UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

# DYNAMIQUE DES COMMUNAUTÉS DE BRYOPHYTES DANS LA PESSIÈRE À MOUSSES DE LA FORÊT BORÉALE: RÔLE DES ÎLOTS DE RÉTENTION APRÈS COUPE

MÉMOIRE

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# AVANT-PROPOS

Conformément aux exigences du programme de maîtrise en biologie, ce mémoire comprend un article rédigé en anglais, portant sur une étude visant à déterminer les facteurs influençant la dynamique des communautés de bryophytes suite à des traitements sylvicoles, ainsi qu'une introduction et une conclusion générale. Cet article sera soumis à la revue scientifique « Canadian Journal of Forest Research ».

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# TABLE DES MATIERES

# LISTE DES FIGURES

# LISTE DES TABLEAUX

Tableau Page

# RÉSUMÉ

En forêt boréale, dans la pessière à mousse de l'ouest du Québec, les feux laissent des îlots intacts après leur passage. Le principal objectif de cette étude est de déterminer quel rôle joue la rétention après coupe, dans un contexte d'aménagement forestier écosystémique, sur la dynamique des communautés de bryophytes et de déterminer les facteurs influençant la capacité des îlots de rétention après coupe à remplir la fonction écologique de refuge. La première hypothèse émise est que les îlots de grande taille devraient être plus efficaces pour servir de refuge. La seconde hypothèse est que le temps depuis la coupe devrait influencer négativement la population d'origine. La troisième hypothèse est qu'il existe un changement graduel de composition de l'îlot de rétention vers la matrice de coupe et que ce changement est plus marqué pour les grands îlots que les petits. Pour répondre aux hypothèses, un dispositif de 195 placettes de 50 m² a été inventorié selon la technique d'inventaire floristique par habitat dans des coupes de différents types de taille et d'âge depuis la coupe.

En général, les résultats démontrent une différence en recouvrement, composition et richesse selon la taille de l'îlot de rétention et le temps depuis coupe. On retrouve un fort recouvrement de *Pleurozium schreberi* dans les grands îlots de rétention et dans des parterres de coupe plus vieux. Aussi, on remarque un changement en composition de bryophytes : de mousses dans les petits îlots de rétention vers un mélange d'hépatiques, de mousses et de sphaignes dans les grands îlots de rétention. Ce changement en composition est aussi remarqué en fonction du temps depuis la coupe. La richesse en bryophyte est plus importante dans les vieux parterres de coupe que dans les jeunes. De plus, on remarque une différence en richesse de bryophytes entre le centre de l'îlot de rétention et les placettes de la matrice de coupe, mais les résultats ne démontrent pas de gradient. En somme, le maintien de longs cycles de coupe permet de préserver une flore importante de la forêt boréale.

**Mots clés :** coupe à rétention variable, îlots résiduels, fonctions écologiques, bryophytes et perturbation

# CHAPITRE I

# INTRODUCTION GÉNÉRALE

## 1.1 Problématique

Afin de répondre aux divers besoins de la population humaine croissante, l'utilisation du territoire tel que l'urbanisation, l'agriculture intensive et la déforestation augmentent. Ces actions, en plus des perturbations naturelles et de l'intensification de l'exploitation forestière, ont des répercussions importantes sur le paysage forestier de l'Amérique du Nord. Ainsi, la forêt a subi des pressions importantes, ce qui a mené à un rajeunissement de la mosaïque forestière et à la raréfaction des forêts matures et anciennes (Cyr *et al.* 2009). Ces enjeux écologiques ont poussé l'adoption de l'approche d'aménagement écosystémique qui vise à une diminution des écarts entre les forêts aménagées et naturelles (Gauthier *et al.* 2008). Avec l'intégration du nouveau régime forestier en 2013, les coupes à rétention variable ont commencé à être intégré dans l'aménagement de la forêt boréale pour réduire un écart important : la complexité au sein de la perturbation (Ministère des Ressources Naturelles 2013). La rétention variable est un régime sylvicole qui permet d'incorporer davantage de complexité dans les aires de coupe forestière (Mitchell & Beese 2002). Des exemples de traitements de rétention variable sont la CRS : coupe avec réserve de semenciers, la CPHRS : coupe avec protection de la haute régénération et du sol; et la CPRS : coupe avec protection de la régénération et du sol, où il est possible d'ajouter de la rétention variable, par exemple des bouquets ou des îlots (Ministère des Ressources Naturelles 2013). Lorsqu'il y a de la rétention dans ces traitements, les îlots de rétention représenteraient des arbres n'ayant pas brûlés ou des îlots résiduels laissés suite à un feu de forêt (Bergeron *et al.* 2001). Les rétentions peuvent avoir différents patrons spatiaux, selon l'objectif de l'aménagement, les rétentions peuvent être agrégées, dispersées et le pourcentage non coupé peut varier (Halpern *et al.* 2012). Les îlots obtenus suite aux coupes à rétentions variables rempliraient diverses fonctions écologiques en permettant de maintenir l'hétérogénéité du paysage (Hazell &

Gustafsson 1999). Cependant, on ne connait pas la quantité et la superficie de rétention à garder dans le paysage et les impacts que ces rétentions ont sur la dynamique forestière.

Dans la forêt boréale, dépendamment des espèces en cause, les îlots résiduels n'ont pas le même impact fonctionnel (Rosenvald & Lõhmus 2008). Certaines espèces sont plus sensibles que d'autres et ne réagiront pas de la même façon aux changements de structure dans leur environnement (Gandhi *et al.* 2004, Lõhmus *et al.* 2006, Aubry *et al.* 2009). Par exemple, les bryophytes, qui contribuent à une grande proportion de la biomasse et de la biodiversité totale dans une variété d'écosystèmes, sont très influencées par les perturbations dans l'environnement (Baldwin & Bradfield 2005, Fenton & Frego 2005, Bradbury 2006). La communauté des bryophytes semble être un ensemble d'espèces végétales idéales pour comprendre l'impact de la rétention verte dans la forêt boréale, car elle y constitue la majorité de la biodiversité de la flore forestière (Qian *et al.* 1998). Par ailleurs, elles sont des indicateurs biologiques de vieilles forêts reconnus pour l'aménagement forestier écosystémique de la forêt boréale (Nordén & Appelqvist 2001). Certaines bryophytes sont considérées comme étant des espèces pérennes associées aux forêts sans perturbation, mais elles peuvent tolérer quelques variations dans leur environnement (e.g *Hylocomium splendens, H. umbratum*; Jonsson & Esseen 1998). Ces dernières espèces, avec les espèces de *Sphagnum*, sont à la base de l'humus de la forêt boréale (Heinselman 1981). Les espèces colonisatrices ou pionnières sont plus associées aux forêts perturbées, telles qu'une zone récemment brulée (e.g. *Pohlia nutans*, *Polytrichum juniperinum* et *P. longisetum*; Jonsson & Esseen 1998, Fenton & Frego 2005). Par ailleurs, ces espèces ont été relevées dans de nombreuses études portant sur la composition et la diversité des communautés végétales après des feux ou d'autres perturbations naturelles (Bradbury 2006, Hylander & Johnson 2010). De plus, les espèces colonisatrices ou pionnières ont aussi été observées suite à différents types de perturbations anthropiques telles que les coupes forestières (Fenton *et al.* 2003, Baldwin & Bradfield 2005).

Cette étude a pour objectif de mieux comprendre la dynamique des communautés de bryophytes associées aux coupes de rétention dans la pessière à mousses. Elle vise plus particulièrement à déterminer si les îlots de rétention après coupe remplissent certaines fonctions écologiques. L'échantillonnage est effectué dans quatre types de rétention variable contenant des îlots de rétention. Ces îlots sont de différents âges, de différentes tailles et sont situés dans des parterres de coupe d'âges différents. Cette étude pourrait apporter des arguments de poids quant à la nécessité de préserver une hétérogénéité spatiale pour la conservation de la flore. Elle aidera à éclairer sur certaines décisions concernant les méthodes entreprises pour l'exploitation forestière ainsi que sur les caractéristiques à conserver au sein des îlots de rétention.

## 1.2 État des connaissances

### 1.2.1 Domaine bioclimatique de la pessière à mousses

Le domaine bioclimatique de la pessière à mousses couvre 27% de la superficie du Québec et fait partie du biome de la forêt boréale. Il est subdivisé en deux sous-domaines : le sous-domaine de l'ouest et le sous-domaine de l'est; cette subdivision est due aux conditions climatiques différentes selon la région (Saucier *et al.* 2003). De plus, selon les caractéristiques du milieu, la forêt boréale peut être constituée d'une variété d'essences telles que l'épinette noire (*Picea mariana* (*Mill.*) B.S.P.), le pin gris (*Pinus banksiana Lamb*.), le bouleau blanc (*Betula papyrifera Marsh*.) et le peuplier faux-tremble (*Populus tremuloides Michx.*). Ces essences sont capables de recoloniser rapidement les zones incendiées grâce à leur stratégies évolutives (Bergeron & Dubuc 1989, Bergeron 2000, Greene *et al.* 2004). La végétation au sol est principalement constituée de mousses (*Pleurozium schreberi* (Brid.), *Ptilium crista-castrensis* et *H. splendens*) ou d'éricacées (*Rhododendron groenlandicum, Kalmia angustifolia* et *Vaccinium angustifolium Ait*; Bergeron *et al.* 1999).

Les feux sont la principale perturbation naturelle la forêt boréale (Zackrisson 1977, Schmiegelow *et al.* 2006). Les cycles de feu historiques sont évalués approximativement entre 100 et 200 ans (Lesieur *et al.* 2002, Gauthier *et al.* 2008), mais ces cycles tendent à s'allonger depuis 1940 (Bergeron *et al.* 2006). De plus, le type de feu et sa sévérité vont influencer la dynamique forestière (Bergeron *et al.* 2007), ce qui aura des répercussions sur la régénération forestière, la succession végétale ainsi que la productivité des sites (Heinselman 1981, Franklin *et al.* 2007), et donc sur l'aspect du paysage, car lorsqu'il y a un feu de forêt, il est rare de voir une sévérité uniforme du feu (Bergeron *et al.* 2002). En effet, l'état de la végétation (Hély *et al.* 2000), la topographie (Cyr *et al.* 2007), les conditions météorologiques (Flannigan & Harrington 1988, Madoui *et al.* 2010) et le moment dans la saison vont modifier la sévérité et l'intensité du feu (Ryan *et al.* 2013). Ainsi, un feu de forêt va laisser des îlots intacts et des zones plus ou moins incendiées après son passage (Gauthier *et al.* 2001, Kafka *et al.* 2001). Lorsque l'intervalle de temps entre deux perturbations par le feu est suffisamment long, il est possible d'observer localement une succession forestière et des changements dans la composition de la canopée (Bergeron & Dubuc 1989). Dans ce type de situation, il est possible d'observer une dynamique par trouée et donc un remplacement des arbres de la canopée (St-Denis *et al.* 2010).

La principale perturbation anthropique de ce domaine bioclimatique est l'exploitation forestière. Par conséquent, la dynamique végétale est influencée selon le type de coupe employée (Aubry *et al.* 1999). Par exemple, si la coupe consiste en une faible rétention, il y a une diminution importante de la canopée et une augmentation de la distance entre les arbres retenus. Ce type de coupe a pour avantage de permettre une meilleure croissance pour les arbres dus à une diminution de la compétition intraspécifique, mais aura des répercussions désavantageuses pour les espèces de sous-bois (Halpern *et al.* 1999) dû à l'ouverture de la canopée. Lorsqu'il y a planification d'une coupe avec rétention variable, trois principaux facteurs sont considérés: les structures à maintenir, le nombre d'îlots de rétention et l'arrangement spatial des îlots (dispersé, aggloméré ou une combinaison; Franklin *et al.* 1997, Aubry *et al.* 1999). Dépendamment des objectifs de l'aménagement, tous ces facteurs vont varier. La diversité structurale forestière varie donc selon les arbres individuels retenus. En effet, la diversité structurale est influencée par la présence d'arbres ayant des caractéristiques distinctives, telles que des cavités, de grosses branches, un gros diamètre à hauteur de poitrine ou un certain niveau de pourriture (Brokaw & Lent 1999). De plus, pour améliorer la diversité structurale, différents stades de décomposition et de grosseurs de chicots et de débris ligneux peuvent être laissés sur place (Lindenmayer & Franklin 1997). Tous ces éléments permettent non seulement de varier la diversité structurale, mais permettent aussi de maintenir la biodiversité en procurant des habitats critiques pour une grande variété d'organismes (Harmon *et al.* 1986) tel que les oiseaux (Lance & Phinney 2001) et les invertébrés (Fenton *et al.* 2013). Par ailleurs, en conservant la structure du peuplement, cela permet de conserver une canopée multiétage et de maintenir des parterres forestiers intacts (Bergeron *et al.* 1999). Ces derniers permettent de servir de refuges pour plusieurs organismes.

En somme, il est important de bien cibler les objectifs d'aménagement après la coupe, de connaître les avantages et les inconvénients qu'un type de coupe engendrera, afin d'appliquer la bonne approche de conservation (Bergeron *et al.* 2007).

### 1.2.2 Îlots de rétention

Il y a trois fonctions écologiques principales qui ont été suggérées dans la littérature pour les îlots résiduels. La première fonction aurait un rôle de refuge « lifeboating » pour les espèces animales et végétales (Rosenvald & Lõhmus 2008). La seconde fonction aurait un rôle de connectivité « stepping stones » : ils permettraient d'augmenter la connectivité entre la forêt autour des coupes (Franklin *et al.* 1997). Finalement, la dernière fonction serait d'augmenter l'enrichissement structural de la forêt en régénération et ainsi contribuer à la diversité structurale de la forêt future (Franklin *et al.* 2007).

Selon la littérature, les îlots de rétention permettraient de maintenir la biodiversité à l'intérieur de la matrice de coupe (Franklin *et al.* 1997, Rosenvald & Lõhmus 2008, Gustafsson *et al.* 2012). Certains des éléments à l'intérieur des îlots de rétention sont obligatoires pour la survie des espèces (Berg *et al.* 1995, Lindenmayer & Franklin 1997) et le maintien des fonctions écosystémiques. Sans ces îlots, certaines espèces plus sensibles pourraient disparaître lors de l'exploitation forestière, car l'habitat dont elles dépendent serait modifié (Gustafsson *et al.* 2012). Alors, la structure des îlots de rétention permettrait d'améliorer les conditions microclimatiques, de procurer un substrat essentiel et de procurer des éléments nutritifs pour les organismes hétérotrophes (Berg *et al.* 1995, Madoui *et al.*

2010). De ce fait, ces îlots sont des parcelles d'habitat dans la coupe qui conservent des microhabitats ressemblant à la forêt d'origine (Jiquan Chen in Franklin *et al.* 1997), ce qui aura pour résultat de procurer un inoculum pour le rétablissement des espèces dans la matrice de coupe pendant la régénération. Ce résultat sera obtenu une fois que le nouveau peuplement forestier et les conditions spatio-temporelles seront idéals. Cela permettra la résilience de la forêt (Hazell & Gustafsson 1999) et d'augmenter le nombre d'espèces pouvant s'y établir. Par ailleurs, la probabilité qu'un îlot serve de fonction refuge change selon plusieurs facteurs. Le premier facteur, cité par plusieurs études, est la configuration des îlots. En effet, les études de Baker & Read (2011), de Halpern *et al.* (2012) et de Rudolphi *et al.* (2014) ont démontré que la probabilité qu'un îlot ait une fonction refuge augmente lorsque la rétention se distribue sous la forme d'agrégat. Un second facteur est le temps depuis la dernière coupe (Rosenvald & Lõhmus 2008). Un dernier facteur est l'habileté des espèces cibles à s'établir et à persister dans l'environnement (Perhans *et al.* 2009).

La rétention aurait également un rôle de connectivité, la coupe par rétention permettrait donc l'amélioration du mouvement des organismes en augmentant la connectivité entre les îlots (Gasaway & Dubois 1985 in DeLong & Kessler 2000). Traditionnellement, l'aménagement forestier structurait la rétention sous forme de corridor, car les scientifiques pensaient que cette technique permettait d'améliorer le déplacement des organismes (Simberloff *et al.* 1992, Mönkkönen & Mutanen 2003). Après certaines études, ils ont remarqué que cette structure du paysage s'appliquait davantage aux vertébrés qu'aux autres organismes (Franklin 1993). Des recherches ont ainsi démontré que les facteurs qui influencent la connectivité perçue entre les îlots de rétention dans la matrice de coupe sont la capacité de dispersion et de migration des organismes, les conditions de la matrice et la distribution spatiale des îlots (dispersé, en agrégat ou un mélange des deux; Franklin *et al.* 1997). En effet, les îlots de rétention permettent de rendre la matrice de coupe moins hostile pour la dispersion, car ils fournissent des zones avec un couvert forestier qui servent d'abris temporaires à travers la matrice (Franklin 1993). En somme, les facteurs qui permettent d'augmenter la connectivité entre les îlots de rétention sont la forme, la grosseur de ces derniers et l'espace entre les îlots (Hanski 1991, Rybicki & Hanski 2013). Par conséquent, pour augmenter la probabilité de dispersion, il faut augmenter la grosseur des îlots de rétention et diminuer l'espace entre les îlots de rétention (MacArthur & Wilson 1967).

Finalement, la dernière fonction, celle qui permettrait d'augmenter l'enrichissement structural de la forêt en régénération (Franklin *et al.* 2007) est enrichie par la coupe par rétention variable verte, car c'est une technique sylvicole permettant d'enrichir la complexité structurale d'un peuplement, de fournir des conditions qui permettent aux espèces de survivre et donc de permettre le rétablissement plus rapide de certaines espèces (Schmiegelow *et al.* 2006). De nombreuses études démontrent comment la coupe par rétention peut enrichir les peuplements des cohortes suivantes et, par ailleurs, fournir des habitats appropriés pour les espèces qui sont généralement rares ou absentes dans les jeunes peuplements (Baker & Read 2011, Halpern *et al.* 2012, Fenton *et al.* 2013).

En somme, les coupes avec rétention offrent des conditions microclimatiques moins stressantes que celles observées dans les coupes totales sans protection de la régénération (Franklin *et al.* 1997). Les fonctions écologiques décrites précédemment ne sont pas étudiées équitablement par les chercheurs. La première fonction, soit celle de refuge, est la plus présente dans la littérature (Rosenvald & Lõhmus 2008). Par contre, l'ensemble des études portant sur les îlots s'accorde sur le fait qu'ils sont d'une grande importance pour la conservation de la biodiversité (Gustafsson *et al.* 2012, Baker *et al.* 2013, Rudolphi *et al.* 2014).

### 1.2.3 Les bryophytes

Les bryophytes occupent une place importante dans la production primaire nette des systèmes boréaux (Turetsky 2003). De plus, elles participent à la rétention des nutriments et de l'humidité (Riely *et al.* 1979), elles créent donc un environnement favorable pour les invertébrés (Peck & Moldenke 2011) et procurent même des sols permettant l'établissement des trachéophytes (Jongmans *et al.* 2001). La communauté de bryophytes permet de stabiliser le substrat (Eldridge 1998) en influençant les caractéristiques du sol, le cycle des nutriments et la germination des trachéophytes. De plus, elles peuvent même servir de matériaux de nidification pour les petits mammifères et oiseaux (Breil & Moyle 1976). Les bryophytes contribuent à une grande variété de fonctions écologiques et jouent un rôle important dans la dynamique forestière.

Les bryophytes sont dépourvues de racine et de stomate, ce qui les distingue des plantes qui ont un système vasculaire plus développé. Elles sont donc poïkilohydriques, ce qui signifie que la majorité de l'eau et des nutriments sont transportés à l'extérieur et l'absorption se fait à la surface de la plante. C'est pourquoi la conservation d'eau et de nutriments est une priorité chez ces êtres vivants (Proctor 1982). De plus, elles possèdent de faibles proportions de tissus respiratoires, car elles croissent à leur apex et meurent par l'autre extrémité, elles ont donc une continuité de jeunes tissus qui sont efficaces à la photosynthèse. En plus, elles ont des périodes de croissance différente des trachéophytes, car dès que les conditions environnementales leur sont favorables, les espèces déjà établies vont croître (Tan & Pocs 2000), même si la luminosité et la température ne sont pas optimales pour les trachéophytes. D'autres facteurs affectent négativement leur croissance lorsqu'ils sont en trop grande quantité dans le milieu tel que la luminosité et la disponibilité des minéraux, et une haute température (Bates 2000). Par conséquent, il ne semble pas y avoir de compétition entre les bryophytes (During & Lloret 2001, Kimmerer 2005), puisque vivre en colonie diminue les désavantages liés aux pertes d'eau et de nutriments.

Grâce à leurs caractéristiques uniques, les bryophytes sont capables de coloniser différents substrats comparativement aux trachéophytes (p.ex. roches, tronc d'arbre; Bates 2000). Ces caractères particuliers font en sorte que certaines espèces se retrouvent sur la totalité des continents, car elles sont de grandes colonisatrices, par contre plusieurs autres espèces sont limitées par la dispersion. Pour se disperser, les bryophytes disposent d'une multitude d'organes sexuels (spores) et asexués (fragment végétatif, gemmae). Ces différents organes sont principalement dispersés par des agents abiotiques et biotiques tels que le vent, l'eau ou les animaux (Glime 2013). Lors de la reproduction sexuée, la probabilité de germination et d'établissement des spores est plus faible que la probabilité de germination et d'établissement des organes végétatifs. Cette probabilité varie en fonction de la grosseur des spores et de la longévité des spores (During 1979). De plus, il y a les conditions environnementales optimales telles que le pH du sol, l'humidité relative et la disponibilité de l'eau qui influencent cette probabilité. En plus, la densité des spores diminue avec la distance de la colonie mère (Söderström & Jonsson 1989). Aussi, la germination et l'établissement des organes végétatifs se font plus rapidement dans de nouveaux habitats et dans des milieux ouverts, car ils se dispersent moins loin que les spores (Kimmerer 1991) et l'habitat n'a pas besoin d'avoir des conditions optimales de germination (Löbel *et al.* 2006).

De plus, le patron de colonisation des bryophytes dépend de la durée de vie de leur substrat, du temps entre les perturbations, de la variété de microhabitats et la disponibilité des microhabitats (Herben *et al.* 1991, Söderström & During 2005). En modifiant les facteurs régissant l'environnement des bryophytes, on modifie la composition de la communauté des bryophytes parce qu'elle va varier en fonction des microhabitats disponibles (Mills & Macdonald 2004, 2005, Cole *et al.* 2008). Un microhabitat est une petite entité dont l'ensemble forme l'habitat (forestier, marin, urbain...) et qui évolue dans le temps sous diverses conditions microclimatiques. Il est donc une composante de l'habitat à très fine échelle (e.g. bois mort, roche, trou d'eau) et chaque microhabitat est optimal pour des espèces particulières (mesurés par l'occurrence des espèces et leur aptitude dans ce microhabitat donné). Par conséquent, les microhabitats possèdent des caractéristiques environnementales favorables ou non à l'établissement d'une communauté de bryophytes (Söderström 1993). En somme, l'échelle temporelle et les modifications dans l'environnement sont des facteurs limitant leur présence dans un environnement (Berg *et al.* 1995, Ross-Davis & Frego 2002, Fenton & Bergeron 2008).

Puisqu'une grande proportion de bryophytes pousse sur des microhabitats qui peuvent être isolés ou agrégés (Peck & Acker 1995) ou sur des substrats éphémères (Rydin 2008), la théorie des métapopulations est incontournable. En effet, les bryophytes suivent un système de populations dans lequel a lieu un changement continuel de la distribution spatiale (Hanski & Simberloff 1997). Ainsi, les conditions environnementales propres à chaque îlot seront propices à une bryoflore donnée (communauté d'espèces formant une population de bryophytes localement). La population de cet îlot sera amenée à interagir avec les populations des autres îlots à l'échelle régionale, on parle de dynamique métapopulationnelle des bryophytes (Hanski & Gilpin 1991). Les populations ont une espérance de vie limitée et sont déterminées par la balance entre l'extinction locale et la colonisation. Les probabilités de colonisation et d'extinction sont régies par divers processus démographiques (taux de naissance, mortalité) et environnementaux (perturbations naturelles). Par ailleurs, la grandeur de la population est associée avec la grosseur de l'îlot (Snäll *et al.* 2003), donc plus un habitat est fragmenté, plus le risque d'extinction augmente (Rybicki & Hanski 2013). De plus, la connectivité entre les parcelles influence le taux d'immigration, donc le risque d'extinction. Elle est influencée non seulement par la taille des îlots et la distance entre ses derniers, mais aussi par la qualité des habitats dans les îlots. Par conséquent, il est possible d'observer un taux d'extinction en augmentation avec la diminution de la taille de l'habitat ou avec une détérioration de la qualité de l'habitat. En somme, il n'y a pas que la dispersion qui influence le risque d'extinction, il y a aussi la probabilité d'établissement d'une colonie (Hanski 1999). En effet, l'étude de Hylander (2009) suggère qu'une combinaison de facteurs influencerait la probabilité de coloniser un milieu chez les bryophytes telles que la probabilité de survie d'une population locale qui permettrait la perpétuité de l'espèce, la probabilité d'une source locale de propagule (une banque de spores) et des conditions environnementales de microhabitats limitées. La qualité d'un substrat varie dans le temps et pendant sa vie; ensemble, tous ces facteurs influencent le risque d'extinction d'une population de bryophyte.

## 1.3 Objectifs et hypothèses

Ce projet vise à documenter si les îlots de rétention après coupe forestière remplissent la fonction écologique de refuge. Un refuge étant ici défini comme un endroit qui héberge une communauté de bryophytes qui permettrait aux bryophytes de coloniser la matrice de coupe. Donc un milieu qui permet d'avoir une grande richesse de bryophyte et une composition en bryophytes reflétant la forêt naturelle.

Nous chercherons à savoir comment les caractéristiques des îlots de rétention influencent la fonction écologique refuge pour la communauté de bryophytes.

Afin de répondre à cet objectif, nous avons formulé trois hypothèses de travail. Premièrement, en se fiant à la théorie de la biogéographie insulaire, la taille des îlots de rétention influencerait la capacité de servir de refuge (Hanski 1999). Les îlots de grande taille devraient avoir une plus grande quantité de microhabitats disponibles pour les bryophytes, par conséquent être plus efficaces pour servir de refuge.

Deuxièmement, selon le principe de la dette d'extinction, le temps depuis la dernière coupe devrait influencer négativement la population d'origine (Hanski, & Ovaskainen 2002). Alors, la capacité de l'îlot de servir de refuge diminuera suite à une perturbation.

Troisièmement, la position de la placette influencera la capacité de servir de refuge. Au centre de l'îlot de rétention, la capacité devrait être plus grande et cela devrait diminuer avec l'éloignement de l'îlot de rétention. Par ailleurs, la grandeur de la population est associée avec la grosseur de l'îlot (Snäll *et al.* 2003), donc plus un habitat est fragmenté, plus le risque d'extinction augmente (Rybicki & Hanski 2013). De plus, la connectivité entre les parcelles influence le taux d'immigration, donc le risque d'extinction. Il est possible d'observer un taux d'extinction en augmentation avec la diminution de l'habitat ou avec une détérioration de la qualité de l'habitat. Aussi, en se fiant au principe de la connectivité, plus la surface d'un îlot est grande, plus on devrait être capable de percevoir un gradient en richesse d'espèces de bryophytes, donc percevoir qu'il y a une richesse d'espèces similaires proche de l'îlot de rétention et diminuer avec l'éloignement de ce dernier. De plus, la composition en bryophytes devrait être plus similaire proche de l'îlot de grande taille que de petite taille et changer en s'éloignant de l'îlot. De plus, proche de l'îlot de rétention, suite à une perturbation la richesse devrait être plus grande et diminuer avec le temps et la distance de l'îlot de rétention

# CHAPITRE II

# DYNAMICS OF BRYOPHYTE COMMUNITIES IN THE SPRUCE MOSS BOREAL FOREST: ROLE OF POST-LOGGING RETENTION PATCHES

# Dynamics of bryophyte communities in the spruce moss Boreal forest: Role of post-logging retention patches.

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## 2.1 Abstract

Variable retention harvest is recommended to reduce the gaps between natural forest, and managed forest patterns because in the spruce-moss western Quebec, fires leave intact patches after their passage. These patches could provide a “lifeboat” for species sensitive to changes associated with logging. However, we don’t know if retention patches can fulfills this function. The aims of this study are to determine if retention patches can fill the “lifeboat” function by comparing retention patches of different size and exposure time, and to see how to their “lifeboat” capacity for bryophytes varies, the main species diversity in the boreal forest. Bryophytes were inventoried in 10 retention patches of different sizes and exposure time: CPRS with small remnants (small / young), CPRS with large islands (large / young), moose islands (large / old) and cut block separators (small / old). The composition of bryophytes was compared between the center of the retention patches and the cut matrix (10, 20 and 50m). Different variables that describe the forest stand in the retention patches were also measured. The recovery of *Pleurozium schreberi* declined after disturbance, but was resilient and since has increased with time. Bryophyte richness and composition showed a similar pattern, with changes with retention patch area, exposure time and plot position relative to retention patch. Also, we note that bryophyte, moss and liverwort richness is greater in the center of large retention patches with old exposure time. In conclusion, we should keep the old retention patch to preserve an important boreal forest flora.

## 2.2 Résumé

La coupe avec rétention variable est préconisée afin de diminuer les écarts entre la forêt naturelle et aménagée parce que dans la pessière à mousse de l'ouest du Québec, les feux laissent des îlots intacts après leur passage. Ces îlots pourraient offrir un refuge pour les espèces sensibles aux changements associés à la coupe forestière. Par contre, nous ne savons pas si la rétention dans sa forme actuelle remplit sa fonction de refuge. Le principal objectif de cette étude est de déterminer si la rétention après coupe remplit la fonction de refuge en comparant la rétention de différentes tailles et âges après coupe. Les bryophytes ont été inventoriées dans 30 îlots de rétentions de différents tailles et âges après coupe (CPRS bouquet (petit/ jeune); CPRS îlot (grand/ jeune); îlots orignaux (grand/ vieux) et séparateur à sec (petit/ vieux)). La composition des bryophytes a été comparée entre le centre de l'îlot de rétention et à différentes distances de cet îlot dans le parterre de coupe (10, 20 et 50m). Différentes variables qui décrivent le peuplement de la rétention ont aussi été mesurées. Le recouvrement de *Pleurozium schreberi* a diminué après la perturbation, mais a été résilient et a augmenté avec le temps. La richesse des bryophytes a suivi un patron semblable. Les résultats démontrent qu'il y a un changement en composition des bryophytes avec le temps depuis la coupe, la taille de l'îlot de rétention et la position de la placette par rapport au centre de l'îlot. Aussi, on remarque que la richesse des bryophytes, mousses et hépatiques est plus grande au centre des îlots de rétention de grandes tailles et d'un temps depuis coupe plus long. En somme, les vieux îlots de rétention permettent de préserver une flore importante de la forêt boréale.

## 2.3 Introduction

Human actions like intensive agriculture and deforestation, in addition to natural disturbances and forestry intensification, have significant impacts on the forest landscape of North America. Thus, the forest has been under considerable pressure, which has led to a homogenization of the forest at stand and landscape scales, and the increasing scarcity of many species associated with mature forests (Munteanu *et al.* 2016). Variable retention harvest is recommended to reduce this growing gap between the natural and managed forests because in the spruce-moss forest of western Quebec, natural disturbances, like fires, leave intact patches in their wake (Madoui *et al.* 2010). Variable retention harvest creates retention patches, which represent trees that haven't burned or residual patches left after a forest fire (Bergeron *et al.* 2001). These retentions may be arranged in different spatial patterns, depending on the aims of management, either aggregated, or dispersed with varying uncut percentages (Halpern *et al.* 2012). However, the spatial arrangement of the retention patches in the landscape (e.g. number, distance between patches) and the spatial structure (i.e. size and shape) of each patch that should be maintained in cut blocks to retain their natural function are unknown. Furthermore, the impact that these retentions have on post-disturbance recovery remains to be investigated. It is therefore necessary to evaluate the factors that influence retention patch function.

Three main functions of retention patches have been described in the literature. The first one is "lifeboating" for wildlife (Rosenvald & Lõhmus 2008). The second one is "stepping stones", which increases the connectivity between the patches (Franklin *et al.* 1997) by allowing organisms to better disperse in the ecosystem by enabling better connectivity between habitats. The last one is to increase the structural enrichment of the regenerating forest, which contributes to the future forest structural diversity (Franklin *et al.*, 2007). In this study, the first function will be treated. The "lifeboat" function maintains biodiversity inside the cut matrix (Franklin *et al.* 1997), because retention patches offer microhabitats similar to the original forest (Jiquan Chen in Franklin *et al.* 1997), keep a structure that improves microclimatic conditions and keeps essential substrates (Berg *et al.* 1995). A microhabitat is a small entity, which when put together form the habitat (forest, marine, urban) and evolves over time in various microclimate conditions. It is therefore a component of the habitat at a very fine scale (dead wood, rock, water hole) and each microhabitat is optimal for specific species (measured by the occurrence of species and their ability to survive in that particular microhabitat).

Bryophytes, which contribute a large proportion of the total biomass and biodiversity in a variety of ecosystems, are strongly influenced by disturbances (Baldwin & Bradfield 2005, Fenton & Frego 2005, Bradbury 2006). The bryophyte community seems to be an ideal group to understand the impact of retention patches in the boreal forest, because it represents the majority of the biodiversity of the forest flora (Qian *et al.* 1998). Some perennial bryophyte species are associated with old growth forests, but they can tolerate some environmental variation (e.g. *Hylocomium splendens, H. umbratum*; Jonsson & Esseen 1998). Colonist-pioneer species are associated with disturbed forests, like those recently burned or harvested (e.g. *Pohlia nutans, Polytrichum juniperinum* and *P. longisetum*; Jonsson & Esseen 1998, Baldwin & Bradfield 2005, Fenton & Frego 2005) and have been identified in previous studies as species affiliated with disturbed areas (both naturally and anthropogenically; Bradbury 2006, Hylander & Johnson 2010). In addition, bryophyte colonization patterns depend on the duration of their substrate, the time between disturbances, microhabitat variety and availability (Herben *et al.* 1991, Söderström & During 2005). Therefore, microhabitats have favorable environmental characteristics or not for a bryophyte community to establish (Söderström 1993). In short, time scale and alterations in the environment are factors limiting their presence in an environment (Berg *et al*. 1995, Ross-Davis & Frego 2002, Fenton & Bergeron 2008). By changing the factors regulating the bryophytes environment, it changes bryophyte community composition because it will vary depending on available microhabitats (Mills & Macdonald 2004, 2005, Cole *et al*. 2008). Without these retention patches sensitive species could disappear after harvest because their habitat will be distorted (Gustafsson *et al.* 2012).

The objective of this study was to determine whether size and exposure time could influence retention patch ability to serve as a "lifeboat" for mature forest species in different post-harvest patterns. The hypotheses of this study were that (1) we expected the ability to serve as a "lifeboat" to be positively correlated with patch size, based on metapopulation theory (Hanski 1999), and the dependence of bryophytes on humid microhabitats consequently the edge effect. A large enough patch, with appropriate environmental conditions, may contain one or more local populations (bryophytes colony; local scale) and these may interact with other populations (patch; regional scale). Therefore, there could be a dynamic of local populations and therefore the whole would conserve a viable metapopulation (Hanski & Gilpin 1991). (2) We also expected the ability to serve as a "lifeboat" to be negatively correlated with exposure time, based on the extinction debt theory. Extinction debt is the time delay when species are still present but habitat conditions for survival are no longer fulfilled (Hanski & Ovaskainen 2002). We will test these hypotheses in the context of the assumption that (3) "lifeboat" ability will be negatively correlated with plot position relative to the retention patches (within, and along a gradient without) and we expected that the ability to serve as a "lifeboat" will be affected by the interaction between the three hypotheses due to the connectivity principle (Baker & Read 2011). Populations have a limited life expectancy and which is determined by the balance between local extinction and colonization. Probabilities of colonization and extinction are regulated by various demographic processes (birth rate, mortality) and environmental factors (natural disturbances). Moreover, the size of the population is associated with the patch area (Snäll *et al.* 2003), so as habitat is fragmented, the risk of extinction increases (Rybicki & Hanski 2013). In addition, connectivity between patches influences the immigration rate, so also the extinction risk. It is influenced not only by the patch area and the distance between them, but also by the habitat quality in the patches. Therefore, it is possible to observe an increase in extinction rate with decreasing the patch area or with deterioration in the habitat quality. In short, there is not only dispersal that influences the extinction risk, but also the probability of establishing a colony (Hanski 1999). These hypotheses will be tested on response variables at different scales with increasing sensitivity to disturbance. The first, cover of common forest species *Pleurozium schreberi* permits a global view of response. The second, bryophyte richness by taxonomic group permits an evaluation of the evolution of specific groups, including the disturbance sensitive liverworts (Fenton and Frego 2005). Finally, community composition gives a global picture, but is sometimes more difficult to interpret. With the results obtained from this study, it will be possible to suggest guideline for retention types in forest management.

## 2.4 Methods

### 2.4.1 Study and experimental design

The study area is in Quebec, Canada, more specifically in the south-west of the administrative region of the North-of-Quebec between 77° 25’ 1" and 79° 8’ 1" W longitude and 49° 10’ 1" and 50° 1’ 1" N latitude. Inside these limits, cut blocks with different patterns of retention were selected for sampling based on dominance of black spruce (*Picea mariana*) in the tree canopy, age of the harvest (i.e. exposure time) and size of the retention patches. A total of 10 sites were selected to represent the combined factors of retention size (over 1ha and less than 1ha) and exposure time (time since harvest: young (2007-2013) vs old (1990-1993)): three sites (cut blocks) with small and young retention (CPRS with small remnants) with an original forest age between 91 and 134 years, three sites of large and young retention (CPRS with retention islands) with an original forest age between 90 and 147 years, two sites of large and old retention (moose islands) with an original forest age of 142 and 222 years and two sites of small and old retention (cut block separators) with an original forest age of 166 and 199 years. In each site, we chose three retention patches for a total of 30 patches. The patches were initially identified using geographic information systems (ArcGis10®) and were verified in the field. The perimeter and area, which permit the determination of the form, were determined with GPS in the field.

The sampling design followed that of a parallel study on post-fire retention patches (Barbé *et al.* unpublished) in order to facilitate comparison between the studies. In each retention patch, we established a North-South transect. For the patches smaller than 1 ha in area, five plots of 50 m² (5 m x 10 m) were established along this transect, one in the center of the patches and four plots outside of the retention patch at 10 and 20m from the edge on the north and south sides. When the retention patches were over 1 ha in area, a second plot in the center was added. Three plots of 50 m² are placed in the matrix of the cut, at 10m, 20m plus another one at least 50 m away from all the retention patches and the edge of the natural forest, to represent the matrix without forest influence. A figure describing the experimental design is presented in appendix (Annexe A). Unfortunately, time did not allow for sampling the 10m, 20m and 50m plot of the transect in the cut block separators.

The GPS coordinates of each plot were recorded and a series of environmental factors that could influence bryophytes were measured. In each plot, canopy cover was measured with a densiometer (scored concave mirror) and organic layer thickness, was measured in three randomly chosen places. Also, we measured the temperature and relative humidity with HOBO data loggers. We installed a HOBO U23 Pro V2 in the center of the retention and another at 15m of the edge (2 per site for each treatment). In parallel, in Louiza Moussaoui's project (Moussaoui *et al.* 2016) we measured the age of the original forest with dendrometric measured.

### 2.4.2 Bryophyte cover

In each plot, we randomly placed three 1 m² quadrats to measure forest floor bryophyte cover. Locations were excluded that included microhabitats like stumps or woody debris. Within each quadrat, approximate percent cover of large forest floor bryophyte species was recorded. Species present less than 1% were all noted as 0.005%.

#### 2.4.2.1 Bryophyte community composition

In each plot, the nature of all microhabitats was noted (e.g. woody debris, tree base, rock, etc.) and the bryophytes species present were sampled. Also, we have taken note of all empty microhabitats to give us an idea of habitat saturation. This method was inspired by the Floristic Habitat Sampling (FHS) of Newmaster (2000 in Newmaster *et al.* 2005) and it is rigorous because it guarantees an effective sampling of all the microhabitats present and increases the probability that all species are collected. In this study, FHS was modified because we noted not only the presence but also the frequency of species so our method is more quantitative than Newmaster which is more qualitative, and we restrained sampling to a specific geographic area. As microscopic identification is required for most bryophyte species, samples were placed in paper bags and the site, plot and microhabitat were identified on the bag in the field. Sample bags were dried and stored until identification. Bryophyte nomenclature follows the "Flore des bryophytes du Québec-Labrador" (Faubert 2012, 2013, 2014).

### 2.4.3 Statistical analyses

Bryophyte composition and richness was studied at two scales. Richness was determined as the number of species present in total and for each taxon group (moss, liverwort and sphagna).

Two canonical correspondence analyses (CCA) were carried out (one at the microhabitat scale and one at the plot scale) to answer hypotheses 1, 2 and 3. In order to summarise overall gradients in species composition and to determine the relative contribution of environmental variables and treatment type (small/young, large/young, large/old and small/old) on bryophyte patterns (for each taxon: liverwort, moss and sphagna). Ordination results in axis scores for each species, with the axes correlated to the most important environmental variables in the analysis. Ordination was performed on presence-absence data of all species occurring more than five times in the entire dataset, to ensure links between the species (Økland 1990). At the microhabitat scale, the ordinated matrix contained 160 species in 943 microhabitats (out of a total of 11 410 microhabitats) and at the plot scale the ordinated matrix contained 160 species in 148 plots (on a total of 165 plots). The software CANOCO was used for the analysis using untransformed data and biplot scaling.

*Pleurozium schreberi* cover (the only species present in a majority of plots) was analysed using linear models to determine by which factors it was influenced using the function lm.

We didn't include random effects because a comparison between the two models with and without random effects (ANOVA) was not significatively different. Due to heteroscedasticity in the residual values, *P. schreberi* cover was square root transformed. Based on bryophyte habitat and les hypotheses théorique, we developed fifteen candidate models that could explain the variation in *P. schreberi* cover (Table 2.1). We ranked these models, based on the second-order Akaike information criterion (AICc) and Akaike weights (wi), using the AICcmodavg package (Mazerolle 2015). The models considered the following habitat parameters and their combinations: organic layer thickness (thick), retention patch age (age_forest), retention patch area (size: small vs large), exposure time (time: young vs old), plot position relative to the retention patch (center vs 10m, 20m and 50m), the interaction between retention patch area and position plot (size:position), the interaction between retention patch area and exposure time (size:time), and the interaction between exposure time and the plot position relative to the retention patch (time:position) were considered. We included a null model, which only contained a constant as an explanatory variable and with the same random effect structure as the other models. We used multimodal inference to compute model-averaged parameter estimates and their unconditional standard errors (Mazerolle 2015). We based our conclusions on 95 % confidence intervals around the estimates. For a given estimate, a 95 % confidence interval excluding 0 indicated that the estimate differed from 0.

In order to determine which environmental factors influence bryophyte species richness, we used general linear mixed-effect models with a Poisson distribution for count data (function glmer, package lme4 version 1.1-10; Douglas *et al.* 2015). Bryophyte species richness was analysed for all species, and subsequently divided taxonomically (mosses, liverworts and sphagna) and was analysed at the two scales (microhabitat and plot). As there was no data for the 10m, 20m and matrix plots in the small, old retention patches (cut block separators), we generated data for these plots from the large, old sites (moose islands) via random sampling with replacement of the species richness values for the equivalent 30 plots. So bryophyte richness at microhabitat scale N= 14 988 and at plot scale N= 195. Different environmental factors were considered as fixed factors (Table 2.2.). Site and retention patches, i.e., variables that describe the spatial structure, were considered as random effects. The same habitat variables as for *P. schreberi* were analysed except that we added an interaction between retention patch area, exposure time and plot position (size:time:position). We made a backward selection as due to the large number of replicates, model selection was not efficient and the importance of the parameters was evaluated from the final model. We performed pairwise comparisons (Tukey's honestly significant difference) to determine which treatment levels differed significantly.

The microclimatic variables temperature and relative humidity were too correlated with other variables to be included in the same model. Therefore, we analysed the effect of those variables individually.

Bryophyte community composition was analysed with CANOCO (ter Braak & Smilauer 2012) while cover and species richness were analysed in R (R Development Core Team 2015).The hierarchical spatial structure of our data was integrated with random effects in mixed effects models (Gelman & Hill 2007).

**Table 2.1** Candidate models explaining *P. schreberi* cover (N=165), bryophyte richness in microhabitats (N=14 988) and in plots (N=195), during the summer of 2014 in four types of treatment (young:small, young:large, old:large, old:small) in northwestern Quebec, Canada. Explanatory variables are: retention patch age (age_forest), organic layer thickness (thick), retention patch area (size: large vs small), exposure time (time: old vs young), plot position relative to the retention patche(position: center/ 10m/ 20m/ 50m), interaction between area and plot position relative to the retention patch (size:position), the interaction between retention patch area and exposure time (size:time), and interaction between exposure time and the plot position relative to the retention patch (time:position).

| **Models** | **Hypotheses** |
|---|---|
| Null | Intercept only, for comparison with other models |
| age_forest | Effect of retention forest age (habitat quality) |
| thick | Organic layer thickness (for some taxon more organic layer is a better habitat quality) |
| size | Effect of retention patch area (answer hypothesis 1) |
| time | Effect of exposure time (answer hypothesis 2) |
| position | Center, 10m, 20m and 50m of the patches (answer hypothesis 3) |
| size+time | Additive effect of retention patch area and exposure time (answer hypotheses 1,2&3) |
| size+time+size:time | Additive effect of retention patch area, exposure time and interaction between them (answer hypotheses 1& 2) |
| size+position | Additive effect of retention patch area and plot position (answer hypotheses 1& 2) |
| size+position+size:position | Additive effect of retention patch area, plot position and interaction between them (answer hypotheses 1& 3) |
| time+position | Additive effect of exposure time and plot position (answer hypotheses 1&3) |
| time+position+time:position | Additive effect of exposure time, plot position and interaction between them (answer hypotheses 2&3) |
| thick+ age_forest+ size+ time+ position | Additive effect of organic layer thickness, retention patch age, exposure time and plot position (answer hypotheses 2&3) |
| thick+ age_forest+ size+ time+ position | Additive effect of organic layer thickness, retention patch age, retention patch area and plot position (answer hypotheses 1&3) |
| thick+ age_forest+ size+time+ position+ size:position+ size:time+ time :position | Global model (answer hypotheses 1,2&3) |

**Table 2.2** Environmental factors explaining bryophytes composition. For *Pleurozium schreberi* and bryophytes richness at microhabitat scale and plot scale, only retention patch area (large or small), exposure time (old or young), retention patch age, organic layer thickness, temperature, relative humidity and canopy openness was environmental factor chosen. For bryophytes richness at plot scale we added percentage of occupied microhabitat.

| Parameters | N | Mean size ($m^2$) | Range size ($m^2$) | Exposure time (range yrs) | Retention patch age ( $\bar{x}$ yrs) | Temperature (°C) | | Relative humidity (%) | | Canopy openness (%) | | Organic layer thickness (cm) | | Nbr microhabitats (%occupied) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Center $\bar{x}$ | Matrix $\bar{x}$ | Center $\bar{x}$ | Matrix $\bar{x}$ | Center $\bar{x}$ | Matrix $\bar{x}$ | Center $\bar{x}$ | Matrix $\bar{x}$ | Center | Matrix |
| Small/young | 9 | 530 | 250- 770 | 2007-2011 | 110 | 16.64 | 16.78 | 81.66 | 80.44 | 57 | 100 | 11 | 4 | 63 | 27 |
| Large/young | 9 | 12110 | 5040-17350 | 2012-2013 | 120 | 15.61 | 16.22 | 94.66 | 79.58 | 38 | 99 | 16 | 8 | 74 | 22 |
| Large/old | 6 | 48670 | 35690-59850 | 1990-1993 | 180 | 15.68 | 15.73 | 90.48 | 91.58 | 27 | 50 | 18 | 19 | 88 | 58 |
| Small/old | 6 | 1410 | 150-2260 | 1990-1993 | 180 | 16.16 | 16.25 | 86.07 | 86.01 | 22 | 51 | 11 | 19 | 80 | 58 |

## 2.5 Results

We analyzed data from 14 988 microhabitats: 7 294 microhabitats with bryophytes and of these 5 782 with mosses, 4 232 with liverworts and 1 370 with sphagna. The number of microhabitats occupied by bryophytes, mosses and liverworts differed between the retention patch center and the cut matrix ($p$ = 2x10-16, $p$ = 2x10-16 and $p$ = 2x10-16 respectively) but it did not differ for the sphagna ($p$ = 0.148). On average, bryophytes occupied 76 % and 41% of microhabitats in the center and cut respectively, mosses occupied 58 % and 33% and liverworts occupied 56 % and 20%.

Richness of all taxa at microhabitat and plot scales was influenced by temperature (Table 2.3, Table 2.4), with higher richness associated with lower temperatures (Figure 2.1, Figure 2.2). Moreover, bryophyte and liverwort richness at the microhabitat and plot scale, and moss richness at the microhabitat scale was influenced by relative humidity (Table 2.3, Table 2.4), with higher richness associated with higher relative humidity (Figure 2.3, Figure 2.4).

**Table 2.3** Parameter estimates for the richness of bryophytes, mosses, liverworts and sphagna in 14 988 microhabitats in 4 types of treatment (young:small, young:large, old:small, old:large) in northwestern Québec, Canada. A p-value < 0.05 indicates that the variable has an effect on a parameter (in boldface type). Explanatory variables are: temperature and relative humidity.

| | Bryophyte | | | Moss | | | Liverwort | | | Sphagna | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *Estimates* | *z-value* | *p-value* | *Estimates* | *z-value* | *p-value* | *Estimates* | *z-value* | *p-value* | *Estimates* | *z-value* | *p-value* |
| Temperature | **-0.54** | **-31.67** | **2x10$^{-16}$** | **-0.47** | **-22.33** | **2x10$^{-16}$** | **-0.79** | **-22.75** | **2x10$^{-16}$** | **-0.16** | **-2.77** | **0.0056** |
| Relative humidity | **0.33** | **33.37** | **2x10$^{-16}$** | **0.24** | **20** | **2x10$^{-16}$** | **0.67** | **33.92** | **2x10$^{-16}$** | -0.06 | -1.57 | 0.117 |

**Table 2.4** Parameter estimates for the richness of bryophytes, mosses, liverworts and sphagna in 195 plots in 4 types of treatment (young:small, young:large, old:small, old:large) in northwestern Québec, Canada. A p-value < 0.05 indicates that the variable has an effect on a parameter (in boldface type). Explanatory variables are: temperature and relative humidity.

| | Bryophyte | | | Moss | | | Liverwort | | | Sphagna | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *Estimates* | *z-value* | *p-value* | *Estimates* | *z-value* | *p-value* | *Estimates* | *z-value* | *p-value* | *Estimates* | *z-value* | *p-value* |
| Temperature | **-0.26** | **-8.177** | **2.91x10$^{-16}$** | **-0.24** | **-5.61** | **2.02x10$^{-8}$** | **-0.43** | **-7.01** | **2.42x10$^{-12}$** | **-0.17** | **-2.18** | **0.029** |
| Relative humidity | **0.31** | **5.42** | **5.92x10$^{-8}$** | 0.02 | 0.735 | 0.462 | **0.44** | **9.39** | **2x10$^{-16}$** | 0.1 | 1.59 | 0.111 |

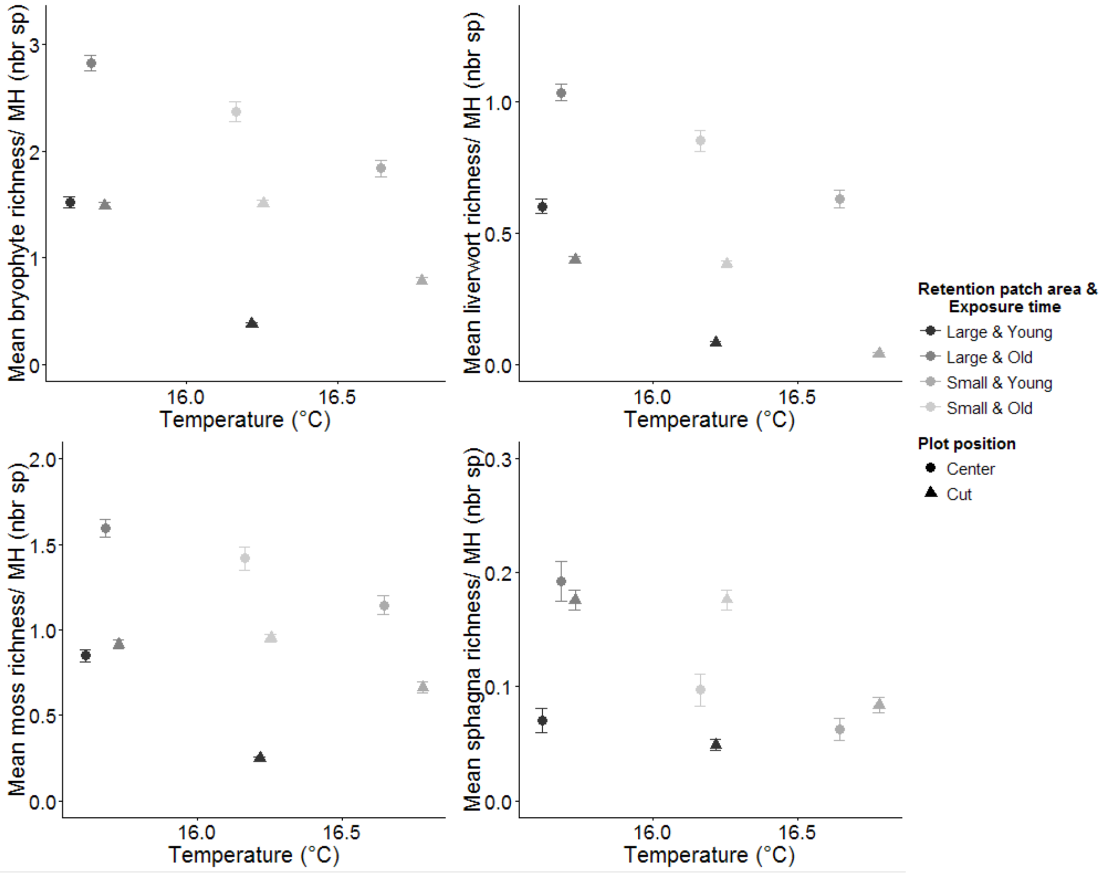

**Figure 2.1** Mean bryophyte, moss, liverwort and sphagna richness at the microhabitats scale depending upon temperature, retention patches area, exposure time and plot position. Error bars represent standard error.

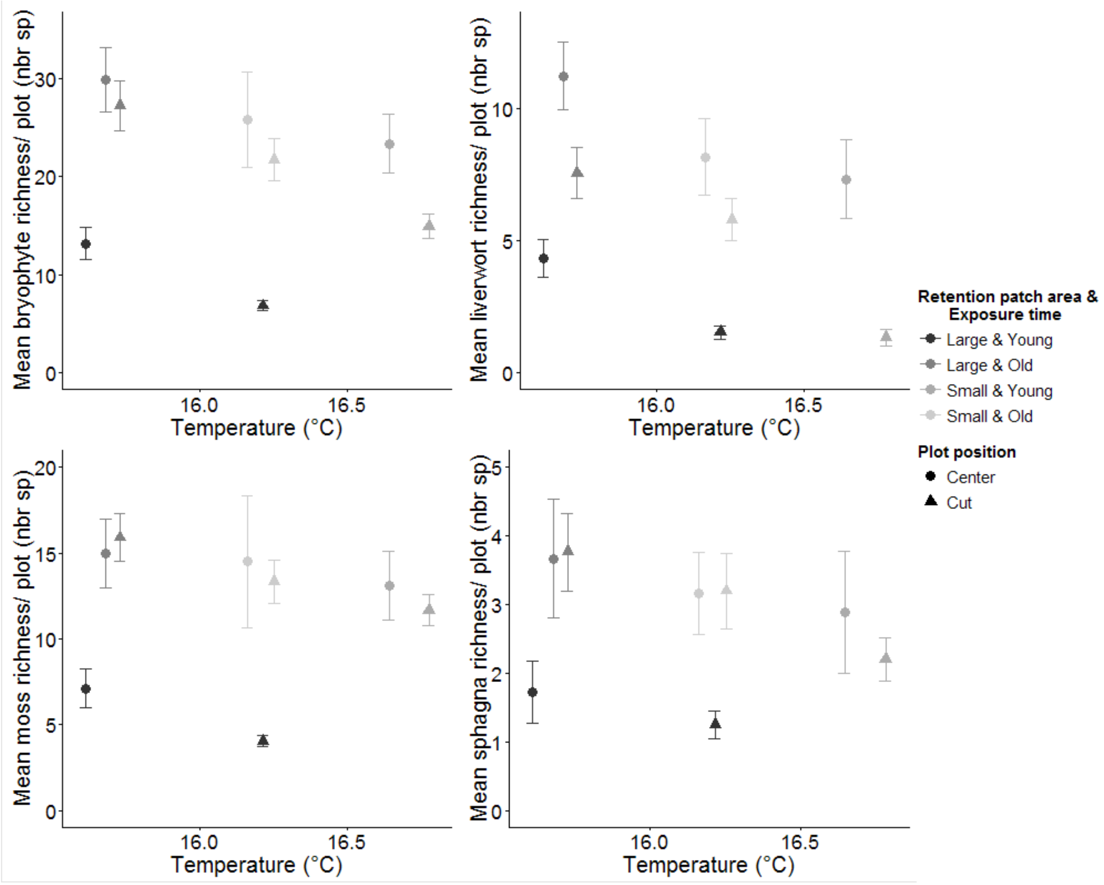

**Figure 2.2** Mean bryophyte, moss, liverwort and sphagna richness at the plot scale depending upon temperature, retention patches area, exposure time and plot position. Error bars represent standard error.

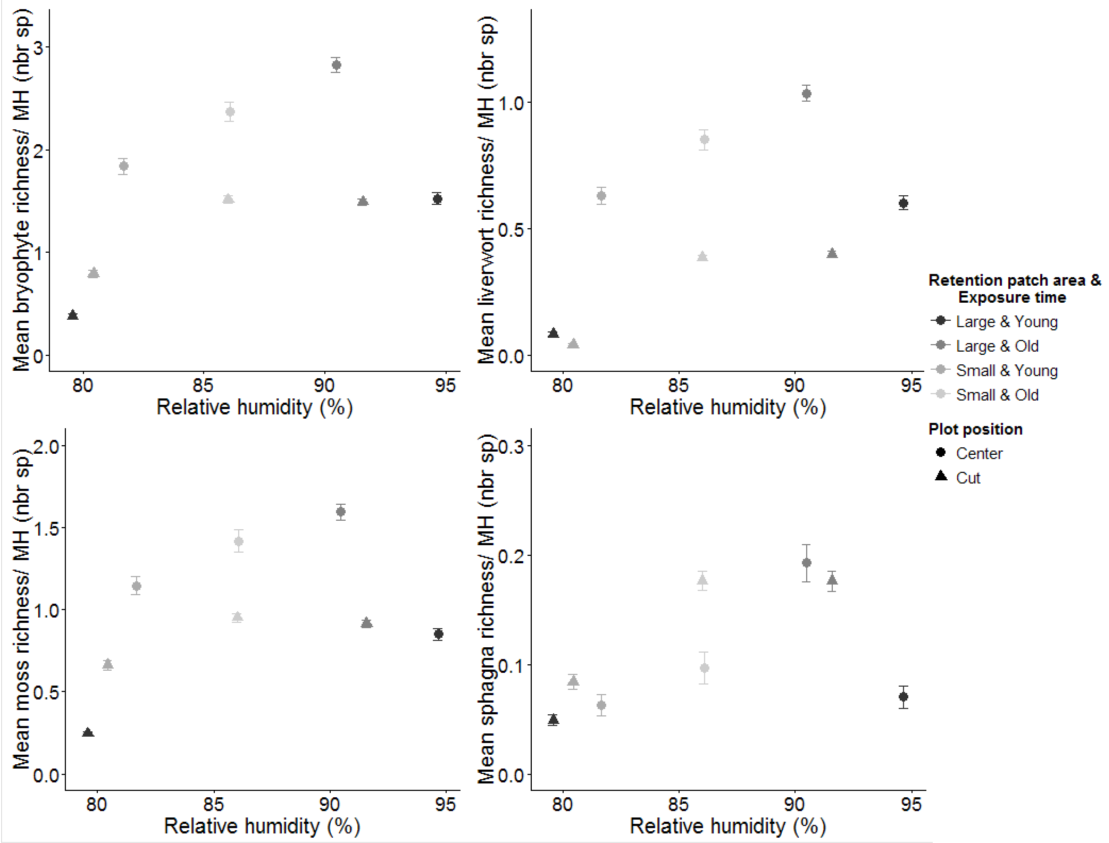

**Figure 2.3** Mean bryophyte, moss, liverwort and sphagna richness at the microhabitats scale depending upon relative humidity, retention patches area, exposure time and plot position. Error bars represent standard error.

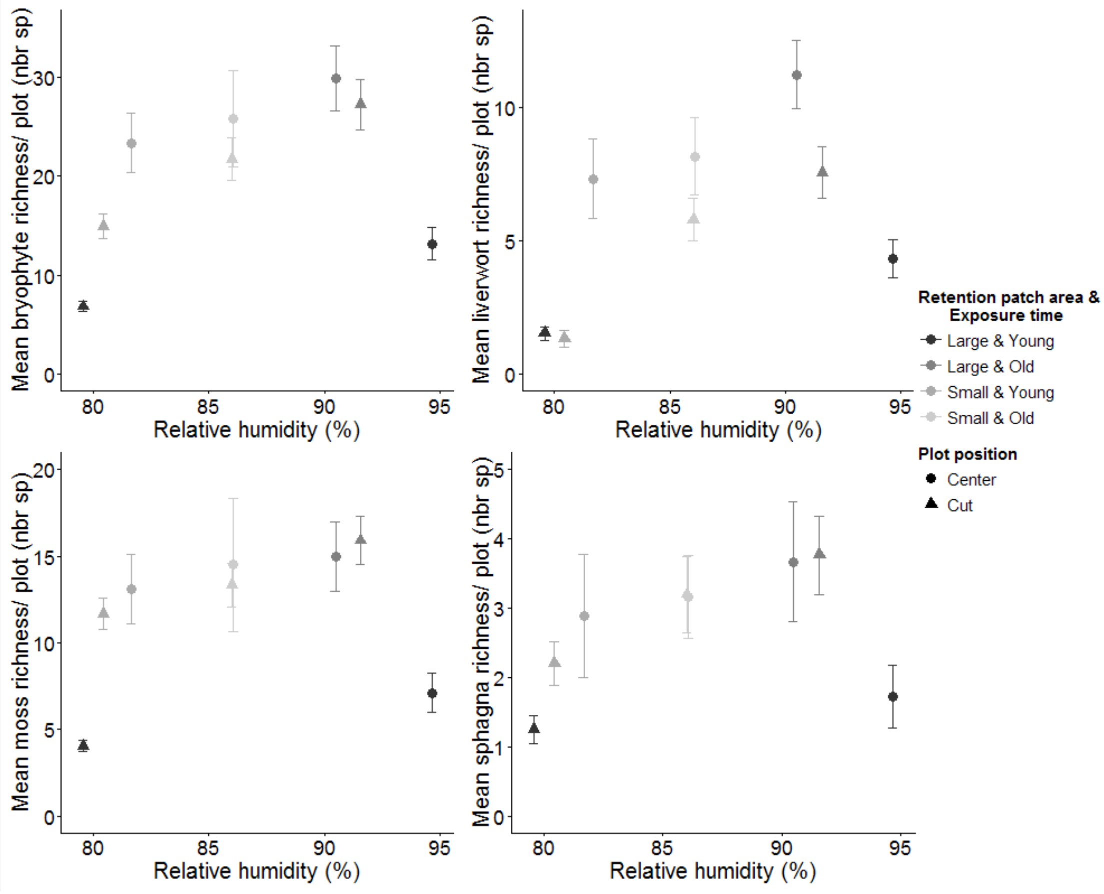

**Figure 2.4** Mean bryophyte, moss, liverwort and sphagna richness at the plot scale depending upon relative humidity, retention patches area, exposure time and plot position. Error bars represent standard error.

### 2.5.1 Bryophyte cover

Two models explaining *P. schreberi* cover had the greatest support, with a ΔAICc < 2 and a combined Akaike weight of 0.74 (Table 2.5). These models included organic layer thickness, retention patch age, retention patch area, exposure time, plot position relative to the retention patch, the interaction between retention patch area and plot position, the interaction between retention patch area and exposure time and the interaction between exposure time and plot position. Multimodal inference indicated that *P. schreberi* cover was influenced by the interaction between retention patch area and plot position relative to the retention patch (Figure 2.5). As predicted by hypothesis 1, cover was greater in large retention patches than in small retention patch (Table 2. 6). Also, as predicted by hypothesis 2, *P. schreberi* cover was influenced by the interaction between exposure time and plot position relative to the retention patch (Figure 2.6) with higher *P. schreberi* cover in young exposure time at the center compared to 20m and 50m positions (Table 2.6). However, no difference in *P. schreberi* cover was found at 20 m and 50 m positions in old exposure time. Otherwise, *P. schreberi* cover was positively associated with organic layer thickness (Table 2.6).

**Table 2.5** Top three lm models of *Pleurozium schreberi* cover in northwestern Québec, Canada, based on the second-order Akaike information criterion (AICc). Differences between each model and the top-ranked model (ΔAICc), together with their Akaike weights (ωi) and the number of estimated parameters (K) are indicated. All other models had a ΔAICc <3. Explanatory variables are: organic layer thickness (thick), retention patch age (age_forest), retention patch area (size: large/ small), exposure time (time: old/ young), plot position relative to the retention patch (position: center/ 10m/ 20m/ 50m), interaction between retention patch area and plot position (size:position), interaction between retention patch area and exposure time (size:time), and interaction between exposure time and the plot position relative to the retention patch (time:position).

| Models | K | AICc | ΔAICc | ωi |
|---|---|---|---|---|
| time+ position+ size:position+ size:time+ time:position | 9 | 748.69 | 0.00 | 0.50 |
| thick+ age_forest+ size+ time+ position | 9 | 750.19 | 1.49 | 0.24 |
| thick+ age_forest+size+ time+ position+ size:position+ size:time+ time:position | 16 | 750.84 | 2.15 | 0.17 |

**Table 2.6** Parameter estimates for the cover of *Pleurozium schreberi* in 165 plots in 4 types of treatments (young:small, young:large, old:small, old:large) in northwestern Québec, Canada. A 95 % unconditional confidence interval excluding 0 indicates that the variable has an effect on a parameter (in boldface type). Explanatory variables are: organic layer thickness (thick), retention patch age (age_forest), retention patch area (size: large/ small), exposure time (time: old/ young), plot position relative to the retention patch (position: center/ 10m/ 20m/ 50m), interaction between area and plot position relative to the retention patch (size:position), interaction between retention patch area and exposure time (size:time), and interaction between exposure time and the plot position relative to the retention patch (time:position).

| Parameter | Estimate | SE | Lower 95 % CI | Upper 95 % CI |
|---|---|---|---|---|
| **thick** | **0.0541** | **0.0224** | **0.0081** | **0.1002** |
| age_forest | -0.01 | 0.01 | -0.02 | 0.01 |
| size (reference = large) | | | | |
| **small** | **-0.93** | **0.41** | **-1.74** | **-0.12** |
| time (reference = young) | | | | |
| old | 1.24 | 0.57 | 0.13 | 2.36 |
| position (reference = center) | | | | |
| **10m** | **-2.15** | **0.48** | **-3.1** | **-1.2** |
| **20m** | **-2.24** | **0.49** | **-3.2** | **-1.28** |
| **50m** | **-3.39** | **1.08** | **-5.51** | **-1.28** |
| size:position (reference= large:center) | | | | |
| small:10m | -1.39 | 1.17 | -3.69 | 0.91 |
| small:20m | -2.08 | 1.18 | -4.4 | 0.24 |
| small: 50m | -0.76 | 1.43 | -3.56 | 2.04 |
| size:time (refence= large: young) | | | | |
| small:old | 0.75 | 1.44 | -2.07 | 3.56 |
| time:position (reference = young: center) | | | | |
| **old:10m** | **2.52** | **1.13** | **0.31** | **4.73** |
| **old:20m** | **3.35** | **1.17** | **1.06** | **5.64** |
| **old:50m** | **3.94** | **1.37** | **1.26** | **6.62** |

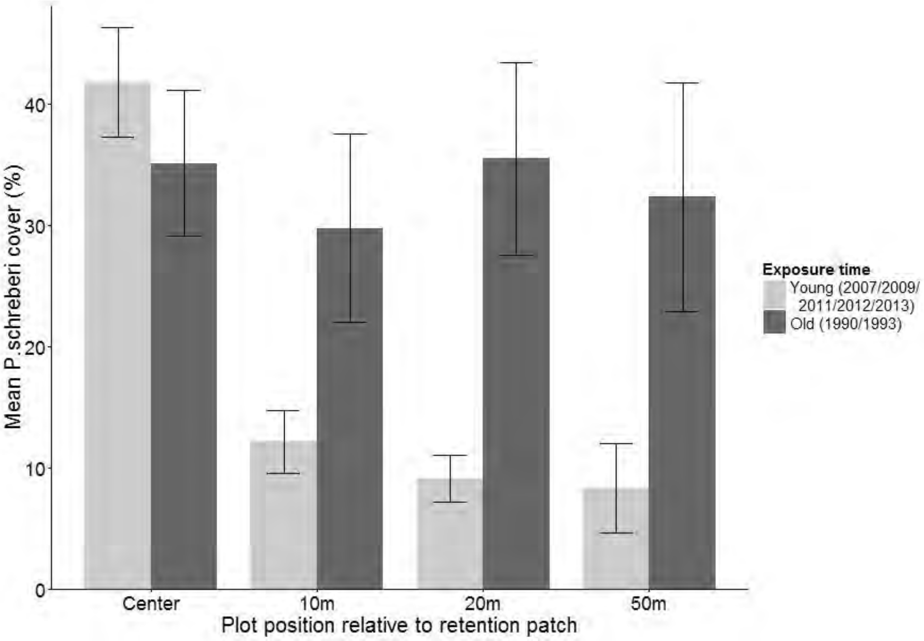

**Figure 2.5** Mean *Pleurozium schreberi* cover by exposure time and plot position relative to the retention patches. Error bars represent the standard error.

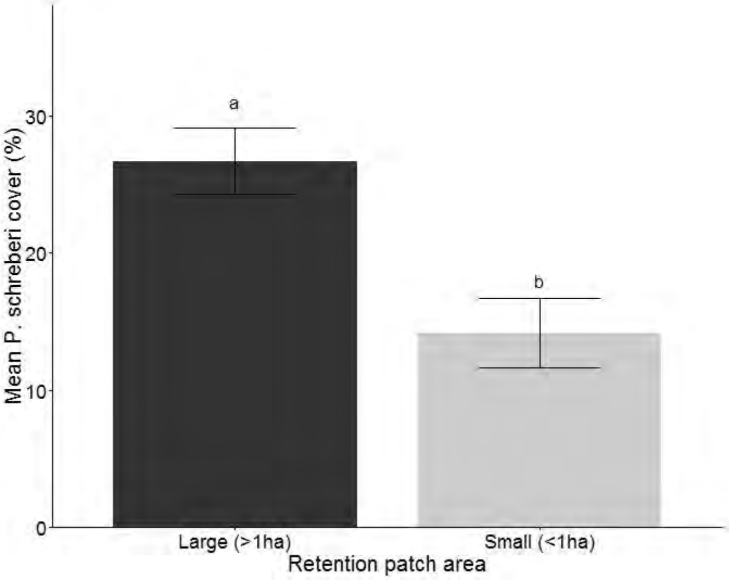

**Figure 2.6** Mean *Pleurozium schreberi* cover by retention patch area. Error bars represent the standard error.

### 2.5.2 Bryophyte community composition

#### 2.5.2.1 Bryophyte composition at the microhabitat scale

The Canonical Correspondence Analysis (CCA) accounted for 4% of the variability in the species pattern. Liverworts were clustered on the left of the diagram with the center plots, while sphagna were found with outer plots and associated with open canopy. The relative importance of the environmental variables in shaping the species pattern (Figure 2.7), indicated that the axis 1 was mainly correlated with canopy openness, increasing forest floor thickness and plot position in the center (1, 0.8 and 0.8% respectively). Temperature, retention patch age, relative humidity, retention patch area (large and small), exposure time (young and old), plot position (sum of 10m, 20m and 50m) accounted respectively for 0.7, 0.7, 0.7, 0.6, 0.6, and 1.0% of the explained variation.

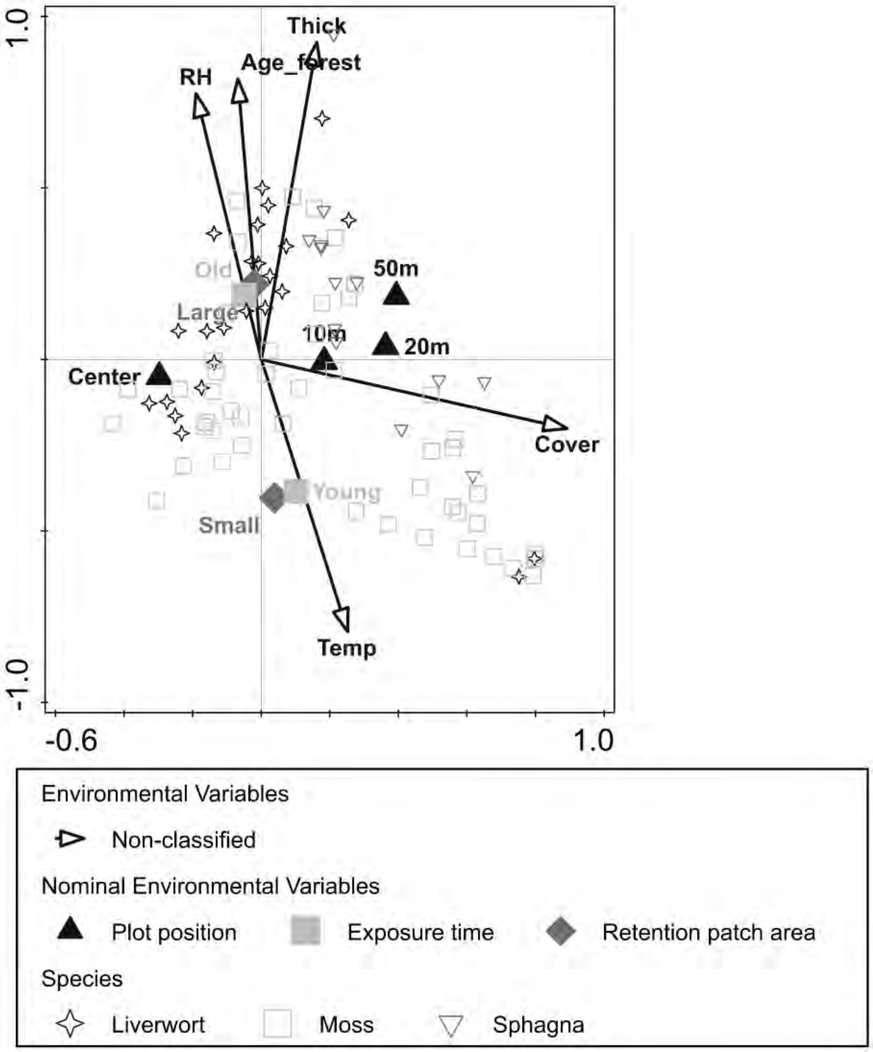

**Figure 2.7** Canonical Correspondence Analysis axes 1 and 2 of bryophyte composition at the microhabitat scale. Filled symbols represent categorical variables: retention patch area (dark gray diamond), exposure time (light gray square) and plot position relative to retention patches (black triangle). Empty arrows represent numerical variables: retention patch age (Age_forest), organic layer thickness (Thick), cover openness (Cover), relative humidity (RH) and temperature (Temp). Empty symbols represent individual species by taxonomic group: liverworts (black star), mosses (light gray square) and sphagna (dark gray down triangle).

### 2.5.2.2 Bryophyte richness at the microhabitat scale

The estimate of model fit, as indicated by the Pearson correlation moment between fitted values and raw data, is 0.179. As expected for hypotheses 1, 2 and 3, the interaction between retention patch area, exposure time and plot position influenced bryophyte richness at the microhabitat scale (Table 2.7). Bryophyte richness was higher in the center than in the matrix for all retention types (Figure 2.8). However there was no significant difference at any one position between the retention types, except for large areas with young exposure time, which had lower species richness than other retention types at several matrix positions.

### 2.5.2.3 Moss richness at the microhabitat scale

The estimate of model fit, as indicated by the Pearson correlation moment between fitted values and raw data, is 0.134. As predicted in hypotheses 1, 2 and 3, the interaction between retention patch area, exposure time and plot position influenced moss richness at the microhabitat scale (Table 2.7). Similarly as for bryophyte richness, moss richness was higher in the center of all retention types than in the cut matrix, and there were few differences among retention types at any one position, apart from general lower richness of large patches with young exposure time. (Figure 2.9).

### 2.5.2.4 Liverwort richness at the microhabitat scale

The estimate of model fit, as indicated by the Pearson correlation moment between fitted values and raw data, is 0.185. As expected for hypotheses 1, 2 and 3, the interaction between retention patch area, exposure time and plot position influenced liverwort richness at the microhabitat scale (Table 2.7). Liverwort richness was higher at the center of large and small areas with young exposure time, than at 10m, 20m and 50m of large and small areas with young exposure time. Also, liverwort richness was higher in the center of large areas with old exposure time, than at 10m, 20m and 50m of small and large areas with young exposure time, and at 10m and 20m of large areas with old exposure time. Liverwort richness was higher at the center of small areas with old exposure time, than at 10m, 20m and 50m of large and small areas with young exposure time, and at 20m and 50m of small areas with young exposure time (Figure 2.10).

#### 2.5.2.5 Sphagna richness at the microhabitat scale

The estimate of model fit, as indicated by the Pearson correlation moment between fitted values and raw data, is 0.118. As expected for hypotheses 1, 2 and 3, the interaction between retention patch area and plot position relative to retention patch and the interaction between exposure time and plot position influenced sphagna richness at the microhabitat scale (Table 2.7). Sphagna richness was higher in the center of large areas, than at 10m of large areas. Also, sphagna richness was lower at the center of small areas, than at 10m of small areas (Figure 2.11). Sphagna richness was higher at the center and at 10m with old exposure time, than at 20m with old exposure time (Figure 2.12).

**Table 2.7** Parameter estimates retain from backward selection for the richness of bryophytes, mosses, liverworts and sphagna in 14 988 microhabitats in 4 types of treatments (young:small, young:large, old:small, old:large) in northwestern Québec, Canada. A p-value < 0.05 indicates that the variable has an effect on a parameter (in boldface type). Explanatory variables are: retention patch age (age_forest), layer thickness (thick), retention patch area (size), exposure time (time), plot position relative to the retention patch (position), interaction between retention patch area and plot position relative to the retention patch (size:position), interaction between retention patch area and exposure time (size:time), interaction between exposure time and the plot position relative to the retention patch (time:position), and the interaction between retention patch area, exposure time and plot position relative to the retention patch (size:time:position).

| | | Bryophyte | Moss | Liverwort | Sphagna |
|---|---|---|---|---|---|
| coefficient of determination | | 0.1786 | 0.134 | 0.1851 | 0.118 |
| | *df* | *f-value* | *f-value* | *f-value* | *f-value* |
| age forest | 1 | NA | NA | NA | NA |
| thick | 1 | 0.07 | **10.58** | **5.73** | **119.68** |
| size | 1 | 1.41 | **4.85** | 0.15 | 1.61 |
| time | 1 | **23.38** | **21.4** | **15.7** | 1.45 |
| position | 3 | **700.42** | **278.24** | **459.92** | **6.53** |
| size: time | 1 | 2.16 | **4.63** | 0.1 | NA |
| size: position | 3 | **17.89** | **17.25** | 0.18 | **12.3** |
| time: position | 3 | **95.67** | **45.18** | **88.82** | **7.12** |
| size: time: position | 3 | **7.5** | **10.24** | **13.71** | NA |

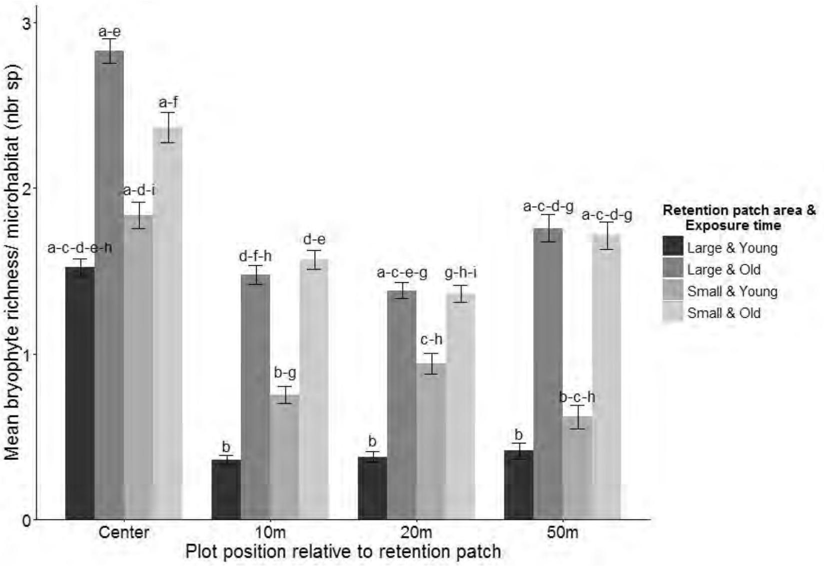

**Figure 2.8** Mean bryophytes richness at the microhabitat scale depending upon retention patch area, exposure time and plot position relative to the retention patches. Error bars represent the standard error. Letter represented significate difference as indicated by a Tukey test.

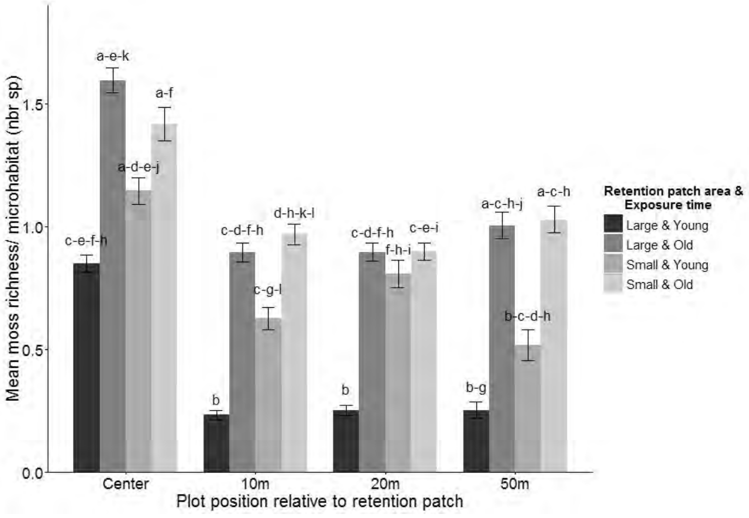

**Figure 2.9** Mean moss richness at the microhabitat scale depending retention patches area, exposure time and plot position relative to the retention patches. Error bars represent the standard error. Letter represented significate difference as indicated by a Tukey test.

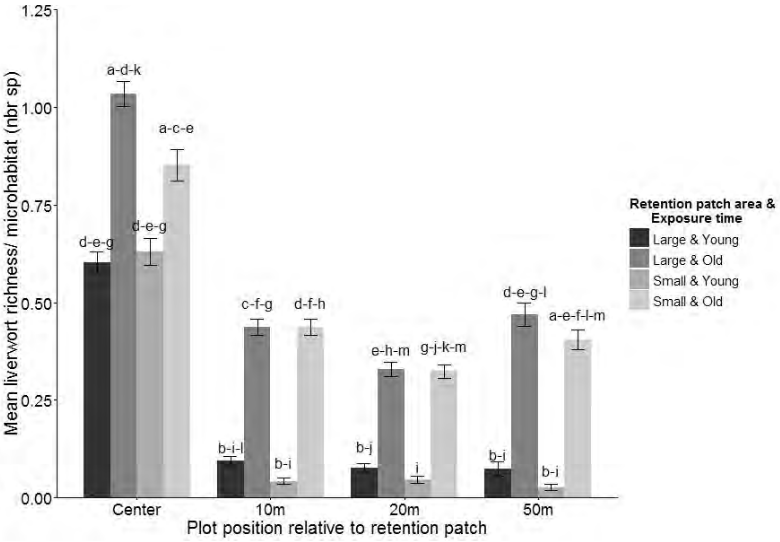

**Figure 2.10** Mean liverwort richness at the microhabitat scale depending upon retention patch area, exposure time and plot position relative to the retention patches. Error bars represent the standard error. Letter represented significate difference as indicated by a Tukey test.

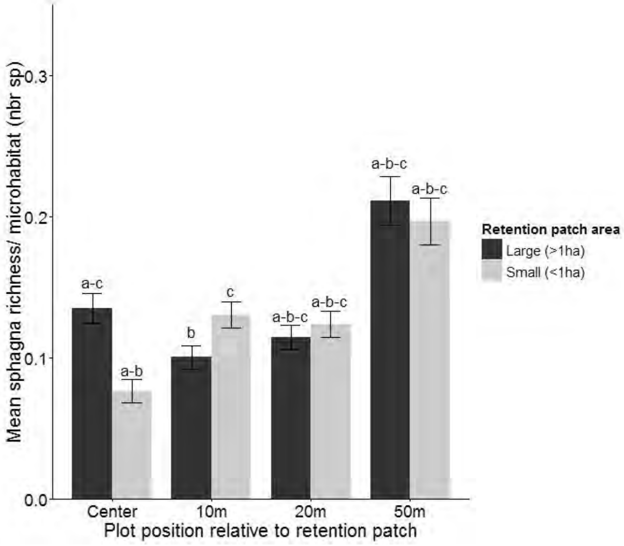

**Figure 2.11** Mean sphagna richness at the microhabitat scale depending upon retention patch area and plot position relative to the retention patches. Error bars represent the standard error. Letter represented significate difference as indicated by a Tukey test.

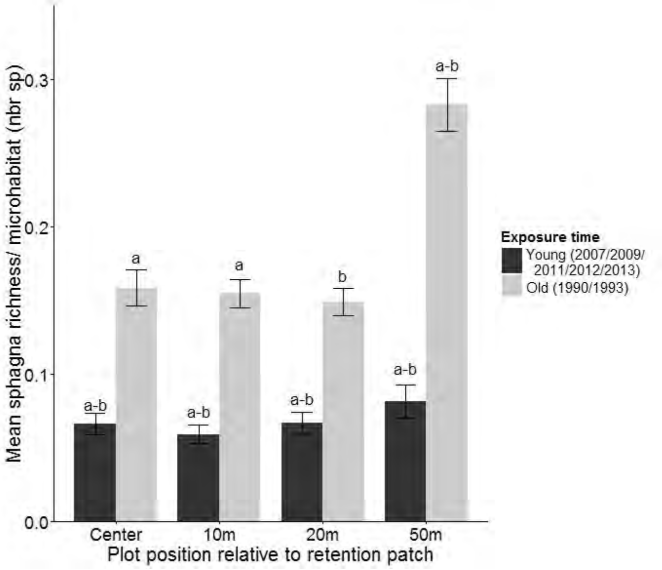

**Figure 2.12** Mean sphagna richness at the microhabitat scale depending upon exposure time and plot position relative to the retention patches. Error bars represent the standard error. Letter represented significate difference as indicated by a Tukey test.

### 2.5.2.6 Bryophyte composition at the plot scale

The Canonical Correspondence Analysis (CCA) accounted for 14.4% of the variability in the species pattern. Liverworts were clustered on the right of the diagram with the center plots, old exposure time and large retention patches area, while sphagna were found with outer plots and associated with canopy openness, young exposure time and small retention area. The relative importance of the environmental variables in shaping the species pattern (Figure 2.13) indicated that the axis 1 was mainly correlated with cover openness, temperature, exposure time (young vs old) and organic layer thickness (2.9, 2.7, 2.5 and 2.5% respectively). Retention patch age, total number of occupied microhabitats, relative humidity, retention patch area (large and small), and plot position (sum of center, 20m and 50m) accounted respectively for 2.4, 2.4, 2.3, 2.2, and 3.7% of the explained variation.

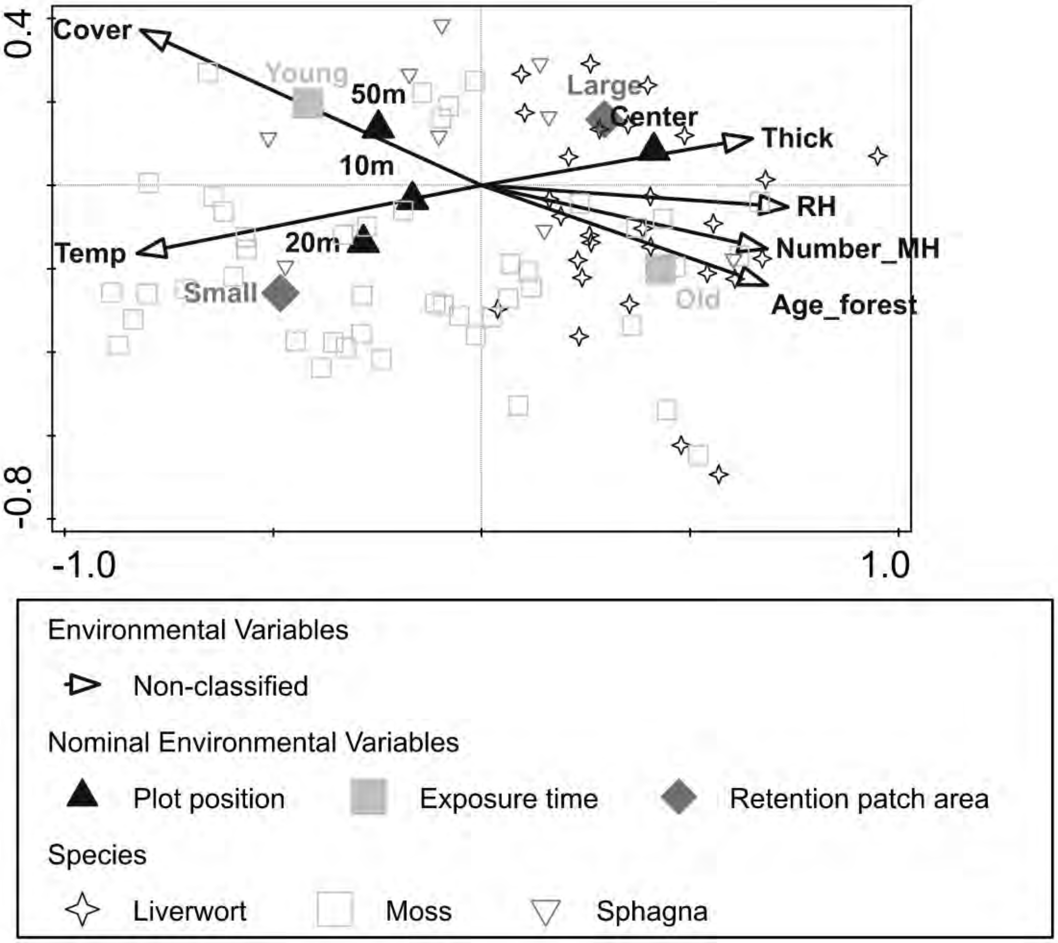

**Figure 2.13** Canonical Correspondence Analysis axes 1 and 2 of bryophyte composition at the plot scale. Filled symbols represent categorical variables: retention patch area (dark gray diamond), exposure time (light gray square) and plot position relative to retention patches (black triangle). Empty arrows represent numerical variables: retention patch age (Age_forest), organic layer thickness (Thick), cover openness (Cover), relative humidity (RH), temperature (Temp) and total microhabitat number occupied (Number_MH). Empty symbols represent individual species by taxonomic group: liverworts (black star), mosses (light gray square) and sphagna (dark gray down triangle).

### 2.5.2.7 Bryophyte richness at the plot scale

The estimate of model fit, as indicated by the Pearson correlation moment between fitted values and raw data, is 0.614. As expected for hypotheses 1, 2 and 3, the interaction between retention patch area, exposure time and plot position influenced bryophyte richness at the plot scale (Table 2.8). Bryophyte richness was higher in the center than in the matrix for all retention types, except for large areas with young exposure time (Figure 2.14). However, like at the microhabitat scale there was no significant difference at any one position between the retention types, except for large areas with young exposure time, which had lower species richness than other retention types at several matrix positions.

### 2.5.2.8 Moss richness at the plot scale

The estimate of model fit, as indicated by the Pearson correlation moment between fitted values and raw data, is 0.534. As expected for hypotheses 1, 2 and 3, the interaction between retention patch area, exposure time and plot position influenced moss richness at the plot scale (Table 2.8). Similarly as for the bryophyte richness, moss richness was higher in the center of all retention types than in the cut matrix, except for large areas with young exposure time, and there were few differences among retention types at any one position, apart from the general lower richness of large patches with young exposure time (Figure 2.15).

### 2.5.2.9 Liverwort richness at the plot scale

The estimate of model fit, as indicated by the Pearson correlation moment between fitted values and raw data, is 0.603. Contrary to hypotheses 1, 2 and 3, only one interaction influenced liverwort richness at the plot scale and it was the interaction between exposure time and plot position (Table 2.8). Liverwort richness was higher at the center of young and old exposure time than at 10m, 20m and 50m of young exposure time (Figure 2.16). And higher in old exposure time than young exposure time overall.

### 2.5.2.10 Sphagna richness at the plot scale

The estimate of model fit, as indicated by the Pearson correlation moment between fitted values and raw data, is 0.611. Contrary to hypotheses 1, 2 and 3, only one interaction influenced sphagna richness at the plot scale and it was the interaction between retention patch area and exposure time (Table 2.8). Sphagna richness was lower in large areas of young exposure time, than in small areas of young exposure time and in large areas of old exposure time (Figure 2.17).

**Table 2.8** Parameter estimates selected from backward selection for the richness of bryophytes, mosses, liverworts and sphagna in 195 plots in 4 types of treatments (young:small, young:large, old:small, old:large) in northwestern Québec, Canada. A p-value < 0.05 indicates that the variable has an effect on a parameter (in boldface type). Explanatory variables are: occupied microhabitats in pourcentage (mh_pt), retention patch age (age_forest), organic layer thickness (thick), retention patch area (size), exposure time (time), plot position relative to the retention patch (position), interaction between retention patch area and plot position relative to the retention patch (size:position), interaction between retention patch area and exposure time (size:time), interaction between exposure time and the plot position relative to the retention patch (time:position), and the interaction between retention patch area, exposure time and plot position relative to the retention patch (size:time:position).

| | | Bryophyte | Moss | Liverwort | Sphagna |
|---|---|---|---|---|---|
| coefficient of determination | | 0.6143 | 0.5334 | 0.603 | 0.6114 |
| | *df* | *f-value* | *f-value* | *f-value* | *f-value* |
| mh_pt | 1 | **60.16** | **28.48** | **108.02** | NA |
| age forest | 1 | NA | NA | NA | NA |
| thick | 1 | **68.99** | NA | NA | **43.14** |
| size | 1 | **16.11** | **23.91** | 0.18 | 3.36 |
| time | 1 | **25.66** | **38.18** | **20.7** | 2.62 |
| position | 3 | **4.04** | 0.51 | **7.97** | NA |
| size: time | 1 | **29.67** | **42.3** | NA | **4.8** |
| size:position | 3 | 2.05 | 0.59 | NA | NA |
| time:position | 3 | 2.05 | 2.47 | **9.03** | NA |
| size:time:position | 3 | 1.86 | 2.38 | NA | NA |

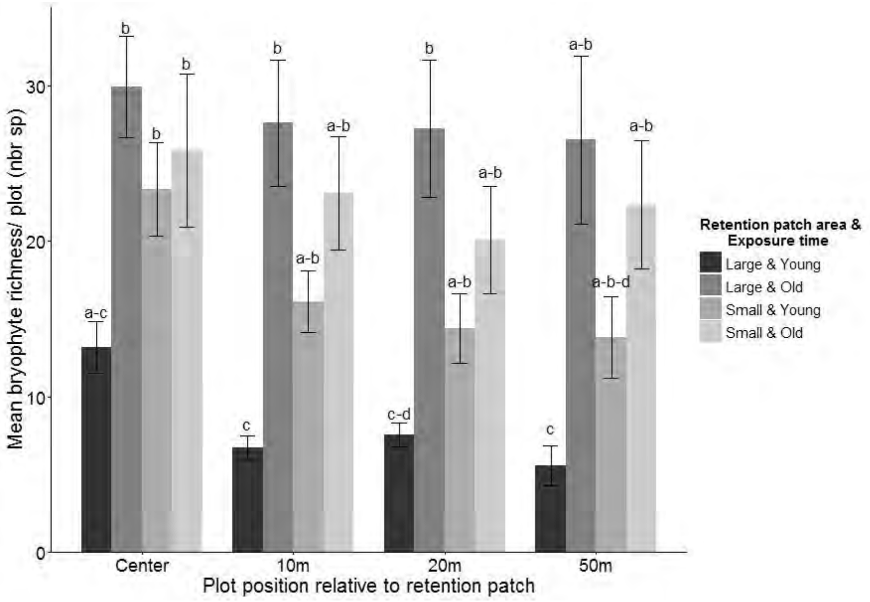

**Figure 2.14** Mean bryophyte richness at the plot scale depending upon retention patch area, exposure time and plot position relative to retention patches. Error bars represent the standard error. Letter represented significate difference as indicated by a Tukey test.

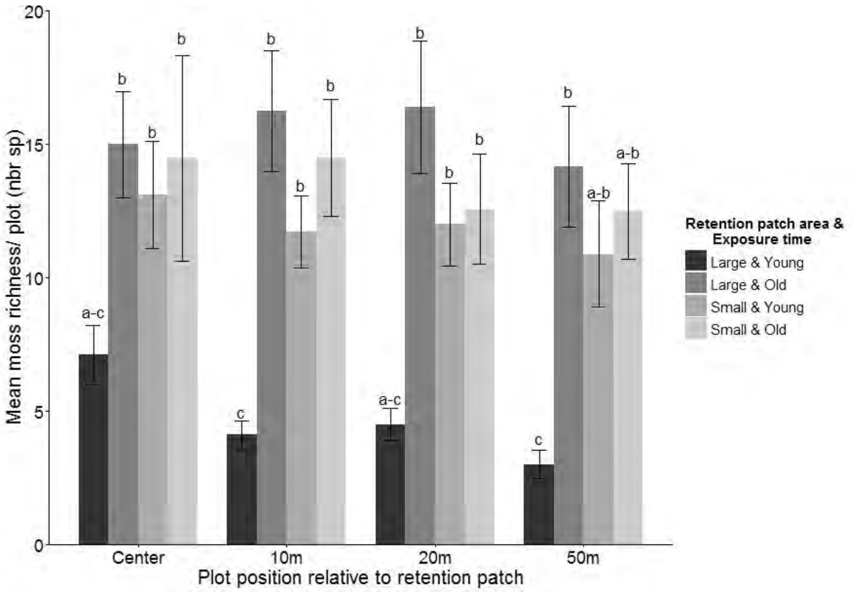

**Figure 2.15** Mean moss richness at the plot scale depending upon retention patch area, exposure time and plot position relative to retention patches. Error bars represent the standard error. Letter represented significate difference as indicated by a Tukey test.

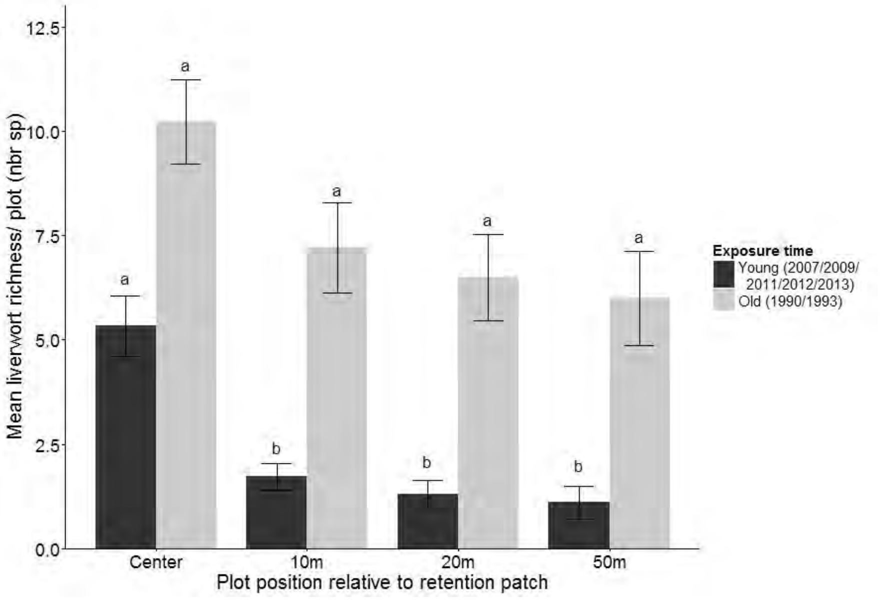

**Figure 2.16** Mean liverwort richness at the plot scale depending upon exposure time and plot position relative to the retention patches. Error bars represent the standard error. Letter represented significate difference as indicated by a Tukey test.

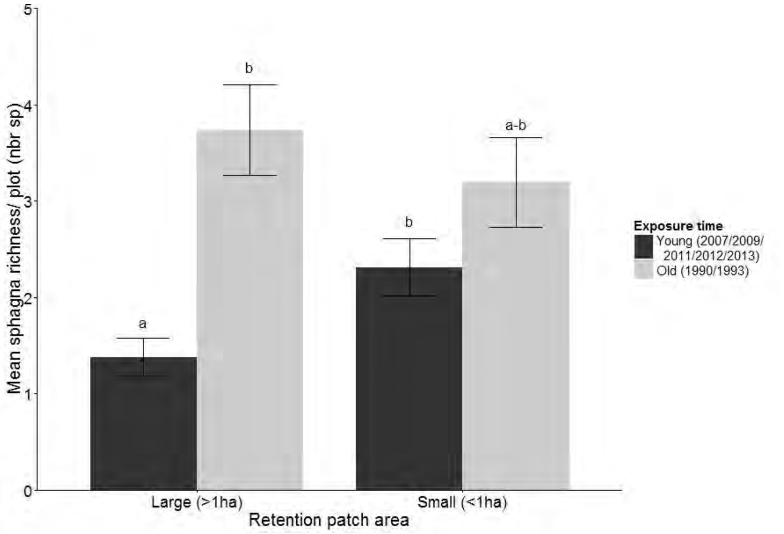

**Figure 2.17** Mean sphagna richness at the plot scale depending upon retention patch area and exposure time. Error bars represent the standard error. Letter represented significate difference as indicated by a Tukey test.

## 2.6 Discussion

The main objective of this study was to understand how post-harvest retention patch characteristics influence their ability to serve as a “lifeboat” for mature forest species. We predicted that the ability to serve as a “lifeboat” will be positively correlated with patch area, and negatively correlated with exposure time. We also assumed that the “lifeboat” ability will be negatively correlated with the distance relative to the retention patch, we tested the interaction between distance from the retention patch and the other factors. The results both support and disprove the hypotheses. Our results demonstrate that globally there is a difference between large and small retention patches and between old and young exposure times. However, the difference was the opposite of our hypotheses, as there was no extinction debt but rather a species enrichment with longer exposure time. Moreover, our results demonstrate that there was a difference between the center and the cut matrix for bryophyte cover and composition, but there was not a gradient in the cut matrix.

### 2.6.1 Retention patch area

Despite the fact that only one species was analyzed for percent cover, we found a difference in cover with retention patch area. We found more *P. schreberi* in large retention areas than in small areas. This may be explained by the greater number of trees present in large retention patches generating a more closed canopy compared to smaller patches. Indeed, as reported by Bescond *et al.* (2011), *P. schreberi* abundance is positively affected with canopy closure and diminished in low-retention cuts compared to untouched forests.

Bryophyte composition results demonstrate a gradient of change in the bryophyte community from moss in small areas to liverwort, moss and sphagna in large areas, as predicted in our hypotheses. Caners *et al.* (2013) found a similar gradient with a change in the liverwort community at any level of retention and a change in moss composition in intact forest compared to a low level of retention.

In contrast to composition, bryophyte richness didn’t reveal an effect of retention area. These results are also consistent with Caners *et al.* (2013) who found no change in moss richness with percent retention in the landscape and with Kimmerer & Driscoll (2000) who found no relation between species richness and boulder area. However, our results are inconsistent with the results of Caners *et al.* (2013) in terms of liverwort richness as their results demonstrated a change in liverwort richness with percent retention in the landscape with an increase of richness with the percent retention kept in the landscape.

Our results could be explained by the edge effect. Indeed, Harper *et al.* (2015) found an edge influence on bryophyte cover due to desiccation with the canopy openness. In the small retention patches, we found different species than in large retention patches because the edge effect could have affected the composition with more colonist-pioneers species in small retention patches than in large patches. However, the similar bryophyte richness between large and small retention patches may be explained by the edge: core ratio, which depends on patch size. Indeed, larger patches can support more microhabitats and therefore house more bryophytes species compared to smaller patches. However, the enhanced edge: core ratio in small compared to large patches may counteracted this effect and bring more species richness because of the increased number of microhabitats found in edges (Murcia 1995; Holland *et al.* 1991).

### 2.6.2 Exposure time

The cover of *P. schreberi* was influenced by exposure time. The *P. schreberi* cover in old exposure sites was higher than in the young exposure sites, which is consistent with the results of Palviainen *et al.* (2005) who found that after a clear-cut *P. schreberi* biomass decreased and then increased.

The bryophyte composition results of this study are also consistent with our hypotheses: there was a difference in composition between old exposure time and young exposure time. Our results avoided bias due to stand age because we obtained no significate difference with the variable retention patch age. Our results demonstrate a gradient of change in the bryophyte community from moss and sphagna in young exposure time to liverwort, moss and sphagna in old exposure time. Our results are consistent with results from Pearce *et al.* (2015) who found a turnover in bryophyte composition with time after harvest.

Bryophyte richness was higher in old exposure time than in young exposure time, these results are inconsistent with our hypotheses but consistent with the results of Paquette *et al.* (2016) who find a higher richness in mature cut than in young cut and with the results of Dynesius & Hylander (2007) who found higher richness in long term after a cut than 2 years after a clear-cut.

Our results could be explained by the species accumulation with time. In young exposure time there is less favorable microhabitats, and with time, there is microhabitat creation and an accumulation of species (Nordén *et al.* 2014). Also, the species accumulation could be explained by the canopy closure. With time, the canopy closes creating more favorable conditions for vascular and nonvascular plants (Hart & Chen 2008).

### 2.6.3 Plot position

Our results also demonstrate a gradient of change in the bryophyte community from moss and sphagna at 10m, 20m and 50m to liverwort and moss at the center. The composition was not so dissimilar between plot positions at 10m, 20m and 50m. The composition change between the cut matrix and the center of retention patches may result from the colonist-pioneer species because these species are shade intolerant and take advantage of canopy openness after a cut (Jonsson & Esseen 1998). With more canopy closure and an old exposure time, there were more liverworts, as these species are sensitive to disturbance (Frisvoll & Presto 1997). Also, canopy openness brings a change in microclimate quality (Schmalholz & Hylander 2009) consequently it also brings a change in the bryophyte community. Our results are consistent with the results from Fenton & Frego (2005) who found a difference in bryophyte communities between remnant patches and open canopy.

Also, we found *P. schreberi* higher in the center of retention patches than in matrix cut. Moreover, a maximum of sphagna richness is at 50m because sphagna is associated with canopy openness (Bisbee *et al.* 2001). Sphagna are heliotrophic species and this is why we find a higher richness with canopy openness, this result is the same found by Fenton & Bergeron (2006). Moreover, our results demonstrate, for all treatments, a maximum of bryophyte, moss and liverwort richness in the center of the retention with a diminution of richness in cut matrix. These results are similar with results of Nelson & Halpern (2005) who found a difference in bryophyte richness between inside forest and cut matrix. Some studies demonstrate that richness is associated with the number of microhabitats found in old forest (Mills & Macdonald 2005) and the total number of microhabitats in the center of large area with old exposure time was the most occupied by bryophytes (Table 2.2). Microhabitat creation could promote colonist species (Økland 1994). Also, bryophyte colonization is affected by limiting dispersal, so the microhabitats should remain long enough to be colonize by bryophyte spores (Hansson *et al.* 1992).

A maximum of bryophyte, moss and liverwort richness is in large areas with old exposure time. For all treatments, after harvest liverwort richness was affected. Even if we keep a large retention patches with old exposure time harvest will bring a change in species richness. This result suggests that to conserve the most sensitive species, it is important to keep high levels of canopy retention for at least 20 years or more. Results from Caners *et al.* (2013) are consistent with our results.

Surprisingly the bryophyte richness was high in the center of small retention areas with young exposure time, this could be caused by microhabitat creation like more downed wood. Our results on the community richness in CPRS with large islands were not what we expected. Surprisingly, richness in the center and in the cut matrix was very low, it may be the result of the difference in temperature and relative humidity or other characteristics we haven’t identify like the degree of isolation for each patch (Baker *et al.* 2013).

## 2.7 Implications for management

The forest rejuvenation is mainly due to the fact that there are harvest that occurs as soon as the stands have reached maturity. It is therefore essential that forest management retains old forests to maintain significant biodiversity in the boreal forest: bryophytes. We should reduce the gap between natural disturbance and anthropologic disturbance to keep a structurally complex landscape.

Forest management aims to reduce the gap in the attributes between natural and managed forests. Our results demonstrate that retention patch provide lifeboats and keep the most sensitive species of bryophytes, such as liverworts. The results show an increase in species richness with time since the last harvest, but the composition of the cut matrix is not similar to the patch center. Indeed, the decline in the microhabitats quality could be the cause of the difference in composition between the liverwort patch centers versus the cut matrix (Ross-Davis & Frego 2002). Long exposure time permits the development and the maturation of a variety of microhabitats important for the recovery of species with specific microhabitat requirements such as numerous liverworts (Fenton *et al.* 2003; Nelson and Halpern 2005).

Maintaining large tree retention areas such as moose islands, it is possible to maintain important forest attributes for the preservation of bryophytes, such as dead wood and microhabitats.

## 2.8 Acknowledgments

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# CHAPITRE III

# CONCLUSION GÉNÉRALE

Cette étude avait pour objectif global de déterminer les facteurs influençant la dynamique des communautés de bryophytes au sein de différents patrons de coupe à rétention variable (coupe avec protection de la régénération et des sols avec rétention de bouquets, d'îlots, de grands îlots orignaux et les séparateurs à sec). Ce projet de recherche s'inscrit dans une démarche globale de validation des prescriptions sylvicoles pour l'aménagement écosystémique des forêts boréales du Québec. Plus spécifiquement, les coupes à rétention variable visent à imiter les îlots résiduels laissés après feu dans le but de répondre à l'enjeu de raréfaction des espèces associées aux vieilles forêts tout en conservant la complexité de l'écosystème forestier.

Afin d'évaluer l'effet des coupes à rétention variables sur ces attributs, nous avons inventorié les conditions d'habitats créées par ces interventions. Puis nous avons inventorié la réponse des communautés de bryophytes. La coupe à rétention variable semble offrir des conditions adéquates à l'installation des bryophytes, quel que soit le patron testé, mais les résultats démontrent que pour qu'il y ait résilience des espèces, il faut laisser ces îlots de rétention, car ils ont un rôle important comme refuge. Cependant, bien que suspectée importante, notre étude ne permet pas de fournir des conclusions quant à la taille requise des îlots de rétention. En effet, les parterres de coupe de CPRS étudiés sont récents et l'effet temporel masque l'effet de la taille des îlots sur les communautés bryophytiques.

En général, le maintien des îlots de rétention après coupe permet de préserver les populations de bryophytes. Les bryophytes jouent un rôle important pour l'établissement des trachéophytes et ont un rôle important dans la production primaire nette, elles ont donc un rôle écologique qui leur confèrent un titre d'espèces clé de l'écosystème forestier. La présence des communautés de bryophytes contribue ainsi à répondre à l'enjeu de maintien de biodiversité.

Cette étude nous permet de poser les bases de la dynamique des communautés de bryophytes et la conservation de l'écosystème suite à l'application de la coupe à rétention variable en forêt boréale de l'Est canadien. Toutefois, après un à deux étés de croissance, les bryophytes issues des CPRS îlots n'ont pas eu le temps de refléter la dynamique des communautés. Il aurait été intéressant de voir au fil des ans la dynamique issue des CPRS îlots. Nous aurions ainsi pu évaluer si la dynamique des communautés de bryophytes issues des CPRS îlots est similaire à ceux des îlots orignaux. Aussi, la création de données pour les séparateurs à sec pour les placettes extérieures ne permet pas réellement de refléter la dynamique à l'extérieur de ces patrons. Un inventaire des placettes extérieures permettrait de mieux documenter la dynamique des communautés de bryophytes en fonction des différents types de rétention. De plus, l'identification des bryophytes selon la composition (colonisatrice, pionnière) permettrait de voir le changement dans la richesse au fils du temps depuis la dernière perturbation. Certaines espèces étant associées aux vieilles forêts pourraient nous indiquer si la taille des îlots résiduels est suffisante pour conserver une biodiversité importante de la forêt boréale intacte.

Ce projet de recherche sur la dynamique des communautés de bryophytes a permis court et moyen terme de déterminer l'impact des coupes à rétention variable sur cette communauté. Le projet était complémentaire à un autre projet en cours impliquant les communautés de bryophytes post-feux, où les facteurs des îlots résiduels post-feux sur la dynamique des communautés de bryophytes sont identifiés. Ces travaux permettront dans leur ensemble de mieux évaluer l'effet des îlots résiduels sur ces espèces dans les forêts boréales du sud de la Baie-James, ainsi que dans des peuplements semblables ailleurs au Québec.

Cette étude permettra également aux représentants des Tables de Gestion Intégrée des Ressources et du Territoire TGIRT, aux aménagistes des ressources naturelles et du territoire, et aux professionnels du Bureau du forestier en chef de mieux comprendre les impacts à court terme et long terme des coupes à rétention variable et de leurs patrons sur la dynamique forestière et, sur la qualité et le succès de la régénération pour une meilleure gestion de scénarios sylvicoles d'aménagement. Elle contribuera ainsi à l'évaluation des effets des Plans d'aménagement forestier intégrés (PAFI) sur les habitats forestiers. Il serait nécessaire de faire le suivi dans les prochaines années afin de mieux évaluer les conséquences de l'effet de la taille des îlots résiduels. En effet, les nouveaux habitats créés par ces interventions étaient constitués de nombreux microhabitats inoccupés. Un suivi à long terme permettrait de dresser un portrait plus complet. De futures études devront être établies pour éviter ces effets confondants et obtenir des réponses sur la taille des îlots à maintenir.

### Implication pour l'aménagement

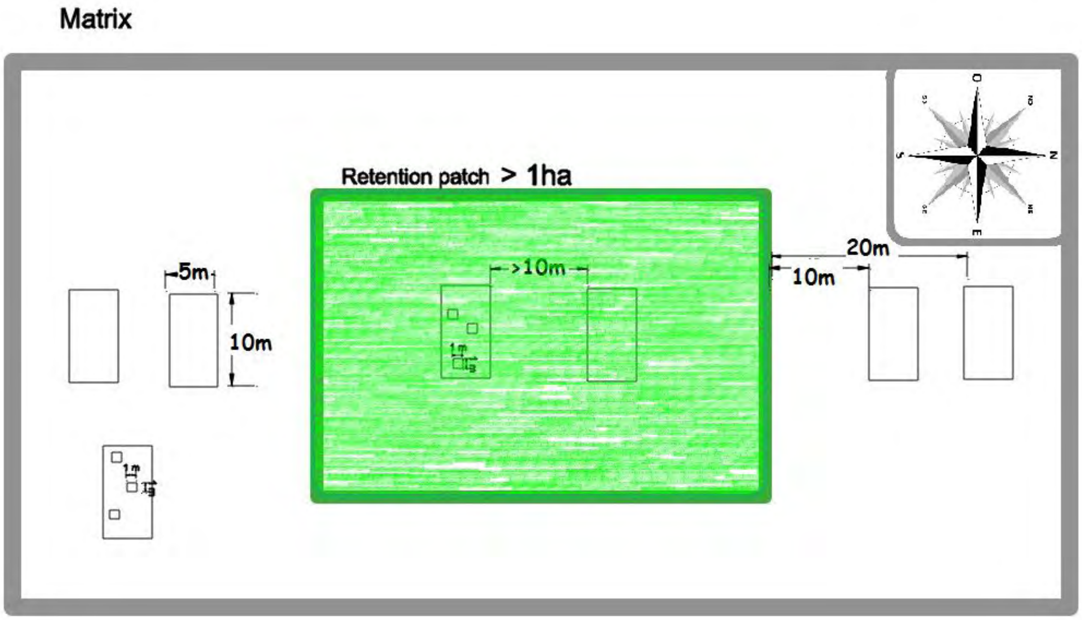
Avec le rajeunissement des peuplements, il y a non seulement une diminution des vieilles forêts, mais il y a aussi une diminution de la richesse des communautés de bryophytes. Ce rajeunissement est principalement dû au fait qu'il y a des coupes qui s'effectuent dès que les peuplements ont atteint leur maturité. Il est donc essentiel que l'aménagement forestier tienne compte des vieilles forêts afin de maintenir une importante biodiversité de la forêt boréale : les bryophytes.

L'aménagement écosystémique a pour objectif de diminuer l'écart des attributs des forêts naturelles de celles aménagées. Nos résultats démontrent que les îlots de rétention servent de refuge et permettent de maintenir les espèces les plus sensibles des bryophytes telles que les hépatiques. Les résultats démontrent une augmentation de la richesse en espèce au fils des années, mais que la composition de la matrice de coupe n'est pas similaire à celle au centre des îlots. En effet, la diminution de la qualité des microhabitats pourrait être la cause de la différence en composition entre la richesse en hépatiques des centres des îlots versus le parterre de coupe (Ross-Davis & Frego 2002).

En conservant des grandes superficies de rétention d'arbre telles que les îlots orignaux, il est possible de maintenir des attributs forestiers importants pour la préservation des bryophytes tels que du bois mort et des microhabitats.

# ANNEXE A –

# LE DISPOSITIF EXPÉRIMENTAL



# BIBLIOGRAPHIE POUR INTRODUCTION ET CONCLUSION GÉNÉRALES

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