

The two experiments in this study are located on the boreal shield in eastern Canada (SAFE), and the boreal plains in western Canada (EMEND) (Figure 4.1). The average annual precipitation ranges from 600 to 1,200 mm in the eastern boreal forest but only from 300 to 600 mm in the western boreal forest (Environment Canada, 2019). This leads to differences in soil moisture availability and fire cycles that range from

~150 years in the east where fires tend to be smaller and less severe, to an average of 75 years in the west where the soil is drier and fires are typically larger and more severe (Bergeron *et al.*, 2014; Hart and Chen, 2006).

The SAFE experiment is located in the Lake Duparquet Research and Teaching Forest (LDRTF) in the Abitibi region of northern Quebec (48°30'N, 79°20'W), in the mixedwood zone of the boreal shield, and the *Abies balsamea* (L.) Mill.- *Betula papyrifera* March (balsam fir-white birch) bioclimatic domain (Saucier *et al.*, 2001). Soils are gray Luvisols that originated from glaciolacustrine clay deposits left by proglacial Lake Ojibway (Vincent and Hardy, 1977). The climate is continental with an average annual temperature of 1°C and annual precipitation of about 989 mm (Mont Brun weather station, average over the last 25 years) (Environment Canada, 2019).

The EMEND experiment is located near the town of Peace River in northwestern Alberta (56˚46′N, 118˚22W), in the Lower Boreal Highlands subregion of Alberta (Alberta Parks, 2015). Soils are fine-textured luvisols that originated from glacio-lacustrine deposits (Kishchuk *et al.*, 2014). The mean annual temperature in the region is 1°C and the mean annual precipitation is 483 mm (Environment Canada, 2019). The dominant tree species are trembling aspen (*Populus tremuloides* Michx.), white spruce (*Picea glauca* (Moench) Voss) and balsam poplar (*Populus balsamifera* L.) (Alberta Parks, 2015).

4.4.2 Experimental design and treatments

We focused on hardwood dominated stands [>70% deciduous (i.e., broadleaf) canopy cover] and mixedwood stands that are common to both experiments (conifer and broadleaf canopy cover, each composing 35–65%) (Dansereau and Bergeron, 1993; Solarik *et al.*, 2012). In the SAFE experiment, four retention levels were applied with three replicates of each retention level for each forest type (Figure 4.1). Harvest was completed during the winters of 1998-1999 and 2000-2001. Experimental units ranged in size from 1 ha to 2.5 ha. In hardwood stands, two partial cut treatments were implemented, the first targeting one third removal of the merchantable basal area (66% of retention level), and the second two thirds (33% of retention level). Thinning from below with removal of non-vigorous stems was the one-third treatment whereas larger, vigorous stems were selected in the two-thirds removal treatment. In mixedwood stands, two partial cut treatments were applied, both of which removed approximately 40% of the total basal area but with two different patterns of retention. One pattern consisted in removing stems in a regular manner (60% retention), while the other consisted of removing stems in gaps of approximately 400m² (60% gap retention). For a more complete description of the harvesting treatments, see Brais *et al.* (2004) and Brais *et al.* (2013).

In the EMEND experiment, retention levels were applied during the winter of 1998-1999 to 10-ha ‘compartments’, with three replicate compartments of each retention level for each forest type (Figure 4.1). Within each compartment, 20 m wide retention strips were established between 5 m wide machine corridors, with the harvesting equipment traversing the machine corridors; thus, minimal disturbance of the forest floor occurred in the retention strips. The retention strips were partially harvested to attain the prescribed retention level for each compartment. For both hardwood and mixedwood stands, the two partial harvesting treatments were 75% and 20% dispersed green tree retention with trees removed without bias towards species or size (Spence *et al.*, 1999)

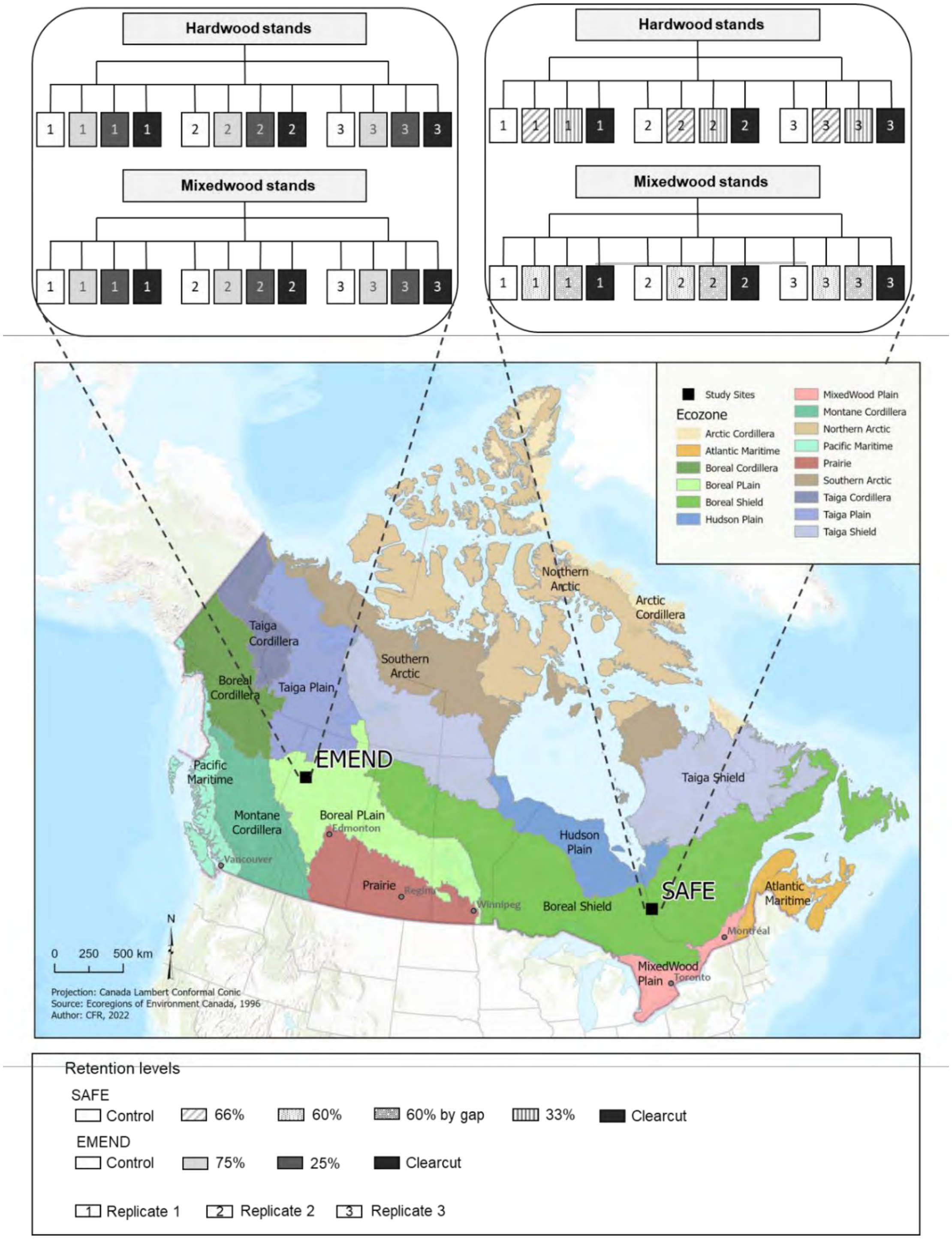


Figure 4.1 Experimental retention levels and locations of SAFE and EMEND experiments (Brais *et al*., 2004; Solarik *et al*., 2012).

4.4.3 Data collection

4.4.3.1 Understory plant species community

Understory plant species community composition and abundance (low shrub < 1.5 m and forb species) have been monitored from the onset of each experiment. During surveys, each individual was identified to the species level utilising reference texts: the *Flore Laurentienne* (Bourlière, 1966) nomenclature for SAFE, and *Flora of Alberta* (Moss, 1983) for EMEND. In the SAFE experiment, between late July and mid-August 2019, forty 1 m^2 quadrats were randomly placed within each replicate for each retention level and forest type combination, and the abundance of each identified species was estimated as percent cover using five classes: <1%, 1–10%, 11%-25%, 26%-50%, >50%. For EMEND, data were collected in late June to late July 2015 (Bartels and Macdonald, 2023). In each replicate of retention level and forest type, cover values were estimated in six 2 × 2 m quadrats using the following system: from 0 to 1 % to the nearest 0.5%, from 1 to 20 % to the nearest 1%, and from 20 to 100% to the nearest 5%. Plants with minimal cover were assigned a value 0.1%. For subsequent analyses cover values per species were averaged to the level of the replicate.

4.4.3.2 Traits

Information on plant traits was obtained both from direct measurements and from existing published values using the Traits Of Plants In Canada database (TOPIC, Aubin *et al.*, 2020). We use the term “trait” in its broader sense and include metrics related to plant morphology, strategy of regeneration, dispersion, environmental performance, and resource utilization. To characterize differences in functional composition of understory communities between the two experiments, we chose to use seven categorical/semi-quantitative traits along with four quantitative traits, which we measured in the field (Tableau 4.1). The selected traits and metrics relate to the capacity for colonization, development, and competition processes in understory plant communities that are directly impacted by forest harvesting.

Categorical traits were extracted for each low shrub (height < 1.5 m) and forb species observed in the different communities. For the quantitative traits we focused on the most abundant species. This decision was based on the "biomass ratio hypothesis" proposed by Grime (1998), which states that the traits of a species influence ecosystem properties in proportion to the contributions of the species to the total biomass of the community, and therefore the number, relative abundance, and identity of the species present (Garnier *et al.*, 2004). In each experiment, forest type and replicate of retention level, we selected the 3 to 4 most abundant low shrub and forb species, whose cumulative cover represented 80% total cover (Garnier *et al.*, 2004). This resulted in 14 species for SAFE and 18 for EMEND for a total of 26 species, with six species shared between the two (data are available in Noualhaguet *et al*., (2023a)).

We measured four quantitative traits, including two morphological and two resources utilization traits, *in situ* for the 26 selected species. The two morphological traits were: 1) Specific Leaf Area (SLA), defined as the ratio between the one-sided area of a leaf to oven-dried leaf mass in $cm^2 g^{-1}$; and 2) Leaf Dry Matter Content (LDMC), which is the oven-dry mass of a leaf divided by its water-saturated fresh mass in $mg g^{-1}$. The two resource utilization traits were: Leaf Nitrogen Content (LNC), the concentration of nitrogen in the foliage; and leaf phosphorous content (LPC), the concentration of phosphorous in the foliage. These *in situ* measurements also allowed us to assess intraspecific trait variability (ITV) for these quantitative traits.

In July 2020 for SAFE and July 2021 for EMEND, we collected fresh leaves of the selected species in each of the 24 replicates of retention level and forest type in each experiment following the standardized protocol of Perez-Harguindeguy *et al.* (2016). Collection was conducted uniformly throughout each replicate of each retention level and forest type. To measure SLA and LDMC, we collected one leaf from each of 20 reproductively mature, healthy-looking individuals, per species per replicate. This represented a total of 180 to 220 samples per retention level of each stand type and experiment. Leaf area was estimated from scanned images (Epson Expression 12000XL, 600ppi resolution) of fresh leaves using the software Winfolia (one sided area, cm2; Regent Instruments Inc, Canada). The fresh weight was recorded after rehydrating the leaves by immersing them in water within than four hours after harvest. Fresh weight was measured between 24 h to 48h after the leaf was hydrated. The constant dry weight was obtained after drying the leaves for at least 48 hours at 70°C. For LNC and LPC, we collected additional leaves (approximately 500g) from each species per replicate, representing a total of 145 samples. Each sample was oven dried for 48 hours at 70°C and then ground for nitrogen and phosphorous analysis in the laboratory (iForêt at Montréal, Québec, Canada). LNC percentage was determined by infrared thermal conductivity after sample combustion at 1040°C. LPC percentage was determined by fluorescence spectrometry induced with X-ray (XRF, 8-50 kV rhodium tube).

From the measurement of these traits, two matrices were developed 1) traits per species for community functional composition analysis, 2) traits per species per replicate of retention level and forest type for ITV analysis. Traits measured in the field were: a) an average per species used in community functional composition analysis; and b) the value of individuals per species per replicate for ITV analysis.

Tableau 4.1 Categorical/semi-quantitative traits[1] selected from the TOPIC (Traits Of Plants in Canada) database, and quantitative traits[2] measured in the field. Adapted from Aubin *et al.,* (2020).

Category	**Traits**	**Value**	**Description**	**Importance**	**Data source**
Environment performance metrics	Raunquier life form[1] (RA)	cha	Chamaephyte: buds between 1 mm & 25 cm from ground	Bud placement relative to forest floor affects ability to survive disturbance (Raunkiaer, 1934)	TOPIC
		geo	Geophyte: buds in the ground		
		hem	Hemicryptophyte: buds on the surface of the ground		
		mcpha	Micro, nano phanerophyte: buds between 25 cm & 8 m from the ground		
		mgpha	Mega, meso phanerophyte: buds ≥ 8 m from the ground		
		the	Therophyte: no bud, annual plant		
	Water preference[1]	0	Habitat xeric or xeric-mesic	Ability to survive in a given condition (Garnier and Navas, 2012)	TOPIC
		1	Habitat mesic		
		2	No preference		
		3	Habitat humid or humid-mesic		
	Light requirement[1]	1	Shade tolerant, <2 hours of direct sunlight	Ability to survive in a given condition	TOPIC

Tableau 4.1 continued

		3	Mid tolerant, 2-5 hours of direct sunlight	(Messier *et al*., 1999)	
		6	Shade intolerant, needs >6 hours of direct sunlight at mid-summer		
Resource utilization	Leaf nitrogen content[2] (LNC)	%	Concentration of nitrogen in the foliage in % dry leaf mass	Ability to acclimate to the environmental conditions (Wright *et al.*, 2004)	TOPIC
	Leaf phosphorous content[2] (LPC)	%	Concentration of phosphorous in the foliage in % dry leaf mass		
Morphology and strategy of regeneration and dispersal	Flowering phenology[1] (Flowering)	0	The presence of flowers in spring	Adaptation to environmental conditions (Garnier and Navas, 2012)	TOPIC
		1	The presence of flowers in summer or in early fall		
	Growth[1]	0	Slow rate of aboveground growth	Ability to colonize available space in disturbed habitats (Garnier *et al*., 2007)	TOPIC
		0.5	Medium rate of aboveground growth		
		1	Rapid rate of aboveground growth		

Tableau 4.1 continued

Lateral extension[1]	0	Absent : no vegetative propagation	Ability to colonize available space in disturbed habitats (Garnier *et al*., 2007)	TOPIC
	0.1	Compact: vegetative propagation by sprouting, root collar sprouts (phanerophyte), by bulbs/bulbettes, corm/caudex, tubers (non-phanerophyte)		
	0.5	Inter: vegetative propagation by layering, root suckers, rhizomes (phanerophyte), by bulbils, layering (non-phanerophyte)		
	1	Extensive: propagation by root suckers, rhizomes (phanerophyte), by rhizomes, stolons, plant fragments (non-phanerophyte)		

Tableau 4.1 continued

Leaf dry matter content^2 (LDMC)	mg/g	The oven-dry weight of a leaf divided by its fresh weight	Adaptation to environmental conditions and eco-physiological properties (Wright *et al.*, 2004)	Field measures
Specific leaf area^2 (SLA)	cm²/g	The ratio of the one-sided area of a leaf to oven-dried leaf mass		
Seed bank persistence^1	0	Short viability : ≤ 1 year	Ensuring population persistence in disturbed habitats (Baskin and Baskin, 2014)	TOPIC
	0.5	Semi-permanent seed bank: > 1-5 years		
	1	Permanent seed bank: >5 years		

4.4.4 Statistical analyses

4.4.4.1 Understory community responses at 20 years post-harvest

To compare community scale multivariate and univariate functional responses to retention levels and between experiments, we analyzed hardwood and mixedwood forest types separately. First, to examine the multivariate community response, we used functional and taxonomic metrics to assess understory response to the different retention level using three distinct matrices: (1) matrix *L* contained cover data per species per replicate in each experiment, (2) matrix *Q* (traits by species) contained species trait value data. For the categorical/semi-quantitative traits, we assigned a value per species based on Aubin *et al.* (2020) (Tableau 4.1). For the quantitative traits measured in the field, the average value per trait, species, experiment and retention level was used. (3) Matrix *R* represented the information on the experiment (SAFE or EMEND) and the level of tree retention applied at harvest 20 years ago. Then we generated a Community-Weighted Mean (CWM) matrix using matrix *L* and matrix *Q* (Ricotta and Moretti, 2011). The CWM matrix was generated by calculating the mean of the trait value present in the community, weighted by the percent cover for each species (Garnier *et al.*, 2004). We then conducted a Principal Component Analysis (PCA) on the CWM matrix to relate patterns of co-occurring traits to retention levels in the two experiments. We performed a priori tests of retention levels and experiments effects on community pattern using distance-based tests of multivariate differences between the different combinations of retention levels-experiments (8 predefined groups in each forest type) using multiple response permutation tests (PERMANOVA), with 9999 permutations (Anderson, 2014).

Second, to look at the response of univariate community scale indices to harvesting, taxonomic richness and functional diversity were calculated and compared among retention levels separately by forest type and for each experiment. Richness was measured using the number of species per replicate of retention level. Functional diversity was calculated using Rao's quadratic entropy index (Rao, 1982; Ricotta and Moretti, 2011). Rao's index describes the variation of species trait composition within the community and is calculated as the sum of pairwise distances between species weighted by their relative abundance. Using the matrices L and Q, the functional diversity was computed as a univariate index. Then to analyze the effect of retention level on these two diversity indices, we used analysis of variance models (ANOVA) and Tukey's HSD (Honestly Significant Difference). The models were fit separately for the two experiments in each of the two forest types. Square root transformations were applied when the residuals did not conform to the assumptions of normality and homogeneity of variance. Finally, Tukey HSD (Honestly Significant Difference) post-hoc tests were used to examine differences between all pairwise combinations of retention levels by experiment and forest type.

4.4.4.2 Intraspecific trait variability

To test how intraspecific trait variability responded to retention levels in each experiment, we studied five of the six species present at both SAFE and EMEND, because they were present in the control stands and at least one retention level: *Aralia nudicaulis* (L.), *Cornus canadensis* (L.), *Linnaea borealis* (L.), *Rubus pubescens* (Raf.) and *Viburnum edule* (Michx.). First, to examine the breadth of intraspecific variability across each species' sampled range, we created density plots, based on Kernel density, showing the relative frequency of morphological (SLA and LDMC) and chemical (LNC and LPC) leaf trait values for each of the five species. The relative frequency represented the proportion of samples that had a certain value of the trait. Second, to determine the impact of retention level in each forest type on the two morphological traits, we used ANOVA and Tukey's HSD for each species and for each experiment and forest type separately. Square root transformations were applied when necessary to ensure normality and homogeneity of variance of the residuals. We note that in some cases species were not observed in the selected retention levels and the retention level doesn't appear in the analysis for that species. Comparisons of the mean value of the trait in the species were made between the different retention levels.

All analyses were conducted using R software (version 4.0.3, R core Team 2020). The functional diversity indices were calculated using the package FD (Laliberté and Legendre, 2010) and the PCA was conducted with the package ade4 (Dray and Dufour, 2007). In all statistical tests, a p value ≤ 0.05 was considered significant.

4.5 Results

4.5.1 Understory community responses 20 years post-harvest

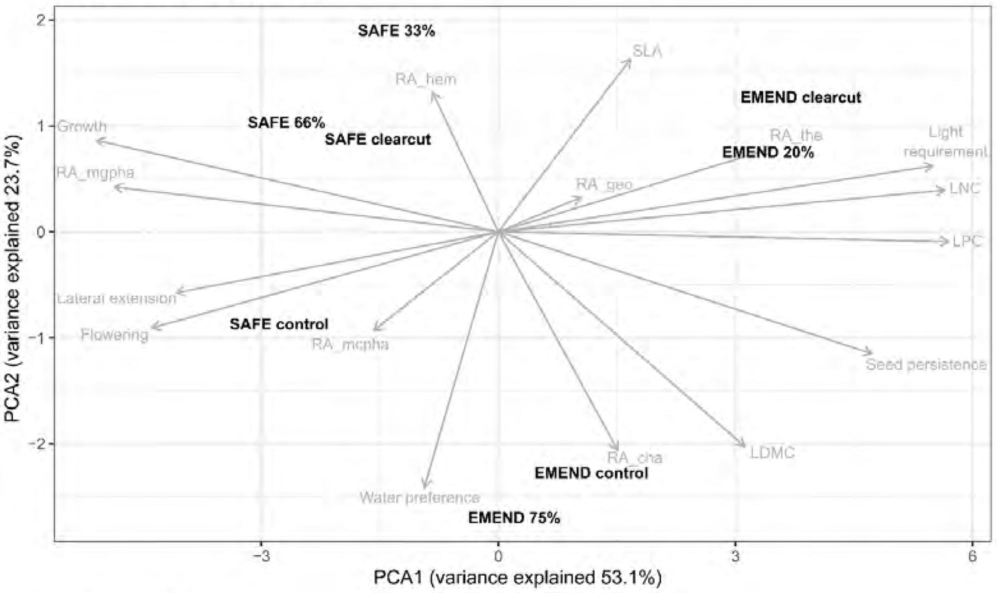
4.5.1.1 Community functional composition

For hardwood dominated stands, the first two axes of the PCA on the community-weighted mean (CWM) explained 76.7% of the total variation (Figure 4.2 a). The community functional composition did not vary significantly between experiments (PERMANOVA results, $F = 2.655$, $R^2 = 0.24117$, $p = 0.2494$) or among retention levels (PERMANOVA results, $F = 1.471$, $R^2 = 0.66801$, $p = 0.4476$). The first axis separates the two experiments, with SAFE stands on the left and EMEND stands on the right, and was associated with functional changes in communities from species with more rapid growth, spring flowering, and an extensive lateral extension, to species that were more shade intolerant, had high seed bank persistence, and high LDMC, LNC and LPC (Figure 4.2 a.). The second axis separates the stands with higher retention levels (controls and 75% EMEND) from the stands with lower retention levels. Separation along axis 2 was predominantly associated with Raunquier life form, LDMC, SLA and soil moisture. Microphanerophytes had higher abundance in SAFE control. Chamaephyte species with a higher LDMC and a preference for higher soil moisture had higher abundance in EMEND control and 75% retention. Hemicryptophytes had higher abundance in SAFE 66%, 33% and clearcut. Therophytes and shade intolerant species with a higher SLA, LNC and LPC had higher abundance in the EMEND 20% and clearcut.

For mixedwood dominated stands, the first two PCA axes explained 71.4% of the total variation in the CWM (Figure 4.2 b). The community functional composition did not vary significantly by experiment (PERMANOVA results, $F = 1.704$, $R^2 = 0.29933$, p

= 0.3998) or retention level (PERMANOVA results, F = 0.598, R^2 = 0.52505, p = 0.7593). The extremes of the gradients are defined by EMEND stands whereas the trait values did not vary much for the four SAFE retention levels. This suggest that differences between retention levels at EMEND were greater than the differences among retention levels at SAFE. We observed four groupings with the EMEND control on the top right, EMEND clearcut on the middle left, the two intermediate levels of retention of EMEND on the bottom right and the two intermediate levels of retention of SAFE on the bottom left. The control and clearcut at SAFE were centrally located. EMEND control was characterized by more chamaephytes and species with extensive lateral extension. EMEND clearcut was characterized by more hemicryptophytes species with higher LPC. Both 75 and 20% EMEND had more microphanerophytes and species with spring flowering and a high seed bank persistence.

a. Hardwood dominated stands



b. Mixedwood stands

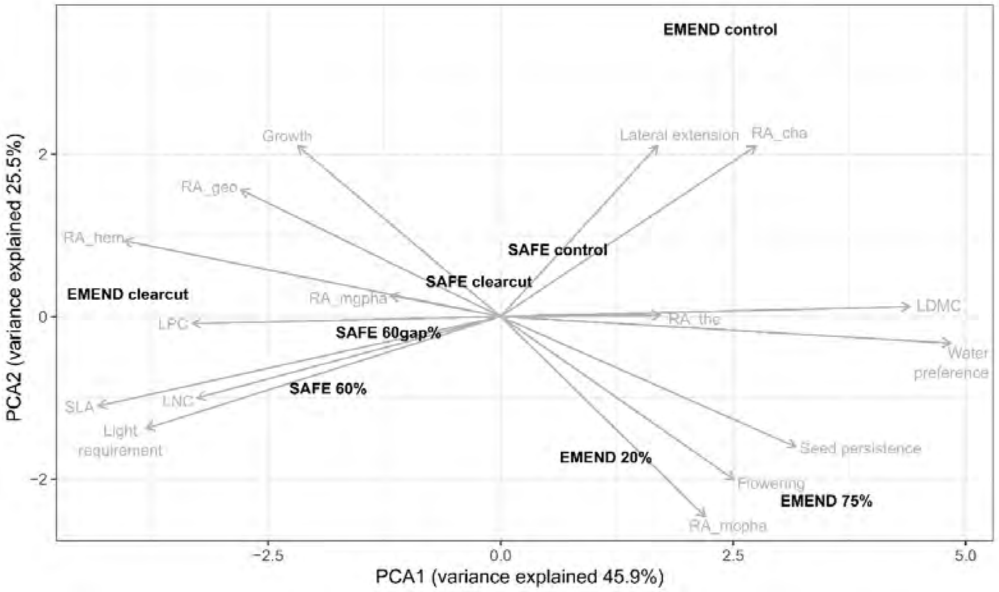


Figure 4.2 First two axes of the principal component analysis conducted on the matrix of Community Weight Mean (CWM) trait × site (experiment (SAFE, EMEND) and retention level) showing the patterns in trait occurrences for the a. Hardwood dominated and b. Mixedwood stands. The experiment and retention level name in bold indicates the centroid of the replicates for that combination. Light grey arrows and their length indicate, respectively, the direction and the strength of the relationships between site and functional traits. See Tableau 4.1 for trait code descriptions.

4.5.1.2 Community scale taxonomic richness and functional diversity

For the hardwood dominated stands, taxonomic richness and functional diversity did not differ statistically among the levels of retention (Annexe D). For SAFE, the mean species richness varied between 26 and 28 among retention levels (Tableau 4.2). The functional diversity varied between 0.175 and 0.210. For EMEND, the mean species richness varied between 35 and 39 among retention levels (Tableau 4.2). The functional diversity varied between 0.186 and 0.212.

Tableau 4.2 Mean and standard deviation of the taxonomic (species richness per replicate of retention level) and functional (Rao univariate index per replicate of retention levels) diversity indices for each experiment and retention level, in hardwood and mixedwood stands. Results of the comparisons based on a Tukey test are indicated by letters. Different letters indicate a significant difference at $p<0.05$. Results of the ANOVA models are presented in Annexe D.

Stand type	Experiment	Diversity index	% Residual trees			
			control	66/75	33/20	clearcut
Hardwood	SAFE	Richness	28.3± 2.1	28.0± 5.2	28.3 ± 5.7	26.7 ± 1.5
	EMEND		38.0 ± 2.0	37.0 ± 1.0	35.3 ± 2.1	39.3 ± 3.8
	SAFE	Rao	0.193 ± 0.026	0.175 ± 0.033	0.210 ± 0.031	0.202 ± 0.024
	EMEND		0.186 ± 0.087	0.198 ± 0.061	0.190 ± 0.068	0.212 ± 0.057
			control	60/75	60gap/20	clearcut
Mixed wood	SAFE	Richness	32.3 ± $3.5^{a.b}$	27.0 ± 2.6^{b}	28.7 ± $3.1^{a.b}$	35.3 ± 1.2^{a}
	EMEND		39.3 ± 1.2^{b}	39.3 ± 3.8^{b}	49.3 ± 4.0^{a}	36.7 ± 3.1^{b}
	SAFE	Rao	0.299 ± $0.002^{a.b}$	0.291 ± 0.005^{b}	0.295 ± 0.002^{b}	0.304 ± 0.003^{a}
	EMEND		0.293 ± 0.002	0.300 ± 0.006	0.296 ± 0.006	0.297 ± 0.006

For the mixedwood stands in SAFE, responses of taxonomic richness and functional diversity to retention level were similar (Annexe D): species richness was higher in the clearcut than in the 60% retention, and functional diversity was higher in the clearcut than in both the 60% retention and the 60%gap. For both, the control had intermediate values for taxonomic richness and functional diversity (Tableau 4.2). In EMEND, taxonomic richness differed among retention levels (Annexe D) with species richness significantly higher in 20% retention than in the other three retention levels, with a mean of 49 species per replicate, compared to a mean of ~37 - 39 species per replicate for the other retention levels (Tableau 4.2). No significant differences were observed among the retention levels for the functional diversity at EMEND (Annexe D).

4.5.2 Species level intraspecific trait variability

4.5.2.1 Breadth of trait distribution

The five studied species had different trait distributions across the experiments and retention levels with differences among species in the mean, the mode and the breadth of their trait distribution (Figure 4.3). For the four traits, *R. pubescens* and *V. edule* had relatively wider breadths of distribution whereas the breadth for *C. canadensis* and *L. borealis* was relatively lower. In terms of traits values, when the species had a maximum frequency at higher LDMC values, they had a maximum frequency at lower SLA, LNC and LPC values. This was observed for *L. borealis* and *C. canadensis.* In contrast, when species had a maximum frequency at lower LDMC values, they had a maximum frequency at higher SLA, LNC and LPC values. This was observed for *A. nudicaulis, R. pubescens* and *V. edule.*

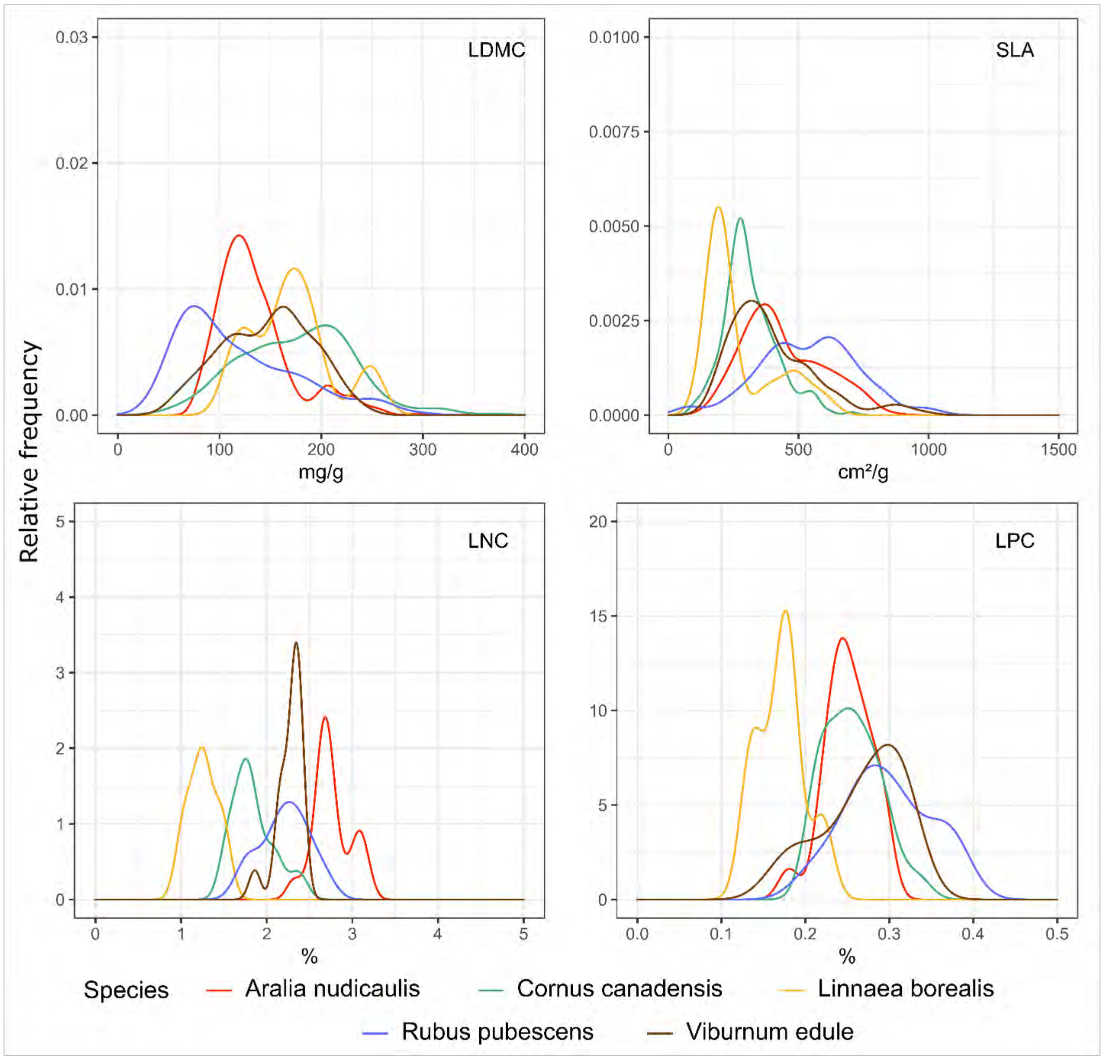


Figure 4.3 Relative frequency based on Kernel density showing the variation in the leaf traits across the range of retention levels for five study species present in both the SAFE and EMEND projects. SLA, specific leaf area; LDMC, leaf dry matter content, LNC, leaf nitrogen content; LPC, leaf phosphorus content.

4.5.2.2 Effects of retention levels on intraspecific variability

Impacts of retention levels on the trait values of the five studied species varied with the experiment and the forest type (Figure 4.4, Figure 4.5, Annexe E, Annexe F).

For the LDMC, lower values, which characterized acquisitive species in an environment with a good availability of light, and soil moisture and available nutrients, were expected for lower retention levels. This was observed in hardwood stands at SAFE, with higher LDMC values in control stands compared to 66%, 33% and clearcut for *R. pubescens* (Figure 4.4). In contrast, *C. canadensis* showed the opposite response with higher LDMC values in clearcut than in control stands. In mixedwood stands, we observed significantly lower LDMC values in clearcut and 60% by gap retention than in control, for *C. canadensis;* and than control for *L. borealis.* For *V. edule* LDMC was lower in 60% and 60% by gap retention than for clearcut or control, which did not differ from one another.

In EMEND for hardwood stands, LDMC was significantly lower in 20% retention than in control for *R. pubescens,* and in clearcut compared to control and 20%, but not 75%, for *V. edule* (Figure 4.4). In mixedwood stands, we observed significantly lower LDMC values in the 75% retention than in the control for *A. nudicaulis* and in 75% and 20% retention compared to control for *L. borealis. V. edule* in mixedwood stands showed a response somewhat opposite to what was expected, with higher LDMC values in 75% and 20% stands than in control stands. *C. canadensis* showed no differences in LDMC values among retention levels for either forest type.

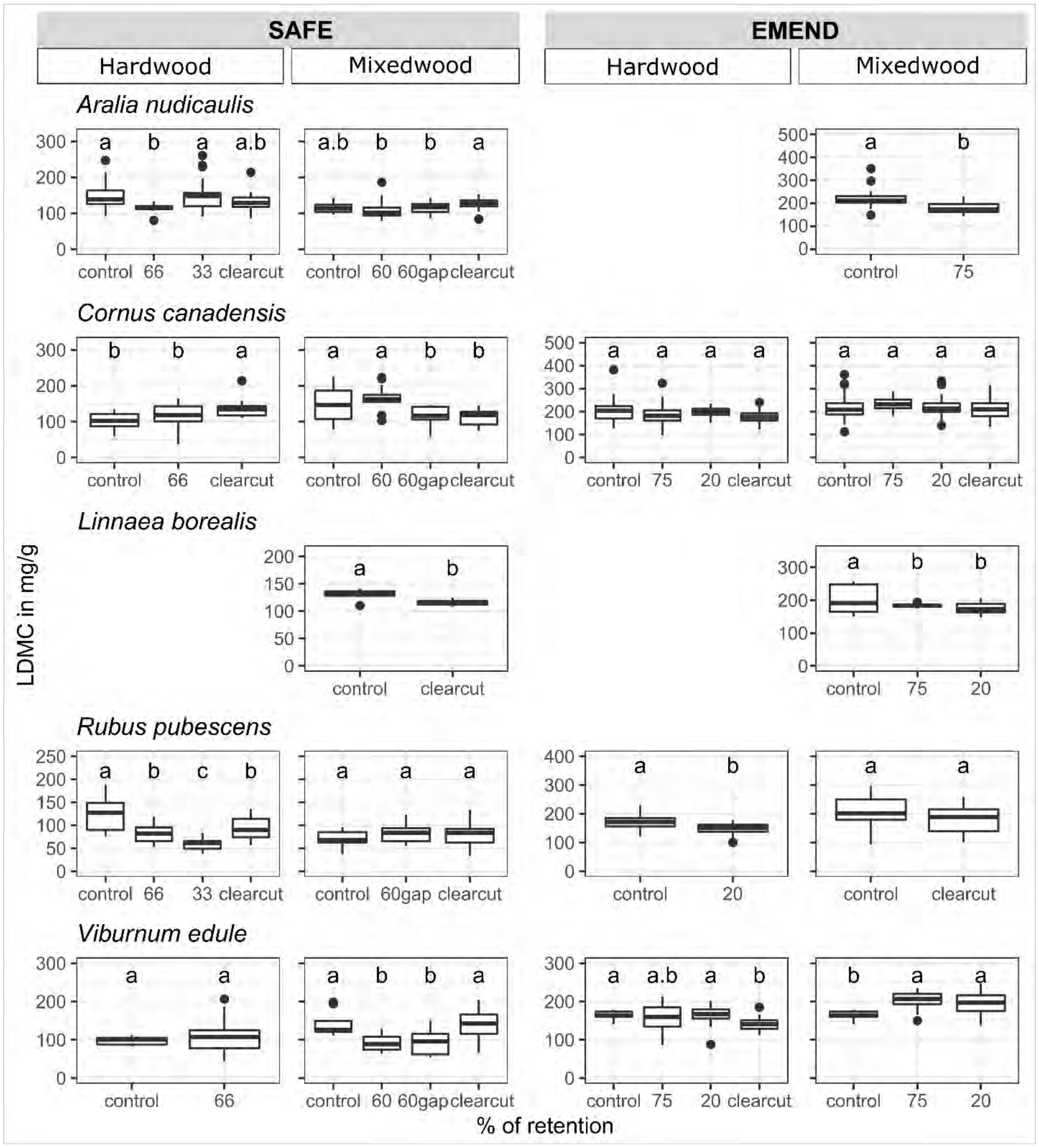


Figure 4.4 Comparison of Leaf Dry Matter Content (LDMC) trait values among retention levels or the five selected species that were found in SAFE and EMEND, by forest type. Results of the comparisons based on Tukey tests are indicated by letters. Different letters indicate a significant difference at $p<0.05$. Results are missing for retention levels and/or forest types for some species because they were not found in that combination. See also Annexe E.

In contrast to LDMC, higher SLA values characterize acquisitive species and thus were expected after lower retention levels. This was sometimes the case at SAFE, with significantly higher SLA values, compared to controls, for *R. pubescens* in hardwood stands in 66%, 33% and clearcuts, and in mixedwood stands for *A. nudicaulis* in 60gap and clearcut (Figure 4.5). Unexpectedly, we in some cases observed significantly lower values of SLA in harvested compared to control stands: for *C. canadensis* in 66%, 60% and clearcut for both hardwood and mixedwood stands and for V. edule in hardwood 66%. *L. borealis, R. pubescens* and *V. edule* in mixedwood stands showed no differences in SLA among retention levels.

Results at EMEND occasionally supported our expectations. Compared to control stands, we observed significantly higher values of SLA for *R. pubescens* in 20% retention hardwood stands, *C. canadensis* in 75% retention hardwood stands, and for *L. borealis* in 75% retention mixedwood stands (Figure 4.5). In contrast to expectations we observed, compared to control, significantly lower values of SLA for *C. canadensis* in 75% retention and for *V. edule* in 75% and 20% retentions in mixedwood stands.

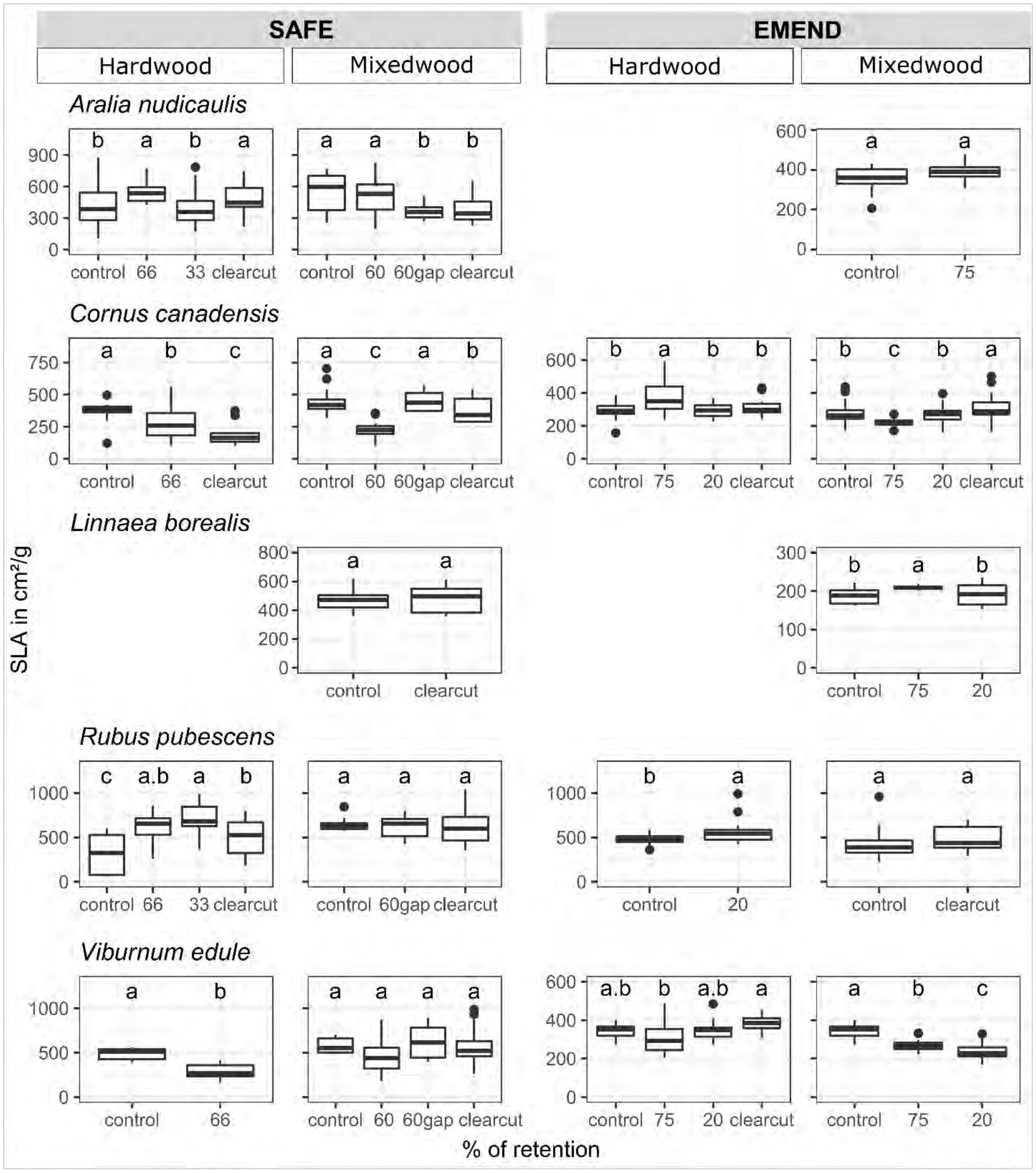


Figure 4.5 Comparison of Specific Leaf Area (SLA) among retention levels for the five selected species that were found in SAFE and EMEND, by forest type. Results of the comparisons based on Tukey tests are indicated by letters. Different letters indicate a significant difference at $p<0.05$. Results are missing for retention levels and/or forest types for some species because they were not found in that combination. See also Annexe F.

4.6 Discussion

4.6.1 Understory community scale response 20 years after retention

In both hardwood and mixedwood stands the community functional composition did not vary significantly by experiment or retention levels (from PERMANOVA) but trends can be observed in the PCA. We hypothesized that traits favored by harvest were those reflecting an acquisitive strategy. However, we observed this trend only for hardwood stands in SAFE experiment, and for hardwood and mixedwood stands in EMEND experiment. EMEND hardwood stands with lower retention (20% and clearcut) were characterized by species that were shade intolerant, with higher LNC and LPC. In EMEND mixedwood stands that were clearcut, species with these attributes were favored, as well as those with faster growth and higher SLA. In the SAFE experiment, species with faster growth were favoured in hardwood 33%, 66% and clearcut retention stands, supporting this hypothesis. However, the results for mixedwood stands did not provide any evidence for this hypothesis as communities were similar across the different retention levels. Noualhaguet *et al*. (2023b) observed for bryophytes, which are known to be sensitive to harvesting (Caners *et al.*, 2013b), that many generalist and common species were shared among all retention levels and forest types in SAFE. We attribute similarity in community traits to the similar microclimatic conditions (soil temperature and understory humidity) found on these sites (Noualhaguet *et al*., 2023b), as understory vascular vegetation is known to be very sensitive to differences in microclimate (Christiansen *et al.*, 2022; Zellweger *et al.*, 2020).

We expected increased taxonomic richness and functional diversity after harvest, as compared to control stands, with the differences between harvest and control stands being more pronounced in the east than in the west, and especially in the older mixedwood forest. We found limited support for this hypothesis. In hardwood stands, taxonomic richness and functional diversity were similar among the levels of retention in both experiments. In the mixedwood stands at SAFE, clearcuts had higher richness and functional diversity than other retention levels. In the mixedwood stands at EMEND, taxonomic richness did not follow the retention levels; rather, it was highest in the 20%. These results could be attributable to changes in richness that accrued over the 20 years since harvesting as stands regenerated. Similar to our results, Bermúdez e*t al*. (2007), in a study of secondary growth laurel forest stands 15 years after harvest, observed only small changes in species diversity following clearcutting. These authors attributed this to the high fertility of the soils and the low disturbance of the forest floor during the harvesting. SAFE and EMEND experiments were harvested in winter when the ground was snow covered so physical soil disturbances (rutting or scarification) were minimal in all treatments (Brais *et al.*, 2004; Sidders and Luchkow, 1998). Our results contrast with previous studies that found a large increase in functional diversity after harvesting in boreal mixedwood and coniferous forests as well as in temperate forests (Dodson *et al*., 2008; Wei *et al*., 2019; Wienk *et al*., 2004). We assume that these differences are due to the different harvest periods, spring for Dodson *et al.* (2008), autumn-winter Wienk *et al.* (2004), and from post-harvest site preparation (plow, disk trenching and burning) in the study of Wei *et al.* (2019). Harvest timing and site preparation are both characteristics that influence soil fertility and available space, and therefore species establishment (Belleau *et al.*, 2006; Frey *et al.*, 2003b). While these practices can be used to promote commercial trees species, they can also be unfavorable to understory vegetation (Dodson *et al.*, 2008; Harvey *et al.*, 2002; Wei *et al.*, 2019; Wienk *et al.*, 2004) as silvicultural operations (harvesting, site preparation, plantation) are mechanical disturbances that are different in nature from natural disturbances (chemical, biological, physical).

Our results suggest that lower retention levels in the SAFE experiment had a more pronounced and longer effect on the functional diversity of communities than at the

EMEND experiment. We suggest that this is due to differences in microclimate between eastern (wetter) and western (drier) regions (Bergeron and Fenton, 2012; Fulton, 1989; Hare and Thomas, 1979). Harvesting in the east likely creates more differences from pre-harvest in the microenvironment (light, temperature, humidity) by opening the canopy (Aerts and Chapin, 1999; Haeussler *et al.*, 2002; Weiher and Keddy, 1995) and exposing the understory to more contrasting conditions than in the west where species are already adapted to tolerate drier conditions. Furthermore, in studies based on seedling establishment and stem regeneration after retention harvesting, lower retention levels in the east had a more pronounced and longer effect than in the west (Gradowski *et al*., 2010; Noualhaguet *et al*., 2023c; Solarik *et al*., 2012). This is likely attributable to edaphic factors such as parent material, surficial deposits, and organic matter accumulation which influence the regeneration and growth of trees following a disturbance (Mansuy *et al*., 2012). The mostly clay deposits in the east Boreal Shield compared to rich mineral deposits in the west Boreal Plains, might explained the longer stands recovery after harvesting observed in the east (Bartels *et al*., 2016). The slower recovery of the stands would play on the slower recovery of the understory communities.

Our hypothesis that the effects of harvesting on species richness would be greater in the older forest (mixedwood) than the younger forest (hardwood) was only partially supported by limited differences apparent only in mixedwood stands. Like between east and west, between hardwood drier and mixedwood wetter stands (Chen and Popadiouk, 2002), communities in hardwood stands might be able to tolerate greater fluctuations in seasonal conditions than species in mixedwood stands. The greater tolerance of hardwood communities could be due to a greater tolerance to changing environmental conditions. Young stands, mostly composed of deciduous trembling aspen (*Populus tremuloides* Michx.) are subjected to stronger seasonal fluctuations in temperature, humidity, irradiance, and wind in the understory (Barbier *et al.*, 2008). Older stands, composed of a mix of deciduous and persistent coniferous species have more moderate seasonal climatic variation in the understory (Barbé *et al.*, 2020). We follow again the results observed by Noualhaguet *et al*., (2023b) for the bryophytes and suggest that species in hardwood dominated stands tolerated more fluctuations in environmental conditions than species in mixed stands.

4.6.2 Species level response 20 years after retention

When we examined the trait breath distribution, the foliar economic spectrum (Wright *et al.*, 2004) was well expressed. As expected, for a given species, SLA, LNC and LPC were inversely related to LDMC. *Rubus pubescens* and *Viburnum edule* had traits consistent with an acquisitive strategy which dominate in early successional communities (Whittle *et al.*, 1997). *Aralia nudicaulis* was also characterized by an acquisitive strategy, however this ubiquitous species is not normally part of early successional post-harvest communities and is more generally characterized by more conservative strategy (Hart and Chen, 2006). *Cornus canadensis* and *Linnaea borealis*, shade tolerant species which are normally part of later successional communities, had traits consistent with a conservative strategy, which are low SLA, LNC and LPC but high LDMC (Hart and Chen, 2006; Rowe, 1983). The different breath and peak in the frequency of functional traits showed the plasticity of these five species. The species studied not having been found in majority in all the retention levels, could have explained the different breath and peak. The realization of density plots, showing the relative frequency only in control stands (figure not presented), showed similar tendencies in the breaths, and in the intervals values of picks but with reduced frequency for the four traits of the five species. Each species had its own distribution of traits, and thus it was not possible to highlight a common pattern. Kumordzi *et al*., (2019) also observed different trait distributions for common species across their distribution in the boreal mixedwoods. These authors also showed an important proportion of the ITV occurred at the local scale (comparison of disturbed vs undisturbed sites) whereas large scale environmental gradients, such as temperature and precipitation, had relatively less impact. In our study, community richness and functional diversity were similar between the different levels of retention/experiments, more differences occurred at the individual scale; i.e., between species.

After harvesting, we expected leaf morphological traits to vary predictably with harvesting; i.e., the lower the retention level, the greater the abundance of individuals with high SLA and lower LDMC compared to control stands (Wright *et al.*, 2004). However, responses differed among the five species and did not follow the retention levels. Community assembly is thought to result from the interaction between three types of processes: environmental filtering, biotic interactions and demographic stochasticity (HilleRisLambers *et al.*, 2012). The distinct responses of the five species, 20 years post retention, might result from a combination of the three like observed by Cardou *et al.*, (2022). With the environmental filtering, the five species which exploit broader niches, have high ITV that have allowed them to modify trait values to find the local adaptive optima and achieve higher fitness at the local scale (Ackerly, 2003). With the influence of biotic factors, like the interspecific competition, the niche overlap should be minimized between coexisting species in a community by maximizing the differences (The limiting similarity theory, (Chesson, 2000)). With the random factor, species respond to the environmental changes in other ways that expected and sometimes without providing a net adaptive advantage (Bolnick *et al.*, 2011; Joner *et al.*, 2012; Moran *et al.*, 2016). These last two factors could explain the distinct and unexpected responses of the five species 20 years after harvest.

Our results imply that there is more than one strategy for achieving consistent presence in forest understory plant communities. Species can rely on different strategies for resource acquisition. They can have range between acquisitive or conservative or they can rely on high level of plasticity. The distinct responses of the species to harvesting implies that the functional response of understory communities to harvesting is very complex and requires species-specific studies. To represent the community functional composition, it is important to understand autecology of each species and to measure range and variation of traits on a large number of individuals and also on different part of the plants (Kumordzi *et al.*, 2019; Poorter *et al.*, 2019). It is also important to recognized that a trait may be present because it was inherited from a previous ancestor and not because it is necessary for adaptation to current habitat conditions (Wang *et al.*, 2018). This make the trait selection a very important step that should be based on precise hypotheses. Certain key traits are often excluded because they are difficult to measure and not readily available in databases (i.e., root traits), limiting the predictive capacity of a trait-based approach (Aubin *et al.*, 2016). However, the choice of traits must be made according to the mechanisms underlying the species' response to its environment, to avoid non-functional traits (i.e., inherited from previous ancestor). These factors make it difficult to isolate the effects of a disturbance like harvesting on an individual trait. Nevertheless, it is essential to recognized that the functional response at community level (i.e. via community weight mean) may differ from that at intraspecific.

4.7 Conclusion

We found that the impacts of harvesting on understory community taxonomic richness, functional diversity, and functional traits were limited 20 years post-harvest. This suggests that retention harvesting has the potential to help maintain functional understory diversity. These results also showed that there is more than one strategy understory plant species to maintain themselves in forest communities through changes associated with a disturbance like harvesting. Although species with acquisitive strategy are favored at the community level, different trait value can be expressed by the species to obtain a better fitness when faced with changing env conditions. This is particularly the case in systems with species having a broad ecological range as in boreal forest. It is therefore needed to assess both inter and intra specific response to obtain a comprehensive portrait of understory community response to disturbance in boreal forest. We found that each species was characterized by a different functional response to the retention levels, showing the species-specific reactions to environmental variation. Thus, species favored in a particular environment might not only be species that show traits we expect to be advantageous but may be those possessing the largest intraspecific variability. While a trait-based approach may be often use for studying plant ecology, it is important to consider its limitations when applying it to different ecosystems or research questions. Effectively the relevance of traits can vary depending on mechanisms underlying the species response' at the environment. Taxonomic, functional and phylogenetic approaches should complement each other increasingly in future research, to improve our understanding of community structure and composition.

CHAPITRE 5

CONCLUSION

En forêt boréale canadienne, la CT est la pratique forestière la plus commune malgré la reconnaissance de ses effets négatifs, notamment la simplification des structures forestières. Cela a conduit à une situation d'urgence de protection et de conservation de la biodiversité où l'évaluation de traitements sylvicoles alternatifs est l'une des priorités de la recherche en foresterie. Ces traitements alternatifs permettraient de maintenir des forêts productives saines, offrant une multitude de services écosystémiques et riches en diversité d'espèces indigènes. C'est l'objectif de l'AFE. Pour l'atteindre, l'AFE suggère une gestion des forêts de manière à les rapprocher, en termes de structure, de fonction et de composition, aux forêts naturelles à tous les stades de développement de la succession. Parvient-on à reproduire la diversité des structures et des compositions forestières observées après perturbations naturelles grâce à une gamme de traitements sylvicoles ? C'est la problématique principale de cette thèse. Pour cela, le suivis des deux dispositifs expérimentaux SAFE au Québec et EMEND en Alberta mis en place il y a 20 ans, nous a servis d'appuis pour évaluer si les intentions sylvicoles établies dans le sens de l'AFE s'appliquent dans le temps suite à différents traitements en forêt boréale mixte. La question soulève différents aspects de réponses qui touche deux domaines qui semblent s'opposer : la productivité et la conservation.

Le premier est principalement abordé dans le Chapitre 2 de cette thèse. Il est représenté par la structure d'âge et composition en espèces commerciales des peuplements localisés dans le dispositif SAFE. Nous montrons que plus la coupe appliquée fut intense, plus le peuplement met du temps à revenir à un état de référence naturel en termes de surface terrière des arbres commercialisables. De plus, les coupes plus intenses favorisent des taux de régénération (gaules) élevés par rapport aux coupes moins intenses. Le second domaine, la conservation, est abordé dans les Chapitres 3 et 4, représentée par les communautés végétales de sous-bois (richesse en espèces de bryophytes et diversité fonctionnelle des plantes vasculaires) et n'est pas indépendant des aspects de productivité (structure et composition des peuplements) présentés dans le Chapitre 2. En effet, nous montrons l'importance du niveau de récolte et du type de peuplement forestier où sont pratiquées les coupes, pour le maintien de la richesse en espèces de bryophytes dans les forêts gérées (Chapitre 3). Même si les peuplements ont été récoltés avec une perturbation minimale des habitats du sol forestier, la structure et la composition des peuplements, incluant la dynamique du bois mort, 20 ans après la récolte ont affecté différemment les habitats forestiers et les conditions de croissance, et par conséquent les communautés. Ces attributs liés à l'humidité, à la température et aux nutriments du sol, sont tous des éléments importants à considérer lors de la mise en place de plan de récolte. Au niveau de la végétation vasculaire de sous-bois (Chapitre 4), la comparaison entre les 2 dispositifs SAFE dans l'est et EMEND dans l'ouest du Canada montre d'une part l'importance des facteurs à grande échelle (précipitations, température, régimes d'incendie) qui peuvent structurer l'assemblage général des espèces de sous-bois. D'autre part, elle montre l'importance relative de la variabilité intraspécifique dans les communautés végétales lorsque nous cherchons à explorer les effets de conditions environnementales contrastées résultant de perturbations locales telles que l'exploitation forestière. Ces résultats ont des implications au niveau des plans d'échantillonnage, dans la sélection des variables de réponse et des variables explicatives pour réaliser des études locales et continentales.

Le Canada présente une grande diversité d'écosystèmes forestiers et de régimes de perturbation, ainsi que des considérations sociales et économiques qui varient d'un endroit à l'autre. Par exemple si dans l'Est, un des objectifs principaux des CP est de favoriser le retour et l'accroissement des conifères souvent par la limitation du retour du peuplier faux-tremble, dans l'Ouest, le peuplier fait partie des composants du paysage et donc les CP cherchent à favoriser son retour ainsi que celui des conifères. Les pratiques de gestion forestière doivent varier en fonction de cette diversité. Aucun système de récolte ou de sylviculture n'est approprié partout. Les systèmes de coupe totale, partielle, de rétention, de coupe progressive ou de sélection peuvent être écologiquement, économiquement et socialement appropriés dans le bon contexte. L'utilisation d'un mélange de systèmes peut aider à obtenir une gamme de tailles et de structures de parcelles dans les peuplements et dans les paysages. Les forestiers doivent choisir le système sylvicole le plus approprié, en fonction de facteurs de sécurité, d'écologie et d'exploitation. Le plus important est peut-être que les forestiers doivent concilier ou équilibrer les objectifs souvent contradictoires de la sylviculture et de la conservation de la biodiversité. Ce que nous montrons possible dans cette thèse avec les CP qui permettent, à moyen terme, le maintien ou la récupération des attributs des peuplements boréaux mixtes en termes de productivité (Chapitre 2) et de conservation de la biodiversité (Chapitre 3, Chapitre 4). Tandis qu'avec les CT, l'emphase porte plus sur la régénération qui permet d'envisager un développement futur des peuplements (Chapitre 2). Toutefois, les CP n'ont pas fait reculer les peuplements à des stades plus précoces avec une exploitation plus intensive, ni même avancer les peuplements à des stades plus tardifs avec une exploitation moins intensive. Elles ont essentiellement eu un impact initial qui semble se dissiper avec le temps. Malgré la confirmation du potentiel de l'AFE de maintenir un plus large éventail de services écosystémiques que les pratiques forestières intensives, nous ne pouvons pas conclure que nous parvenons à imiter la complexité des peuplements générés par les régimes de perturbation naturelle. Mais voulons-nous vraiment imiter les perturbations naturelles ?

Le sujet relève de plus en plus de discussions aujourd'hui. S'inspirer des perturbations naturelles est un principe fondamental qui guide la gestion forestière dans l'écozone boréale de l'Amérique du Nord depuis la mise en place de l'AFE (Attiwill, 1994; Chen et Popadiouk, 2002; Gauthier *et al.*, 2009). L'hypothèse était que les pratiques de gestion forestière (en grande partie l'exploitation et la régénération) qui reproduisent le plus fidèlement les perturbations naturelles permettraient de mieux préserver l'ensemble des valeurs forestières. Cependant les défis posés par la mise en œuvre de cet aménagement sont multiples.

Tout d'abord, la nature même de la foresterie commerciale (c'est-à-dire l'enlèvement du bois) rend impossible l'imitation précise des perturbations naturelles. Aucune perturbation naturelle n'enlève les troncs d'arbres et laisse tout le reste derrière elle (Palik *et al.*, 2002). Les opérations sylvicoles (récolte, préparation de terrain, dégagement de plantation) sont des perturbations mécaniques dont la nature est différente des perturbations naturelles (chimiques, biologiques, physiques). Les effets des deux types de perturbations seront différents même si le régime peut être semblable (Bergeron *et al.*, 2017; Brais *et al.*, 2013; Simard *et al.*, 2001). Malgré cela, l'observation des structures et des modèles de peuplements à travers les paysages produits par les perturbations naturelles a fourni des modèles potentiels pour les conditions souhaitées des peuplements et des paysages aménagés. Cependant, les perturbations naturelles sont de toutes formes et de toutes tailles, à de multiples échelles temporelles (Attiwill, 1994) de sorte qu'il est toujours possible de trouver qu'une action de gestion est d'une manière ou d'une autre « fondée sur » une perturbation naturelle. Il est donc essentiel de déterminer dans quelle mesure un peuplement doit être similaire à l'état jugé « naturel » pour atteindre les objectifs de l'AFE et ne pas penser que presque tout puisse passer pour cette approche. Au Québec, il y a un registre qui référence 17 états jugés naturels représentant les objectifs de gestion à atteindre après les coupes. Ces états sont définis en fonction de composants d'intérêt comme la structure, composition et bois morts des peuplements retrouvés dans les forêts préindustrielles (Bouchard *et al.*, 2011). Cependant jusqu'à ce jour, de nombreuses études ont révélé la complexité spatiale de l'hétérogénéité des peuplements laissée après les perturbations naturelles à laquelle s'ajoute la complexité temporelle de retrouver les états naturels d'après perturbations (Bergeron *et al.*, 2014; McCarthy, 2001, Oliver et Larson, 1996). Ces hétérogénéités à l'échelle des peuplements nichées dans les paysages sont encore mal comprises et les résultats de cette thèse le démontre. En étudiant le dispositif SAFE où les peuplements ont été récoltés manuellement, sans grosse perturbation physique du sol, les arbres récoltés sectionnés un par un, nous ne sommes pas parvenus à « orienter » le développement des peuplements tel que nous le souhaitions avec les CP (Chapitre 2). Nous n'avons pas fait reculer les peuplements à des stades plus précoces avec une exploitation plus intensive, ni même avancer les peuplements à des stades plus tardifs avec une exploitation moins intensive, nous avons essentiellement eu un impact initial qui semble se dissiper avec le temps.

Donc aujourd'hui il ne faudrait peut-être pas essayer de « copier » ces perturbations mais plutôt essayer de s'adapter à ces perturbations surtout si elles sont susceptibles d'augmenter dans le futur. De nombreuses études reportent l'évolution des régimes de perturbations naturelles, notamment en raison du réchauffement climatique suggérant qu'il peut ne pas être souhaitable d'émuler la gamme complète du type, de l'échelle et de la sévérité des perturbations présentes. Par exemple, les incendies de forêt ont perturbé des zones trois fois plus grandes que l'échelle de l'activité d'exploitation forestière (Natural Resources Canada, 2021). Les infestations du dendroctone du pin ponderosa (*Dendroctonus ponderosae* Hopkins, 1902), au début des années 1990, ont touché plus de 18 millions d'hectares de forêt en Colombie-Britannique et en Alberta (Cooke and Carroll, 2017), celles de la tordeuse des bourgeons de l'épinette plus de 13 millions d'hectares au Québec en 2020 (MFFP, 2020). L'augmentation de la sécheresse a entraîné une mortalité et une réduction générales de la croissance des arbres (Gray et Hamann, 2011; Hogg *et al.*, 2017), en particulier dans l'Ouest canadien sujet à la sécheresse (Hogg et Bernier, 2005). Par conséquent, même si l'imitation de la nature s'est imposée comme une stratégie de gestion forestière permettant de maintenir à la fois les produits du bois et la biodiversité, il n'est peut-être pas nécessaire de tenter d'imiter véritablement les perturbations naturelles. Il est peut-être temps de revenir à l'objectif initial de l'AFE : soutenir le plus large éventail de valeurs forestières (Hunter, 1990). Les nombreuses études portant sur l'imitations des perturbations naturelles nous guident sur les approches futures de gestion forestières pour atteindre cet objectif général.

En gardant à l'esprit que l'AFE nécessite une bonne compréhension de la dynamique naturelle des peuplements, il est impératif que les objectifs et les prescriptions sylvicoles soient basés à la fois sur les conditions actuelles des peuplements et sur la dynamique anticipée de la végétation, c'est-à-dire le recrutement, la croissance et la mortalité, après différents traitements. En outre, il est probable que les forêts primaires restantes dans les paysages aménagés seront les plus vulnérables aux incendies qui devraient augmenter en raison du changement climatique (Bergeron *et al.*, 2017a; Grondin*, et al.*, 2021). Nous pourrions assister à un effet additif du changement climatique et de la gestion forestière, renforçant les menaces actuelles qui pèsent sur les forêts boréales. Face à ce scénario, les stratégies d'aménagement écosystémique devraient tenir compte de ces risques pour mieux adapter les pratiques sylvicoles à ce nouveau contexte. Par exemple, appliquer des pratiques de restauration (drainage, plantation) pour améliorer la résistance et la résilience des forêts moins productives. Promouvoir la variabilité des CP comme alternative aux CT dans les forêts les plus productives permettrait également de maintenir les fonctions et services écosystémiques qu'elles fournissent déjà. Ensuite, nous devons adapter nos pratiques en fonction des enjeux de récolte. Sont-ils plus économique, sociétale, environnementale, les trois combinés ou seulement deux ?

Les avantages des forêts ont de multiples facettes et ne doivent pas être limités à une fausse division entre la production de bois et tous les autres services écosystémiques. Les compromis et les interactions sont complexes, dépendent du contexte et sont susceptibles de changer en fonction des priorités sociétales et de l'évolution des conditions écologiques. Ainsi, forestiers, écologistes et scientifiques appliqués apportent des contributions importantes et indissociables à la gestion des forêts. Les forestiers gestionnaires doivent reconnaître les risques auxquels sont exposées les forêts et être prêts à les intégrer dans les plans de gestion. En accord avec cela, les écologistes appliqués et les chercheurs forestiers doivent également s'adapter pour comprendre les outils économiques, sociaux et politiques utilisés par les gestionnaires. Grâce à cette compréhension, ils peuvent s'efforcer de trouver les questions de recherche importantes qui éclairent la gestion et la politique forestières face à la demande croissante de bois (Betts *et al.*, 2021; Kok *et al.*, 2018).

Ce projet de recherche a abordé des aspects clefs de l'AFE pour évaluer l'efficacité de multiples intensités de coupes dans le but de promouvoir la croissance des arbres résiduels, de favoriser la régénération et de minimiser les pertes de biodiversité. Toutefois, pour avoir une évaluation plus complète dans un contexte de gestion durable des forêts, il faudrait réaliser des études supplémentaires focalisées sur d'avantage d'aspect économique, de conservation, de services écosystémiques et de temps de récupération des attributs forestiers. Un des grands avantages des dispositifs expérimentaux SAFE et EMEND est l'existence de parcelles permanentes d'échantillonnage qui garantit le suivi des systèmes sylvicoles dans le temps et le développement des recherches futures. De plus, ils se trouvent dans des domaines très importants pour la productivité forestière au Canada. Les recherches déjà menées et celles de ce doctorat contribuent donc directement à l'industrie du bois. Enfin, les grands jeux de données accumulés pendant 20 ans peuvent compléter nos connaissances sur la complexité des écosystèmes forestiers. Bien souvent pour améliorer l'efficacité de la gestion ou pour atteindre d'autres objectifs sociétaux, les structures et modèles naturels ont été simplifiés (Beese *et al.*, 2019). Par exemple dans cette thèse, nous avons étudier l'effet des coupes sur différentes strates des peuplements forestiers, soit les arbres vivants et morts, les bryophytes et la végétation de sous-bois mais sans jamais vraiment regarder l'interaction entre ces strates. Pourtant, les processus d'interactions multiples sont considérés comme les principaux moteurs de la dynamique des écosystèmes forestiers et notamment de la dynamique de régénération forestière (Binkley et Fisher, 2012; Callaway, 1995; Grace et Tilman, 1990; HilleRisLambers *et al.*, 2012). La quantification de l'influence des interactions positives, négatives ou neutres, directes ou indirectes dans la dynamique forestière et la compréhension des mécanismes sous-jacents sont nécessaires pour mieux comprendre les effets de l'AFE. Ainsi le développement d'études dans ce sens nous permettrait de mieux comprendre quand, pourquoi et comment les différents processus sont importants dans la structuration des écosystèmes forestiers pour les considérer dans la planification des récoltes forestières.

ANNEXE A

Results of model on the bryophyte richness in function of treatment and cohort

Results of the generalized linead mixed model on the total bryophyte richness in function of treatment and cohort.

Random effects	Variance	Standard deviation
BLOC	0.0006488	0.025

Fixed effects	Estimate	Standard error	t-value	p-value
Intercept	3.01	0.06	50.81	<0.001
cohort2	0.08	0.08	0.99	0.32
cohort3	0.04	0.08	0.44	0.66
treatmentCC	-0.33	0.09	-3.70	<0.001
treatmentPC1/3	-0.09	0.08	-1.12	0.26
treatmentPC2/3	-0.03	0.08	-0.41	0.68
treatmentPCgap	-0.20	0.08	-2.41	<0.05
treatmentPCreg	-0.25	0.08	-3.05	<0.005
cohort2:treatmentCC	-0.01	0.12	-0.04	0.97
cohort3:treatmentCC	0.24	0.12	1.96	0.05

ANNEXE B

Mean values and standard errors for stand structures, microhabitats and climate variables by treatment and cohort

Mean values and standard errors for stand structures, microhabitats and climate variables by treatment and cohort. Variable are compared between treatments of the same cohort. Statistical significance determined by Tukey tests is indicated by letters. When no letter is mentioned, it means that no difference was found between treatments of the same cohort. Different letters indicate a significant difference by panel. PC, partial cut; CC, clearcut; BA, basal area; Nb, number.

Variables	Cohort 1				Cohort 2				Cohort 3	
	Control	PC 1/3	PC 2/3	CC	Control	PC reg	PC gap	CC	Control	CC
Stand structure										
Harwood (BA/ha)	42.6 ± 12.8^{a}	34.7 ± 10.8^{a}	17.9 ± 7.5^{b}	14.2 ± 5.1^{c}	29.4 ± 8.5^{a}	14.4 ± 6.0^{b}	12.4 ± 5.9^{b}	4.4 ± 3.7^{c}	9.8 ± 8.6^{a}	8.3 ± 5.2^{a}
Coniferous (BA/ha)	5.1 ± 3.3	5.1 ± 2.4	5.9 ± 3.3	2.7 ± 2.5	15.9 ± 3.9	15.8 ± 4.9	13.3 ± 5.9	12.6 ± 2.9	13.7 ± 4.8^{a}	4.3 ± 3.5^{b}
Canopy closure (%)	61.64	55.68	64.27	68.78	66.42	69.13	64.55	64.76	64.76	67.01
Microhabitats										
Stumps (nb/ha)	144.2 ± 92.5 ^{a}	266.7 ± 105.5 $^{a.c}$	415.0 ± 177.2 $^{b.c}$	750.0 ± 258.8 ^{b}	270.0 ± 146.1	458.3 ± 186.3	425.0 ± 172.4	536.7 ± 252.5	169.6 ± 120.2	257.7 ± 165.3
Snags (nb/ha)	168.3 ± 82.1	118.3 ± 79.9	159.6 ± 42.7	82.1 ± 64.1	307.1 ± 135.3 ^{a}	257.1 ± 137.4 ^{a}	181.7 ± 129.0 ^{b}	53.1 ± 20.9 ^{b}	182.1 ± 91.7	119.4 ± 148.0
Fresh dead wood (m^3/ha)	59.1 ± 35.3	17.8 ± 14.6	43.4 ± 22.1	2.5 ± 2.0	65.5 ± 40.7	44.9 ± 19.3	42.2 ± 30.2	19.0 ± 20.9	18.4 ± 12.7	2.6 ± 1.5

Old dead wood (m^3/ha)	60.1 ± 15.8	44.0 ± 30.4	70.8 ± 25.5	15.3± 11.6	45.1 ± 14.6	53.6 ± 11.7	61.6 ± 13.7	57.0 ± 18.9	36.6 ± 1.9	63.1± 11.9
Climate										
Min soil temperature (°C)	3.5 ± 1.9	1.0 ± 2.5	2.6 ± 2.1	2.4 ± 0.4	1.1 ± 1.2 0.4	0.8 ± 3.5	2.7 ± 5.2	0.1 ± 5.8	1.3 ± 1.3	0.9 ± 2.9
Max soil temperature (°C)	32.2 ± 1.5	32.8 ± 0.9	31.3 ± 0.6	30.6 ± 0.4	32.0 ± 0.7	31.7 ± 0.9	33.1 ± 1.7	36.1 ± 10.0	31.7 ± 0.9	32.7 ±2.5
Min soil moist (%)	4.5 ± 2.6	1.8 ± 2.3	5.4 ± 4.1	9.4 ± 5.8	6.5 ± 9.0	14.5 ± 4.7	1.9 ± 2.5	23.3 ± 8.6	3.2 ± 4.0	2.9 ± 4.9
Max soil moist (%)	43.9 ± 6.6	40.6 ± 12.3	46.3 ± 9.8	50.9 ± 8.1	45.2 ± 5.3^{a}	43.1 ± 16.9$^{a.b}$	41.7 ± 15.9^{b}	50.3 ± 3.7^{a}	49.7 ± 7.6	53.0 ± 3.0

ANNEXE C

Number of occurrences for each bryophyte species found in each forest type, in each treatment

Number of occurrences for each bryophyte species found in each forest type, in each treatment. Nomenclature follows Faubert (2012-2014). Species are presented by life forms. n refers to the number of species in each forest type. * Represents species considered rare on the surveyed sites (abundance < 6). PC, partial cut; CC, clearcut.

Taxon	Species code	Cohort 1 : Aspen dominated stands				Cohort 2 : Mixedwood stands				Cohort 3: Coniferous mixedwood stands	
		Control	PC 1/3	PC 2/3	CC	Control	PCreg	PCgap	CC	Control	CC
# of species		61				56				48	
ACROCARPOUS											
Aulacomnium palustre	Aulpal	9	1	1		5	2	2		1	1
Dicranum flagellare	Dicfla	1	3	1						6	15
Dicranum fuscescens	Dicfus	19	14	28	13	40	29	22	36	39	42
*Dicranum majus**	Dicmaj	1				1				1	
Dicranum montanum	Dicmon	15	10	19	7	17	15	14	11	41	29

Dicranum polysetum	Dicpol	5	7	7	5	13	24	18	36	7	7
Dicranum scoparium	Dicsco	2	5	2	3	2				6	6
Dicranum viride *	Dicvir	2									
*Hedwigia ciliata**	Hedcil		1								
Mnium spinulosum	Mnispi	6	4	2	1	13		4	1	1	1
Oncophorus virens	Oncvir	2	1	2	1		2	2	2	3	2
Plagiomnium cuspidatum	Placus	20	18	30	16	56	33	18	10	9	8
Plagiomnium drummondii	Pladru			9	2	9	7	1	1		
Plagiomnium ellipticum	Plaell	3	2	6	5	2			6	8	16
*Plagiomnium medium**	Plamed					1					
Pohlia nutans	Pohnut	8	5	3	1	1				14	3
Polytrichum juniperinum	Poljun	1		2	2				4	2	1
Rhizomnium punctatum	Rhipun	1				5	2	1	1	4	3
Tetraphis pellucida	Tetpel	2	14	4	2	2		1	1	23	28

PLEUROCARPOUS											
Amblystegium serpens	Ambser	1	2	4	7	7	3	6	8		4
Brachythecium acuminatum	Braacu	5	5	8	4	12	1	5			
Brachythecium acutum	Braact	54	79	60	47	13	17	22	8	29	32
Brachythecium campestre	Bracam	109	119	140	89	136	95	103	148	65	88
Brachythecium curtum	Bracur	16	22	30	7	16	41	7	3	28	20
*Brachythecium falcatum**	Brafal				1						
Brachythecium reflexum	Braref	59	57	61	55			2	4	37	38
*Brachythecium rutabulum**	Brarut	1		1	2						
Brachythecium starkii	Brasta	20	38	24	29	29	21	14	18	24	24
Brotherella recurvans	Brorec	7	1		1				1		
Callicladium haldanianum	Calhal	57	44	58	32	23	23	27	43	109	120
Campyliadelphus chrysophyllus	Camchr	20	32	44	24	5	19	33	11	10	17
Campylophyllum hispidulum	Camhis	29	12	11	10	17	8	15	8	1	8

Eurhynchiastrum pulchellum	Eurpul		3		1	3		8	1	9	1
Herzogiella turfacea	Hertur				6	3					
Hylocomium splendens	Hylspl	2	1	2		10	5	10	5	2	
*Hypnum fauriei**	Hypfau					1					
Hypnum imponens	Hypimp	12	5	4		1	5	5		3	5
Hypnum pallescens	Hyppal	14	5	9	7	4	8	9	7	6	12
Plagiothecium cavifolium	Placav		1		2					17	17
*Plagiothecium denticulatum**	Pladen					1				2	
Platygyrium repens	Plarep					1		6	3	4	1
Pleurozium schreberi	Plesch	8	25	28	6	64	95	80	91	45	35
Ptilium crista-castrensis	Pticri	1	16	14		14	50	27	26	12	4
Pylaisia intricata	Pylint	10	2			14	9	9	3	1	
Pylaisia polyantha	Pylpol	24	18	7		12	7	8			1

Rhytidiadelphus triquetrus	Rhytri	3		7	2	16	4	4	4	1	
Sanionia uncinata	Sanunc	71	74	72	14	133	79	79	60	43	28
LIVERWORTS											
*Aneura pinguis**	Anepin			1							
*Barbilophozia attenuata**	Baratt		1								
Barbilophozia barbata	Barbar	2	1	2	2					9	
Bazzania trilobata	Baztri	2	5	1							
Blepharostoma trichophyllum	Bletri	10	4	6	1	5	6	7		4	
Cephalozia lunulifolia	Ceplun	7	2	6	7					5	3
*Chiloscyphus graveolens**	Chigra			1							
Chiloscyphus profundus	Chipro	36	14	32	15	75	59	64	53	32	18
*Frullania inflata**	Fruinf					1					
Frullania oakesiana	Fruoak	1	1			16	2	1	1	9	2
Geocalyx graveolens	Geogra	18	28	29	9	14	15	23	13	12	23

*Homalia trichomanoides**	Homtri					1		1			
Jamesoniella autumnalis	Jamaut	68	41	57	23	46	41	46	32	35	24
Lepidozia reptans	Leprep	1		4	3	5	3		3	7	3
Lophozia guttulata	Lopgut	1	4	2	1					4	
Nowellia curvifolia	Nowcur	8	1	9	2	14	7	21	12		
*Nowellia unifolia**	Nowuni		1								
Ptilidium ciliare	Pticil	14	7	14	6	18	8	32	17	5	2
Ptilidium pulcherrimum	Ptipul	27	18	30	17	60	60	66	49	36	19
*Radula complanata**	Radcom		1			4					
*Riccardia latifrons**	Riclat					1					
*Scapania apiculata**	Scaapi							3			

ANNEXE D

Results of the models testing for differences in the two diversity indices (taxonomic richness and functional diversity (Rao)) between the retention levels

Results of the ANOVA models testing for differences in the two diversity indices (taxonomic richness and functional diversity (Rao)) between the retention levels. p-value indicates if the difference was significant with *. df degrees of freedom.

Stand	Experiment	Diversity indices	df	Sum of squares	Mean squares	Statistic F	p-value	
Hardwood	SAFE	Richness	3	5.67	1.89	0.11	0.949	
		Rao	3	0.002	0.0006	0.80	0.528	
	EMEND	Richness	3	25.58	8.53	1.44	0.301	
		Rao	3	0.001	0.0004	0.09	0.966	
Mixed wood	SAFE	Richness	3	125.70	41.89	5.59	0.0231	*
		Rao	3	2.83e-4	9.43e-5	10.10	0.004	*
	EMEND	Richness	3	281.00	93.67	9.07	0.006	*
		Rao	3	8.08e-5	2.69e-5	0.91	0.476	

ANNEXE E

Results of the models testing for differences in leaf dry matter content (LDMC) between the retention levels

Results of the ANOVA models testing for differences in leaf dry matter content (LDMC) between the retention levels. p-value indicates if the difference was significant with *. Exp, Experiment; df degrees of freedom (varies because species were not always present in all retention levels).

Stand	Exp	species	df	Sum of squares	Mean squares	Statistic F	p-value	
HARDWOOD	SAFE	*Aralia nudicaulis*	3	23648	7883	6.65	<0.001	*
		Cornus canadensis	2	14487	7243	7.79	1.02e-03	*
		Rubus pubescens	3	43321	14440	24.56	<0.001	*
		Viburnum edule	1	1386	1385.7	1.43	0.239	
	EMEND	*Cornus canadensis*	3	8736	2912	1.96	0.124	
		Rubus pubescens	1	6838	6838	11.51	1.63e-03	*
		Viburnum edule	3	7518	2506	4.14	9.03e-03	*
MIXEDWOOD	SAFE	*Aralia nudicaulis*	3	8168	2722.7	8.13	<0.001	*
		Cornus canadensis	3	40435	13478	10.35	<0.001	*
		Linnaea borealis	1	2170	2170	42.83	<0.001	*
		Rubus pubescens	2	2780	1390.1	2.29	0.108	
		Viburnum edule	3	51340	17113	15.52	<0.001	*
	EMEND	*Aralia nudicaulis*	1	19272	19272	16.63	<0.001	*
		Cornus canadensis	3	7275	2425	1.30	0.276	
		Linnaea borealis	2	18442	9221	11.57	<0.001	*
		Rubus pubescens	1	8484	8484	3.68	0.060	
		Viburnum edule	2	17621	8810	17.76	<0.001	*

ANNEXE F

Results of the models testing for differences in surface leaf area (SLA) between the retention levels

Results of the ANOVA models testing for differences in surface leaf area (SLA) between the retention levels. p-value indicates if the difference was significant with *. Exp: Experiments; df degrees of freedom (varies because species were not always present in all retention levels).

Stand	Exp	species	df	Sum of squares	Mean squares	Statistic F	p-value	
HARDWOOD	SAFE	*Aralia nudicaulis*	3	634403	211468	9.38	<0.001	*
		Cornus canadensis	2	325562	162781	18.39	<0.001	*
		Rubus pubescens	3	1929048	643016	16.9	<0.001	*
		Viburnum edule	1	399952	399952	75.53	<0.001	*
	EMEND	*Cornus canadensis*	3	81557	27186	10.38	<0.001	*
		Rubus pubescens	1	68361	68361	6.47	0.015	*
		Viburnum edule	3	65733	21911	7.54	<0.001	*
MIXEDWOOD	SAFE	*Aralia nudicaulis*	3	1126967	375656	19.5	<0.001	*
		Cornus canadensis	3	733958	244653	33.18	<0.001	*
		Linnaea borealis	1	2170	2170	42.83	<0.001	*
		Rubus pubescens	2	29708	14854	0.70	0.500	
		Viburnum edule	3	208624	69541	2.12	0.103	
	EMEND	*Aralia nudicaulis*	1	10796	10796	4.03	0.052	
		Cornus canadensis	3	181366	60455	12.69	<0.001	*
		Linnaea borealis	2	8182	4091	9.46	<0.001	*
		Rubus pubescens	1	52892	52892	2.96	0.091	
		Viburnum edule	2	150929	75464	59.17	<0.001	*

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