UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

DYNAMIQUE DES COMMUNAUTÉS BRYOPHYTIQUES EN PESSIÈRE NOIRE À MOUSSES DE L'OUEST DU QUÉBEC : RÔLES DES ÎLOTS RÉSIDUELS POST-FEU

THÈSE

PRÉSENTÉE

COMME EXIGENCE PARTIELLE

DU DOCTORAT EN SCIENCES DE L'ENVIRONNEMENT

PAR

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OCTOBRE 2016

« L’ART DE CHERCHER UNE AIGUILLE DANS UNE BOTTE DE FOIN ! »

REMERCIEMENTS

Sans vouloir oublier personne ni trop en faire, en sachant pertinemment que l'on faillira à ces deux points, les remerciements sont peut-être, après mûre réflexion, la partie la plus délicate à rédiger d'une thèse. Peu à l'aise avec les épanchements sentimentaux, je comparerais cet exercice à l'arrachage d'un pansement : en un seul coup, sans se poser trop de questions !

Sans plus attendre, je souhaite alors m'excuser auprès de ceux que je m'apprête à oublier, qu'ils ne m'en tiennent pas rigueur et qu'ils reçoivent mes plus sincères remerciements !

Que serait un doctorant sans directrice(eur) ni codirectrice(eur) ? Une âme esseulée dans les couloirs d'une quelconque université certainement. C'est pour cette raison, que, le plus chaleureusement du monde, à la manière dont elle m'a accueillie à bras ouverts sur le tarmac de l'aéroport de Rouyn-Noranda un soir de 23 janvier 2013 où les températures nocturnes ont chuté sous la barre des -45 °C, je remercie la Dre Nicole Fenton, ma directrice. Je souhaite à quiconque doit faire un doctorat d'avoir la chance d'être dirigé par une directrice aussi disponible, attentive, réactive et ouverte que Nicole. Présente du début à la fin, elle n'a jamais ménagé ses efforts pour bonifier ce travail et était toujours partante pour explorer les questions les plus rocambolesques, merci Nicole de ta patience et de ta passion ! De même, mes plus sincères remerciements se dirigent vers le Dr Yves Bergeron, mon codirecteur, dont l'expertise pointue et les commentaires pertinents ont contribué à améliorer chacune des étapes de ce travail. Merci Nicole et merci Yves d'avoir misé sur moi, puisse votre audace être récompensée par l'aboutissement de ce travail.

Aussi, que serait une thèse sans d'éreintants étés de terrain ? Un vif merci à mes assistants : Flora Joubier, Louis Dubois et Philippe Heine. Je vous ai usé jusqu'à la corde et vous n'avez jamais bronché, vous êtes des machines humaines !

Je me dirige maintenant d'un pas décidé à remercier celles qui sont partout et sans qui rien ne serait possible, celles qui sont à la fois le sourire et le cœur de l'UQAT, j'ai nommé Marie-Hélène Longpré et Danièle Laporte. Votre bonne humeur contagieuse est la seule chose que j'envie aux étudiants dont les bureaux jouxtent les vôtres. Merci à vous deux de votre sympathie, de votre gaieté et de votre professionnalisme, vous avez éclairé chacune de mes journées au Québec !

Se lancer dans une thèse c'est comme se décider à partir en pleine mer. Dans le même bateau que des dizaines d'autres étudiants avec lesquels seront partagés tempêtes déchaînées, liesses à la vue d'une terre, mutineries et pourquoi pas, le scorbut dans le pire des cas. Autant donc s'entourer d'un équipage agréable puisque le voyage sera long et semé d'embûches. J'ai eu cette chance et je remercie alors chacun de mes compagnons de bordée et particulièrement : Dalenda Ben Amar, Joëlle Castonguay, Noémie Graignic, Morgane Higelin, Aurore Lucas, Mélissande Nagati, Marine Pacé, Raphaële Piché, Pauline Suffice, Sarah Verguez-Moniz, Arun Bose, Benjamin Gadet. Un merci particulier à Louiza Moussaoui et Chafi Chaieb avec lesquels je partage bon nombre des données utilisées dans cette thèse.

Merci aussi aux professeurs et professionnels de l'UQAT et de l'UQAM qui ont chacun amené leurs grains de sel à ce travail : Danielle Charron, Annie Desrochers, Mélanie Desrochers, Ann Gervais, Francine Tremblay, Pascal Drouin, Philippe Duval, Raynald Julien, Ahmeed Koubaa, Frédéric Normand et Benoit Plante.

Un petit détour pour un grand merci à mes coauteurs Richard Caners, Pierre Drapeau, Jean Faubert, Louis Imbeau, Martin Lavoie et Marc Mazerolle qui ont bien voulu se joindre à cette aventure et m'éclairer de leurs expertises respectives. Une mention spéciale est ici décernée à une collègue devenue une amie et avec qui je partage le point commun d'aimer poursuivre des chimères. Un sincère merci à Émilie Chavel, j'espère que nous aurons encore la chance de partager des idées aussi extravagantes que transcendantes !

Et pour finir, et non des moindres, je remercie encore Louis Dubois, mon plus fidèle assistant de terrain qui a poussé le masochisme à son apogée en récidivant trois années de suite ! Merci à toi Louis, qui est devenu un peu plus qu'un assistant de terrain et qui m'a accompagné dans cette aventure de bout en bout…

Je ne serai personne si j'omettais de remercier chacun des membres de ma famille qui m'ont offert le plus beau cadeau en acceptant de me laisser partir, au risque que je m'attache au Québec et particulièrement à un Québécois ! Merci donc à mon père, ma mère, ma grand-mère et ma sœur cadette qui ont été présents chaque minute durant ces trois ans et demi. Je vous dédie cette thèse et vous remercie de votre soutien depuis les tout premiers jours d'une scolarité qui s'est éternisée jusqu'à aujourd'hui…

AVANT-PROPOS

Cette thèse est présentée sous forme de quatre articles et deux articles annexes et s'articule donc en quatre chapitres et deux chapitres annexes assortis d'une introduction et d'une conclusion générales. Les articles, selon leurs avancements, sont, pour certains déjà publiés et, pour d'autres, en préparation pour soumission dans des revues scientifiques avec comité de lecture. Selon la revue visée, la forme des articles varie sensiblement. Chacun des chapitres présentés dans ce document résulte de relevés de terrain effectués sur un territoire d'étude commun ayant abouti à l'obtention d'une base de données globale qui sera considérée en intégralité ou partitionnée selon les objectifs dudit chapitre. Les répétitions, bien qu'elles rendent la lecture redondante, sont alors inéluctables.

Les quatre chapitres présentés ici sont le fruit d'une étroite collaboration entre chacun des coauteurs y ayant participé. Selon les traditions scientifiques et académiques, ayant contribué à la collecte des données, à la réalisation des analyses statistiques et à la rédaction, je me trouve première auteure de chacun d'eux. La première coauteure est ma directrice la Dre Nicole J. Fenton. L'ultime place de coauteur revient à mon codirecteur le Dr Yves Bergeron. Tous deux ont pleinement participé à chacune des étapes de cette thèse, de ses balbutiements jusqu'à son aboutissement. Le cinquième chapitre compte parmi ses auteurs le Dr Richard Caners qui a fourni de précieux conseils statistiques, bryologiques et rédactionnels.

Les lecteurs les plus opiniâtres trouveront, à la fin de cet ouvrage, deux chapitres placés en annexe. La première annexe, conjointement réalisée avec une autre étudiante au doctorat, Émilie Chavel, sera aussi intégrée dans la thèse de cette dernière. En effet, ce travail est issu d'une collaboration entière entre Émilie et moi-même. Nous avons toutes deux participé à la récolte des données, à la réalisation des analyses statistiques et à la rédaction de ce chapitre. La place de première auteure fut difficile à départager et me fut cédée seulement au terme d'un combat acharné de « pierre-feuille-ciseaux », lequel je remportais glorieusement ! Émilie Chavel est donc la deuxième auteure de ce papier, les places de coauteurs reviennent à chacun de nos directeurs et codirecteurs respectifs : Dre Nicole J. Fenton, Dr Louis Imbeau, Dr Marc J. Mazerolle, Dr Pierre Drapeau et Dr Yves Bergeron. L'article rapporté dans la seconde annexe est, quant à lui, issu d'un travail collaboratif avec un étudiant en géographie de l'Université Laval encadré par la Dre Nicole J. Fenton et moi-même durant son stage de fin d'études. Ayant réalisé l'intégralité des cartes, la deuxième place de coauteur revient à cet étudiant, Louis Dubois. Le spécialiste québécois de la bryologie, Jean Faubert, qui nous a fourni les données de base pour la réalisation de ce travail, me fait l'honneur de son expertise et occupe la troisième place de coauteur de cet article. Le cinquième coauteur de ce travail est le Dr Martin Lavoie, superviseur de stage de fin d'études de Louis Dubois à l'Université Laval. La Dre Nicole J. Fenton et le Dr Yves Bergeron occupent respectivement les quatrième et dernière places de coauteurs.

Chapitre II. Barbé, M., Fenton, N.J. & Bergeron, Y. Are post-fire residual forest patches refugia for boreal bryophyte species? Implications for ecosystem based management and conservation. En revision dans *Biodiversity and Conservation*, Octobre 2016.

Chapitre III. Barbé, M., Fenton, N.J. & Bergeron, Y. Boreal bryophyte response to natural fire edge creation. En revision dans *Journal of Vegetation Science*, Octobre 2016.

Chapitre IV. Barbé, M., Fenton, N.J. & Bergeron, Y. So close and yet so far away: long distance dispersal events govern bryophyte metacommunity re-assembly. *Journal of Ecology*, 104(6): 1707-1719.

Chapitre V. Barbé, M., Fenton, N.J., Caners, R. & Bergeron, Y. Time changes everything: inter-annual variation in bryophyte dispersal. En préparation pour *Oecologia*.

Annexe I. Barbé, M., Chavel, É.E., Fenton, N.J., Imbeau, L., Mazerolle, M.J., Drapeau, P. & Bergeron, Y. Dispersal of bryophytes and ferns is facilitated by small mammals in the boreal forest. *Ecoscience*, DOI: 10.1080/11956860.2016.1235917.

Annexe II. Barbé, M., Dubois, L., Faubert, N.J., Lavoie, M., Bergeron, Y. & Fenton, N. Distribution range extension of 35 bryophyte species from sampling in the neglected south of Northern-Québec (Canada). En préparation pour *Canadian Field Naturalist*.

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RÉSUMÉ

La conscientisation aux problématiques environnementales survenue il y a une trentaine d'années a engagé une refonte de la foresterie. Il s'agit alors de s'inspirer des patrons écologiques issus de la dynamique forestière naturelle. Sous l'égide de l'aménagement écosystémique, l'objectif principal de cette thèse est de rendre compte du rôle des îlots résiduels post-feu et des caractéristiques qui soutiennent ces rôles, dans la dynamique des communautés bryophytiques. Conjointement, nous ambitionnons d'améliorer les connaissances sur la dynamique des bryophytes en forêt boréale nord-américaine.

Les bryophytes furent échantillonnnées dans trois types de peuplement illustrant un gradient de sévérité de perturbation : forêts non perturbées témoins (données de C. Chaieb), îlots résiduels post-feu et matrices brûlées. La variété des microhabitats en bordure des îlots résiduels expliquerait leurs richesses en bryophytes. En revanche, l'absence de plusieurs espèces forestières sensibles aux perturbations ne permet pas de définir les îlots résiduels comme des refuges *i.e.*, habitats aux caractéristiques environnementales et à la composition en espèces similaires à celle des forêts non perturbées. Cependant, les îlots résiduels de plus de 56 ans et 0.20 ha et de complexité structurelle modérée arboraient une communauté bryophytique plus similaire à celle des forêts non perturbées qu'à celles des matrices brûlées. La stratégie gagnante pour optimiser la richesse en bryophytes et maintenir les espèces sensibles consiste à imiter ces caractéristiques dans les îlots de rétention tout en conservant des peuplements forestiers non perturbés.

Dans les mêmes trois types de peuplements, en divisant les îlots résiduels en habitats de cœur (forêt à l'intérieur de l'îlot) et de bordure (zone de transition entre la matrice brûlée et le cœur de l'îlot), nous avons mis en évidence la réponse des bryophytes à l'effet de bordure. L'hypothèse comme quoi les vieux et larges îlots résiduels abriteraient des communautés plus similaires à celles des forêts non perturbées en raison de la moindre pénétration de l'effet de bordure à l'intérieur du peuplement est rejetée. Les îlots résiduels, même de 3 à 11 ha, étaient dépourvus de cœur. Ce changement de communauté face à la création de bordures est naturel, ouvrant à la discussion quant à l'interprétation de la réponse des espèces à la création de bordures anthropiques.

En comparant la communauté bryophytique des îlots résiduels et des matrices brûlées aux espèces présentes dans la pluie de propagules aériennes interceptées dans les mêmes habitats, nous avons démontré leur non-concordance. La faible similarité entre ces communautés était expliquée par la prépondérance du transport à longue distance des propagules. Ce résultat suggère que les îlots résiduels, comme sources de propagules potentielles, ont une influence sur la recolonisation de la matrice brûlée à l'échelle locale, mais surtout régionale. Nous insistons donc sur la

nécessité de penser l'aménagement forestier à l'échelle régionale, et rapportons l'occurrence d'un processus controversé chez les bryophytes : la dispersion à longue distance.

La dépendance accrue des bryophytes aux conditions environnementales est un fait avéré. Pourrait-elle expliquer les patrons interannuel et intersaisonnier des pluies de propagules aériennes interceptées en pessière noire ? Oui, et la dispersion des propagules serait impactée par les conditions environnementales (principalement la température, l'humidité et la durée de l'hiver) concomitantes au relargage des propagules, mais aussi en amont de la libération des propagules (durant les phases de fertilisation et de croissance/maturation du gamétophyte). Cette étude préliminaire et ponctuelle recquiert d'être complémentée par des études à plus long terme. Cependant, elle représente une avancée considérable dans la compréhension des patrons de dispersion des espèces, sujet de première importance dans le contexte des changements globaux.

Pour poursuivre, nous avons étudié le recours, par les bryophytes, à des agents biotiques de dispersion. Le brossage de micromammifères capturés en pessière noire a permis de démontrer que 50 % d'entre eux transportaient des propagules viables de bryophytes. La dynamique métapopulationnelle des bryophytes est assurée par cette interaction journalière avec les micromammifères, qui contribueraient à la dispersion d'une quantité substantielle de propagules.

Nous concluons en actualisant la Flore des bryophytes du Québec-Labrador et en redessinant l'aire de répartition de 35 bryophytes, dont 20 nouvelles pour notre région d'étude. L'extension de l'aire de répartition de ces espèces renvoie à la nécessité de poursuivre les campagnes d'échantillonnages bryologiques, d'autant plus dans des endroits riches d'une bryoflore aussi remarquable que la pessière noire, où chercher une mousse revient un peu, avouons-le, à chercher une aiguille dans une botte de foin !

À l'issue de cette thèse, nous soulignons le bénéfice d'étudier les bryophytes afin de s'inspirer des patrons de perturbations naturelles et de mitiger les impacts délétères des coupes forestières sur l'écosystème. Un soin particulier quant à la conception des îlots résiduels à l'échelle locale, mais aussi quant à leur agencement à l'échelle du paysage est requis pour conserver une bryo-diversité maximale. Ces conclusions soulèvent, de plus, l'impérieuse nécessité de préserver des peuplements forestiers âgés et continus pour conserver les espèces sensibles aux perturbations et à haut risque d'extirpation. Maintenir la bryoflore en forêt boréale exploitée est le prérequis indispensable à la régénération optimale des peuplements et à la résilience de cet écosystème, patrimoine naturel des plus remarquable de l'Amérique du Nord.

PROLOGUE

En toute innocence vous venez ici de franchir le seuil de tout un univers. Ouvrir ce document c'est comme s'autoriser à partir en voyage. Pourtant nous ne partons pas si loin, non, contentons-nous de baisser les yeux et par la même occasion de baisser notre garde… Nous partons au cœur du sous-bois et nous allons, par curiosité davantage que manque de pudeur, nous glisser sous les jupes des épinettes noires, figures emblématiques des forêts boréales nord-américaines et plus précisément de la pessière noire à mousses. Je vous emmène à la rencontre des plus minimes occupantes du sous-bois, et non des moindres !

En effet, quels végétaux peuvent se targuer de marquer le passage entre la vie terrestre et aquatique ? D'avoir conquis l'intégralité des continents ? Lesquels peuvent encore, à l'instar du Phoenix qui renaît de ses cendres, s'enorgueillir de posséder le don de reviviscence ? Si les arbres avaient autant de qualités, peut-être auraient-ils mérité notre intérêt, mais, et au risque de froisser les « trachéophytologues », les voilà ici supplantés par celles mêmes qui leurs lèchent les bottes, nous entendons bien parler des bryophytes ! Discrètes, mais non désuètes, à qui sait se pencher et écouter, elles livreront leurs plus intimes secrets. À l'Université du Québec en Abitibi-Témiscamingue, au cœur de la forêt boréale, mieux vaut donc être atteint de surdité, puisqu'elles sont nombreuses, et elles en ont des choses à dire ! Nous avons alors tendu l'oreille, et, au terme de ces trois années et demie, nous venons vous présenter ce qu'elles ont bien voulu laisser entendre.

Je vous abandonne alors à ces quelques menues pages et vous laisse entrer dans l'univers des bryophytes qui incarne sobriété, naturel et quiétude, valeurs fondamentales à l'opposé même de ma personnalité ! Je vous offre cette ode aux bryophytes et espère faire naître un nouvel attrait et, pourquoi pas même, une nouvelle passion chez certains d'entre vous, car, comme l'écrit si justement Véronique Brindeau : « pour qui s'éprend des mousses, le monde s'éclaire d'une nouvelle et minuscule fenêtre » (Brindeau, 2012), une fenêtre qui plus jamais ne se refermera.

CHAPITRE I

INTRODUCTION GÉNÉRALE

1.1 Sujet d’étude

De la lyrique « mousse plume » en passant par l’ostentatoire « hypne dorée » pour finir par la survoltée « queue de chat électrique », les bryophytes ont de quoi attiser les curiosités. Ainsi, et au risque de paraître sectaire, commençons pour une fois par le commencement : les bryophytes !

1.1.1 Terminologie et nomenclature

L’origine grecque du mot bryophyte se rapporte à leur capacité à gonfler sous l’effet de l’hydratation (Vanderpoorten & Goffinet, 2009). Sous cette dénomination sont regroupés les trois *phyllum Bryophyta* (mousses et sphaignes), *Marchantiophyta* (hépatiques) et *Anthocerophyta* (anthocérotes ; Figure 1.1 ; Glime, 2013). En réalité le mot « bryophyte » est peu utilisé en français, excepté par les initiés, et on lui préfère dans le langage courant, le mot « mousse ».

Seulement, vous l’aurez compris, l’utilisation du mot « mousse » pose le problème de ne plus pouvoir distinguer le règne du *phyllum*. Ce raccourci m’a d’ailleurs valu plusieurs « discours de sourds » et les plus familiers avec l’excellent « Dîner de cons » (Veber, 1998) comprendront le parallèle à l’échange entre Pierre Brochant et François Pignon à propos d’un certain Juste Leblanc ! C’est pourquoi vous rencontrerez dans la littérature la terminologie « mousses s.l. » soit « mousses *sensu largo* » qui renvoie aux bryophytes et « mousses s.s. » soit « mousses *sensu stricto* » pour parler du *phyllum Bryophyta*.

De plus, récemment, Crum (2001) a introduit le *phyllum Sphagnophyta* pour distinguer les sphaignes des mousses, originellement regroupées sous les *Bryophyta*. Par souci de clarté, et bien que cette division ne fasse pas l'unanimité chez les taxonomistes, le terme bryophyte sera utilisé dans la suite de ce document pour parler des mousses, sphaignes et hépatiques divisées en trois *phyllum* distincts. Les anthocérotes ne seront pas abordées étant donné qu'aucune n'a été relevée dans la région d'étude considérée.

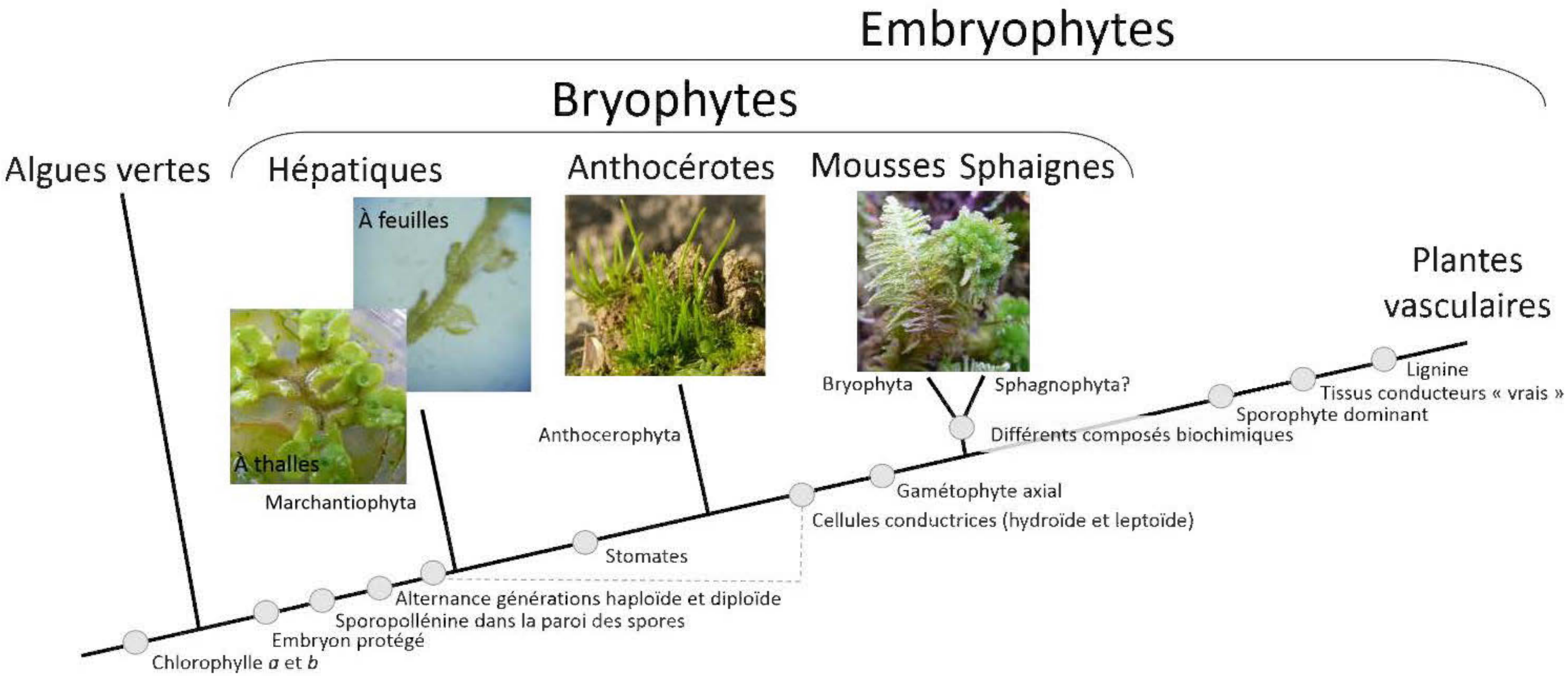

Figure 1.1 Cladogramme des végétaux. Les cercles gris renvoient aux caractères évolutifs à la base de la différentiation entre les *phyllum* présentés. La ligne grise pointillée souligne que ce caractère évolutif, rapporté par Ligrone *et al.* (2000) à la fois chez certaines hépatiques et chez certaines mousses, remets en question l'organisation du présent cladogramme. Adapté de Glime (2013) ; Raven *et al.* (2014) et Vanderpoorten & Goffinet (2009).

Les bryophytes occupent aujourd'hui une place à part entière dans le règne végétal et pourraient même représenter un sous-règne à elles seules (Glime, 2013). D'ailleurs, le mot « mousse » proviendrait du latin « *mulsa* » soit la boisson des Dieux : l'hydromel, utilisé métaphoriquement pour décrire ces plantes (CNRTL, 2012). L'ascension dans le cladogramme végétal n'aura pourtant pas été aisée. En effet, dans les années 1600, les bryophytes étaient dédaigneusement considérées comme des fœtus de plantes avortés (Crum, 2001). Aussi, en se référant à mes lointains aïeux, les Gaulois, le mot « mousse » dériverait de « *mudia* », qui décrivait les souillures et les déjections au sol (CNRTL, 2012). Les clichés ont la vie dure puisque la fâcheuse tendance à décrire les bryophytes par ce qui leur fait défaut davantage que par ce qui les rend singulières perdure encore. On parle alors de plantes non vasculaires, en référence à leur absence de tissus spécialisés dans la conduction de l'eau et des nutriments (Vanderpoorten & Goffinet, 2009). Cependant, la mise en évidence par Ligrone *et al.* (2000), de cellules conductrices internes chez certaines hépatiques et mousses, invalide l'usage de cette appellation réductrice pour décrire la deuxième famille végétale la plus diversifiée de la planète (Frahm, 2008 ; Glime, 2013). On estime en effet entre 15 000 (Gradstein *et al.*, 2001) et 25 000 (Crum, 2001) le nombre d'espèces de bryophytes. De surcroît, les bryophytes occupent une part conséquente de la biomasse globale de la plupart des écosystèmes (*e.g.*, 6.66 % de la biomasse globale des forêts décidues Atlantique, 98 % de la biomasse des près humides Arctique ; Longton, 1992 ; Rieley *et al.*, 1979).

Taxonomiquement parlant, les bryophytes sont le chaînon liant les algues vertes aux plantes vasculaires (Figure 1.1). Plusieurs caractères évolutifs les distinguent des algues vertes tels que des spores contenant de la sporopollénine et un embryon protégé dans le gamétophyte femelle. Les bryophytes sont donc les plus primitives des Embryophytes et sont les seuls végétaux terrestres chez qui la phase gamétophytique (la plante mère) est dominante (Figure 1.2 ; Vanderpoorten & Goffinet, 2009). La phase sporophytique (organe reproducteur contenant les spores) est réduite et matrotrophe, soit parasite de la plante mère. Selon Graham et Wilcox

(2000), la matrotrophie serait l'avantage évolutif qui aurait permis la diversification des bryophytes et leur ascension au rang de plantes terrestres. Parmi les bryophytes, les hépatiques sont les plus primitives et leur affiliation aux Embryophytes est remise en cause par de récentes études paléontologiques (VanAller Hernick *et al.*, 2008). De plus, les études moléculaires rapportent des résultats contradictoires concernant quel *phyllum* des bryophytes serait le plus proche voisin des plantes vasculaires (Nishiyama *et al.*, 2003 ; Qui *et al.*, 2006). Tous les taxonomistes s'accordent cependant sur une chose, les bryophytes marquent la conquête du milieu terrestre il y a plus de 400 millions d'années et leur extirpation de l'eau et un des évènements majeurs de l'histoire de notre planète qui aurait conduit à l'avènement des plantes terrestres et à l'environnement tel qu'il nous est familier aujourd'hui (Vanderpoorten & Goffinet, 2009).

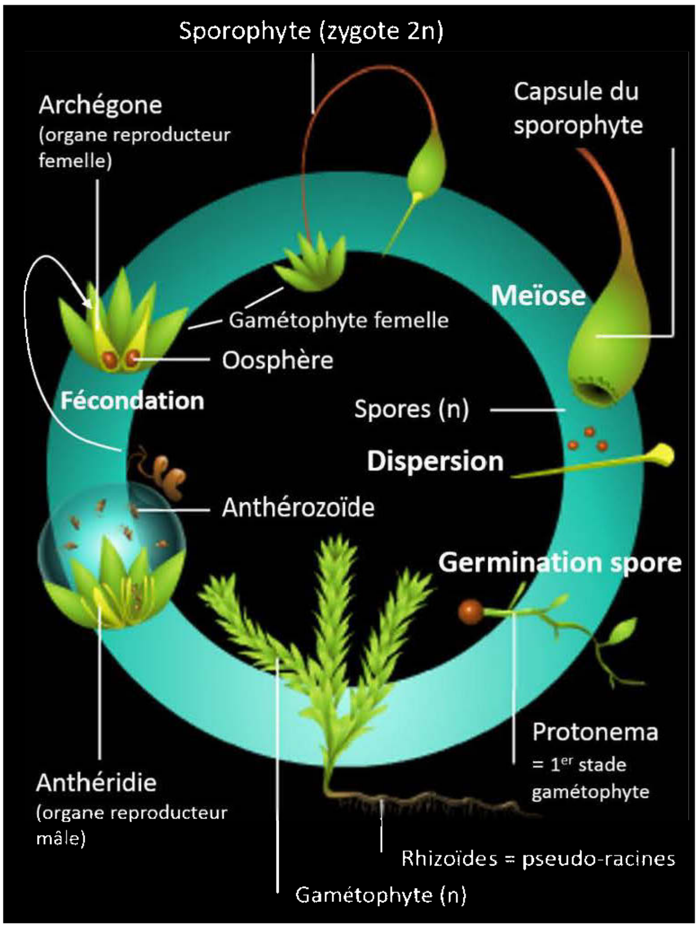

Figure 1.2 Cycle phénologique d'une bryophyte typique, la mousse *Funaria hygrometrica*. Adapté du Larousse (2006).

1.1.2 Dispersion

Les bryophytes sont retrouvées sur tous les continents et sous toutes les latitudes excepté les eaux salines et les écosystèmes gelés en permanence (Vanderpoorten & Goffinet, 2009). De plus, contrairement aux végétaux vasculaires, les bryophytes ne répondent pas au gradient latitudinal de diversité croissant des pôles vers l'équateur ni ne possèdent des taux élevés d'endémisme (Frahm, 2008 ; Hodgetts, 1996 ; van Zanten & Pócs, 1981). Certaines espèces ont une aire de répartition continue sur plusieurs voire tous les continents (*e.g., Bryum argenteum, Pleurozium schreberi*) et sont alors qualifiées de cosmopolites ou d'ubiquistes. D'autres taxons possèdent des aires de distribution disjointes (*e.g., Isothecium holtii* présente sur les îles Britanniques, l'ouest de la France et de la Norvège ainsi qu'en Turquie sans jonction entre ces localités ; Sabovljević *et al.*, 2005) expliquées par la dérive des plaques continentales, des phénomènes d'extinctions locales et par leurs modes de dispersion (Frahm, 2008).

Les bryophytes peuvent en effet se reproduire de façon sexuée et asexuée, chacune dévolue à un type de dispersion donné. La reproduction asexuée est réalisée par le biais de propagules produites à la base des feuilles (gemmae) ou de fragments végétatifs (fragments de tiges ou feuilles qui se développeront pour donner un nouvel individu ; Benscoter, 2006 ; Mälson & Rydin, 2007; Rochefort *et al.*, 2003). Les propagules asexuées sont principalement utilisées pour la dispersion à courte distance et pour l'expansion locale de la population étant donné leur taille et leur fort potentiel germinatif, même en conditions suboptimales (Kimmerer, 1991 ; Löbel *et al.*, 2006). *A contrario*, la reproduction sexuée est effectuée par l'intermédiaire de propagules sexuées (spores) qui sont produites dans la capsule du sporophyte (Figure 1.2). Ce mode de reproduction est dédié à la dispersion à plus longue distance et expliquerait l'intercontinentalité des bryophytes (van Zanten & Gradstein, 1988 ; van Zanten & Pócs, 1981).

Cependant, la capacité de dispersion des bryophytes demeure un sujet controversé (Frahm, 2008) et la courbe de distance leptokurtique typique des bryophytes illustre que l'on peine à imaginer leur dispersion au-delà des océans (Figure 1.3 ; Mogensen, 1981). En effet, des études ont démontré que, chez certaines espèces 43 % à 94 % des spores tombaient à moins de 3 m de la colonie mère (Roads & Longton, 2003 ; Söderström & Jonsson, 1989 ; Stoneburner *et al.*, 1992). Miles et Longton (1992) ont aussi mis en évidence une déposition moyenne chutant drastiquement de plus de 13 000 à moins de 1000 spores/cm^2 après un éloignement de 30 cm du centre de la colonie mère (Figure 1.3). Néanmoins, Stenøien *et al.* (2011) soutiennent l'incidence fréquente de dispersions intercontinentales et des spores de sphaignes ont même été collectées dans le Svalbard alors qu'aucune colonie source n'est présente à moins de 1000 km de distance (Sundberg, 2013).

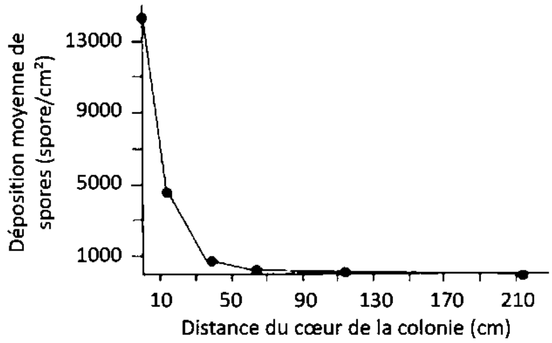

Figure 1.3 Déposition moyenne des spores mesurée durant 30 jours en fonction de la distance au cœur d'une colonie d'*Atrichum undulatum*. La courbe présentée représente un patron de dispersion leptokurtique typique soit une « distribution exponentielle à queue épaisse » où la majorité des spores est déposée dans les premiers centimètres de la source et un nombre moindre à plus longue distance [adapté de Vanderpoorten & Goffinet (2009) issu de Miles & Longton (1992)].

Les bryophytes ont majoritairement recours, pour la dispersion de leurs propagules (gemmae, fragments végétatifs et spores confondus), à des agents abiotiques de dispersion (eau et vent). Pour ce faire, chaque espèce y va de sa stratégie. Pour exemple, chez l'hépatique *Marchantia polymorpha*, les gemmae sont éjectés des corbeilles ou « splash-cups » où ils sont concentrés suite à l'impact des gouttes d'eau (Brodie, 1956 ; Figure 1.4 a, b). Les sphaignes (*Sphagnum* spp.) sont-elles plus proactives. À la manière d'un pot de confiture qui « pop » elles peuvent expulser leurs spores à plus de 20 cm du sol en réponse aux changements de température et d'humidité (Sundberg, 2010 ; Figure 1.4 c, d). Le même mécanisme est utilisé chez plusieurs hépatiques qui possèdent, dans leurs capsules, des ressorts appelés élatères qui agissent comme de véritables frondes (Ingold, 1959 ; Figure 1.4 e, f). D'autres espèces se sont alliées de collaborateurs plus « exotiques ». C'est ainsi que les Splachnacées se sont parées de couleurs carnassières et libèrent une vive odeur de viande putréfiée en vue d'attirer leurs pollinisateurs attitrés, les mouches (Marino *et al.*, 2009 ; Figure 1.4 g, h). En effet, les animaux peuvent être des disperseurs de choix et les interactions entre les bryophytes et les oiseaux, ovins, chauves-souris et invertébrés ont plusieurs fois été observées (Osorio-Zuñiga, 2014 ; Pauliuk *et al.*, 2011 ; Rudolphi, 2009).

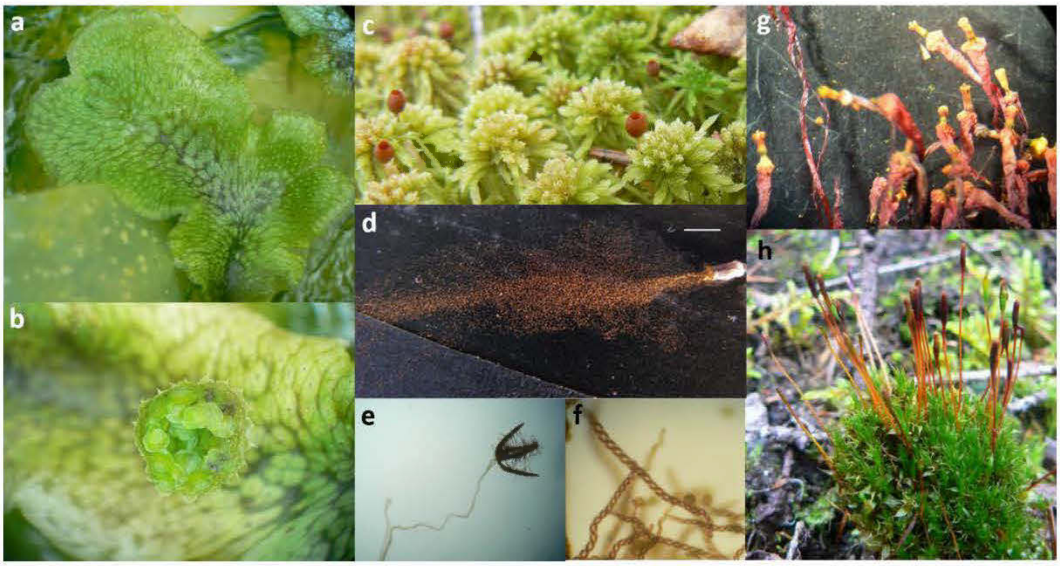

Figure 1.4 Stratégies de dispersion de différentes espèces de bryophytes. (a) Thalle et (b) corbeilles à propagules de *Marchantia polymorpha* ; (c) sporophytes de *Sphagnum angustifolium* ; (d) capsule de *Sphagnum centrale* après explosion, la traînée de spores orange est visible [issu de Sundberg (2010)] ; (e) sporophyte déhiscent et (f) élatères présents dans le sporophyte de *Ptilidium pulcherrimum* ; (g) sporophytes déshydratés de *Splachnum ampullaceum* et (h) sporophytes transformés pour attirer les mouches de *Tetraplodon angustatus*.

1.1.3 Une dépendance accrue aux microclimats et microhabitats élevant les bryophytes au rang d'espèces bio-indicatrices

Proctor (2000) rapporte « le paradoxe des bryophytes : tolérance à la dessiccation – évasion de la sécheresse ». Tout est dit. En effet, les bryophytes sont poïkilohydriques et dépourvues de système racinaire, ainsi, leur contenu en eau est directement régulé par l'humidité ambiante (Proctor, 1990). Les bryophytes sont donc totalement dépendantes de l'eau à toutes les phases de leur cycle phénologique et particulièrement durant la fertilisation étant donné le caractère natatoire des gamètes mâles (anthérozoïdes ; Frahm, 2008). Rien d'étonnant donc à ce que dans le calendrier républicain, le nom « Mousse » soit attribué au 2ème jour du mois de pluviôse (20 janvier au 18 février dans le calendrier grégorien) où les pluies tombent en abondance (d'Eglantine, 1794). Cependant, les bryophytes sont retrouvées dans tous les écosystèmes et sur tous les substrats. Ainsi, les espèces de milieux désertiques ou vivant sur des substrats soumis à la dessiccation (*e.g.*, rochers, branches), peuvent maintenir un métabolisme quasi normal même en conditions sous-optimales (synthèse de composées biochimiques) ou évitent le stress hydrique en entrant en dormance (During, 1979, *c.f.* Glime, 2015). À ce titre Maheu (1902) rapporte la régénération d'un protonema de *Tortula muralis*, la mousse des murs, d'un gamétophyte conservé déshydraté durant 14 ans. Aussi, La Farge *et al.* (2013) ont observé la résurrection de spécimens de bryophytes après 400 ans enfouis sous les glaciers !

Ajoutée à l'humidité, la température est un facteur de première importance pour les bryophytes puisqu'elle régule quantité de mécanismes (photosynthèse, libération des spores ; Vanderpoorten & Goffinet, 2009). Les différentes stratégies utilisées par les bryophytes pour la survie du gamétophyte en conditions non optimales de lumière, température ou humidité ont conduit à la classification des formes de vie de During (1979, 1992). Cette classification considère aussi l'énergie allouée à la reproduction et à la fréquence de production des sporophytes et *gemmae* (Ódor *et al.*, 2013). On y oppose les espèces pérennes qui allouent peu d'énergie à la reproduction et tolèrent des stress sévères, aux espèces colonisatrices allouant une grande part de leur énergie à la reproduction, particulièrement sexuée, et évitant les stress sévères par entrée en dormance des propagules [Pohjamo (2008) adapté de During (1979) ; Appendix H].

Les relations intimes entre les bryophytes et les conditions environnementales expliquent leurs dépendances aux microclimats et microhabitats. Par microhabitat nous entendons la plus petite unité de l'habitat (*e.g.*, bois mort, rocher, trou) dont l'ensemble forme l'habitat et évolue dans le temps et l'espace. Chaque microhabitat sera donc optimal pour une espèce durant une période de temps limité. En conséquence, l'on s'attend à des changements de composition des communautés en réponse aux changements de conditions microclimatiques et de microhabitats (Cole *et al.*, 2008 ; Mills & Macdonald, 2004, 2005). Ainsi, puisque les bryophytes réagissent de façon prédictible et mesurable aux changements environnementaux, elles sont de parfaites espèces bio-indicatrices de la qualité de l'habitat (Gignac, 2001, 2011). Les espèces supportant des variations microclimatiques plus importantes et pouvant, de ce fait, occuper des microhabitats plus variés seront qualifiées de « généralistes » (Frahm, 2008). Corollairement, ces espèces sont aussi les moins sensibles aux perturbations, on y retrouve les espèces colonisatrices et pionnières (*e.g.*, *Ceratodon purpureus*, *Pleurozium schreberii*, *Pohlia nutans* ; Baldwin & Bradfield, 2010 ; Hylander & Johnson, 2010 ; Jonsson & Esseen, 1998). D'autres espèces sont en revanche plus « délicates » et inféodées à un nombre restreint de microhabitats, on parle d'espèces « spécialistes ». C'est le cas de nombreuses hépatiques inféodées aux bois morts (epixyliques ; *e.g.*, *Nowelia curvifolia*, *Ptilidum pulcherimum*) ou encore de certaines mousses liées aux rochers (saxicoles *e.g.*, *Brachythecium erythrorizon*, *Racomitrium microcarpum*). Ces espèces sont plus sensibles aux modifications de l'habitat et plus généralement liées à des conditions microenvironnementales plus stables telles que retrouvées dans les forêts matures et non perturbées (Anderson & Hytteborn, 1991 ; Fenton & Frego, 2005 ; Lesica *et al.*, 1991).

1.1.4 Rôles des bryophytes au sein de l'écosystème

Jadis, les bryophytes étaient utilisées pour divers usages domestiques. Par exemple, en Suède et en Norvège, on calfeutrait les murs des chaumières avec des hypnes (*Hypnum* spp.) ; les balais et les brosses étaient confectionnés avec le Polytric commun (*Polytrichum commune*) ; les sphaignes (*Sphagnum* spp.), en mélange aux poils de rennes, servaient à rembourrer les matelas ; l'hypne triquètre (*Rhytidiadelphus triquetrus*) était utilisée pour emballer la porcelaine (d'Orbigny, 1846). Aujourd'hui, les sphaignes ont un intérêt économique et sont utilisées comme isolant, comme substrat en horticulture pour la culture des champignons et le rempotage des bulbes d'orchidées, mais aussi comme combustible. En Irlande, les briques de tourbe représentaient 25 % de la consommation en combustible dans les années 1980 (Glime, 2007). En Écosse, on utilise les sphaignes pour la fabrication de certains whiskys (Golinski, 2016) !

Mais, davantage que ces usages anthropiques, c'est au sein de l'écosystème que les rôles des bryophytes sont les plus marqués. Les bryophytes sont pleinement impliquées dans le fonctionnement des écosystèmes et participent ardemment à la production primaire nette (Turetsky, 2003, Turetsky *et al.*, 2012). Les bryophytes, et particulièrement les sphaignes, participent à la séquestration de l'azote suite à l'association avec des cyanobactéries (Turestky, 2003) et contribueraient à la fixation de plus de 50% de l'azote inorganique atmosphérique (3.4 kg N ha/an) en forêts montagneuses Costa-ricaine (Clark *et al.*, 2005). Les bryophytes participent aussi au cycle du carbone (Vitt et Wieder, 2009) et les taux lents de décomposition des sphaignes justifient l'appellation de « bombes à retardement » des tourbières. Le tiers du carbone total mondial se serait accumulé dans ces écosystèmes durant le dernier millénaire et leur décomposition pourrait augmenter le taux de CO_2 de l'atmosphère de plus de 50 % (O'Neill, 2000 ; Vanderpoorten & Goffinet, 2009). De plus, les bryophytes participent au cycle des nutriments et les rendent disponibles pour d'autres organismes (Brown & Bates, 1990 ; Coxson & Nadkarni, 1995) et à la dynamique hydrique des écosystèmes (Rixen & Mulder, 2005). Dans les forêts riches en épiphytes, elles sont de véritables « éponges ». Kürschner et Parolly (2005) ont estimé qu'elles retiendraient près de 15 000 kg H_2O/ha en forêt tropicale Équatorienne et Chang *et al.* (2002) rapportent que les bryophytes absorberaient de 0.23 à 1.28 g H_20/g poids sec/h dans les forêts de montagnes taiwanaises. De surcroît, les bryophytes, qui sont les premières à recoloniser l'habitat suite à une perturbation (Ah-Peng, 2007), participant à la formation des sols elles facilitent alors l'établissement des plantes vasculaires en agissant de substrats de germination (Jongmans *et al.*, 2001 ; Morgan, 2006). Pour finir, les bryophytes fournissent nourriture et abris pour nombres d'invertébrés, de micro et mésomammifères (Glime, 2014 ; Longton, 1992 ; pers. obs. 2015 Figure 1.5).

Figure 1.5 Destruction d'un tapis d'*Hylocomium splendens* transplanté en pessière noire à mousses de l'été 2014 à l'été 2015. Le suspect, un micromammifère, a été identifié grâce aux défécations laissées sur place (cercle rouge). La zone définie par la ligne noire représente la partie broutée (pour consommation ou élaboration d'un nid), une section non endommagée du transplant est visible en bas à droite de l'image.

1.2 La forêt boréale comme terrain de jeu

Les bryophytes sont une composante élémentaire de la forêt boréale où elles atteignent des diversités, abondances et biomasses substantielles (Turetsky *et al.*, 2010 ; Turetsky *et al.*, 2012), un terrain de prédilection pour les bryologues.

La forêt boréale ceinture l'hémisphère nord sur une superficie de 6.7 millions de km² et représente environ 26 % des forêts mondiales ce qui en fait un des biomes les plus étendus de la planète (Scott, 1995). Au Canada, la forêt boréale couvre 560

000 km². Plus localement, au Québec, elle est divisée en deux domaines bioclimatiques : la sapinière à bouleau blanc et la pessière noire à mousses, elles-mêmes subdivisées, sur la base des précipitations et du relief, en sous-domaines de l'est et de l'ouest (MRNQ, 1999 ; Saucier *et al.*, 2009). En résultent alors des différences fondamentales dans les régimes de perturbation, mais aussi dans la proportion des essences végétales dominantes. Nous nous en tiendrons dans cette étude à la pessière noire à mousses de l'ouest du Québec.

1.2.1 Région d'étude

La pessière noire à mousses ouest-québécoise s'étend sur 154 184 km² et est délimitée, à l'ouest par la frontière ontarienne et, à l'est, par le bassin versant des rivières Péribonka et Manouane. Au nord elle prend fin où commence la taïga et au sud où commence la sapinière à bouleaux blancs de l'ouest (MRNQ, 1999). La pessière noire à mousses occupe alors une bande continue de 300 km entre le 48° 38' et le 52° 00' de latitude nord.

Les peuplements de conifères dominent la région d'étude. L'essence principale est représentée par l'épinette noire (*Picea mariana* (Mill.) Briton), en mélange au pin gris (*Pinus banksiana* Lamb.), au peuplier faux-tremble (*Populus tremuloides* Michx.), au sapin (*Abies balsamea* (L.) Mill.), au mélèze (*Larix laricina* (Du Roi) K. Koch) et au bouleau à papier (*Betula papyrifera* Marshall). Les éricacées dominent le sous-bois (*e.g.*, *Rhododendron groenlandicum* (Oeder) Kron & Judd) tandis que le sol est recouvert d'un tapis continu de mousses hypnacées (*Pleurozium schreberi* (Brid.) Mitt., *Hylocomium splendens* (Hedw.) Schimp., *Ptilium crista-castrensis*) cédant la place aux sphaignes dans les sites mal drainés et plus acides (Saucier *et al.*, 2009).

L'intégralité de la région d'étude est située sur la Ceinture d'argile s'étendant du nord-est de l'Ontario au nord-ouest du Québec (Allard, 1974). Les dépôts d'argile laissés suite à la sédimentation du lac pro-glaciaire Barlow-Ojibway durant le Wisconsinien atteignent par endroit 60 m d'épaisseur (Vincent & Hardy, 1977). Le relief est peu accidenté et l'altitude varie en moyenne entre 200 et 300 m. Le climat est subpolaire continental avec une température moyenne annuelle de 1 °C et des précipitations annuelles moyennes de 927.8 mm (relevés pour la période de 1981-2010, station météorologique de Lebel-sur-Quévillon, Environnement Canada, 2015). La région est marquée par de longs hivers (précipitations neigeuses annuelles moyennes de 312.9 cm) et par une saison de croissance courte (140 à 160 jours).

Notre région d'étude couvre une superficie de 73 197 km^2 (79° 69' O, 50° 71' N - 74° 50' O, 50° 71' N - 79° 69' O, 48° 83' N et 74° 50' O, 48° 83 N ; Figure 1.6). Ce territoire est intégralement localisé dans la région administrative du Nord-du-Québec, sur le territoire d'Eeyou Istchee Baie James. Nous y avons sélectionné six zones de feu de taille, forme, âge et origine variés (Table A2.1) dans lesquels les communautés bryophytiques ont été échantillonnées. En parallèle, des peuplements de forêts continues non brûlées ont été sélectionnés sur le même territoire dans le cadre d'un autre projet et seront utilisés à titre de témoins dans plusieurs des chapitres de cette thèse (Chaieb *et al.*, 2015).

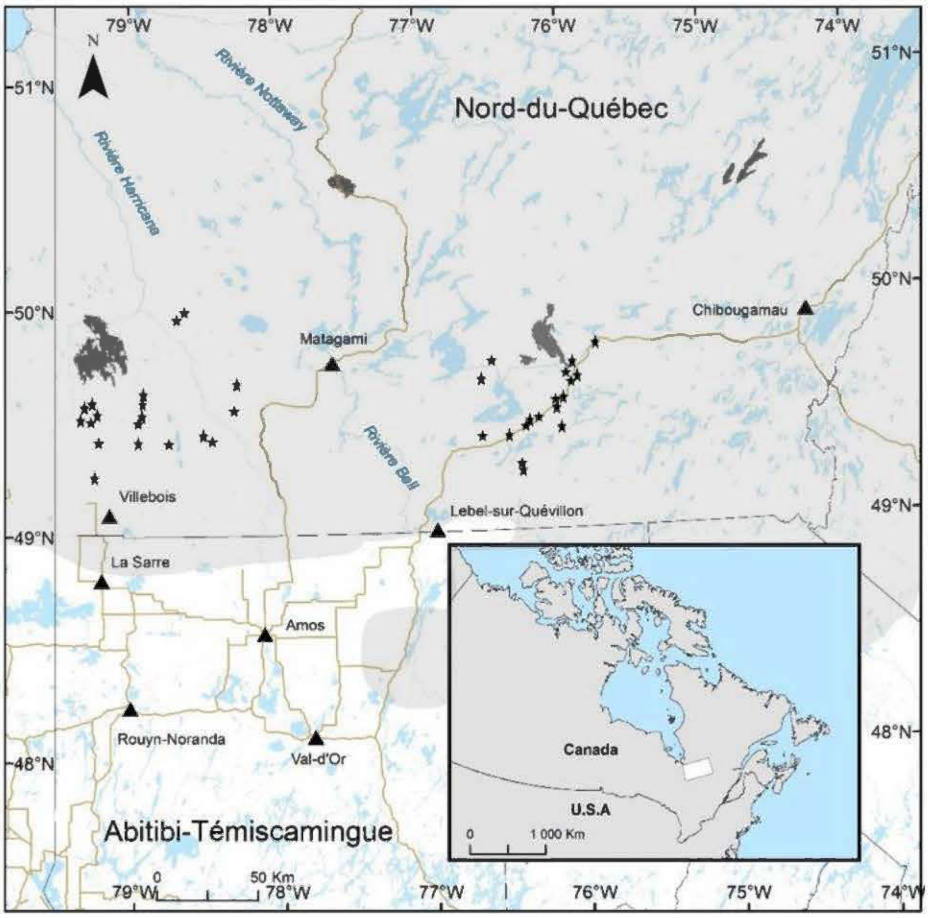

Figure 1.6 Région d'étude en pessière noire (zone gris clair), Québec, Canada. Les six sites de feux sont représentés en gris foncé, les peuplements de forêts continues non-brûlées sont indiqués par les étoiles (données issues de C. Chaieb). Les lignes gris clair représentent les limites des régions administratives du Québec. Les routes principales sont indiquées par les lignes brunes.

1.2.2 Les feux de forêt et les îlots résiduels

Les feux de forêt représentent, avec les épidémies d'insectes, les maladies et les chablis, les principales perturbations naturelles de la forêt boréale (Pothier, 2001 ; Schmiegelow *et al.*, 2006). Dans la région d'étude considérée, la perturbation dominante est le feu, dont le régime (fréquence et sévérité) couplé à la végétation présente pré-perturbation, vont influencer la succession forestière post-perturbation (Franklin *et al.*, 2007 ; Heinselman, 1981). Le cycle des feux dans la région d'étude été estimé à 101 ans en 1850, 135 ans de 1850 à 1920 et à 398 ans depuis 1920, conduisant à un âge moyen des peuplements de 150 ans (Bergeron *et al.*, 2004). L'allongement des régimes de feu depuis les années 1850 est expliqué par la modification des conditions climatiques et, plus récemment par l'addition des actions anthropiques (*i.e.*, suppression des feux, coupes) interférant avec les patrons de perturbations naturelles (Bergeron *et al.*, 2006).

La particularité première des perturbations naturelles résulte dans la création d'une matrice forestière diversifiée. En effet, le feu a un impact hétérogène sur le paysage conduisant à une mosaïque de peuplements d'âges, de compositions et de structures variables (Cyr *et al.*, 2009) où les zones brûlées jouxtent des parcelles de forêts rescapées des flammes (Bergeron *et al.*, 2002 ; Madoui *et al.*, 2010). Les conditions météorologiques durant l'épisode de feu, la topographie du milieu (*e.g.*, les dépressions humides et les parois rocheuses peuvent agir comme des pare-feu naturels) ainsi que la susceptibilité locale de la matrice à l'ignition expliquent cette hétérogénéité (Ouarmim *et al.*, 2015 ; Turner *et al.*, 1994).

Les confettis de forêt rescapés du feu sont appelés « îlots résiduels » (Figure 1.7). La proportion des îlots résiduels dans la matrice brûlée est en moyenne de 10 % en pessière noire à mousses québécoise (Madoui *et al.*, 2011), mais cette proportion varie en fonction de la taille et de la sévérité du feu (DeLong & Tanner, 1996). De taille et forme variables, les îlots résiduels sont rarement distants de plus de 700 m de leur plus proche voisin (Perron *et al.*, 2008). Certains îlots résiduels peuvent avoir été épargnés « par chance » due à une modification soudaine des conditions météorologiques (*e.g.*, changements de direction du vent, ondées) alors que d'autres seraient épargnés du feu de façon récurrente. Ces derniers représentent des îlots séculaires et pourraient avoir survécu au feu depuis plusieurs millénaires en raison de conditions stationnelles les rendant peu susceptibles à l'ignition (Bergeron & Harper, 2009 ; Ouarmim *et al.*, 2015).

Figure 1.7 Îlots résiduels de forêts.

Les îlots résiduels sont des habitats eux-mêmes hétérogènes, composés d'un cœur (forêt au centre de l'îlot) et d'une bordure (Holland *et al.*, 1991). Les conditions microclimatiques et environnementales peuvent différer entre les cœurs et les bordures des îlots résiduels qui pourront alors varier en termes de luminosité, type de substrat, conditions hydrologiques, et complexité structurelle et pourront alors abriter une diversité et une composition en espèces distinctes (Didham & Lawton, 1999 ; Murcia, 1995).

1.2.3 Rôles présumés des îlots résiduels

Les îlots résiduels post-feu sont pleinement impliqués dans le fonctionnement à long terme de la matrice perturbée et dans la régénération de la forêt suite à la perturbation (Gandhi *et al.*, 2001). Parmi les rôles qu'on leur prête, ceux de refuges et de sources de semences pour la recolonisation de la matrice brûlée (Fenton & Frego, 2005 ; Perhans *et al.*, 2009 ; Lõhmus *et al.*, 2006). En effet, et c'est particulièrement vrai pour les îlots séculaires, ils agiraient comme des arches de Noé en contribuant à la survie de certaines espèces suite à la perturbation. On considère qu'on y trouverait une composition en espèces similaire à celle avant feu et donc à celle des forêts non perturbées alentour, d'où leur dénomination de refuge. Épargnées du feu, ces communautés pourront agir de « semencières » et faciliter la régénération de la matrice brûlée. Parallèlement, les îlots résiduels contiennent des legs biologiques (*e.g.*, bois mort au sol ou sur pied, arbres rémanents) qui représentent des microhabitats de qualité pour les espèces dépendantes de conditions microenvironnementales stables et de microhabitats spécialisés (Anderson & Hytteborn, 1991 ; Fenton & Frego, 2005 ; Lesica *et al.*, 1991). Ces legs biologiques sont des sources desquelles peut reprendre la colonisation de la matrice et orientent la succession forestière post-perturbation (DeLong & Kessler, 2000 ; Lindenmayer *et al.*, 2006 ; Seidl *et al.*, 2014). Les îlots résiduels seraient donc des *inocula* et garantiraient le maintien d'espèces qui auraient sinon disparu à long terme du paysage, étant donné leurs sensibilités aux perturbations et leurs capacités de dispersion réduite.

Les îlots résiduels agiraient aussi comme des connecteurs pour les espèces mobiles et participeraient à l'enrichissement structurel de la matrice brûlée (Franklin *et al.*, 2007 ; Nappi *et al.*, 2004 ; Neitlich & McCune, 1997). Les îlots résiduels réduisent les distances à parcourir au sein de la matrice perturbée hostile et sont alors qualifiés de « pas japonais » ou « stepping stones » (Chan-Mcleod & Moy, 2007 ; DeLong & Kessler, 2000). Les organismes, selon leurs capacités de dispersion respectives, requerront différents agencements spatiaux des îlots résiduels (dispersé, en agrégat).

La résilience de l'écosystème, définie comme « le taux, la manière et le degré auxquels les caractéristiques initiales d'une communauté sont restaurées suite à une perturbation » (Halpern, 1988), est donc dépendante des îlots résiduels qui assurent la survie de certaines espèces après la perturbation. La diversité des espèces fonctionnellement équivalente (« redondance fonctionnelle ») maintenue dans l'écosystème après la perturbation en assure la résilience (Rosenfeld, 2002). Par conséquent, la physionomie (aire et taille), l'âge, l'agencement spatial et la complexité structurelle des îlots résiduels qui déterminent leurs qualités de refuges, de sources de propagule et de pas japonais définissent le potentiel régénératif d'un écosystème (Drapeau *et al.*, 2009 ; Honnay *et al.*, 1999 ; Lee *et al.*, 2015).

1.3 Une aspiration : l'aménagement écosystémique

Depuis les dernières décennies, en réponse à la demande croissante en produits ligneux et dérivés, l'exploitation forestière s'est intensifiée modifiant considérablement le paysage forestier nord-américain. La raréfaction des peuplements anciens et surannés au profit d'un rajeunissement de la mosaïque forestière (Cyr *et al.*, 2009), en plus de la fragmentation du territoire engendrée par les coupes forestières, ont conduit à la perte des écosystèmes naturels et à l'isolement des populations. En Fennoscandinavie, où l'exploitation des ressources forestières précède de près de 100 ans celle de l'Amérique du Nord (Mönkkönen & Welsh, 1994), les études réalisées font office de pionnières et rapportent la diminution de la biodiversité suite à l'exploitation (Imbeau *et al.*, 2001 ; Siitonen, 2001). Cela laisse entrevoir des risques encourus en forêt boréale nord-américaine où les espèces les plus sensibles aux perturbations et les moins mobiles, comme c'est le cas des bryophytes, sont alors en sursis (Hazell & Gustafsson, 1999 ; Vanderpoorten & Goffinet, 2009). L'addition des coupes forestières aux épidémies d'insectes et aux feux, perturbateurs naturels de la forêt boréale nord-américaine, a accru la vulnérabilité des écosystèmes aux prises désormais à l'action simultanée des perturbations anthropiques et naturelles (Gauthier *et al.*, 2008). Ces constats, abordés durant le Sommet de la Terre de Rio de Janeiro (1992) et lors du Processus de Montréal (1994) ont conduit à l'élaboration de critères et d'indicateurs d'aménagement forestier durable précipitant la refonte de la foresterie. Il s'agit désormais de réduire les écarts entre les forêts aménagées et naturelles en reproduisant les patrons spatiotemporels issus des perturbations naturelles afin de poursuivre l'exploitation forestière en maintenant conjointement la biodiversité et la fonctionnalité des écosystèmes (Gauthier *et al.*, 2008 ; Perera *et al.*, 2004).

En forêt boréale canadienne, la portraitisation des patrons spatiaux et temporels des perturbations a débuté il y a 20 ans (Bergeron & Harvey, 1997 ; Cyr *et al.*, 2009) et a mené à l'émergence de plusieurs alternatives d'aménagement écosystémique. Parmi celles-ci, on retient, dans le contexte de ce projet, les coupes à rétentions variables (« green tree retention » ; Franklin et Forman, 1987). Ces coupes visent à maintenir la complexité spatiale et structurelle du paysage *via* le maintien de bouquets d'arbres dans la matrice de coupe, comme ce serait le cas après un feu qui épargne, çà et là, des îlots résiduels (Bergeron et al. 2002 ; Bergeron *et al.*, 2006). La taille, le nombre et l'agencement spatial (agrégé ou dispersé, bouquets ou îlots) des parcelles de rétention, mais aussi le nombre et les essences d'arbres laissés sur pied varient selon l'objectif d'aménagement encouru (Halpern *et al.*, 2005). Dans le meilleur des mondes on vise à imiter au mieux les desseins du feu en conservant des parcelles de rétention qui auraient des rôles équivalant aux îlots résiduels post-feu. Seulement, pour ce faire, il apparaît nécessaire de préalablement posséder une connaissance du rôle de ces îlots post-feu.

1.4 Objectifs

Cette thèse prend ici tout son sens et vise, dans une optique d'aménagement écosystémique, à élucider le rôle des îlots résiduels post-feu dans la dynamique des communautés bryophytiques en vue de s'en inspirer lors de la mise en place des îlots de rétention dans les parterres de coupes. Bien que les rôles des îlots résiduels aient été substantiellement étudiés suite aux perturbations anthropiques, les études réalisées suite aux perturbations naturelles et notamment aux feux sont rares et rapportent des résultats ambivalents (Hylander, 2009 ; Snäll *et al.*, 2005 ; Swanson et Franklin, 1992). De plus, aucune étude n'a encore été entreprise en pessière noire à mousses québécoise pourtant soumise à des régimes de feu singuliers. Formée d'une mosaïque d'îlots résiduels, cet écosystème représente un système naturel prédestiné pour les études portant sur la fragmentation, la biogéographie insulaire (MacArthur et Wilson, 1967) et la dynamique des métapopulations (Hanski et Simberloff, 1997).

L'intérêt d'utiliser les bryophytes pour répondre à cette question résulte de leur ubiquité en pessière noire à mousses, mais aussi de leur capacité à répondre finement aux modifications des conditions microenvironnementales (Pardow et

Lakatos 2013 ; Pharo et Zartman, 2007). De plus, les bryophytes sont parmi les premières à recoloniser le territoire suite à une perturbation (Ah-Peng, 2007 ; Jongmans *et al.*, 2001). Initiatrices de la régénération forestière, elles constituent alors un modèle biologique original et robuste pour étudier la résilience de l'écosystème face aux perturbations.

Ce projet se divise en deux volets: (i) aménagement écosystémique, en vue de bonifier les connaissances sur les patrons de perturbations naturelles à des fins de gestion forestière ; (ii) bryologie, avec pour objectif d'améliorer les connaissances fondamentales dans ce domaine.

Le volet « aménagement écosystémique » est scindé en trois sous-objectifs :

1.1. Documenter le rôle des îlots résiduels post-feu comme refuges pour les communautés bryophytiques (Chapitre II). Par refuge, nous entendons un habitat ou un microhabitat capable de supporter des conditions environnementales et une communauté bryophytique similaire à celle retrouvée dans une forêt non perturbée (basée sur Lancaster et Belyea, 1997 et Sedell *et al.*, 1990). Dans un refuge les effets de la perturbation sont atténués voire inexistants, nécessité fondamentale au maintien de nombreuses espèces de bryophytes sensibles aux perturbations et à haut risque d'extirpation (Fenton et Frego, 2005 ; Frisvoll et Prestø, 1997 ; Gustafsson et Hallingbäck, 1988). Un refuge offrirait un « pied à terre » aux bryophytes afin de leur faciliter la recolonisation de la matrice brûlée.

1.2. Estimer l'existence d'un effet de bordure dans les îlots résiduels post-feu et la réponse des bryophytes à celui-ci (Chapitre III). L'effet de bordure a été démontré comme délétère pour de nombreuses espèces dans des systèmes anthropisés (Boudreault *et al.*, 2008 ; Hylander, 2005 ; Nelson et Halpern, 2005), qu'en est-il de bordures issues de perturbations naturelles ? Quelles conclusions en tirer ?

1.3. Attester du rôle de sources de propagules des îlots résiduels post-feu pour les communautés bryophytiques (Chapitre IV). Le rôle de refuge est intimement lié à son corollaire de source de propagules puisque les colonies ayant survécu à la perturbation dans les îlots résiduels seront des sources de propagules potentielles. L'agencement spatial des îlots résiduels devrait influer sur les patrons de dispersion des bryophytes (Baker *et al.*, 2013 ; Chan-Mcleod et Moy, 2007).

Le volet « bryologie » est, lui, divisé en quatre sous-objectifs :

2.1 Estimer les distances moyennes de dispersion des bryophytes en pessière noire à mousses et valider ou réfuter le paradigme de la faible distance de dispersion des bryophytes (Miles et Longton, 1992 ; Sundberg, 2013 ; Chapitre IV).

2.2 Analyser la réponse des différentes phases du cycle phénologique des bryophytes aux conditions climatiques en vue d'expliquer les patrons de dispersion observés (Chapitre V)

2.3 Attester du recours à des agents biotiques de dispersion par les bryophytes (Annexe I).

2.4 Fournir un portrait bryologique préindustriel de la pessière noire à mousses nord-américaine *via* l'actualisation de la Flore des bryophytes du Québec-Labrador (Faubert, 2012-2014 ; Annexe II).

CHAPITRE II

ARE POST-FIRE RESIDUAL FOREST PATCHES REFUGIA FOR BOREAL BRYOPHYTE SPECIES? IMPLICATIONS FOR ECOSYSTEM BASED MANAGEMENT AND CONSERVATION

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En révision dans *Biodiversity and Conservation*, Octobre 2016

2.1 Abstract

Residual forest patches remaining after natural or anthropogenic disturbance may facilitate regeneration of the fragmented forest. However, residual forest patch function remains unclear, especially after natural wildfire. We investigate the role of residual boreal forest patches as refugia for bryophytes and ask the question, do post-fire residual forest patches house bryophyte communities similar to those encountered in undisturbed forests? Bryophytes were sampled in three habitat types in black spruce boreal forests illustrating a gradient of disturbance severity: undisturbed forests, residual patches and burned matrices. Temporal, disturbance severity, spatial and structural variables of habitats were also recorded. Bryophyte community composition differed among habitat types with residual forest patches characterized by loss of forest specialists and the addition of disturbance-prone species. Consequently, residual patches were richer in species than undisturbed forests. As residual patches did not conserve all species and especially forest specialists, they were not refugia, but their high bryo-diversity suggests that they represent habitats of high quality for post-disturbance community assembly. Furthermore, we identify some temporal, spatial and structural characteristics of residual patches that maintain bryophyte communities closest to that of undisturbed forests. The distinct bryoflora housed by residual forest patches and undisturbed forests suggests that they represent complementary habitats. Consequently, both of these habitats need to be conserved in order to not lose species and to maintain landscape bryo-diversity.

Key-words: black spruce forest; community assembly; disturbance prone species; forest remnant; forest interior species, forest remnant, liverworts.

2.2 Résumé

Les îlots résiduels issus de perturbations d'origines naturelles et anthropiques sont supposés impliqués dans la régénération forestière. Cependant, les fonctions de ces îlots résiduels, et particulièrement de ceux issus de feux de forêt naturels, demeurent confuses. Nous avons étudié le rôle de refuge des îlots résiduels post-feu pour les bryophytes. Ces îlots résiduels abritent-ils des communautés bryophytiques similaires à celles retrouvées dans les forêts non perturbées ? Les bryophytes ont été échantillonnées dans 39 forêts non perturbées et six feux naturels composés d'îlots résiduels et de matrices brûlées de sorte à obtenir trois types d'habitats illustrant un gradient d'intensité de perturbation. Des variables temporelles, de sévérité de feu, spatiales et structurelles ont aussi été relevées dans les différents types d'habitats. La composition des communautés différait selon les types d'habitats et les îlots résiduels étaient caractérisés par l'absence de certaines espèces forestières et par la présence d'espèces favorisées par la perturbation. Les îlots résiduels étaient plus riches en espèces que les forêts non perturbées. Bien que le confinement de plusieurs espèces strictement forestières aux forêts non perturbées ne permette pas de décrire nos îlots résiduels comme des refuges, nous soutenons qu'ils sont des habitats de haute qualité participant au re-assemblage d'une communauté bryophytique riche post-perturbation. Nous avons, en parallèle, identifié des caractéristiques temporelles, spatiales et structurelles des îlots résiduels leur permettant de supporter des communautés plus comparables à celles des forêts non perturbées qu'à celles des matrices brûlées. Les bryoflores distinctes des îlots résiduels et des forêts non perturbées suggèrent qu'ils représentent des habitats complémentaires qui doivent être conservés de concert afin de ne pas perdre d'espèces et de maintenir la bryo-diversité de l'écosystème.

Mots-clés : assemblage des communautés ; espèce favorisée par la perturbation ; espèce forestière ; fragment forestier ; hépatiques ; pessière noire à mousses.

2.3 Introduction

Ecosystems are intrinsically subject to disturbances of various intensities and frequencies (e.g. storms, wildfires, insect outbreaks), which temporarily modify their functions. Following Halpern's (1988) definition, resilience is "the rate, manner, or degree to which initial community characteristics are restored" after a disturbance. Resilience is believed to be enhanced by the diversity of functionally equivalent species in an ecosystem (functional redundancy; Rosenfeld 2002). However, functions provided by individual species could be lost after disturbance if species inter-relationships change or species are lost (Walker 1995; Creed 2000). As anticipating the future roles of species after environmental changes is a challenge, a precautionary approach is appropriate and all species, including the infrequent or rare, should be conserved in order to ensure that ecosystem functions persist. Our study was designed to identify habitats that fulfill a "life-boat" role for species in a naturally disturbed landscape in order to ensure species conservation and re-assembly of a functional post-disturbance community, and therefore ecosystem resilience (Walker 1995).

Various ecosystems are naturally disturbed by wildfire (e.g. savannah, boreal forest; Payette 1992; Higgins et al. 2000), which has heterogeneous impacts (Carlson et al. 2011). In many systems, patches of unburnt forest ("residual patches"; Andison 2014) that have partially or entirely escaped fire persist in the burned matrix. The characteristics of this mosaic of unburned patches (i.e. spatial arrangement, size) depend on fire frequency and severity as well as on the physical characteristics of the landscape (i.e. topography, flammability) and the vegetation present at the time of fire (Madoui et al. 2010; Leonard et al. 2014). These residual forest patches are believed to serve several functions such as refugia for species during the fire event, and as propagule sources during landscape recolonization (Rosenvald and Lõhmus 2006; Perhans et al. 2009; Robinson et al. 2013). Residual patches also reduce the travelling distance across the matrix for mobile species and promote structural diversity in the regenerating landscape (Nappi et al. 2004). Consequently residual patches will influence, together with the vegetation present before disturbance, the composition, structure and successional trajectory of post-fire vegetation (Clarke 2002). However, the definition of refugia is not clear as they may be defined as areas where the negative impacts of disturbance are diminished compared to the surrounding area (based on Sedell et al. 1990 and Lancaster and Belyea 1997) but at different scales, such as habitats (forest stands) or even microhabitats (i.e. biological legacies such as dead wood). The working definition used here is that refugia contribute to the recovery of biotic communities to a pre-disturbance state, and therefore ensure the ecosystem functionality and resilience of the forest landscape.

Over the last decade, the literature has focused on the importance of post-harvest retention patches as refugia for species (Dynesius and Hylander 2007; Perhans et al. 2009; Lee et al. 2015) but there are few studies on post-fire residual forest patches (Hylander and Johnson 2010; Robinson et al. 2013). Therefore, the natural role that post-harvest retention patches are meant to emulate is yet undetermined. Furthermore, no clear patterns in retention patch characteristics that influence refugia capacity have emerged, as different studies around the globe highlight the importance of spatial variables (e.g. size affects invertebrates diversity; Lee et al. 2015), structural variables (e.g. deadwood affects bird and bryophyte communities; ; Rambo 2001; Drapeau et al. 2009), temporal variables (e.g. forest age affects plant diversity; Honnay et al. 1999), and landscape variables (topography influences refugia potential; Leonard et al. 2014; Chia et al. 2015; Robinson et al. 2016). However, in North America, both the role of post-fire residual forest patches and the characteristics that influence their value as refugia remain unclear (Schmiegelow et al. 2006; Robinson et al. 2013). In this study we attempt to clarify both of these elements by focusing on bryophyte assembly in a natural post-fire patch system in the boreal forests of eastern North America.

Bryophytes dominate the boreal forest in terms of plant biomass and species richness (Turetsky et al. 2012). They occupy a variety of microhabitats, from the forest floor for large feather mosses, to boulders, dead wood and tree bases for specialist species (Dynesius and Hylander 2007). Forest bryophytes, and particularly their early life stages (protonemata), are dependent on humid microclimates (Löbel and Rydin 2010). Consequently, both natural and anthropogenic disturbances that generate dry conditions may induce a local reduction in bryophyte diversity (Ross-Davis and Frego 2002). This is particularly true for drought-sensitive species that have a high local extirpation risk and require specific substrates, such as dead wood, to be maintained in the landscape (Rambo 2001; Pharo and Lindenmayer 2009). Residual forest patches from fire or harvest may house such substrates and therefore may act as refugia to mitigate the species extinction debt (sensu Tilman et al. 1994; Hylander and Johnsson 2010).

Specifically, through the comparison of three habitat types i.e. undisturbed forests as control, residual forest patches and recently burned matrices, this study examines the role of post-fire residual patches as refugia for bryophytes by addressing two questions: 1) do post-fire residual forest patches act as refugia for bryophyte species? And, 2) what characteristics influence the ability of post-fire residual forest patches to act as refugia? Following our working definition, a refugium refers to a residual forest patch that contains a community of species (from common to infrequent species) and environmental characteristics similar to those found in undisturbed forests.

We hypothesise that residual patches share species with both recently burned sites and undisturbed forests and therefore contain a higher species richness than either of these other habitat types (H1), as implied by the intermediate disturbance hypothesis (Connell 1979). We also expect that the presence of liverworts, given their affinities with closed canopies and stable micro-climates and habitats (Lesica et al. 1991; Fenton and Frego 2005), generates a shift in bryophyte community composition from burned matrix to undisturbed forests (H2). We also suppose that stand age is the best predictor of bryophyte composition whereas stand structure is the best predictor of bryophyte richness (Pipp et al. 2001) (H3). In contrast to the overall composition, the presence of liverwort species that are most sensitive to forest harvest (Nelson and Halpern 2005), will be positively associated with stand age and size [which is believed to enhance microhabitat quantity and quality (Pipp et al. 2001; Fenton and Bergeron 2008)] and microhabitat diversity (Mills and Macdonald 2004) (H4).

2.4 Methods

2.4.1 Study area

The study area covers a total of 73 197 km² (79˚69 W, 50˚71 N - 74˚50 W, 50˚71 N - 79°69 W, 48°83 N - 74°50 W, 48°83 N) in the boreal black spruce (*Picea mariana* Mill., Briton)-feather moss (*Pleurozium schreberi* (Brid.) Mitt.) forest of western Québec, eastern Canada (Grondin 1996; Figure 2.1a). Stands are dominated by *P. mariana* with *Pinus banksiana* Lamb., *Populus tremuloides* Michx, *Abies balsamea* (L.) Mill., and *Betula papyrifera* Marshall as secondary species. The understory is dominated by ericaceous species [e.g. *Rhododendron groenlandicum* (Oeder) Kron & Judd] and bryophyte species (feather mosses are replaced by sphagna under more humid conditions). The region is relatively flat and the altitude varies from 200 to 300 m above sea level. The main surface deposits are clays left by the withdrawal of the lake Barlow-Ojibway after the Wisconsonian glaciation (Vincent and Hardy 1977). The climate is subpolar continental and average annual temperature and precipitation are respectively 1 °C and 927.8 mm (1981 to 2010), recorded at Lebel-sur-Quévillon, Québec, which is located at the center of the study area (Environment Canada 2015).

The natural dynamics of the forests of the study area are primarily driven by stand replacing wildfires. The fire cycle was estimated at 398 years since 1920 (Bergeron et al. 2004), consequently, the average age of the forest is in excess of 150 years.

Fires burn unevenly and leave residual patches of unburned forests within the burned matrix (Madoui et al. 2010). The proportion of residual patches varies with the wildfire area, but was not linked with the presence of wetlands (Madoui et al. 2010). Moreover, Moussaoui et al. (in prep.), working on the same set of residual patches, have demonstrated that residual forest patches have a structural complexity in the natural range of undisturbed forests.

This boreal landscape composed of scattered residual forest patches enables us to investigate the roles of post-fire residual forest patches. Six wildfires and 39 undisturbed forests were selected across the study area (Figure 2.1b). Wildfires varied in age (8 to 42 years), size (6 915 to 25 517 ha) and origin (lighting or human) and within each fire we identified five residual forest patches and three burned matrix areas. Stratified random sampling was used to select undisturbed forests and residual forest patches with the following criteria: black spruce dominance, accessibility (< 2 km from road for the undisturbed forests and < 600 m for residual forest patches) and generally flat topography. The undisturbed forests and residual patches varied in size (0.05 to 1 820 ha), shape (circular to irregular), stand age (36 to 3 840 years), forest structure (from 0 to 5 600 stems / ha) and fire severity. Fire severity refers to the quantity of the organic/duff layer left unburned sensu Miyanishi and Johnson (2002) (Appendix A).

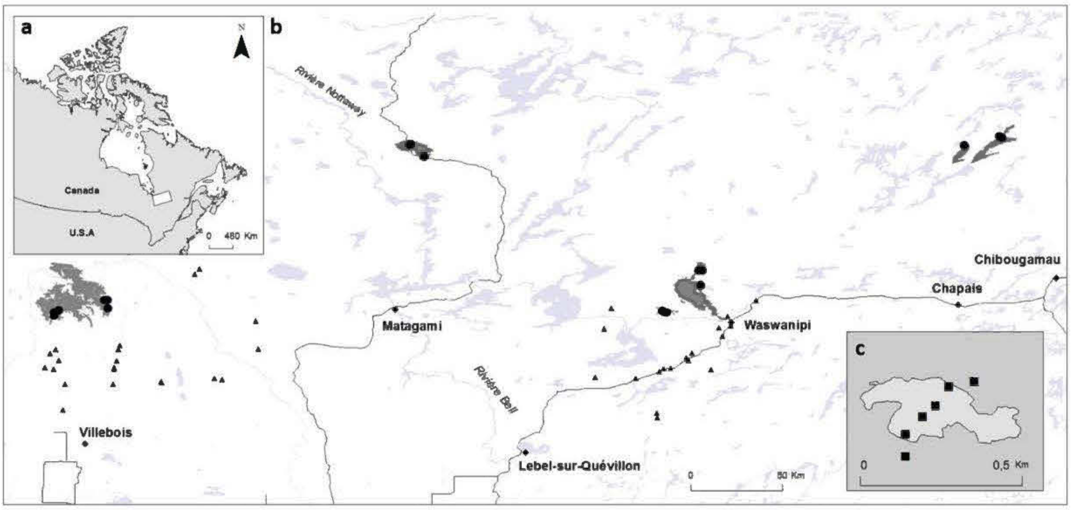

Figure 2.1 Location of the study area in the province of Québec (a), of the six wildfires studied (dark grey; b) and design used for bryophyte sampling in one residual forest patch (c). The main cities and rivers are indicated as well as lakes (light grey). Circles, residual forest patches (5 per wildfire, some are superimposed because of the map scale); triangles, undisturbed forests (39 sites). (c) Sampling design used in a residual forest patch (light grey) larger than 1 ha (in residual forest patches smaller than 1 ha, only one core plot was sampled).

2.4.2 Bryophyte sampling

The bryophyte community was sampled in 5 × 10 m rectangular plots (50 m^2) in the undisturbed forests during the summers of 2008 and 2009 (Chaieb et al. 2015), and in the wildfires during the summer of 2013. Within each undisturbed forest, three plots, distant at least 10 m from each other, were placed along a line crossing the center of the stand, but at least 50 m from the edge of the undisturbed forest. Within each residual forest patch, a north-south linear transect was established crossing the patch from edge to edge (Figure 2.1c). In residual forest patches smaller than 1 ha, five plots at least 10 m apart were placed along the transect, two in the burned matrix adjacent to the residual forest patch, two straddling the edges of the patch and one in the core of the patch. In residual forest patches larger than 1 ha a second core plot was added for a total of six plots. Each plot was therefore at one of three positions: fire, edge and core. Edge and core plots were considered as residual forest patch plots. In each wildfire, three additional 50 m^2 plots of burned matrix were placed as far as possible from all residual forest patches (from 200 to

8 500 m) to ensure that as much of the bryophyte diversity of the burned matrix was sampled as possible. In total, the bryophyte community was sampled in 117 plots in 39 undisturbed forests, 108 plots in 30 residual forest patches, and 78 plots of burned matrix (2 plots surrounding the residual forest patches × 30 residual forest patches plus 3 additional plots × 6 fires) for a total of 303 plots.

The bryophyte community was sampled with a modified form of "floristic habitat sampling" (Newmaster et al. 2005). In the original method, all habitats are searched for species with no specific reference to area. Here it was restricted to the 50 m^2 plots and all potential microhabitats (e.g. coarse woody debris, tree bases, peat mounds and water holes) within the plots were searched and the bryophytes present placed in individually marked paper bags. All microhabitats per plot were pooled in order to obtain the species richness of the community per plot. Bryophyte samples were dried until identification in the laboratory and vouchers are stored at the Université du Québec in Abitibi-Témiscamingue, Canada. Nomenclature follows Faubert (2012-2014) except for *Sphagnum subtile* (Russ.) Warnst., which follows the nomenclature of the Flora of North America Editorial Committee (2007).

2.4.3 Environmental variables sampling

The relative effect of four categories of environmental variables (i.e. temporal, severity, spatial and structural; Appendix A) on bryophyte composition and richness were studied. The temporal variable 'age of forest (years)' is defined as the time since the last fire. Forest age was estimated by coring ten dominant trees with an increment corer in a circular plot 11.28 m in radius (400 m^2) placed at the core of the undisturbed forest and residual forest patches (Chaieb et al. 2015, Moussaoui et al. 2016). The age of the oldest tree was established as the minimum age of the forest. In the forest stands were the ten dominant trees approached the maximum life span of black spruce (i.e. > 180 years old), ^{14}C dating of charcoal particles from a soil pit was used (Simard et al. 2007). The age of burned matrices was defined as the time since the last fire.

Fire severity was assessed using the thickness of the organic layer between the top charcoal layer and the mineral soil of the soil pit (Miyanishi and Johnson 2002). When the residual organic layer was > 4 cm, sites were categorized as originating from a low-severity fire (Greene et al. 2007).

Spatial variables consisted of proxies of site area and shape and were calculated using ArcGis 10.3.1 (ESRI 2015). Buffer zone width (m) is defined as the average of five distances from the core plot to five points placed along the edge of residual forest patches and undisturbed forests. A low value corresponds to a reduced distance from the core to the disturbed area (i.e. burned matrix). Buffer zone width was used instead of area as it better represents the isolation of the core bryophyte community from the surrounding disturbed areas. Similarly, the residual forest patch and undisturbed forest shape was estimated using the standard deviation (SD) of the five distances used to determine buffer zone width. A low SD value corresponds to low variability in the five distances and to a relatively rounder shape (i.e. approaching a circle), whereas a high SD value corresponds to a more elongated or irregular shape. Buffer zone width and shape both equalled 0 in burned matrix sites.

Structural variables include tree and snag density (number of stems / ha), mean tree height (m), volume of coarse woody debris according of the decay class (m^3 / ha), tree species richness (number of species), number of different microhabitats, and the presence or absence of water holes. Tree and snag density, and volume of coarse woody debris were calculated in the 400 m^2 circular plots at the core of each undisturbed forest and residual forest patch, while the line intersect method was used at the edge and in the fire plots surrounding each residual patch. As these values were not measured in the fire matrix plots, we calculate the mean value of the two fire plots associated with all five residual forest patches in each fire and used this value. All trees and snags with DBH > 9 cm and all coarse woody debris

> 5 cm in diameter were measured. Coarse woody debris were categorized using Thomas et al.'s (1979) decay classification system for snags and dead woods: classes 1 and 2 were grouped and correspond to "recently" fallen dead trees with bark and branches intact; class 3 refers to dead woods without bark nor branches and with softening wood; and classes 4 and 5 were grouped and refer to dead woods with a collapsed shape. Mean tree height of the ten dominant trees in the 400 m^2 circular plots was estimated with a clinometer. Tree species richness was determined for each plot as the number of species present both in the plot and at less than 1 m surrounding the plot (i.e. intersection with the plot edge or with branches or canopy that can drop litter in the plot). The number of different microhabitats and water hole presence / absence were recorded for each plot.

2.4.4 Data analyses

In order to overcome the different number of sites sampled per habitat type, analyses were conducted at the plot level and we described the bryophyte community of the three different habitat types along the disturbance severity gradient: burned matrix > residual forest patch > undisturbed forest.

R software 3.2.1 (R-Development-Core-Team 2015) was used for all statistical analyses with a significance level of $\alpha = 0.05$. As we used a nested design we tested whether the spatial structure of the sampling influenced the models in the different analyses with a LogLik ratio test (Pinheiro and Bates 1995). In all analyses, the spatial structure had a significant effect, we therefore used mixed models. Random effects corresponded to the forest stand and to the wildfire in which plots were sampled. When normality and homoscedasticity assumptions were met, linear mixed models (lme) were used with the package "nlme" 3.1-121 (Pinheiro and Bates 2015). A square root transformation was applied as needed to fit a normal distribution. If this was insufficient, no other transformations were investigated because of their non-intuitive interpretation (Warton and Hui 2011), and generalized linear mixed models (glmer) were applied with the package "lme4" 1.1-8 (Bates et al. 2015), with the appropriate link function. Models were followed by post-hoc tests equivalent to Tukey HSD for mixed models with the package "multcomp" 1.4-1 (Hothorn et al. 2015).

2.4.4.1 Bryophyte richness and composition

Bryophyte species were classified by their presence in a habitat type and by life forms. We obtained four species richness datasets: total (all life forms), true mosses, liverworts and sphagna. The same life form divisions were applied to the species only present in one of the three habitat types. We therefore obtained total, true mosses, liverworts and sphagna richnesses for species only found in undisturbed forests, residual forest patches or burned matrices, defined as "restricted richnesses" of each habitat type.

Bryophyte richness and composition were calculated at the plot level (n = 303) and compared as total and means among the three habitat types. Individual fires and forest stands were included as random variables to take into account the nested data (see above). In the analyses, no species richnesses were transformed except sphagna richness, which was square root transformed. Total and sphagna species richness were treated with linear mixed models (lme) due to their normal distributions whereas generalized linear mixed models (glmer) were used for the six other species richnesses, with Poisson distributions.

In order to determine whether overall community composition differed among habitat types, Correspondence Analysis (CA; Lepš and Šmilauer 2003*)* was performed on presence-absence data of all species occurring more than five times in the entire dataset (117 of 208 taxa; as required by the algorithm) using the package "vegan" 2.3-0 (Oksanen et al. 2015). Specimens identified only to genus for whom other species of the same genus were present were also removed from the analysis, resulting in an ordination matrix of 110 species and 303 plots. The significance of the differences in community composition among habitat types was determined by Multi-Response Permutation Procedure (MRPP) with 2000 permutations.

2.4.4.2 Relationships between environmental variables, habitat types, bryophyte richness and composition

Two analyses were undertaken to determine the relationship between bryophyte richness and community composition and environmental variables. In order to only examine non-correlated variables, relationships among numerical environmental variables were tested through non-parametric Spearman rank correlations. Variables with correlation coefficients < - 0.70 or > 0.70 and with P-values < 0.05 were removed from the analyses. Similarly, boxplots were used to examine relationships between numerical and categorical variables. Retained environmental variables were subsequently compared among undisturbed forests, residual forest patches and burned matrices via generalized linear mixed model (glmer), except for "number of microhabitats" and "tree and snag density" that were tested via linear mixed models (lme) because they followed normal distributions.

First, the relative influences of the categories of environmental variables (temporal, severity, spatial and structural) on bryophyte richness were assessed for total, true mosses, liverworts and sphagna richness datasets. Of the "restricted" species richness groups, we examined in detail species richness of the true mosses and liverworts only found in undisturbed forests in order to understand what main environmental characteristics of the stands justify their absence from residual forest patches and burned matrices. A model selection procedure using 32 candidate models generated from combinations of the environmental variables plus the null model was performed for each richness variable (Table 2.1). As the two spatial variables (area and shape) were correlated, they were never included together in one model. We therefore have two global models, each including one of the spatial variables. They are followed by 12 models testing each category of environmental variables (with 2 models for the correlated spatial variables). The 18 other models tested biologically relevant combinations of variables of different categories and interaction terms (see Table 2.1 for details) with duplication of the models for each of the spatial variables. The lack of convergence of certain models was corrected by optimization of the model algorithm via the bobyqa function of the glmerControl parameter (Powell 2009). The explanatory variable dataset (environmental variables) was standardised (on columns) to account for the different scales of measurement. Candidate models were ranked based on the Akaike's Information Criterion corrected for small sample size (AICc) (Burnham and Anderson 2002) using the package AICcmodavg 2.0-3 (Mazerolle 2015). Models with a delta AICc (ΔAICc) > 2.0 were considered to have substantially lower empirical support (Burnham and Anderson 2002). The model with the lowest delta AICc was considered the most parsimonious and indicated the environmental predictors that best explained variations in species richness. In the case where several models had a delta AICc < 2, evidence-ratio tests were performed to compare their respective explanatory weight. Multimodel inference was used to illustrate the effect of each explanatory variable of the most parsimonious model. When the value of the evidence ratio between the two best models was weak, no one model was the considered the best and multimodel inference was performed. We obtained 95% confidence intervals and model predictions using the modavgpred function of the AICcmodavg 2.0-3 package (Mazerolle 2015). Variables with 95% confidence intervals excluding 0 have a significant effect on the explanatory variable (the different species richnesses) and their predicted values were subsequently plotted against values of the explanatory variable. No interaction terms excluded 0. An estimate of model adjustment was indicated by Spearman's Rho.

Table 2.1 Models tested and number of parameters estimated (K; includes random effects) for the model selection procedure performed with glmer (K_{glmer}), except for total and sphagna species richnesses that were tested with lme (K_{lme}) (see Methods for details). The 12 parameters retained were grouped in four categories: temporal, severity, spatial and structural.

Model name	Variable used (variable category)	K_{glmer} / K_{lme}
Each class of variable separately		
Mod1	Age (Temporal)	5/6
Mod2	Severity (Severity)	5/6
Mod3	Area ($\text{Spatial}_{\text{area}}^{!}$)	5/6
Mod4	Shape ($\text{Spatial}_{\text{shape}}^{!}$)	5/6
Mod5	Tree & snag density ($\text{Structural}_{\text{LS}}^{*}$)	10/11
Mod6	CWD-1&2 ($\text{Structural}_{\text{LS}}$)	10/11
Mod7	CWD-3 ($\text{Structural}_{\text{LS}}$)	10/11
Mod8	CWD-4&5 ($\text{Structural}_{\text{LS}}$)	10/11
Mod9	Nb tree species ($\text{Structural}_{\text{LS}}$)	10/11
Mod10	Mean tree height ($\text{Structural}_{\text{LS}}$)	10/11
Mod11	Nb of different microhabitats ($\text{Structural}_{\text{FS}}^{\dagger}$)	6/7
Mod12	Water hole ($\text{Structural}_{\text{FS}}$)	6/7
Other models		
Mod13	Temporal+Severity	6/7
Mod14	Temporal+$\text{Spatial}_{\text{area}}$	6/7
Mod15	Temporal+$\text{Spatial}_{\text{shape}}$	6/7
Mod16	Temporal+$\text{Structural}_{\text{LS}}$	12/11
Mod17	Temporal+$\text{Structural}_{\text{FS}}$	7/8
Mod18	Severity+$\text{Spatial}_{\text{area}}$	6/7
Mod19	Severity+$\text{Spatial}_{\text{shape}}$	6/7
Mod20	Severity+$\text{Structural}_{\text{LS}}$	11/12
Mod21	Severity+$\text{Structural}_{\text{FS}}$	7/8
Mod22	$\text{Spatial}_{\text{area}}$+$\text{Structural}_{\text{LS}}$+$\text{Spatial}_{\text{area}}$:$\text{Structural}_{\text{LS}}^{1}$	12/13
Mod23	$\text{Spatial}_{\text{shape}}$+$\text{Structural}_{\text{LS}}$+$\text{Spatial}_{\text{shape}}$:$\text{Structural}_{\text{LS}}^{1}$	12/13
Mod24	$\text{Spatial}_{\text{area}}$+$\text{Structural}_{\text{FS}}$+$\text{Spatial}_{\text{area}}$:$\text{Structural}_{\text{FS}}^{2}$	9/10
Mod25	$\text{Spatial}_{\text{shape}}$+$\text{Structural}_{\text{FS}}$+$\text{Spatial}_{\text{shape}}$:$\text{Structural}_{\text{FS}}^{2}$	9/10
Mod26	$\text{Structural}_{\text{LS}}$+$\text{Structural}_{\text{FS}}$	12/13
Mod27	Temporal+$\text{Spatial}_{\text{area}}$+$\text{Structural}_{\text{LS}}$+$\text{Spatial}_{\text{area}}$:$\text{Structural}_{\text{LS}}^{1}$	13/14
Mod28	Temporal+$\text{Spatial}_{\text{shape}}$+$\text{Structural}_{\text{LS}}$+$\text{Spatial}_{\text{shape}}$:$\text{Structural}_{\text{LS}}^{1}$	13/14
Mod29	Temporal+$\text{Spatial}_{\text{area}}$+$\text{Structural}_{\text{FS}}$+$\text{Spatial}_{\text{area}}$:$\text{Structural}_{\text{FS}}^{2}$	10/11
Mod30	Temporal+$\text{Spatial}_{\text{shape}}$+$\text{Structural}_{\text{FS}}$+$\text{Spatial}_{\text{shape}}$:$\text{Structural}_{\text{FS}}^{2}$	10/11
Global models		
Global1	$\text{Spatial}_{\text{area}}$+Temporal+Severity+Structural+$\text{Spatial}_{\text{area}}$:$\text{Structural}^{1,2}$	18/19
Global2	$\text{Spatial}_{\text{shape}}$+Temporal+Severity+Structural+$\text{Spatial}_{\text{shape}}$:$\text{Structural}^{1,2}$	18/19
Null model		
Null	Nested data structure alone	5/4

CWD, coarse woody debris by decay class (1 to 5) from Thomas et al. (1979); Nb, number.

"!" The two spatial variables "area" and "shape" are correlated and are therefore placed in distinct models.

"*" $\text{Structural}_{\text{LS}}$ refers to structural variables at large scale.

"†" $\text{Structural}_{\text{FS}}$ refers to structural variables at fine scale.

"+" addition of the parameters included in the model; ":" interaction between the two parameters included in the model.

[1] Interaction is only made with the structural variable at large scale ($\text{Structural}_{\text{LS}}$) CWD-1&2, the spatial variables determined the volume of coarse woody debris in early decay classes (1 & 2), which is expected to increase in largest and more heterogeneous undisturbed forests and residual forest patches. Interaction with volume of coarse woody debris in advanced decay classes (3, 4 & 5) are not influenced by spatial variables because they are fallen long time ago, possibly before the fragmentation of the forest into residual forest patches.

[2] Interaction is made with the two structural variables at fine scale ($\text{Structural}_{\text{FS}}$) Nb of different microhabitats & Water hole, the spatial variables determined the number of microhabitats and the presence of water holes, which are expected to increase in largest and more heterogeneous undisturbed forests and residual forest patches.

Secondly, the influence of the same set of environmental variables on community composition was assessed using a Multivariate Regression Tree (MRT; Larsen and Speckman 2004). MRT permits the analysis of a whole community of species and multiple explanatory variables within a single model or tree (Larsen and Speckman 2004) via constrained clustering where the data are recursively partitioned to minimise the dissimilarity within the resulting groups using different levels of the explanatory variables. MRT is a robust method that makes no assumptions about the relationships between species and explanatory variables or among explanatory variables. Trees are described by their fit (i.e. inverse of relative error RE), which varies from 1 (0% of the variance explained by the tree) to 0 (100% of the variance explained by the tree); and their predictive accuracy estimated by the cross-validating error (CVRE), which varies from 1 (poor predictive power) to 0 (good predictive power). In this study, wildfires were included as dummy variables to take into account the spatial structure of the dataset. The mean values of environmental variables for each leaf (or end group) were subsequently calculated. Environmental variables explaining each split were examined and their explanatory power summed until a total of 90% of the split was reached. MRT was applied to the entire community with presence/absence data (i.e. both 110 common 82 infrequent species = 192 species) and 303 plots (117 of unburned forest, 108 of residual forest patch and 78 of burned matrix) to determine which category of environmental predictors accounted for a larger proportion of the explained variance in the model, and whether plots of the different habitat types were separated. Plots that MRT was not able to classify represent remaining observations and were not treated in the analyses (i.e. 3 plots sampled in one residual forest patch in our case).

2.5 Results

2.5.1 Bryophyte communities in the different habitat types

In total 192 taxa, including 100 true mosses, 74 liverworts and 18 sphagna, were found. Of the species sampled, 82 occurred less than five times in the entire data base (i.e. 42.7% are infrequent species). The three habitat types considered shared 106 species and each habitat type housed a distinct pool of species (Appendix B) but both undisturbed forest and burned matrix housed on average 0.20 restricted species per plot (24 species / 117 plots sampled and 16 species / 78 plots sampled respectively) compared to 0.13 restricted species per plot on average for residual forest patch (14 species / 108 plots sampled).

Mean total species richness per plot of residual forest patches was significantly higher than that of undisturbed forests ($P < 0.001$) and burned matrices ($P = 0.034$; Figure 2.2a). Mean species richness per plot of true mosses, liverworts and sphagna were significantly lower in undisturbed forests than in residual forest patches and burned matrices ($P < 0.001$; Figure 2.2a). However, overall undisturbed forests contained the highest liverworts richness (62 species versus 53 species in both residual forest patches and burned matrices). Significantly fewer species restricted to residual forest patches were found per plot compared to the burned matrices ($P < 0.004$, Figure 2.2b), while there was no difference in the number of species restricted to undisturbed forests compared to the other habitat types. The mean species richness of "restricted" true mosses was significantly lower in undisturbed forests than in burned matrices ($P < 0.038$), but it did not differ from residual forest patches. Residual forest patches were significantly less rich in "restricted" liverworts than undisturbed forests and burned matrices ($P < 0.037$ and $P < 0.033$ respectively). "Restricted" sphagna were only found in the burned matrix. In summary, residual forest patches had the highest mean species richness per plot but had fewer "restricted" species per plot on average than undisturbed forests and burned matrices.

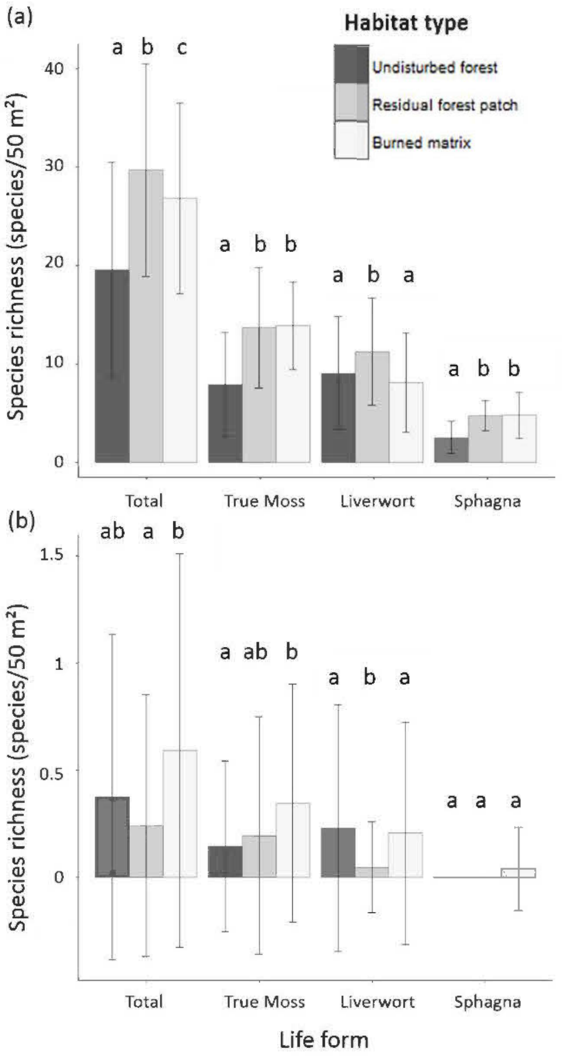

Figure 2.2 Mean species richness per 50 m^2 plots of (a) bryophytes per habitat type and life forms and of (b) "restricted" bryophytes per habitat type and life forms. Error bars refers to SD. Generalized linear mixed models were used to compare mean species richness datasets among habitat types except for the mean richness of total and sphagna species for which linear mixed model were used. Bars topped by different letters are significantly different as indicated by post-hoc tests equivalent of Tukey HSD.

Seven of the species found are classified as rare in the province of Québec (but not necessarily in our database), including six liverworts: *Cephalozia macrostachya*, *Chiloscyphus coadnatus* var. *rivularis*, *Cladopodiella francisci*, *Schistochilopsis capitata*, *Schistochilopsis grandiretis*, and *Schistochilopsis laxa*, and the true moss *Campylium protensum* (Faubert et al. 2014+).

Community composition differed among the habitat types (MRPP, $P < 0.001$). The first CA axis (Eigenvalue = 0.24, gradient length = 2.66 S.D. unit; Figure 2.3) separated species generally associated with forest habitats (e.g. *Anastrophyllum hellerianum*, *Blepharostoma trichophyllum*, *Hylocomium splendens*, *Platygyrium repens*) from species associated with open and disturbed habitats (e.g. *Cephalozia loitlesbergeri, Dicranella heteromalla, Polytrichum piliferum, Polytrichum juniperinum*). Species linked with specific microhabitat requirements (e.g., dead wood) and moist habitats are grouped to the left of the ordination (e.g. *Nowelia curvifolia*, *Tetraphis pellucida*). The second CA axis was less clear (Eigenvalue = 0.12, gradient length = 2.23 S.D. units) but illustrated a trend from species on rocks or tree trunks (e.g. *Hygroamblystegium varium*, *Hypnum pallescens*) to species inhabiting bogs and ferns (e.g. *Dicranum undulatum, Leiomylia anomala, Sphagnum* spp.). However, considering the positions of the habitat type ellipses on the ordination, the second CA axis may reveal a gradient of disturbance severity. Some species were specific to each habitat type whereas a pool of common and ubiquitous species was shared amongst them (e.g. *Aulacomnium palustre, Pleurozium schreberi*, *Ptilium crista-castrensis*). A small set of species favoured by disturbance characterized the burned matrices (bottom-right of the ordination) compared to a larger set of species found in forest habitat types (i.e. undisturbed forests and residual forest patches, top-left of the ordination).

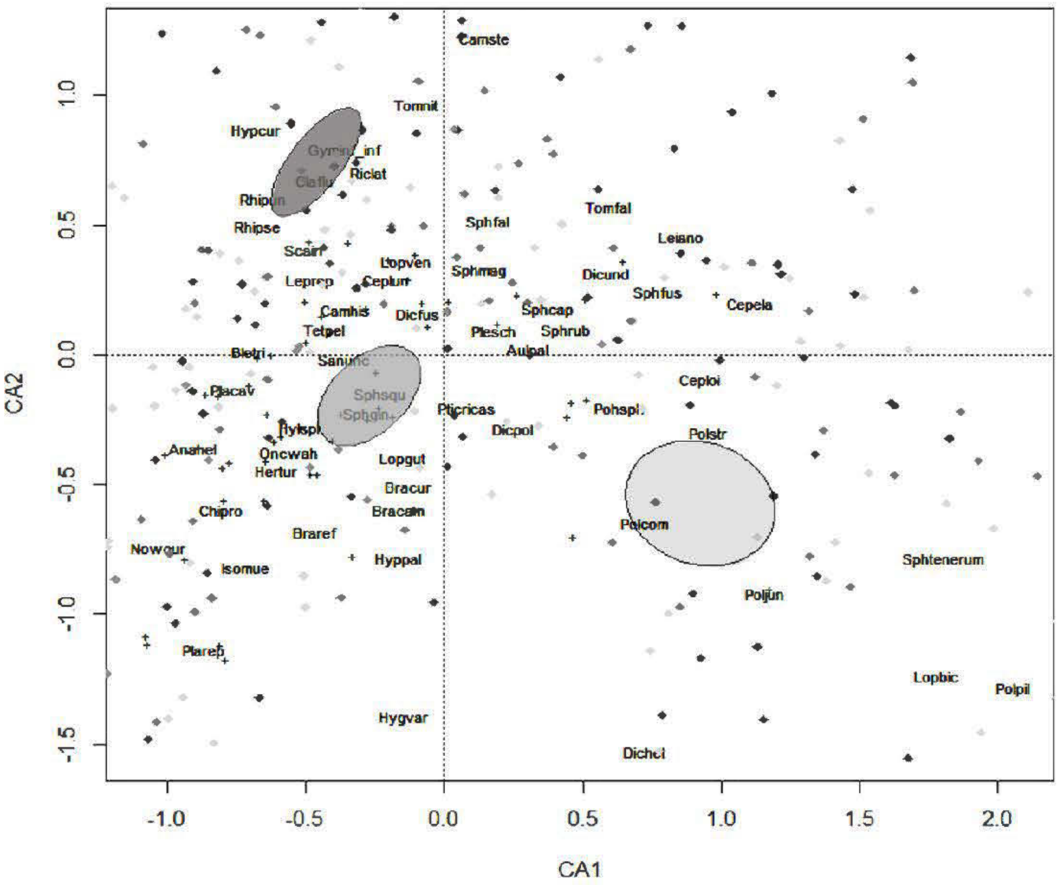

Figure 2.3 Species and site plot of the Correspondence Analysis (CA) of the total matrix of 303 plots: black diamonds, undisturbed forest plots; grey squares, residual forest patch plots; light grey triangles, burned matrix plots. Only the 45 most frequent species are indicated, positions of less frequent species are indicated by +. For complete names see Online Resource 2. The ellipses indicate habitat types centroids with a 95% confidence interval: dark grey, undisturbed forests; grey, residual forest patches; light grey, burned matrices

2.5.2 Environmental characteristics of each habitat type

Only the spatial variables "area" and "shape" were correlated (correlation coefficient > 0.70 with $P < 0.05$; Appendix C) and several environmental variables differed among habitat types (Appendix D). Undisturbed forests were older, larger and had a more heterogeneous shape than residual forest patches ($P < 0.001$). The burned matrix were not tested statistically because of a value of 0 in all sites for the spatial variables (Appendix D). Undisturbed forests contained significantly higher tree species diversity and coarse woody debris volume (principally in decay stages

4 and 5; $P < 0.001$) but had significantly fewer microhabitats ($P < 0.001$). Coarse woody debris volume in decay stage 3 was significantly lower in residual forest patches than in burned matrices and undisturbed forests ($P < 0.001$). Not surprisingly, residual forest patches and undisturbed forests differed from burned matrices by the presence of taller trees, but also by the presence of more water holes ($P < 0.001$ and $P < 0.033$ respectively). Furthermore, structural complexity [i.e. coarse woody debris volume, canopy openness (Moussaoui et al. in prep.) as well as humidity (calculated through the presence of water holes)] of post-fire residual forest patches are situated in the natural range of variability found in undisturbed forests.

2.5.3 Relationships between bryophyte richness and composition, and environmental variables

The relationships between species richness and the 12 retained environmental variables were examined through a model selection procedure. The strength of the relationship between total, true mosses, liverworts and sphagna richness datasets and the best models (i.e. with the lowest AIC_c) were strong ($\rho > 0.68$, Table 2.2), and the weakest relationships were found for the richness of true mosses and liverworts restricted to undisturbed forests ($\rho = 0.34$ and $\rho = 0.42$ respectively). Global model 2 (with the spatial variable shape) was the best model for the total, true mosses, liverworts and sphagna richnesses. For liverwort and sphagna richnesses, Global model 1 (with the spatial variable area) was respectively only 2.48 and 1.12 times less parsimonious than Global model 2. For the richness of species restricted to the undisturbed forests, the best models were not the global models but those that included stand structural variables (Table 2.2).

Table 2.2 Model selection results for the different species richnesses (both global and restricted to undisturbed forest given species taxonomic groups). Model selection was performed on generalized linear mixed models (glmer) except for total and sphagna species richnesses that were tested with linear mixed models (lme). Only models with $\Delta AIC_c < 2$ are presented, with number of parameters included (K), second-order Akaike information criterion (AIC_c), distance from the best model (ΔAIC_c), Akaike weight (w_i), estimate of model adjustment by Spearman's Rho (ρ), and value of the evidence-ratio between the best model and the second model.

Species richness datasets	Model name*	Log-likelihood	K	AIC_c	ΔAIC_c	w_i	ρ	Evidence-ratio
Total	Global2	-757.74	19	1557.34	0.00	0.79	0.89	
True Mosses	Global2	-587.90	18	1215.26	0.00	0.92	0.90	
Liverworts	Global2	-613.56	18	1266.57	0.00	0.71	0.86	2.48
	Global1	-646.64	18	1332.56	66	0.26	0.86	
Sphagna	Global2	-426.31	18	892.07	0.00	0.53	0.68	1.12
	Global1	-426.42	18	892.30	0.22	0.47	0.69	
Restricted true mosses	Mod26	-31.23	11	87.29	0.00	0.79	0.34	
Restricted liverworts	Mod26	-51.71	11	128.27	0.00	0.42	0.42	

"*" See Table 2.1 for details.

Model-averaged estimates of the coefficients of the different parameters of the models with delta AIC_c (ΔAIC_c) < 2 showed that species richness of the different taxonomic groups did not always respond to the same environmental variables (Table 2.3).

Table 2.3 Model-averaged estimates of coefficients of parameters explaining species richness patterns. Unconditional standard error and lower and upper 95% confidence intervals are also shown. Significant parameters are indicated in bold with the sign of the relationship indicated between parentheses.

Species richness datasets	Parameters of the best models	Estimate	SE	Lower CI	Upper CI
Total	Age	-1.26	0.9409	-3.10	0.58
	Severity	-1.46	0.79	-3.00	0.08
	Shape (-)	**-3.82**	**1.03**	**-5.85**	**-1.79**
	Tree & snag density (-)	**-2.72**	**1.28**	**-5.24**	**-0.21**
	Number of tree species	0.87	0.82	-0.73	2.47
	Mean tree height (+)	**4.38**	**1.14**	**2.15**	**6.62**
	CWD-1&2	-1.60	1.04	-3.65	0.44
	CWD-3	1.03	0.78	-0.48	2.56
	CWD-4&5	1.46	1.01	-0.52	3.45
	Number of different microhabitats (+)	**3.98**	**0.62**	**2.76**	**5.20**
	Water hole	-0.18	0.54	-1.25	0.88
	Shape : Number of different microhabitats	-0.27	0.60	-1.44	0.90
True Mosses	Age	-0.06	0.04	-0.14	0.02
	Severity	-0.05	0.03	-0.12	0.01
	Shape (-)	**-0.25**	**0.05**	**-0.36**	**-0.15**
	Tree & snag density	0.00	0.06	-0.11	0.11
	Number of tree species (+)	**0.10**	**0.04**	**0.02**	**0.18**
	Mean tree height	0.03	0.05	-0.06	0.14
	CWD-1&2	-0.06	0.05	-0.16	0.04
	CWD-3	0.06	0.03	-0.00	0.13
	CWD-4&5	0.05	0.04	-0.04	0.14
	Number of different microhabitats (+)	**0.18**	**0.02**	**0.12**	**0.24**
	Water hole	-0.05	0.02	-0.09	0.00
	Shape : Number of different microhabitats	-0.00	0.03	-0.06	0.06
Liverworts	Age	-0.01	0.05	-0.12	0.09
	Severity	-0.02	0.04	-0.11	0.06
	Area	-0.05	0.06	-0.16	0.06
	Shape	-0.06	0.06	-0.18	0.05
	Tree & snag density (-)	**-0.23**	**0.07**	**-0.38**	**-0.08**
	Number of tree species	0.08	0.05	-0.01	0.18
	Mean tree height (+)	**0.41**	**0.07**	**0.28**	**0.55**
	CWD-1&2	-0.05	0.06	-0.16	0.06
	CWD-3	0.01	0.05	-0.08	0.11
	CWD-4&5	0.06	0.06	-0.05	0.17
	Number of different microhabitats (+)	**0.19**	**0.03**	**0.13**	**0.26**
	Water hole	0.03	0.02	-0.01	0.09
Sphagna	Age	-0.01	0.04	-0.12	0.09
	Severity	-0.07	0.04	-0.16	0.01
	Shape (-)	**-0.32**	**0.57**	**-0.43**	**-0.21**
	Tree & snag density	-0.03	0.07	-0.18	0.11
	Number of tree species (-)	**-0.14**	**0.054**	**-0.24**	**-0.05**
	Mean tree height	-0.02	0.07	-0.16	0.11
	CWD-1&2	-0.11	0.06	-0.23	0.00
	CWD-3	-0.03	0.05	-0.12	0.06
	CWD-4&5	0.05	0.06	-0.06	0.16
	Number of different microhabitats (+)	**0.12**	**0.04**	**0.04**	**0.21**
	Water hole	-0.04	0.04	-0.11	0.03

Species richness datasets	Parameters of the best models	Estimate	SE	Lower CI	Upper CI
Sphagna (*continued*)	Shape : Number of different microhabitats	-0.05	0.05	-0.15	0 .04
	Area : Number of different microhabitats	-0.06	0.05	-0.16	0.03
Restricted true mosses	Tree & snag density	0.36	0.51	-0.64	1.37
	Number of tree species	0.51	0.27	-0.02	1.05
	Mean tree height	0.18	1.03	-1.84	2.21
	CWD-1&2	-0.37	0.51	-1.39	0.63
	CWD-3	-0.11	0.60	-1.29	1.06
	CWD-4&5	0.01	0.43	-0.84	0.87
	Number of different microhabitats	0.25	0.40	-0.53	1 .03
	Water hole	-0.03	0.37	-0.75	0.69
Restricted liverworts	**Tree & snag density (-)**	**-0.76**	**0.32**	**-1.39**	**-0.13**
	Number of tree species	0.23	0.17	-0.10	0.57
	Mean tree height (+)	**2.32**	**0.95**	**0.46**	**4.18**
	CWD-1&2 (-)	**-0.99**	**0.45**	**-1.87**	**-0.10**
	CWD-3	0.18	0.38	-0.57	0.94
	CWD-4&5	-0.44	0.41	-1.24	0.36
	Number of different microhabitats	0.47	0.25	-0.02	0.97
	Water hole	-0.27	0.25	-0.76	0.21

CWD, coarse woody debris by decay class (1 to 5) from Thomas et al. (1979), see methods for details.

“:” interaction between the two parameters included in the model.

Tree and snag density as well as shape generally negatively influenced total, true moss, liverwort and sphagna richnesses (Table 2.3 and Figure 2.4) while mean tree height and number of microhabitats also positively influenced on the same variables. Mean tree height also positively influenced the richness of the liverworts restricted to undisturbed forests, while tree and snag density and volume of coarse woody debris in decay classes 1 & 2 had a negative influence (Table 2.3). The richness of true moss restricted to undisturbed forests did not respond to any of the variables (coefficients all include 0).

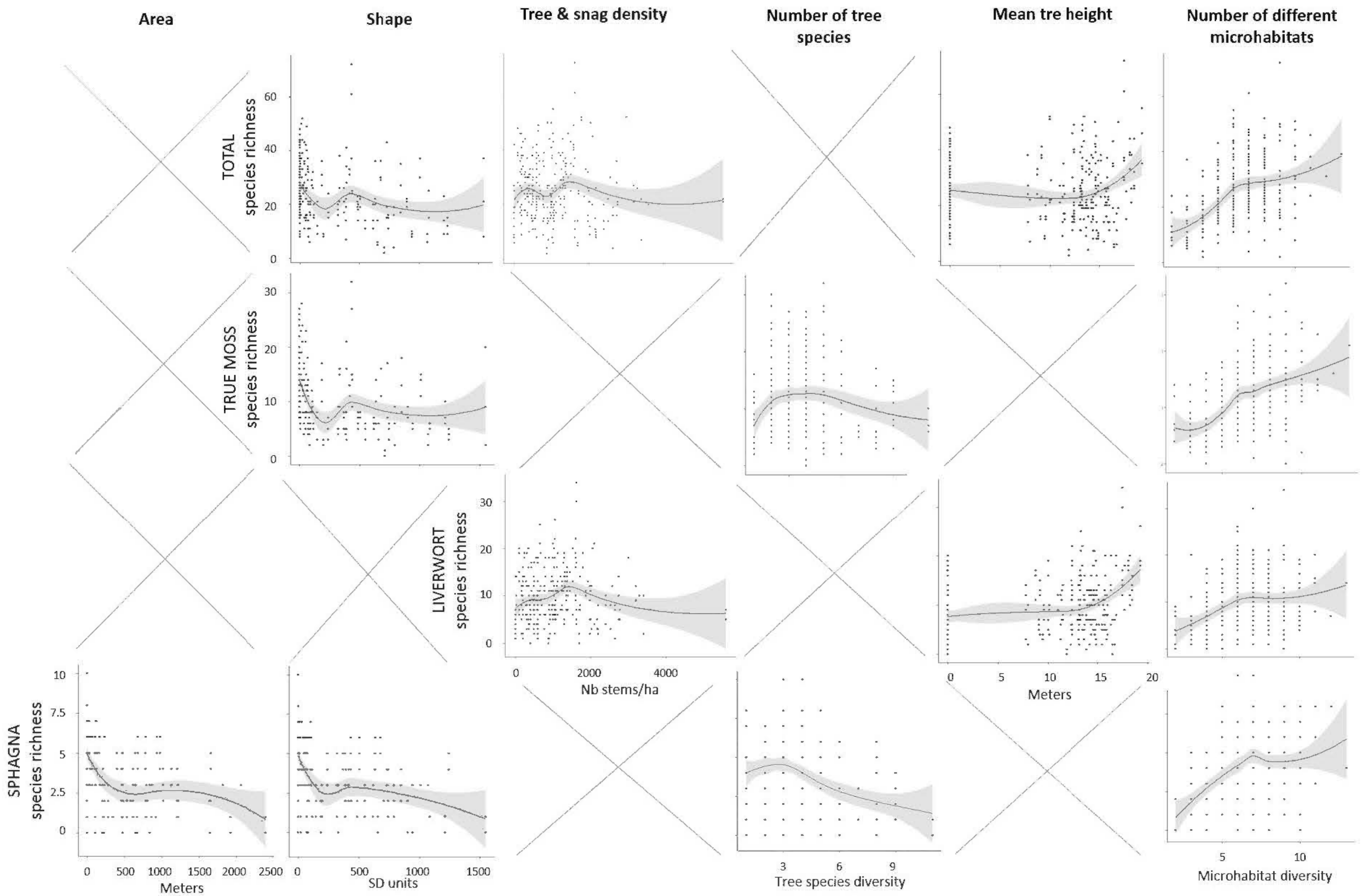

Figure 2.4 Relationships between environmental variables with a 95% confidence interval excluding 0 after model-averaging procedures and total, true mosses, liverworts and sphagna richnesses. In rows, species richness; in columns, environmental variables. Large crosses indicate no relation between the bryophyte taxonomic group and the environmental variable. On each panel: grey shade, 95% confidence interval of the relationship (indicated as a black solid line between dots that are raw data) between species richness and the environmental variable. For details on the signs of the relationships see Table 2.3.

In the MRT used to explore the relationship between the environmental variables and bryophyte composition, environmental variables explained 14.3% of the bryophyte composition variability in a five-split, six-group model (Figure 2.5). The first split was based on the two correlated spatial variables "area" and "shape" and the temporal variable "forest age" (5.73%) and separates the small and young residual forest patches and burned matrices (under 56 years old and with buffer zone width < 24.84 m and circular shape) from larger and older residual forest patches and undisturbed forests (exceeding 56 years old, 24.84 m buffer width and with a more heterogeneous shape). The second level split was generated by "area" (3.63%) and divided the undisturbed forests and residual forest patches into two groups, those with buffer zones over 190 m made up exclusively of undisturbed forests (groups 1 & 2), and smaller areas made up of a mix of undisturbed forests and residual forest patches (groups 3) and exclusively residual forest patches (group 4). Groups 1 & 2 and 3 & 4 were generated only by structural variables. The third level split, at the extreme right of the MRT was based on "fire severity" and "age" (1.88%) and lead to group 5 containing a mix of residual forest patches and burned matrices and to group 6 containing exclusively burned matrices. As a result there is a gradient from left to right in the groups from undisturbed forests, to residual forest patches to burned matrices and 25 of the 30 residual forest patches (i.e. 83%) were grouped, closer to the undisturbed forests rather than the burned matrices.

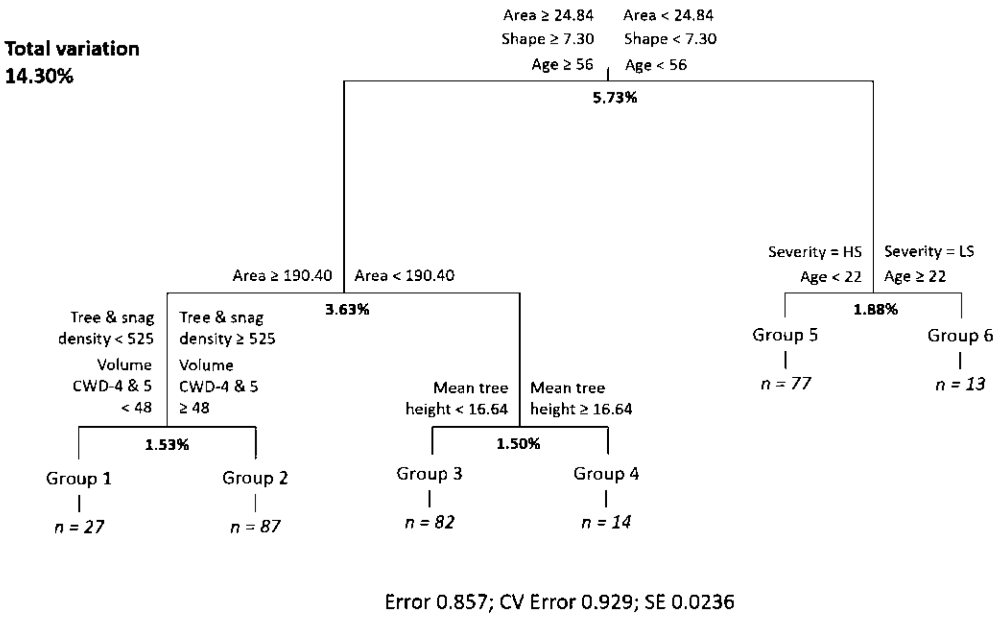

Figure 2.5 Multivariate regression tree (MRT) of bryophyte community composition. The five-split, six-group model was the best model as selected by parsimony and cross validated error (CVRE). The amount of variation explained by the tree is the inverse of the error. This total is decomposed into the percentage explained by each split. The CV error indicated the potential for the unsuccessful classification of additional samples and therefore illustrate the predictive power of the model (i.e. between 0 and 1, with 1 indicating poor predictive power). Each leaf is assigned the number of plots within each group is indicated (*n*). For more details on terminal groups' compositions see Table 4. Abbreviations: CWD, coarse woody debris by decay class (1 to 5) from Thomas et al. (1979); LS, low severity of fire; HS, high severity of fire.

Environmental variables varied among terminal groups with clear shifts in groups in age, area and shape (Table 2.4). Groups 1, 2 and 3 were composed of habitats over 440 years old and 89 ha in size and with a very irregular shape. In contrast, groups 5 and 6 were characterized by their young age (< 30 years old), their small area (< 4 ha) and their rounder shape. Group 4 was composed of habitats of intermediate age (average 160 years old) but of relatively large area (around 95 ha) and with a more or less rounder shape. The spatial structure of the data was not the primary driver of the observed species composition, as wildfires included as dummy variables were not selected.

Table 2.4 Composition and mean values of environmental variables of MRT terminal groups. Group composition is represented by the number of plots from each habitat type (n_{total} = 303). Plots sampled in a single continuous forest stand or residual forest patch were never separated in MRT final groups. Three plots all from one residual forest patch were "remaining observations" and were not classified by the MRT.

Group composition	Group1	Group2	Group3	Group4	Group5	Group6
Undisturbed forest (n = 117)	27	87	3	0	0	0
Residual forest patch (n = 108)	0	0	79	14	12	0
Burned matrix (n = 78)	0	0	0	0	65	13
Temporal						
Age	1285	325	443	162.5	31.8	36.3
Severity						
Severity (LS/HS)*	27/0	48/39	32/39	4/10	0/77	13/0
Spatial						
Area	929.1	823.9	89.4	94.5	3.5	0
Shape	563.2	578	44.9	41.1	1.6	0
Structural						
Tree & snag density	219.4	1264.6	1514.1	1094.6	488.7	166.8
Number of tree species	4.5	4.9	2.8	3.1	3.4	3.1
Mean tree height	8	14.4	13.4	18.2	1.8	2.1
CWD-1&2	5.8	28.8	13	30.6	8.1	2.8
CWD-3	2.4	21.8	7.3	29.3	16.3	21.9
CWD-4&5	7.5	17.3	2.3	3.1	2.1	3.3
Number of microhabitats	4.4	5.4	6.9	6.8	7.5	7.4
Water hole (Y/N)*	11/16	48/36	34/48	5/9	16/61	8/5

CWD, coarse woody debris by decay class (1 to 5) from Thomas et al. (1979), see methods for details. "*" For categorical variables: Y, presence of water hole; N, absence of water hole; LS, low severity; HS, high severity.

2.6 Discussion

Bryophyte richness and composition varied between the three habitat types studied. Community composition distinctness was driven by the shift in species taxonomic groups with the increase of the disturbance severity. In contrast, the differences in bryophyte richness are generated by the presence of infrequent species and species restricted to one of the habitat types. This suggests that spatial and structural attributes of the post-fire residual forest patches were suboptimal for the most sensitive species as they were absent from these habitats. However, as mean species richness was particularly high in residual forest patches, we define these as high quality habitats rather than refugia. The distinctness of the communities of the undisturbed forests and of the residual forest patches suggests that each of these habitat types are complementary and bring their own bryoflora to the landscape.

In light of these results, we make recommendations about management programs that could maximize bryophyte diversity and therefore ecosystem resilience (Walker 1995).

2.6.1 Residual forest patches: hight quality habitats rather than refugia

Residual forest patches were on average more species rich than undisturbed forests and burned matrices (10 more species per plot in average), confirming our first hypothesis. This may be in part explained by the intermediate disturbance hypothesis (Connell 1979), as newly arrived species cohabit with species that survived the disturbance and the new conditions. While controversial (Fox 2013; Sheil and Burslem 2013), the meta-analysis of Kershaw and Mallik (2013) confirmed the validity of this theory in fire-prone boreal landscapes, even though they have also pointed out the necessity of future studies performed in landscapes with high cryptogam diversity. Furthermore, the environmental selection of the species and the heterogeneity of residual forest patches may also be used to explain their high species richness. Residual forest patches, composed of both edge and core habitats that vary in light, substrate and moisture conditions results in high microhabitat diversity (Araújo 2002), opening up the field of possibilities for a large variety of species with specific microhabitat requirements. Residual forest patches therefore represent transient habitats where newly arrived species co-habit with late seral species that have survived the disturbance.

Over half of the species were common to the three habitat types, including several ubiquitous species (e.g. *Dicranum polysetum, Pleurozium schreberi, Ptilium crista-castrensis*) and habitat specialists inhabiting dead wood or rocks (e.g. *Lophozia ventricosa, Oncophorus whalenbergii, Plagiothecium cavifolium*). In contrast, 42.7%

of the species occurred less than five times in the database, and both undisturbed forests and burned matrices were richer in restricted species than residual forest patches. Furthermore, sphagna, true moss and liverwort taxonomic groups dominated the burned matrices, residual forest patches and continuous forests respectively. This shift in species composition along the gradient of disturbance severity was also reported in previous studies (Fenton and Frego 2005; Hylander and Johnson 2010). Our second hypothesis was also supported as there was a shift from species typically found in open stands and exposed substrates such as rocks or burned soils to liverworts that are found under closed canopy conditions, are drought-sensitive and are associated with mature substrates such dead wood in advanced decay classes (Rambo 2001). The first group of species is defined in the literature as disturbance-prone species and are expected to be found directly after a disturbance event. In contrast, the second species group are typical of forest interiors and are associated with undisturbed and continuous forest habitats (Baldwin and Bradfield 2010). Species that inhabit spatially and temporally discrete pocket habitats such as specialized liverworts and certain true mosses are repeatedly cited as driving the difference between undisturbed forests and other habitat types (Dynesius and Hylander 2007; Fenton and Bergeron 2008). As these species were lacking from our residual forest patches, these patches cannot be defined as refugia but rather as high quality habitats after fire. However, 83% of the residual forest patches studied (i.e. 25/30) have a bryophyte community composition more similar to the undisturbed forests than to the burned matrices, which suggests that some environmental attributes are lacking in the remaining 17% of residual forest patches.

2.6.2 Spatial, temporal and structural attributes govern bryophyte richness and composition

Undisturbed forests and residual forest patches each harbour distinct bryophyte communities. However, key environmental variables can increase the similarity of the bryophyte community of residual forest patches to the bryophyte community of undisturbed forests and therefore the potential of residual forest patches to be refugia. As indicated in other studies, and predicted by our third hypothesis, stand age, area and shape were the best predictors of bryophyte composition whereas stand structure mainly explained bryophyte diversity (Pipp et al. 2001; Fenton and Bergeron 2008). Spatial characteristics of the site (area and shape) are negatively correlated with bryophyte richness (see signs of the significant parameters of the selection model procedure in Table 2.3), and also influenced on community composition (see MRT results on Figure 2.5). These relationships may be explained by edge effects and the fact that edges are particularly rich in microhabitats (Murcia 1995). Consequently, in the smallest stands, where the edge: core ratio is enhanced, bryophyte richness is higher than in the larger sites. On the other hand, the larger the site (or the wider the buffer zone), the better protected are the species promoting forest interior species richness. This leads to the distinctiveness of bryophyte communities found in undisturbed forests that are large in size and in residual forest patches that are of moderate size.

Furthermore, stand structural attributes such as mean tree height and density, tree species diversity and dead wood volume influenced bryophyte richness, as has also been found in other systems (Szövényi et al. 2004; Arseneault et al. 2012). Dead wood volume (measured directly but also indirectly through mean tree height) is an important predictor of bryophyte richness (Lesica et al. 1991; Rambo 2001) and is positively linked to bryophyte richness, as well as stand height that influences on micro-environmental gradients (c.f. Barbier et al., 2008; c.f. Baker et al. 2014). The negative correlation between bryophyte richness and stand density may be explained by suppression of the understorey species and the lower dead wood availability in denser stands (c.f. Barbier et al. 2008; Moussaoui et al. 2016). The negative influence of tree species diversity on true mosses and sphagna richnesses may be explained by changes in micro-environmental gradients (e.g. light, humidity, soil pH) generated by a high diversity of trees. Indeed, the addition of broadleave trees might be modified soil litter and pH, which may be deleterious for some bryophyte species such as *sphagnum* linked with acidic substrates (Gough et al. 2000). For instance, the addition of deciduous species in coniferous stands changes leaf litter composition and diminishes soil acidity and vice versa (c.f. Barbier et al. 2008).

2.6.3 Forest interior species structural requirements

Our fourth hypothesis is only indirectly supported as the relationship between the richness of species restricted to forest interiors and stand age is implied but not directly demonstrated. Richness of liverwort species confined to undisturbed forests only depends indirectly on forest age through its relationship with structural attributes (Lesica et al. 1991). In this study, 24 species, of which 13 were liverworts, were restricted to undisturbed forests (Appendix B). The richness of liverworts restricted to undisturbed forests was associated with moderate stand structural complexity: < 8 m tree height, density of 500 stems/ha and less than 10 m^3/ha of coarse woody debris in early classes of decay. This relationship is logical as many liverworts are epixylics and are closely linked with dead wood in advanced decay classes (Rambo 2001). Moreover, mean tree height influences associations with corticolous bryophytes (Szövényi et al. 2004) and in denser stands, dead wood volume is lower (Moussaoui et al., 2016). Forest interior species as well as less frequent species deserve particular attention because their dependence on discrete and pocket habitats enhances their vulnerability to disturbance (Økland et al. 2003; Fenton and Bergeron 2008). However, the paucity of records of these species (some occurred less than 5 times in the database), weakens our conclusions about their habitat preferences and their distribution patterns. Furthermore, the large width of the confidence intervals presented here suggests that additional mechanisms, not considered in this paper, governed bryophyte richness and composition patterns. Neutral stochasticity and founder effects are mechanisms that imply that community composition depends on the identity of species composing it before disturbance (Vellend et al. 2014) and on the order of species arrival (Herben 1995). They have been used to explain the limited prediction ability of environmental variables on bryophyte diversity patterns (Fenton and Bergeron 2013). These concepts are not investigated in this study, but may explain the limited power of our models, and this is especially true for exclusive true moss richness, which was unrelated to the set of variables used.

2.6.4 Implications for management and conservation

Threats to the environment generated by forest harvest intensification have led to the development of ecosystem based management, which aims to reduce differences between natural and managed forests. One proposed strategy within ecosystem based management is the use of post-fire residual forest patches as templates for post-harvest retention patches (Cyr et al. 2009). Bryophyte species ill-adapted to anthropogenic disturbances are vulnerable to forest harvest and their loss can threaten ecosystem resilience (Fenton and Frego 2005). We have shown that some characteristics of residual forest patches (less than 56 years old, 0.20 ha in area i.e. 25 m of buffer zone width) may result in a bryophyte community similar to that found in the burned matrix. These patches, even though they contribute to landscape spatial complexity, mainly house disturbance-prone species with high dispersal and establishment capacities (sensu colonist species), which do not require dedicated efforts to be maintained in the landscape. Residual forest patches over 56 years old and from 0.20 to 11 ha in area (buffer zone from 25 to 190 m width), and with a moderate tree height (< 8 m) can support a bryophyte community more similar to that encountered in undisturbed forests. These characteristics seem to enhance the "life-boat" potential of the residual patches. However, the poor predictive power of our analyses suggests that additional studies on the subject are needed before these features should be emulated in post-harvest retention patches. Despite this, these results highlight the importance of stand size and shape on bryophyte richness and composition. We suggest that retention blocks left for moose (*Alces alces*) between 3 to 10 ha as proposed by Samson et al. (2002), may be more suitable for conserving forest interior bryophytes than the retention patches less than 0.20 ha used in cut blocks in the boreal forest of Québec (Pouilot et al. 2010).

2.7 Conclusions

Despite not being refugia for bryophytes, residual forest patches house a highly diversified bryophyte community. Residual forest patches house a wide variety of bryophytes including four rare species for Québec. While residual forest patches have been suggested as refugia for species sensitive to disturbance (Fenton and Frego 2005; Nelson and Halpern 2005), they do not maintain forest interior species that remain confined to undisturbed forest stands in black spruce boreal forests. Indeed, characteristics found in undisturbed forests such as their advanced age, large size, and abundance of trees, snags and dead wood seem to be the key characteristics linked with the presence of forest interior species. In the fire-prone boreal ecosystem studied, residual forest patches are not refugia but complementary habitats to undisturbed forests. Together, these habitats promote the landscape bryo-diversity. Consequently, our results highlights the need for the preservation of undisturbed forest stands in addition to use of forest retention in cutting stands.

2.8 Acknowledgements

This study was funded by the Université du Québec en Abitibi-Témiscamingue (UQAT) and the National Science and Engineering Research Council (NSERC) in partnership with Tembec, Eacom and Resolute Forest Products.

The authors especially thank Chafi Chaieb who has provided bryophyte samples from the undisturbed forest sites and Julie Arseneault for their identification. Authors also sincerely thank Emilie E. Chavel and Louiza Moussaoui who have provided some of the environmental data used in this paper; Myriam Paquette, Flora Joubier, Louis

Dubois and Philippe Heine for their field assistance; Danielle Charron, Philippe Duval, Raynald Julien, Danièle Laporte, Marie-Hélène Longpré, and Michel Poitras for their technical support; Marc J. Mazerolle for his relevant statistical advice; and Jean Faubert for his precious help in the identification of the most difficult bryophyte sample.

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CHAPITRE III

BOREAL BRYOPHYTE RESPONSE TO NATURAL FIRE EDGE CREATION

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En révision dans *Journal of Vegetation Science,* Octobre 2016

3.1 Abstract

Question: Changes in species richness and composition in plant communities as a result of edge creation are well-documented in anthropogenically modified landscapes, but what happens after natural disturbance? We investigate the responses of boreal bryophytes to edge creation in a post-wildfire residual forest patch system.

Location: Boreal black spruce-feather moss forest of western Québec, Canada.

Methods: Bryophyte community was sampled in 50 m² plots: 117 plots in 39 undisturbed forest cores (control) and 108 plots in 30 residual forest patches from wildfire divided, into 48 core plots, 30 north-facing edge plots and 30 south-facing edge plots. Temporal, severity, spatial and structural characteristics of the stands were also recorded to explain bryophyte communities composition.

Results: We found that residual edges and cores were more species rich than undisturbed cores, with the highest species richness found in the north-facing edges of residual patches. Bryophyte community composition differed between undisturbed cores and residual cores but did not differed between residual cores and edges. Furthermore, species restricted (present in only one forest type) and over represented (present more than 50% of time in one forest type) in undisturbed cores and residual edges were identified as indicators of each of these forest type~~s~~. Spatial variables such as stand area and buffer zone width explained variations in community composition after edge creation. Core and edge communities differed more in patches over 3 ha than in smaller patches, but remained clearly different in composition than undisturbed cores.

Conclusion: Change in community composition in response to edge creation is observed in this naturally disturbed landscape. While edge influence is reduced in large patches, the bryophyte community remains distinct from undisturbed cores, which permit us to determine a 170 m distance of edge influence (DEI) inside residual patches. This natural response to edge creation forces us to no longer consider anthropogenic edges as a control in the study of species response to fragmentation, and reinforces the point that residual forests are not substitute of continuous and undisturbed forests. The case of anthropogenic forest retention in cuttings stands is therefore open to discussion.

Key-words: black spruce forest; edge influence; fragmentation; indicator species; liverwort; moss; sphagna; wildfire.

3.2 Résumé

Question : Les modifications de la richesse spécifique et de la composition des communautés végétales en réponse à la création de bordures sont principalement documentées dans les paysages perturbés anthropiquement. Seulement, qu'advient-il suite à des perturbations naturelles ? Nous étudions la réponse de bryophytes boréales à la création de bordures dans un système naturel composé d'îlots résiduels post-feu.

Localisation : Pessière noire à mousses de l'ouest du Québec, Canada.

Méthodes : La communauté bryophytique a été échantillonnée dans des placettes de 50 m^2 : 117 placettes dans 39 cœurs de forêts non perturbées (contrôle) et 108 placettes dans 30 îlots résiduels post-feu, divisés en 48 placettes de cœur, 30 placettes de bordure orientées au nord et 30 placettes de bordure orientées au sud. Les caractéristiques temporelles, de sévérité de la perturbation, spatiales et structurelles des peuplements ont aussi été relevées afin d'expliquer la composition des communautés.

Résultats : Nous avons observé que les cœurs et les bordures d'îlots résiduels étaient plus riches en espèces que les cœurs de forêts non perturbées, avec la plus grande richesse spécifique trouvée dans les bordures orientées au nord par rapport à celles orientées au sud. La composition de la communauté bryophytique différait entre les cœurs de forêts non perturbées et les cœurs d'îlots résiduels, mais ne différait pas entre les cœurs et les bordures d'îlots résiduels. De plus, les espèces exclusives (présentes dans seulement un type d'habitat) et les espèces surreprésentées (présentes à plus de 50% dans un seul type d'habitat) des cœurs de forêts non perturbées et des bordures d'îlots résiduels ont été identifiées comme des indicateurs de chacun de ces types d'habitats. Les variables spatiales telles que l'aire du peuplement et la largeur de la zone tampon expliquaient les variations observées dans la composition des communautés après la création des bordures. Les communautés de cœur et de bordure différaient davantage dans les îlots résiduels excédant 3 ha que dans les îlots résiduels de tailles inférieures, mais demeuraient cependant clairement distinctes de celles des cœurs de forêts non perturbées.

Conclusions : Un changement de la composition des communautés en réponse à la création de bordures est observé dans cet écosystème perturbé naturellement. Bien que l'effet de bordure soit limité dans les îlots résiduels de plus grandes tailles, la communauté bryophytique demeure distincte de celle trouvée dans les forêts non perturbées. Cela nous permet d'identifier la distance d'influence de la bordure jusqu'à 170 m à l'intérieur des îlots résiduels. Cette réponse des bryophytes à l'effet de bordure est naturelle et nous contraint à ne plus utiliser les bordures créées anthropiquement comme des contrôles lors de l'étude de la réponse des espèces à la fragmentation. De plus, ces conclusions soulignent que les forêts résiduelles ne sont pas des substituts des forêts continues et non perturbées. Le maintien d'îlots de rétention dans les parterres de coupes est donc ouvert à réflexion.

Mots-clés : effet de bordure, espèces indicatrices, feu de forêt, fragmentation, hépatique, mousse, pessière noire à mousses, sphaigne.

3.3 Introduction

The effects of habitat fragmentation on forest communities have and continue to stimulate research in ecology as it is a major concern for biodiversity conservation. Fragmentation, defined as the restriction of communities to forest habitat patches of reduced size surrounded by an inhospitable matrix, is intimately associated with edge effects (Fahrig 2003). Edges represent transient zones between disturbed areas and forest interiors that do not experience the direct effects of disturbance (Holland et al. 1991). Edge creation results in modified microclimatic conditions, such as increased light transmittance, wind velocity, humidity and/or temperatures (Saunders et al. 1991; Harper & Macdonald 2001; Harper et al. 2005). Communities respond to these modified abiotic conditions with changes in species richness and composition. Both habitat change and community response are not restricted to the edge but can extend far inside the core of the forest (Murcia 1995; Harper & Macdonald 2001) and therefore threaten forest interior species that require stable micro-environmental conditions to survive (Rambo & Muir 1998; Newmaster et al. 2003).

The depth-of-edge influence (DEI; Harper & Macdonald 2001; Ries et al. 2004) estimates how far the edge effect is felt inside the forest interior, in terms of changes in environmental conditions but also in species richness and composition. DEI is clearly ecosystem- and species-dependent and an alteration in microclimatic conditions has been reported from studies on different forest ecosystems and varies from 60 m from the edge in mixed-wood boreal forests (Harper & Macdonald 2002) to 40 m in temperate rainforests (Davies-Colley et al. 2000). Community changes in response to these modified microclimatic conditions have been documented 50 to 60 m from the edge for bryophytes and lichens in temperate and boreal Canadian forests and wetlands (Moen & Jonsson 2003; Rhéault 2003; Baldwin & Bradfield 2005; Boudreault et al. 2008) and 75 to 200 m from the edge for epiphytic ferns and bryophytes in Ethiopian forests (Hylander et al. 2013).

The nature of the edge (generated by natural or anthropogenic disturbance), time since disturbance and patch shape influence the DEI. Indeed, edges are dynamic and an edge effect is expected to decrease over time as the contrast between the two sides of the edge are reduced (Harper & Macdonald 2002; Harper et al. 2014). Edge effects are therefore expected to be less pronounced at regenerated edges (i.e., long time since the disturbance, old patches) due smaller differences in temperature, or solar energy on each side of the edge (Zheng & Chen 2000; Baker et al. 2013). Furthermore, residual patch characteristics such as small size and shape complexity can increase edge effects (Ewers & Didham 2006, 2008; Laurance 2008). Similarly, a reduction in distance to the nearest forest source can mitigate community response to edge effects via an increased probability of recolonization at the edges, which is particularly important for species with reduced dispersal capacities (Lõhmus et al. 2006; Baker et al. 2013).

Predicting edge influence and estimating DEI is therefore crucial for biodiversity conservation. This is especially true in ecosystems with increased anthropogenic pressure, which leads to the proliferation of edges and to the substitution of core habitats by edges (Harper et al. 2005). In boreal forests, wildfires generate many edge habitats, particularly in fire skips or residual unburned patches within fire matrices (Harper et al. 2014), they are therefore ideally suited to perform studies on edges. However, despite the rich body of work on edges, most studies have focused on anthropogenic edges, including riparian edges, and on bryophytes, lichens and invertebrate species (Hylander et al. 2005; Stewart & Mallik 2006; Boudreault et al. 2008; Lee et al. 2015). Edges from natural disturbances are substantially less documented (Larrivée et al. 2008; Harper et al. 2014; Franklin et al. 2015). Consequently, the use of continuous forests rather than natural edges as a control in the study of species responses to anthropogenic edge effects might have led to misinterpretation.

Bryophytes dominate boreal forest vegetation both in terms of plant biomass and species richness (Turetsky et al. 2012). They occupy a variety of microhabitats, from the forest floor for large feather mosses to boulders, dead wood and tree bases for specialist mosses and liverworts (Dynesius & Hylander 2007). The poïkylohydric character of bryophytes (i.e. absence of specialized mechanisms for regulating uptake and loss of water; Proctor 1990) generates their strong dependence on moist microclimates (Proctor et al. 2007; Löbel & Rydin 2010). Edges created by both natural and anthropogenic disturbances are drier than forest interiors due to the opening of the canopy and wind penetrance (Holland 1991;

Baker et al. 2013), and the composition of the bryophyte community is expected to change, specifically by the loss of the most drought-sensitive species (Ross-Davis & Frego 2002; Fenton et al. 2003; Rosenvald & Lõhmus 2008). This effect may be amplified at sun-exposed compared to shaded edges (Kivisto & Kuusinen 2000; Hylander 2005).

We therefore propose to reconsider the response of species to edges focusing on bryophytes and using a system of residual patches from natural wildfires. The general objective of this study is therefore to determine the response of bryophytes to the creation of natural fire edges in boreal forests. This will generate a natural control to better appreciate the response associated with anthropogenic edges. In a related study (Barbé et al. in revision, refers to the Chapter II), we have demonstrated that residual forest patches were richer in bryophyte species and differed from undisturbed forests in terms of community composition. However, we have not split residual forest patches into core and edge, we propose to bring this level of comparison in this study comparing bryophyte richness and composition among three forest types: undisturbed cores, residual cores and residual edges. Three questions are successively investigated: (i) are bryophytes sensitive to the creation of natural edges? (ii) is orientation of the edges a factor? and (iii) are residual patches composed of "true cores" i.e. do they house a community similar to that found in undisturbed forests? Indicator species of undisturbed forest cores and of edges will be identified and the depth-of-edge influence for bryophytes will be determined.

The "mass effect" implies the coexistence of a myriad of species in transient zones due to overlapping niches leading to the cohabitation among early-successional (colonists), mid-successional and late-seral species [perennial stayers, sensu During (1992)] (Shmida & Wilson 1985; Auerbach & Shmida 1987). Given that together with the results of Barbé et al. (in revision, refers to the Chapter II), we assume that residual edges are more species rich than undisturbed and residual cores (H1). We also expect that community composition of undisturbed and residual cores are distinct from communities found at residual edges given the association of liverworts with closed canopies, humid and stable microhabitats (Lesica et al. 1991; Fenton & Frego, 2005; H2). Subsequently, we assume to find more drought-sensitive species such as liverworts in more humid and less sun-exposed north-facing residual edges, while south-facing residual edges are expected to mainly house stress-tolerant species (Kivistö & Kuusinen 2000; Hylander 2005). Finally, we have demonstrated that patch area and age influenced on bryophyte composition (Barbé et al. in revision, refers to the Chapter II), we therefore aim to link these findings with edge influence. We hypothesize that larger or older patches house a community more similar to undisturbed cores given the enhanced isolation of core communities and the prolonged time offered for microhabitat differentiation and maturation in the core (Fenton & Bergeron 2008) (H3). In contrast, we hypothesize that the compositional similarity between residual cores and residual edges will be enhanced in small or young patches (H4).

3.4 Methods

3.4.1 Study area

The study area covers 73 197 km² (79°69 W, 50°71 N - 74°50 W, 50°71 N - 79°69 W, 48°83 N - 74°50 W, 48°83 N) within the black spruce (*Picea mariana* Mill., Briton)-feather moss (*Pleurozium schreberi* (Brid.) Mitt.) forest of western Québec, eastern Canada (Saucier et al. 2009; Figure 3.1a). Stands are dominated by *P. mariana* Mill., Briton with secondary species *Pinus banksiana* Lamb., *Populus tremuloides* Michx, *Abies balsamea* (L.) Mill., and *Betula papyrifera* Marshall. The understory is dominated by ericaceous and bryophyte species (sphagna replace feather mosses under more humid conditions). The topography of the region is flat and the altitude varies from 200 to 300 m. The climate is subpolar continental with average annual temperature and precipitation of 1 °C and 927.8 mm respectively (1981 to 2010; Environment Canada 24th February 2015).

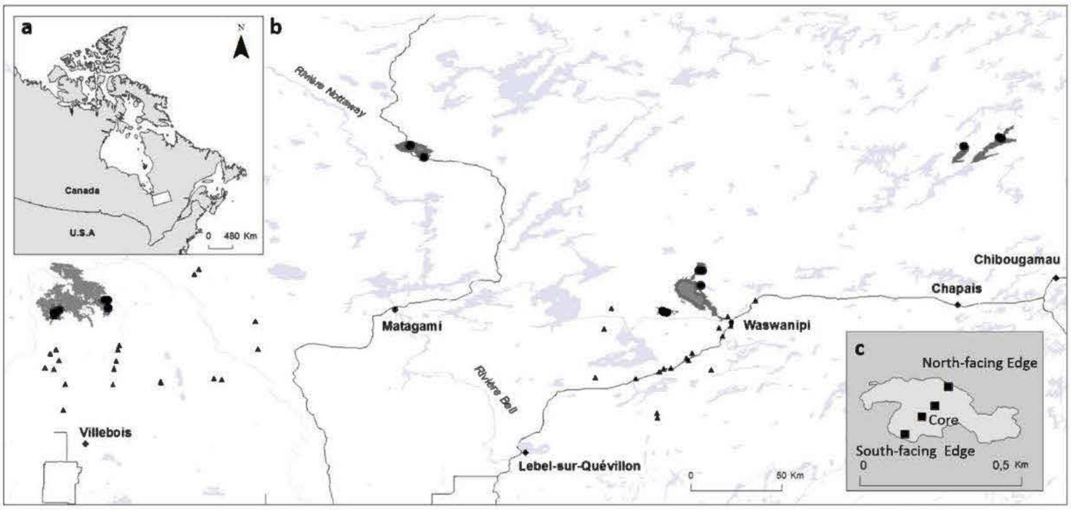

Figure 3.1 Location of the study area in the province of Québec (a), of the six wildfires studied (dark grey; b) and of the design used for bryophyte sampling in one residual forest patch (c). The main cities and rivers are indicated as well as lakes (light grey). Circles, residual forest patches (5 per wildfire, some are superimposed because of the map scale); triangles, undisturbed forests (39 sites). (c) a residual forest patch (light grey) larger than 1 ha, the surrounding burned matrix from the wildfire is indicated in darker grey. Squares represent the 50 m² plots in which bryophytes were sampled with the orientation of the edge plots. In residual forest patches smaller than 1 ha, only one core plot was sampled. The sampling design in undisturbed forest sites consists in only 3 plots of core distant at least 10 m from each other.

Natural dynamics of the forests in the study area are driven by wildfires with a fire cycle estimated at 398 years since 1920 with an average age of the forest in excess of 150 years (Bergeron et al. 2004). Fire impact on the landscape is heterogeneous, leading to a mosaic of unburned residual forest patches within the burned matrix (Madoui et al. 2010).

We selected six wildfires of various ages (8 to 42 years), size (6915 to 25 517 ha) and origin (lighting or human), as well as 39 undisturbed forests as controls (i.e. housing an undisturbed bryophyte community). Five residual patches were identified in each wildfire in order to obtain 30 residual patches divided into cores (forest inside the patch) and edges (transient zone between core forest and burned matrix). Edges were themselves subdivided into north-facing and south-facing orientations. The 30 residual patches and the 39 undisturbed forests were all chosen based on the following criteria: black spruce dominance, accessibility (< 600 m from path for residual patches and < 2 km from roads for undisturbed forests), flat topography with no obvious signs of seasonal flooding.

3.4.2 Bryophyte sampling

The bryophyte community was sampled following the method described in Chaieb et al. (2015) and Barbé et al. (in revision, refers to the Chapter II). Three rectangular plots of 50 m^2 (5 × 10 m) were placed along a line crossing the centre of the undisturbed forest stands (undisturbed cores). Within each wildfire, five residual forest patches were selected and a north-south linear transect was designed to cross each patch from edge to edge (Figure 3.1b, c). In residual patches smaller than 1 ha, three plots at least 10 m apart were used, two straddling the edges (one at the north and one at the south) and one at the core of the patch. In residual patches larger than 1 ha in area a second core plot was added for a total of four plots. Each plot was therefore at one of two positions in residual patches: edge or core. The north or south orientation of the edge plots was also considered.

The bryophyte community sampling protocol was inspired by "floristic habitat sampling" (Newmaster et al. 2005), and species were searched in all the microhabitats available (e.g. coarse woody debris, tree bases, waterholes) within the 50 m^2 plots. Bryophytes collected were placed in individually marked paper bags. All microhabitats present in one plot were pooled in order to obtain the bryophyte species richness at the plot level. Bryophyte samples were identified in the laboratory and vouchers are stored at the Université du Québec in Abitibi-Témiscamingue, Canada. Nomenclature follows Faubert (2012-2014) except for *Sphagnum subtile* (Russ.) Warnst., which follows the nomenclature of the Flora of North America Editorial Committee (2007).

3.4.3 Explanatory forest type variables

Five categories of environmental variables (i.e. temporal, severity, spatial and structural at coarse and fine scales) were recorded in each undisturbed forest and residual patch to describe forest types (Appendix E). For further details about the sampling of these variable see Barbé et al. (in revision, refers to the Chapter II). Undisturbed forests were characterised by their greater age, their large area, their high tree species diversity and coarse woody debris volume in advanced decay classes (Appendix F). Residual patch cores were characterised by their richness in trees and snags, their complex structure and the saturation of their microhabitat [number of occupied microhabitat/number of microhabitat available (occupy + empty)]. Residual patch edges contained a high volume of dead wood in decay class three but there were not differences in terms of environmental variables between north and south orientations.

Subsequently, age (yr), time since fire (yr), area (ha), shape (m), buffer zone width (m) and isolation (m) were used to explain the bryophyte community similarity between undisturbed cores and residual cores and between residual cores and edges. The age of the forest was estimated by coring ten dominant trees with an increment corer in a circular plot of 11.28 m radius (400 m^2) placed at the core of the undisturbed forest and residual forest patch (Chaieb et al. 2015; Moussaoui et al. 2016). The age of the oldest tree was established as the minimum age of the forest. In the sites were the ten dominant trees approached the maximum life span of black spruce (i.e. > 180 years old), ^{14}C dating of charcoal particles from a soil pit was used (Simard et al. 2007). The time since the last fire was determined from the SOPFEU digital map (2011; 094-3003-regecol.2 Geo83-P map, Society of forests protection against fire, Val d'Or, Canada).

Area (ha), shape (m), buffer zone width (m) and isolation (m) and were calculated using ArcGis (Version 10.3.1, ArcGis Dekstop, ESRI, Redlands, US) after tracing the shape of the residual patches with GPS in the field (GPSmap 62® Garmin Ltd.). Buffer zone width is defined as the average of five distances from the core plot to five points placed randomly at the edge of residual forest patches and undisturbed forests. A low value corresponds to a reduced distance from the core to the burned matrix. Buffer zone width was used in addition to area as it better represents the isolation of core bryophyte communities from surrounding edges. Shape of the residual forest patch and undisturbed forest was estimated using the standard deviation of the same five distances used for the estimation of the buffer zone width. A low value of SD corresponds to low variability in the five distances and to a relatively homogeneous shape (i.e. close to circle), whereas high SD value corresponds to a more crooked shape. Isolation corresponds to the minimal distance of a residual patch from the nearby undisturbed forest and refers to "forest influence" that affects the probability of re-establishment of the species and the environmental conditions at residual patch edges (Baker et al. 2013). This measure equals 0 for undisturbed forests.

3.4.4 Data analyses

The bryophyte community was sampled in 225 plots in 69 forest stands: 117 plots in 39 undisturbed forests and 108 plots in 30 residual patches. In total, 165 plots were core (48 core plots in 30 residual patches + 3 core plots × 39 undisturbed forests), the 60 plots remaining correspond to edge (2 edge plots × 30 residual patches). Of the edge plots, half are north-facing plots (n = 30) and half south-facing plots (n = 30). Each of the residual patches was affiliated with one wildfire zone corresponding to the wildfire from which originated. Undisturbed forests were assigned to the closest wildfire zone in order to take into account the spatial structure of the data in analyses (distance ranged from 1.75 to 97 km).

In order to verify our first hypothesis we analysed both species richness and composition among the three forest types (undisturbed cores, residual cores and edges).). A subsequent analysis considered the north-south orientation of the edges. Species richness was studied dividing bryophytes by life forms (true moss, liverwort, sphagna and total i.e. the three life forms grouped together). The same life-form divisions were applied to the species only present in one of the three forest types, defined as "restricted species". We therefore obtained total, true moss, liverwort and sphagna richnesses for species only found in undisturbed forests and residual forest patch cores and edges. All species richnesses followed Poisson distributions and had homoscedastic variances and were therefore treated with generalized linear mixed models with random effect (glmer; see models below).

Community composition was summarized using Correspondence Analysis (CA; Lepš and Šmilauer, 2003) performed on presence-absence data of all species occurring more than five times in the entire dataset (78 taxa) using the package "vegan" (Version 2.3-0; statistical package R). Specimens identified only to genus for whom other species of the same genus were present were removed from the analysis (14 taxa), resulting in an ordination matrix of 100 species and 225 plots. The significance of the resulting pattern was determined by Multi-Response Permutation Procedure (MRPP) with 2000 permutations.

To verify our second hypothesis, we developed two types of indicator species: species restricted to one of the forest type (described above) and species over represented in one forest type. Only species that were present at least ten times in the entire data set were considered. Over represented species were determined by calculating the proportion of occurrences within a given forest type when considering all of the occurrences in a pair of forest types (undisturbed cores vs residual cores; residual cores vs edges; north vs south edges). The difference in number of plots per forest type was accounted for by weighting the number of occurrences by the number of plots in each forest type. The observed frequency was compared to a null hypothesis of no a priori association between species forest types. The difference between observed and expected frequencies was tested for significance with a Chi-square test (χ^2). A significant result indicated that the species was over/under represented in the two habitat types compared. This method of pairs of comparison was used instead of a comparison among the three forest types together to avoid irrelevant combinations of forest types. Moreover this method is more conservative given the expected frequency used in the Chi-square tests was fixed at 50% whereas it would be reduced to 33% in comparison with three habitat types. We therefore selected less indicator species.

In order to explain the differences in frequency of the restricted and over represented species in the different pairs of forest types we compared their life forms (acrocarp, pleurocarp, liverwort, sphagna), life strategy (colonist, perennial, shuttle, dominant; adapted from During 1992), substrate preference (bog, obligate or facultative epixylic, epiphytic, generalist, terricolous, rock, other; based on Faubert 2012-2014), sexual mode (dioïque, autoïque, multiple, other; based on Faubert 2012-2014), association or not with humid habitats (based on Faubert 2012-2014), and whether they were early- or late-successional species (pioneer vs mature species; based on Faubert 2012-2014) using Kruskal-Wallis tests (see models below). In these analyses, restricted and over represented species of a forest type were pooled together to represent patterns of indicator species as a whole for a forest type.

Finally, in order to address third and fourth hypotheses, we compared the compositional similarity between undisturbed coress and residual cores and then between residual cores and edges. Jaccard's index of similarity was calculated between the community of undisturbed cores (n = 117 plots) and residual cores (n = 48 plots). Jaccard's index was chosen because it compares the number of shared species to the total number of species in the combined assemblage while Sørensen's index compares the number of shared species to the mean number of species in a single assemblage; Jost et al. 2011). The area, age, time since fire, shape, buffer zone width and isolation of residual patches were used to explain the similarity between the communities, using linear mixed models (lme; see models below).

The same procedure was repeated to explain the similarity between residual cores (n = 48 plots) and edges (n = 60 plots) using the same set of environmental variables. A high level of similarity between core and edge communities indicates that the edge influence penetrates deep inside the core of the patch, which leads to the homogenisation of the bryophyte community. While, not measured by the traditional method of a linear transect of consecutive plots from the edge to the core described in previous papers (Rhéault et al. 2003; Baldwin & Bradfield 2005; Harper et al. 2014), we estimated the depth-of-edge influence (DEI) on bryophytes via the size and the buffer zone width of residual patches with the highest core-edge similarity.

3.4.5 Models used

R software (Version 3.2.1, R Foundation for Statistical Computing, Vienna, AT) was used for all statistical analyses with a significance level of $\alpha = 0.05$. Results with *p*-values between 0.1 and 0.05 are also discussed as "marginally significant" because they suggest trends in the data, which are important to consider in order to identify fine scale biological responses (Murtaugh 2014; de Valpine 2014). As we used a nested design, we tested whether the spatial structure of the sampling influenced the models in the different analyses with a LogLik ratio test (Pinheiro & Bates 1995). In all analyses the spatial structure had a significant effect, we therefore used mixed models with the random effects "wildfire" and "forest stand". When normality and homoscedasticity assumptions were met, linear mixed models (lme) were used with the package "nlme" (Version 3.1-121; statistical package R). When the response variable was not normal or homoscedastic no transformations were investigated because of their non-intuitive interpretation (Warton & Hui 2011) and generalized linear mixed models with random effects (glmer) were applied with the package "lme4" (Version 1.1-8; statistical package R), with the appropriate link function. Models were followed by post-hoc tests equivalent to Tukey HSD for mixed models performed with the package "multcomp" (Version 1.4-1; statistical package R). When the assumption of homoscedasticity was violated, Kruskal-Wallis non-parametric tests equivalent to one-way ANOVA were used, followed by post-hoc multiple comparison tests performed with the package "pgirmess" 1.6.2; statistical package R).

3.5 Results

3.5.1 Bryophyte richness and composition of the different forest types

In total 176 species, including 92 true mosses, 68 liverworts and 16 sphagna, were found. Of the species sampled, 76 occurred less than five times in the entire data base (i.e. 43% are infrequent species). The three types of sites shared 97 species and 46 species were exclusively found in undisturbed cores and residual cores (Appendix G). Twenty-seven species (11 true mosses, 15 liverworts, and 1 sphagna) were restricted to undisturbed cores, and 5 species (2 true mosses, 2 liverworts, and 1 sphagna) to residual cores. Eleven species (8 true mosses and 3 liverworts) were only found in residual edges, of which six were only recorded at north-facing edges and four at south-facing edges.

In total 141 species were found in undisturbed cores, 124 in residual cores and 141 in residual edges (131 species at the north and 107 at the south). Mean total, true moss and sphagna richness per plot in undisturbed cores was significantly lower and mean liverwort richness per plot was marginally lower than in residual cores ($p < 0.001$, $p < 0.001$, $p < 0.001$, $p = 0.053$ respectively) and edges ($p < 0.001$, $p < 0.001$, $p < 0.001$, $p = 0.069$ respectively; Figure 3.2a). Mean richness of true mosses per plot was also significantly lower in residual cores than in edges ($p = 0.044$). In the edge plots, mean total and true moss richness were significantly higher and mean liverwort richness was marginally higher at the north-facing edge than at the south-facing edge ($p = 0.002$, $p = 0.039$ and $p = 0.080$ respectively). Mean total and true moss richness per plot were also significantly higher at north-facing edges than in residual cores ($p = 0.008$ and $p = 0.003$ respectively). Residual north-facing and south-facing edges and cores did not differ in sphagna mean species richness per plot. Mean richness of liverworts per plot was significantly higher at the north-facing edges of residual patches than in undisturbed cores ($p = 0.024$).

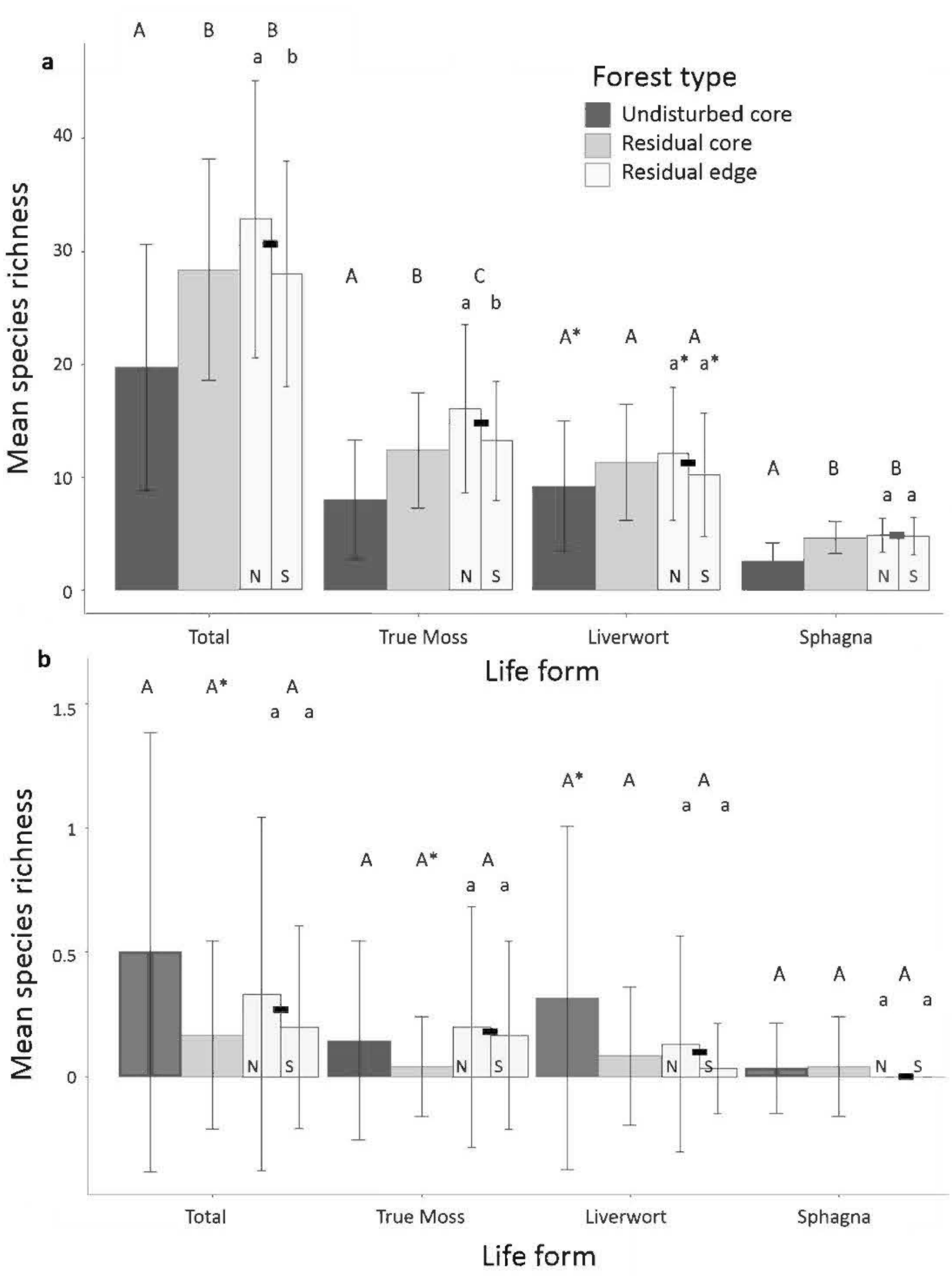

Figure 3.2 Mean bryophyte species richness (a), and mean bryophyte richness of "restricted species" (b) per forest type and life form. Mean richness refers to the mean number of species recorded in the 50 m^2 plots of each forest type. Residual edges are presented by orientation (N, north-facing; S, south-facing), the bold line indicates the mean richness of the "total" edge without division into north and south. Error bars refer to SD. Generalized linear mixed models were used to compare mean species richness among forest types (upper case) and orientation of residual edges (lower case). Bars topped by different letters are significantly different as indicated by post-hoc tests equivalent of Tukey HSD; marginal significance of the tests is indicated by "*" ($0.1 < \alpha < 0.05$). Bars topped by an upper case letter indicate that the forest types differed significantly, bars topped by a lower case letter indicate that the north- and south-facing edges were significantly different.

For species restricted to one forest type, the mean total species richness per plot was marginally higher in undisturbed cores than in residual cores (*p* = 0.050) but did not differ from edges (Figure 3.2b). Residual patch edges were marginally richer in restricted true mosses than cores (*p* = 0.076) but did not differ from undisturbed cores. Furthermore, mean liverwort richness per plot was marginally higher in undisturbed cores than in residual cores and edges (*p* = 0.096 and *p* = 0.055 respectively). No difference in mean richness of sphagna per plot restricted to one forest type was recorded. Overall, undisturbed cores tended to be globally less species rich than residual cores but housed more restricted species, particularly liverworts. Edges of residual patches and particularly north-facing edges tended to be more species rich than cores.

Community composition differed among the forest types (MRPP, $p < 0.001$). Community composition patterns illustrated by the CA were difficult to interpret, however the first CA axis (Eigenvalue = 0.19, gradient length = 2.49 S.D. unit; Figure 3.3) seems to separate species linked to closed forest habitats (e.g. *Herzogiella turfacea, Plagiothecium cavifollium, Lophozia ascendens*) from species associated with open habitats (e.g. *Sphagnum capillifolium, Sphagnum fuscum, Dicranum undulatum, Cephaloziella elachista*). The second CA axis (Eigenvalue = 0.13, gradient length = 1.98 S.D. units) seems to separate species along a humidity gradient, with species affiliated to humid habitats found at the bottom of the ordination (e.g. *Tomenthypnum nitens, Riccardia latifrons, Scapania irrigua*) and species linked to drier habitats at the top (e.g. *Ceratodon purpureus, Polytrichum commune, P. juniperinum*). North-facing edges were more similar to the undisturbed core community than the south-facing edge community. Residual core communities were intermediate between north-facing and south-facing edges communities.

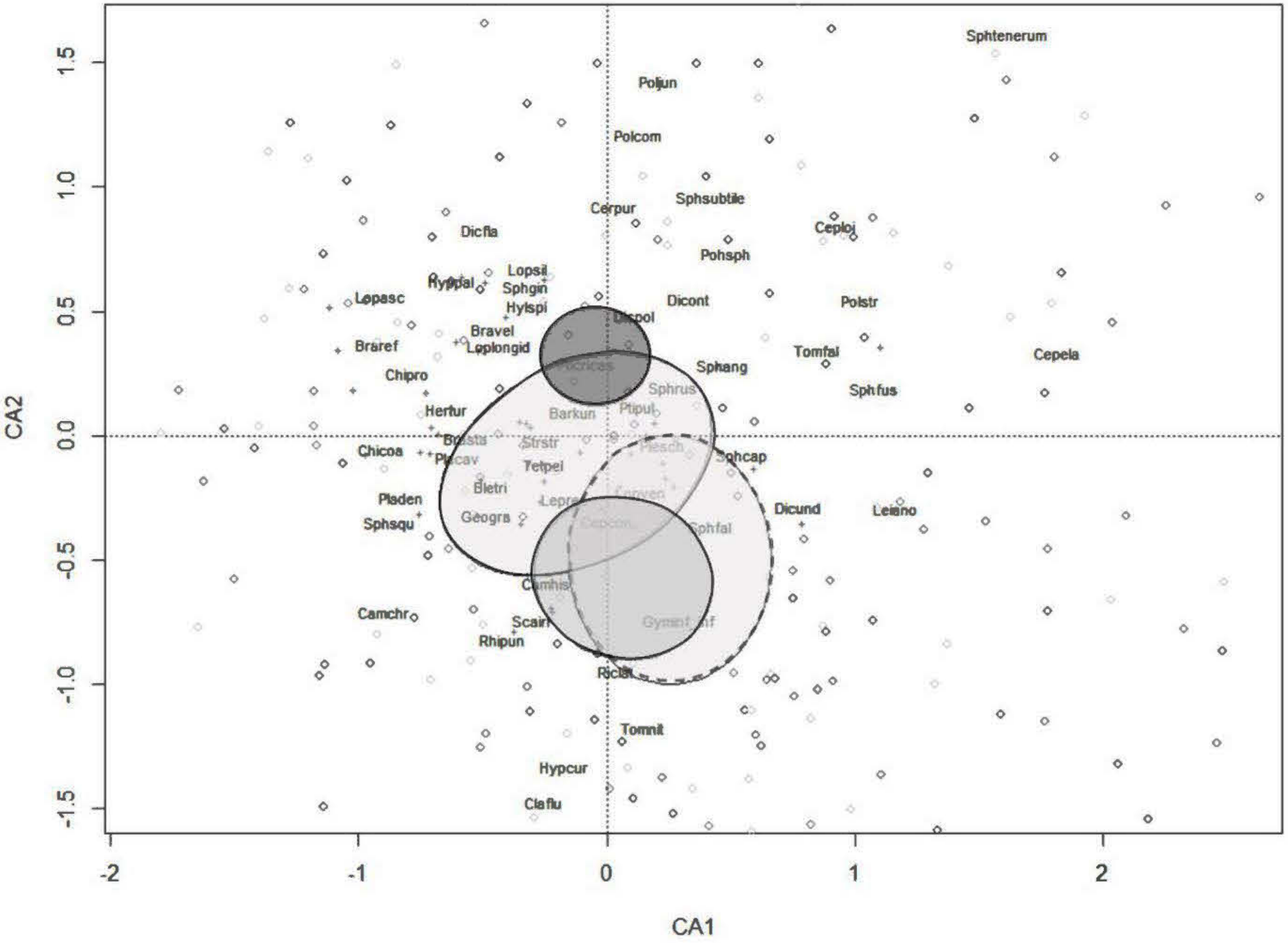

Figure 3.3 Species and site plot of the Correspondence Analysis (CA) of the total matrix of 117 plots of undisturbed cores, residual cores and edges. Only the 55 most frequent species are indicated, positions of less frequent species are indicated by +. For complete names and details on species life form see Appendix G. Symbols indicate plots and ellipses indicate type of forests: dark grey, undisturbed cores; grey, residual cores; light grey full line, residual north-facing edge; light grey hatched line, residual south-facing edge.

3.5.2 Indicator species of undisturbed cores and of residual edges

3.5.2.1 Identification of the restricted and over represented species

A total of 72 species were examined individually in the comparison between undisturbed cores and residual core communities (i.e. restricted and over frequent species of one forest type). Of these, 32 species [27 restricted (15 liverworts) and 5 over represented] were indicators of undisturbed cores and 40 species were indicators of residual cores (5 restricted and 35 over represented; Tables 3.1 and 3.2).

The comparison between residual edges and cores identified 61 species as restricted and over frequent. The dataset of edge-indicator species was composed of 24 species [11 restricted (8 true mosses) and 13 species over represented] compared to the set of 37 species (5 restricted and 32 over represented) that indicated residual cores. Furthermore, 17 restricted and over represented species were identified for residual north- and south-facing edges, 12 indicator species of north edges and five of south edges.

Table 3.1 Life form, life strategy, substrate preference and humidity affinity of the 53 species identified as indicators of undisturbed cores and of residual edges. Affiliation to south (S) or north (N) edges are indicated as exponents.

	Species	Life form	Life strategy	Substrate preference	Humidity affinity*
Indicators of undisturbed cores					
Restricted	*Barbilophozia floerkei*	L	P	R	No
	Bazzania tricrenata	L	P	R	Yes
	Blindia acuta	A	C	T	Yes
	Brachythecium acutum	P	P	T	Yes
	Bryhnia gramnicolor	P	P	T	No
	Calliergon giganteum	P	P	B	Yes
	Cephalozia catenulata	L	C	EO	Yes
	Cephalozia macrostachya	L	P	B	Yes
	Chiloscyphus pallescens	L	C	T	Yes
	Chiloscyphus polyanthos sensu lato	L	C	T	Yes
	Cladopodiella fluitans	L	P	B	Yes
	Hamatocaulis vernicosus	P	P	B	Yes
	Leiocolea heterocolpos	L	C	EF	No
	Lophozia obtusa	L	C	T	No
	Meesia triquetra	A	P	B	Yes

	Mylia taylori	L	P	EF	No
	Orthotrichum ohioense	A	P	EP	No
	Paludella squarrosa	A	P	B	Yes
	Platydictya subtilis	P	P	EO	No
	Pylaisia polyantha	P	P	EP	No
	Riccardia palmata	L	C	EO	Yes
	Scapania mucronata	L	C	T	No
	Schistochilopsis capitata	L	C	T	Yes
	Schistochilopsis grandiretis	L	P	B	No
	Sphagnum cuspidatum	S	D	B	Yes
	Tritomaria quinquedentata	L	P	R	No
	Ulota coarctata	A	P	EP	No
Over represented	*Cepaloziella hampeana*	L	C	G	No
	Hypnum imponens	P	P	EF	No
	Rhizomnium pseudopunctatum	A	S	T	Yes
	Riccardia latifrons	L	C	EF	Yes
	Tomentypnum nitens	P	P	B	Yes
Indicators of residual edges					
Restricted	*Barbilophozia hatcheri*	L	C	R	No
	Cladopodiella francisci^{N}	L	C	T	Yes
	Dicranum fulvum^{S}	A	P	R	No
	Dicranum spurium^{S}	A	S	R	No
	Frullania eboracensis^{N}	L	S	EF	No
	Orthotrichum speciosum^{S}	A	S	EP	No
	Plagiomnium medium^{N}	A	S	T	Yes
	Pohlia elongata^{S}	A	C	R	No
	Polytrichum commune var. *perigoniale*^{N}	A	P	T	No
	Polytrichum longisetum^{N}	A	S	B	No
	Splachnum ampullaceum^{N}	A	C	F	No
Over represented	*Brachythecium reflexum*	P	P	EF	No
	Brachythecium starkei^{N}	P	P	G	Yes
	Calypogeia muelleriana^{N}	L	C	G	Yes
	Cephalozia connivens^{N}	L	P	B	No
	Cephaloziella rubella	L	C	G	No
	Ceratodon purpureus	A	C	G	No
	Dicranum scoparium	A	P	G	No
	Jamesoniella autumnalis^{N}	L	C	G	No
	Plagiothecium cavifolium^{N}	P	P	G	No
	Plagiothecium denticulatum^{N}	P	P	EF	No
	Polytrichum juniperinum	A	P	T	Yes
	Tomentypnum falcifolium	P	P	B	Yes
	Sphagnum wulfianum^{S}	S	D	T	Yes

*, bryophytes require water and moisture at different phases of their phenology (Vanderpoorten & Goffinet 2009) but we distinguish here the species that are the most dependent on humid microhabitats for their survival (based on Faubert 2012-2014).

Abbreviations for life forms: A, acrocarps; L, liverworts; P, pleurocarps; S, sphagna. Abbreviations for life strategies (based on During 1992): C, colonist; D, dominant; P, perennial; S, shuttle. Abbreviations for substrate preferences (based on Faubert 2012-2014): B, bog; EF, facultative epixylic; EO, obligate epixylic; EP, epiphyte; G, generalist; F, faeces; T, terricolous; R, rock.

Table 3.2 Comparison of the life traits and substrate preferences of the species identified as indicators (i.e. restricted and over represented species pooled together) of undisturbed cores and of residual edges following the three pairs of comparison. Values are number of species, frequencies are given in square brackets. N, number of species involved in the comparison; n, number of species in each of the habitat type compared. Kruskal-Wallis tests were used for comparisons. Bold, significant test ($\alpha < 0.05$); "*", marginally significant test ($0.1 < \alpha < 0.05$).

Pairs of comparison	Undisturbed CORE (UC) – residual CORE (RPC) (n = 72)		Residual EDGE (RPE) – residual CORE (RPC) (n = 61)		EDGE NORTH (N) – EDGE SOUTH (S) (n = 17)	
	UC (n = 32)	RPC (n = 40)	RPE (n = 24)	RPC (n = 37)	N (n = 12)	S (n = 5)
Life form	$p = 0.256$		**$p = 0.016$**		$p = 0.329$	
Pleurocarp	8 [25%]	9 [22%]	5 [21%]	8 [21%]	3 [25%]	0
Acrocarp	6 [19%]	8 [20%]	11 [46%]	7 [19%]	4 [33%]	4 [80%]
Liverwort	17 [53%]	16 [40%]	7 [30%]	16 [43%]	5 [41%]	0
Sphagna	1 [3%]	7 [17%]	1 [4%]	6 [25%]	0	1 [20%]
Life strategy	**$p = 0.033$**		**$p = 0.007$**		$p = 0.363$	
Perennial	19 [60%]	15 [37%]	10 [41%]	13 [35%]	5 [11%]	1 [20%]
Colonist	11 [34%]	17 [42%]	8 [33%]	17 [46%]	4 [33%]	1 [20%]
Shuttle	1 [3%]	1 [2%]	5 [21%]	1 [3%]	3 [25%]	2 [40%]
Dominant	1 [3%]	7 [17%]	1 [4%]	6 [16%]	0	1 [20%]
Substrate preference	$p = 0.286$		$p = 0.733$		$p = 0.142$	
Obligate epixylic	3 [9%]	11 [27%]	0	10 [27%]	0	0
Facultative epixylic	4 [12%]	3 [7%]	3 [12%]	2 [5%]	2 [16%]	0
Generalist	1 [3%]	10 [25%]	7 [30%]	11 [30%]	4 [33%]	0
Terricolous	9 [28%]	7 [17%]	5 [21%]	6 [16%]	3 [25%]	1 [20%]
Bog	9 [28%]	9 [22%]	3 [12%]	8 [21%]	2 [16%]	0
Epiphyte	3 [9%]	0	1 [4%]	0	0	1 [20%]
Rock	3 [9%]	0	4 [16%]	0	0	3 [60%]
Faeces	0	0	1 [4%]	0	1 [8%]	0
Sexual mode	$p = 0.847$		$p = 0.111$		$p = 0.186$	
Dioïque	20 [62%]	18 [45%]	11 [46%]	17 [46%]	6 [50%]	0
Autoïque	8 [25%]	9 [22%]	3 [12%]	9 [24%]	2 [16%]	1 [20%]
Multiple[‡]	3 [9%]	8 [20%]	4 [16%]	7 [19%]	2 [16%]	1 [20%]
Other[†]	3 [9%]	5 [12%]	5 [21%]	3 [8%]	0	3 [60%]
NA	0	0	1 [4%]	1 [3%]	2 [16%]	0
Humidity affiliation	$p = 0.051$*		$p = 0.716$		$p = 0.381$	
Yes	18 [56%]	16 [40%]	7 [30%]	15 [40%]	4 [33%]	0
No	14 [44%]	24 [60%]	17 [71%]	22 [59%]	8 [67%]	5 [100%]
Successional Statute	**$p = 0.016$**		$p = 0.929$		$p = 0.301$	
Pioneer	0	5 [12%]	5 [21%]	5 [13%]	2 [16%]	1 [20%]
Mature	1 [3%]	4 [10%]	0	4 [11%]	0	0
NA	31	31	19	28	10	4

NA, not-available.

"‡" Multiple means that the species can use more than one type of sexual reproduction.

"†" The sexual modes monoïque, paroïque, phyllodioïque, and synoïque are grouped together in this category.

3.5.2.2 Life traits and habitat preferences of restricted and over represented species

Restricted and over represented species of undisturbed cores significantly differed in life strategies and successional statute (*p* = 0.033 and *p* = 0.016 respectively; Table 3.2) from species found in residual cores. Undisturbed cores were significantly richer in perennial species and less rich in colonist and pioneer species than residual cores. Species tended to be affiliated with more humid microhabitats in undisturbed cores (*p* = 0.051, with 56% of the species linked to humidity in undisturbed cores compared to 40% in residual cores; Table 3.2).

Residual cores and edges were also distinct in terms of the life form and strategy of the restricted and over represented species (*p* = 0.016 and *p* = 0.007 respectively; Table 3.2). Perennials and acrocarps were mainly found in the edges compared to residual cores that were characterised by liverwort and colonist species. There were no differences in life traits and substrate preference of the species found between north- and south-facing edge orientations.

3.5.3 Bryophyte community similarity between forest types and distance of edge influence (DEI)

In order to determine if post-fire residual patches have "true cores" and to estimate the DEI of bryophytes in boreal black spruce forests, Jaccard's index of similarity was used. Similarity between undisturbed cores and residual cores and between residual cores and edges varied from 2.05% to 49.80% and from 24.8% to 71% respectively. Among the six environmental variables tested through the linear mixed models, similarity between undisturbed forests and residual cores was negatively correlated with residual patch area (*p* = 0.029, r = -0.56; Figure 3.4a) and continuously diminishes with the increasing area of the patch.

On the other hand, similarity between the core and the edge of one residual patch was significantly negatively correlated to its area (*p* = 0.044, r = -0.67; Figure 3.4b) and to the width of its buffer zone (*p* = 0.030, r = -0.86; Figure 3.4c). The highest similarity was in residual patches less than one ha and averaging 3 ha in area and with less than 50 m in buffer zone width, the edge influence was thereby felt until 50 m into residual patches. This corresponds to the DEI. Age, time since fire, shape, and isolation did not explain any of the similarity patterns observed.

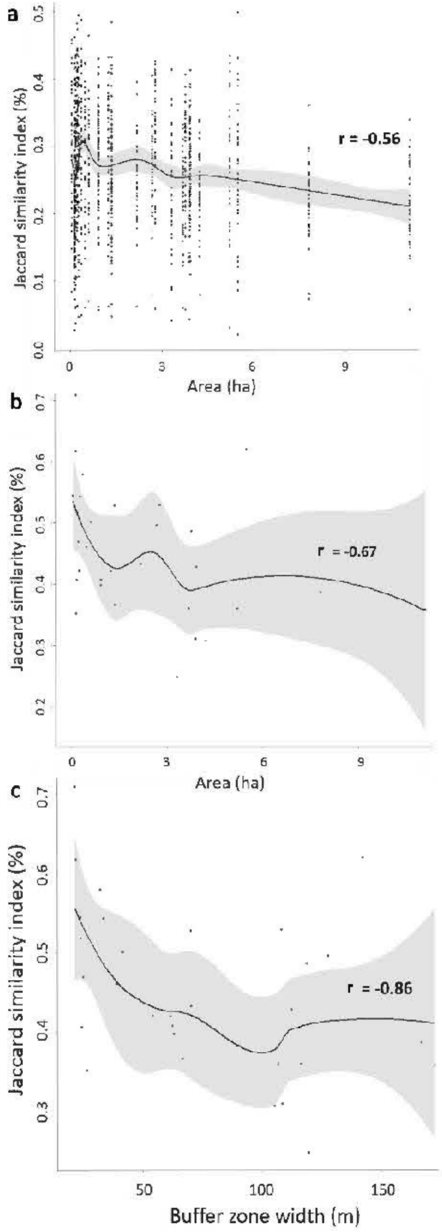

Figure 3.4 Regression plots of the Jaccard similarity index between undisturbed cores (n = 117 plots) and residual cores (n = 48) in function of residual patch area (a), and between residual cores (n = 48) and edges (n = 60) in function of the area (b), and in function of the buffer zone width (c). Dark line, regression curve with the coefficient of regression (R^2); full grey lines, 95% confidence interval; dotted grey lines, prediction curves.

3.6 Discussion

Residual patches, and especially north-facing edges, represent sites of high bryophyte richness. However, bryophytes were negatively affected by edges in a species-dependant manner, and indicator species of undisturbed cores and residual edges were identified. Although the edge influence was mitigated in larger patches, bryophyte communities in undisturbed cores and residual cores remained distinct, as already found in Barbé et al. (in revision, refers to the Chapter II) for the residual patch considered as a whole (i.e. including the edges). The absence of "true cores" in post-fire residual patches and the clear change in community composition associated with these fragmented forest type represents the natural response of bryophytes to edge creation. These conclusions offer new insights to bryophyte response to edge creation that have up to now been only examined on anthropogenic edges.

3.6.1 Bryophyte response to edge influence and the identification of edge-sensitive and edge-preferring species

Not surprisingly, species richness was higher in residual patches (cores and edges confounded) than in undisturbed cores, with the most species richness found in residual edges (Barbosa & Marquet 2002; Duelli et al. 2002; Baldwin & Bradfield 2005). Furthermore, as found in Swedish boreal forest and in Mediterranean Quercus forests, edge orientation was influential (Hylander 2005; Belinchón et al. 2007) with north-facing edges richer than south-facing edges. Our first hypothesis is therefore confirmed. The high species richness of edges may be due to the fact that they are at the interface between two distinct habitats (Holland et al. 1991; Magura 2002), but also due to their structural complexity (i.e. reduced canopy, greater dead wood volume and higher snag density; Chen et al. 1992; Oosterhoorn & Kappelle 2000). This results in high microhabitat diversity, opening a field of possibilities for the coexistence of a myriad of species (Araújo 2002), as suggested by the "mass effect" (Shmida & Wilson 1985; Auerbach & Shmida 1987).

Furthermore, the lower level of microhabitat saturation may indicate that some species cannot tolerate the environmental conditions of the edge, but the large number of species suggests rather that these empty microhabitats represent opportunities for colonization by new species.

We identified 69 species as indicators of undisturbed cores and residual edges. Thirty-two of the species found were significantly more frequent or even restricted to undisturbed cores. This included numerous perennial stayers associated with bogs, and infrequent liverworts that are typically associated with closed-canopies, high humidity and significant deadwood volume in advanced decay classes (Baldwin & Bradfield 2005, 2007, 2010; Hylander et al. 2005; Hylander & Johnson 2010). Moreover, the abundance of sphagna-associated species (e.g., *Calliergon giganteum, Tomenthypnum nitens*) was expected because of the paludified state of some undisturbed old-growth stands in black spruce forests (Fenton et al. 2005). This set of species that negatively responded to edge creation may be used as indicators of undisturbed forests, where structural attributes and microhabitats have diversified over time resulting in increased species colonization and stable microclimatic conditions (Fenton & Bergeron 2008; Pharo & Lindenmayer 2009). The absence of these species from both residual cores and edges may also be explained by the alteration of the regional dispersal processes as a result of fragmentation of the forest landscape. Their metapopulation dynamics was disrupted in response to the increased dispersal distance that change regional distribution patterns but also local abundance of the species (Löbel et al. 2006).

In contrast, some bryophyte species [7 liverworts (71% colonists) and 16 true mosses (68% acrocarps)] were positively affected by edge creation. These edge-preferring species have a high tolerance of disturbance but also have opportunistic strategies such as high dispersal capacities and large niche breathe (c.f. Baldwin & Bradfield 2005; c.f. Ewers & Didham 2006). Therefore, not surprisingly, edges house more acrocarps and shuttle species (*sensu* Paquette et al. 2016 adapted from During 1992), which inhabit long-lived substrates such as granitic rocks and with both high sexual and vegetative reproduction effort. Edge-indicator species are linked to dry and exposed substrates, especially at the south-facing edges, which are characterized by species inhabiting rocky substrates with marked humidity variations (e.g. *Dicranum fulvum*, *Dicranum spurium*, *Orthotrichum speciosum*). The more humid and colder conditions of north-facing edges (Hylander 2005; Stewart & Mallik 2006) are more favourable for species vulnerable to dry microclimates such as liverworts (Esseen & Renhorn 1998; Moen & Jonsson 2003), which explains the similarity in community composition between north-facing edges and undisturbed cores (c.f. CA analysis). However, our north- and south-facing edges did not differ in terms of humidity (Appendix F), due to either the short six month period used to measure microclimatic variables or to an inherent property of edges in boreal black spruce forests prone wildfires. Indeed, in such ecosystems, the rapid recovery of *Sphagnum* spp. in response to post-fire canopy opening brings humidity and limits soil exposition to sunlight, reducing differences on either side of the edge. The *Alnus* spp. belt surrounding some of our residual patches can also have a similar effect.

Together, these results suggest that the bryophyte community of residual cores were more similar to edges than to undisturbed cores communities, and therefore there is little or no core. However, the inherent properties of boreal black spruce forest described above, together with the richness of liverworts and overall community composition of north edges indicated by the CA evoke the question: are these residual patches essentially edges or are do the edges have core characteristics? We cannot answer the question but as the cores do not meet our definition of a “true core”, we reject our second hypothesis.

3.6.2 Bryophyte response to edge creation is mediated by residual patch stand structure

Studies report that edge influence diminish over time and with increasing residual patch area, shape homogeneity and proximity to forest sources (i.e. forest influence), which result in dynamic boundaries (Ewers & Didham 2006; Laurance 2008; Baker et al. 2013; Harper et al. 2014). Consequently, we hypothesized that old and large residual patches would house a core community more similar to undisturbed cores than younger and smaller ones. Our results indicate the opposite, as even in old (more than 3000 years old) or large (from 4 ha to more than 10 ha) residual cores' bryophyte communities remain consistently distinct from undisturbed core communities. Moreover, counterintuitively, similarity between residual and undisturbed cores is negatively correlated with residual patch size and the other spatial and temporal characteristics of patches were not influential on community patterns. As stressed by Jokimäki et al. (1998) for invertebrates and St-Laurent et al. (2007) for birds and small mammals in boreal forests, these results suggest that bryophyte community composition is primarily driven by structural attributes rather than by temporal or spatial characteristics of the stand.

In parallel, in spite of the dissimilarity between residual and undisturbed cores, regardless of patch age, larger patches exhibited more distinct core and edge communities. In boreal forest, both Jalonen & Vanha-Majamaa (2001) and Moen & Jonsson (2003) have demonstrated that small residual patches (less than 1 ha) are strongly influenced by edge creation leading to bryophyte richness decrease and a decline in cover of liverworts. In this study the threshold value below which similarity between cores and edges increased was 3 ha. For Baldwin & Bradfield (2007) in temperate rain-forests, 3 ha also represents a threshold size that provides a number of microhabitats capable of sustaining a diverse array of bryophyte functional groups. Our fourth hypothesis is therefore only partially validated: even if patches over 3 ha displayed contrasting bryophyte core and edge communities, all of our residual patches did not contain "true cores" and housed communities that were more similar to residual edges than to undisturbed cores. Larger patches can hold a broader set of microhabitats (Baldwin & Bradfield 2007) and larger trees for microhabitat generation (e.g. dead wood; Moen & Jonsson 2003). Consequently, the importance of the patch area is indirect and carried by stand structural attributes that mediate bryophyte diversity after edge creation.

3.6.3 Implications for conservation and management

The apparent dissimilarity between undisturbed and residual cores in terms of environmental conditions but also community composition leads us to contradict some previous studies that have determined the DEI of bryophytes and lichens in temperate and boreal Canadian forests at 50 to 60 m from the edge (Rhéault 2003; Baldwin & Bradfield 2005; Boudreault et al. 2008). The highest similarity between residual cores and edges bryophyte communities was identified in patches with 50 m buffer zone width, however we demonstrate that 11-ha residual patches (with 170 m buffer zone width) house a bryophyte community distinct of undisturbed cores. While both the initial community composition and environmental variables are unknown, long-lived compositional and environmental dissimilarities between residual patches and undisturbed forests remain visible up to 170 m inside residual patches, a possible indication of the DEI. Consequently, as also indicated by Barbé et al. (in revision, refers to the Chapter II), the conservation of the most infrequent and sensitive species requires the preservation of undisturbed forest stands. The presence of significant edge influence in natural communities suggests that the real challenge in planning retention in boreal forests is not to avoid edge influence but to rather design retention patches in such a way as bryophyte compositional changes in response to anthropogenic edges creation remain inside the range of compositional changes generated by natural edges. As schematised in Figure 3.5, in the context of ecosystem based management we aim to create retention patches inside the limits of natural edge creation as (2) or (3), although the habitat is essentially composed of edge, and to avoid to create retention patches as (4).

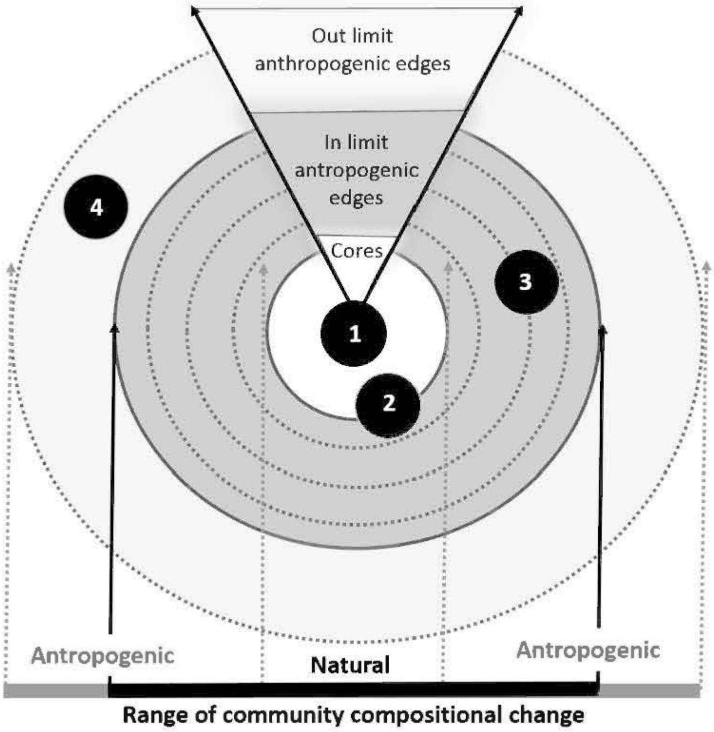

Figure 3.5 Conceptual schema of the changes in bryophyte community composition in response to natural (i.e., wildfire, insect outbreaks) and anthropogenic (i.e., forestry) edge creation. From the interior to the exterior of the successive ellipses: undisturbed forest cores to edges within and outside boundaries of the edges created by natural disturbances. Forest stands are represented by black circles. (1) Forest stands such as undisturbed that house a disturbance sensitive bryophyte community; residual patches situated inside the white circle are composed of "true cores" and support communities isolated from edge influence. (2) Other residual patches containing both a core community that has changed inside the range of natural edge creation. (3) Residual patches that are essentially composed of edge but that house a community that has changed inside the range of natural edge creation. (4) Forest stands that have experienced a change in community composition that is outside the range of natural edge creation.

3.7 Conclusions

The response of bryophytes to natural edge creation gives us new insights and provides a "true control" to better appreciate their response to edge influence. Our study can be used as a guide to design retention patches where community compositional changes remain inside the natural disturbance boundaries. Exceeding the boundaries of the natural range of variability associated with edge creation will cause compositional but also environmental changes outside the natural limit, which can threaten the resilience of the ecosystem. Species compositional change in response to edge creation is not only a character of anthropogenic edges, but is a natural component of the boreal forest dynamic. Finally, this study also re-emphasizes that some species can only be maintained by the conservation of old growth stands, as they are not found in edges but neither in cores of residual forest patches and therefore sustainable forest management needs to include both residual forest stands and undisturbed old growth forests.

3.8 Acknowledgements

Funding for this project was provided by the Université du Québec en Abitibi-Témiscamingue (UQAT) and the National Science and Engineering Research Council (NSERC) in partnership with Tembec, Eacom and Resolute Forest Products.

The authors especially thank Chafi Chaieb who has provided bryophyte samples from the undisturbed forest sites and Julie Arseneault for their identification. Authors also sincerely thank Emilie E. Chavel and Louiza Moussaoui who have provided some of the environmental data used in this paper; Myriam Paquette, Flora Joubier, Louis Dubois and Philippe Heine for their field assistance; Danielle Charron, Philippe Duval, Raynald Julien, Danièle Laporte, Marie-Hélène Longpré, and Michel Poitras for their technical support; and Jean Faubert for his precious help in the identification of the most difficult bryophyte sample.

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CHAPITRE IV

SO CLOSE AND YET SO FAR AWAY: LONG DISTANCE DISPERSAL EVENTS GOVERN BRYOPHYTE METACOMMUNITY RE-ASSEMBLY

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***Journal of Ecology* 104(6): 1707-1719**

4.1 Abstract

1. Metapopulation dynamics have been used to explain bryophyte dispersal patterns and they predict that population abundances vary with the spatial distribution of habitat and with species traits. However, results from stand and landscape studies are contradictory as both distance dependant and independent patterns have been found. These studies have typically included only a few species, which limits inter species comparison. It is the time to investigate bryophyte dispersal at the metacommunity scale.

2. We studied bryophyte dispersal patterns in a system made up of burned matrices containing unburned residual forest patches. The importance of short versus long distance dispersal was examined by comparing extant and propagule rain communities in residual forest patches of three fire sites using both species and life strategies.

3. Extant and propagule rain communities were distinct. Several propagule rain species, of all life strategies, did not originate from the closest extant community, suggesting that regional dispersal events are important, following the inverse isolation hypothesis.

4. Temporal, spatial and structural characteristics of the environment had a greater influence on dispersal than distance, which only influenced similarity patterns at the regional scale, highlighting the importance of propagule source attributes for the conservation of bryophyte metacommunities.

5. *Synthesis*. Long distance dispersal may be the rule and not the exception in bryophyte metacommunities. Therefore bryophyte metacommunity dynamics depend on several dispersal scales, and residual forest patches can contribute both to local and regional diaspore clouds. Species' environmental tolerance during establishment and their ability to produce copious amounts of spores may be more important filters in bryophyte metacommunity dynamics than dispersal distance.

Key-words: bryophyte, geographic distance, inverse isolation hypothesis, life strategies, local dispersal, metapopulation theory, propagule cloud, regional dispersal.

4.2 Résumé

1. La dynamique des métapopulations est souvent utilisée pour expliquer les patrons de dispersion des bryophytes et prédit que l'abondance des populations varie avec la distribution spatiale de l'habitat et les traits des espèces. Cependant, des études réalisées à l'échelle du peuplement et du paysage rapportent des résultats ambivalents, démontrant tantôt la distance-dépendance et tantôt la distance-indépendance des patrons de dispersion des bryophytes. Ces études impliquent généralement un nombre restreint d'espèces limitant les comparaisons interspécifiques. L'heure est venue d'étudier la dispersion des bryophytes à l'échelle de la métacommunauté entière.

2. Les patrons de dispersion des bryophytes ont été étudiés dans trois sites de feux composés d'une mosaïque de parcelles brûlées et d'îlots résiduels non brûlés. L'importance relative de la dispersion à courte et longue distances fut examinée en comparant la communauté bryophytique présente « sur place » dans les îlots résiduels à la composition de la pluie de propagules interceptée dans ces mêmes îlots résiduels.

3. La communauté présente « sur place » et la pluie de propagules étaient distinctes. Plusieurs espèces de la pluie de propagules n'étaient pas originaires de la communauté « sur place » la plus proche, suggérant l'importance de la dispersion régionale, en accord avec l'hypothèse d'isolement inverse.

4. Les patrons de dispersion des bryophytes sont davantage influencés par les caractéristiques temporelles, spatiales et structurelles de l'environnement que par la distance géographique, qui influence seulement les patrons à l'échelle régionale. Cela souligne l'importance des caractéristiques des îlots résiduels i.e. sources

potentielles de propagules pour la conservation des métacommunautés bryophytiques.

5. *Synthèse*. La dispersion à longue distance pourrait être la règle et non l'exception chez les bryophytes. Ainsi, la métacommunauté bryophytique dépend de plusieurs échelles de dispersion et les îlots résiduels post-feu contribuent à la fois à la pluie de propagules locale et régionale. La dynamique des métacommunautés de bryophytes serait donc dépendante de la tolérance environnementale des espèces lors de l'établissement et de leur capacité à produire de larges quantités de spores davantage que de la distance géographique.

Mots-clés : bryophyte, dispersion locale, dispersion régionale, distance géographique, hypothèse d'isolement inverse, nuage de propagules, stratégie de vie, théorie des métapopulations.

4.3 Introduction

Dispersal is a key process in regulating population dynamics, along with establishment and persistence (Clobert *et al.* 2012). This is particularly true for species whose habitat is spatially discontinuous, either due to natural or anthropogenic fragmentation (e.g. forest fire or forest harvest) or its inherently patchy nature (e.g. deadwood) (Johst, Brandl & Eber 2002). Local populations of these species are spatially segregated from others in an unhospitable matrix and their persistence through time depends on a positive balance between population colonization and extinction, i.e. the metapopulation concept (Hanski 1998; Freckleton & Watkinson 2002). Populations are not isolated but exchange migrants with neighbouring populations at a frequency that varies with matrix permeability and mean dispersal distance (Snäll, Ribeiro & Rydin 2003; Löbel, Snäll & Rydin 2006; Johst *et al.* 2011). This concept can be extended to the metacommunity when multiple species are considered (Jacobson & Peres-Neto 2010).

It has long been thought that short distance dispersal (SDD) dominates most metacommunities following the theory of island biogeography (MacArthur & Wilson 1967), with long distance dispersal (LDD) occurring only sporadically. However, it has also been recently suggested that the "inverse isolation hypothesis" is more appropriate for species with fat dispersal tails and that LDD is therefore more frequent than previously expected (Klein, Lavigne & Gouyon 2006; Szövényi, Sundberg & Shaw 2012; Sundberg 2013). This theory suggests that in sites isolated from diaspore sources a higher proportion of diaspores originate from a large set of distant sources rather than from the nearest source. This leads to high genetic variation and species richness at these isolated sites (Sundberg 2005; Klein, Lavigne & Gouyon 2006).

Bryophytes are an interesting group for studying dispersal as their habitats are spatially and temporally patchy, they have large distribution ranges (Söderström 1998), their small and light spores (generally < 20 µm) are primarily dispersed by the wind (During & van Tooren 1987), and they have rapid population colonisation/extinction rates (Snäll, Ehrlén & Rydin 2005). However, bryophyte dispersal is not yet clearly understood. Two paradigms are suggested: (1) bryophyte dispersal is spatially limited to the local scale (Miles & Longton 1992; Laaka-Lindberg, Korpelainen & Pohjamo 2006) and (2) as small bryophyte spores are produced in great numbers, the few percent dispersed beyond the local scale represent significant numbers (During & van Tooren 1987). In other studies, distance independent dispersal has also been found (Sundberg 2013; Lönnell, Jonsson & Hylander 2014) with the suggestion that local habitat characteristics, such as microsite limitation (i.e number of logs, quality of the substrate, Hylander 2009; Wiklund & Rydin 2004) and physical barriers limiting wind availability (i.e. canopy or stand closure, Fenton & Bergeron 2006; Sundberg 2013), may influence dispersal and colonisation. However studies dealing with LDD remain sparse and typically use proxies, such as the genetic similarity of disjunct populations (Studlar, Eddy & Spencer 2007; Lewis, Rozzi & Goffinet 2014). To our knowledge this study is the first to examine the relative importance of short and long distance dispersal (i.e. SDD vs LDD) at the community level.

An interesting natural system for studying bryophyte metacommunity dynamics is found in boreal forests. Forest fires are the dominant disturbance type in North American boreal forests and they heterogeneously impact the landscape (Perera *et al.* 2009; Carlson, Reich & Frelich 2011) leaving patches of unburnt forest ("residual patches") that have partially or entirely escaped fire (Burton *et al.* 2008; Ouarmim *et al.* 2015). They may act as refuges for species during the fire disturbance and as sources of propagules during recolonisation after the fire, particularly for species with limited dispersal capacities extirpated from the disturbed matrix. Consequently dispersal of species from these potential sources to new suitable areas may govern the long-term survival of the metacommunity, particularly in a dynamic landscape. In this study we examine three large fires each with several residual forest patches nested within them across a 10 000 km^2 region.

The general objective of this study was to determine the relative contribution of the extant bryophyte community to the propagule rain at a given site. To achieve this, three specific objectives are addressed. First, the propagule rain community composition is compared to the extant bryophyte community in both the burned matrix and the residual forest patches. Second, we aim to determine whether geographic proximity results in greater compositional similarity between propagule and extant communities. Our third objective is to investigate the relative roles of geographic distance and environmental characteristics of the residual forest patches in driving the dispersal patterns. Finally, in a fourth objective community composition among propagule rains is compared. This comparison eliminates the bias associated with the emergence method used to germinate propagules, which only considers the species able to germinate on an artificial substrate.

We hypothesise that the species found in the propagule rain community reflect the extant community composition in terms of species richness and in proportion of species life forms and life strategies (H1). We expect that the similarity between the propagule rain and the extant community will be negatively correlated with geographic proximity and consequently that SDD occurs more than LDD (H2). We also expect that the similarity between the propagule rain and extant communities will be partially explained by spatial, temporal and structural attributes of the residual forest patches in addition to geographic distance at local scales (H3). Finally, we do not expect a relationship between the similarity of the propagule rain community in two sites and their geographic proximity (H4). Indeed, SDD dominance would produce as many propagule clouds as propagule sources in the landscape and low similarity of propagule clouds regardless of the distance between them.

4.4 Materials and methods

4.4.1 Study area

The study was conducted in the boreal forest in western Québec, Canada, within the black spruce (*Picea mariana* Mill., Briton)-feather moss (*Pleurozium schreberi* (Brid.) Mitt.) forest bioclimatic domain (Grondin 1996). Average annual temperature and precipitation are respectively 1 °C and 927.8 mm (1981 to 2010), recorded at the nearest weather station, Lebel-sur-Quévillon, Québec (55 to 140 km from sites; Environment Canada 2015). Stands are dominated by *P. mariana* with *Pinus banksiana* Lamb., *Populus tremuloides* Michx, *Abies balsamea* (L.) Mill., and *Betula papyrifera* Marshall as secondary species. The understory is dominated by ericaceous species [*e.g. Rhododendron groenlandicum* (Oeder) Kron & Judd] and bryophyte species (primarily sphagna and feather mosses).

Natural fires dominate the disturbance regime, and the average forest age is approximately 140 years (Bergeron *et al.* 2002). Fires burn unevenly and leave residual patches of unburned forests within the burned matrix (Madoui *et al.* 2010). The proportion of residual patches varies with the total area burned, but does not exceed 8% of the burned area, with five one-ha or smaller residual patches per 100 ha (median), situated from 0 to 700 m from each other (Perron, Bélanger & Vaillancourt 2008).

4.4.2 Site selection and sampling of bryophytes and environmental variables

Three fires in natural boreal black spruce forest were chosen in the North of Québec (50° 56' N, 77° 53' W; 49° 75' N, 76° 29' W; 49° 91' N, 76° 13' W). Fires varied in age from 18 to 29 years (i.e. two have occurred in 1997 and one in 1986) and in size from 2 537 to 25 516 ha (SOPFEU 2011). Within each fire we identified three residual forest patches, and three burned matrix areas, for a total of nine residual forest patches and nine areas of burned matrix. Residual forest patches were all dominated by black spruce but varied in size, age, isolation and forest structure (Table 4.1).

Table 4.1 Temporal, spatial and structural variables measured in each of the residual forest patch and burned matrix area in the study. Isolation and canopy openness are means ± standard errors, all other variables are absolute values.

			Temporal variables		Spatial variables				Forest structure variables		
Fire	Sites[1]	Position	Time since fire (year)	Estimated age of forest (year)	Area (ha)	Distance from closer continuous forest (m)	Distance to closest residual patch (m)	Isolation (m)	Canopy openness (%)	Trees and snags density (number of stems/ha)	Holdridge complexity indices (C_{HLC})
LQY	RP8	Edge	18	140	3.69	1360	174	86.2±121.3	44.10±5.14	1100	99.99
LQY	RP8	Core	18	140	3.69	1389	157	209.4±108.2	45.14±13.55	1525	210.78
LQY	RP9	Edge	18	240	11.11	557	1943	555.6±136.5	48.96±17.77	950	94.85
LQY	RP9	Core	18	240	11.11	496	2000	765.6±264.8	29.86±4.21	1375	144.04
LQY	RP10	Edge	18	173	2.69	1209	114	73±86.8	15.28±5.24	1000	122.24
LQY	RP10	Core	18	173	2.69	1134	214	245.2±104.9	29.17±6.83	1325	146.69
LQY	B1	Fire	18	18	0.015	984	658	634±210.1	59.72±22.88	314.3	0
LQY	B2	Fire	18	18	0.015	1536	393	275.6±99.6	62.84±17.81	314.3	0
LQY	B3	Fire	18	18	0.015	978	224	323.8±143.4	69.44±11.47	314.3	0
LQO	RP16	Edge	29	82	4.24	829	110	192±248.1	9.72±9.68	650	33.34
LQO	RP16	Core	29	82	4.24	883	165	333.8±208.5	15.63±13.78	2750	587.58
LQO	RP18	Edge	29	80	0.05	555	90	104±52.7	47.92±17.77	1050	62.30
LQO	RP18	Core	29	80	0.05	554	91	114.6±52.7	12.85±6.69	2200	329.82
LQO	RP20	Edge	29	171	2.2	868	535	284.8±139.4	36.46±18.52	1250	183.45
LQO	RP20	Core	29	171	2.2	949	479	376.6±141.6	26.74±6.61	1875	582.19
LQO	B1	Fire	29	29	0.015	1550	717	186.4±35.1	37.85±7.31	212.5	0
LQO	B2	Fire	29	29	0.015	480	474	328.4±140.6	46.18±25.00	212.5	0
LQO	B3	Fire	29	29	0.015	670	546	551.8±226.4	25.35±9.84	212.5	0
MAT	RP27	Edge	18	183	0.17	1591	100	841.8±479.8	52.08±29.70	1400	92.45
MAT	RP27	Core	18	183	0.17	1561	113	879.8±473.2	16.67±8.13	1925	286.98
MAT	RP28	Edge	18	216	1.36	770	230	561.8±774.5	14.93±9.68	800	40.62
MAT	RP28	Core	18	216	1.36	835	198	651.4±775.4	27.08±1.04	1525	294.48
MAT	RP30	Edge	18	79	0.15	1672	93	618.4±415.2	34.72±5.74	500	8.17
MAT	RP30	Core	18	79	0.15	1678	101	645.8±411.3	21.18±6.77	1025	28.00
MAT	B1	Edge	18	18	0.015	313	7195	815.8±137.3	62.85±18.35	240	0
MAT	B2	Fire	18	18	0.015	2290	1101	1128.2±312.2	42.36±7.39	240	0
MAT	B3	Fire	18	18	0.015	1772	1054	1303.2±360.9	55.55±35.62	240	0

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[1] B, burned matrix area; RP, residual forest patch.

The extant bryophyte community was sampled in 5 × 10 m rectangular plots (50 m²) in the residual forest patches and in the burned matrix during the summer of 2013. Within each residual forest patch, a north-south linear transect was established, crossing the patch from edge to edge (Figure 4.1). In the three residual forest patches smaller than 1 ha, three plots at least 10 m apart were placed along this linear transect, two at the edges of the patch and one in the core of the patch. Two positions were subsequently obtained: edge and core. In the six residual forest patches larger than 1 ha, a second core plot was added for a total of four plots. Three rectangular plots of 50 m² were placed in the burned matrix of each fire as far as possible from all residual forest patches (from 200 to 8 500 m). In total, the extant bryophyte community was sampled in 42 rectangular plots spread across three fires (i.e. 33 in the residual patches and 9 in the burned matrix). Sampling of the extant bryophyte community proceeded by a modified form of "floristic habitat sampling" (Newmaster *et al.* 2005), where all the habitats are searched for species with no specific reference to area. Here it was restricted to the 50 m² plots and all microhabitats (e.g. coarse woody debris, tree bases, peat mounds and water holes) within each plot were sampled and the bryophytes present placed in individually marked paper bags. Bryophyte samples were dried and stored until identification.

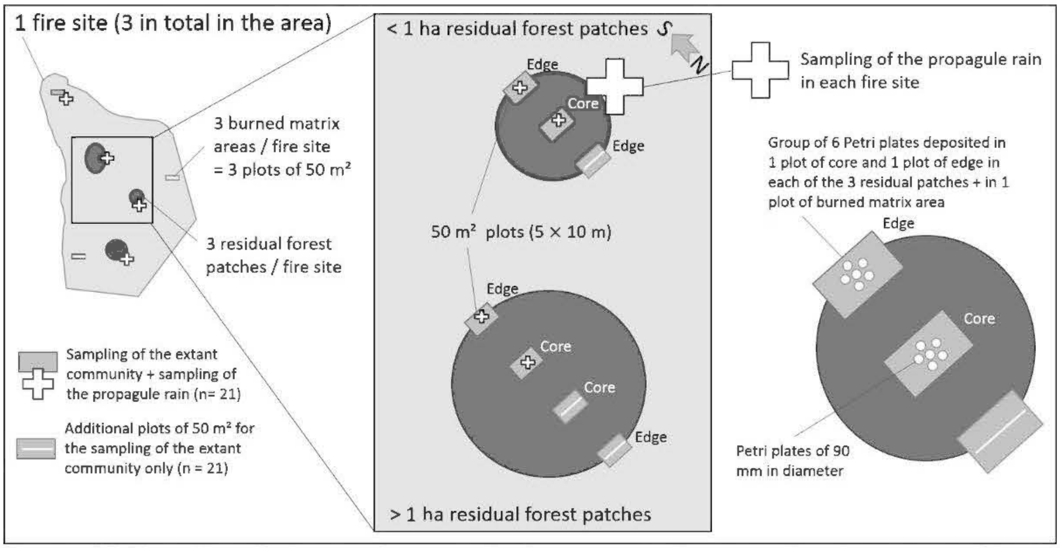

Figure 4.1 Sampling design used to sample the extant and propagule rain communities of bryophytes in boreal black spruce-feather moss forest of western Québec, Canada.

Propagule rain was sampled by the "emergence method" (Rudolph 1970; Ross-Davis & Frego 2004). Petri plate traps (90 mm in diameter) were filled with 78.5 cm^2 of nutrient agar made in sterile laboratory conditions [Parker Thompson's basal nutrient medium of Klekowski (1969), described by *C-Fern* Project © (1995-2014)]. All bryophyte propagule types were included (i.e. spores, gemmae and possible vegetative fragments dispersed *via* the air; During & van Tooren 1987). In each residual forest patch, a group of six Petri plates was placed in the centre of one core and one edge 50 m^2 extant community plot. In addition, a group of six Petri plates was also placed in one of the three burned matrix plots per fire. Propagule rain was trapped during four sessions: the 11th and 16th August (summer) and the 4th and 13th September (autumn) of 2013 as well as the 9th and 11th June (spring) and the 14th and 19th September (autumn) of 2014. Two days are required in each trapping session due to the distance among the fire sites (average of 128 km). The total number of Petri plates exposed over the four sessions is 504 [$(6 \times 2 \times 9 + 3 \times 6) \times 4$]. Petri plates were deposited in the forest for six hours from early morning when capsules are moistened by dew to early afternoon when capsules are dried and temperatures are the warmest. During this period propagule release is triggered by hydration-dehydration of the capsule and elators (Vanderpoorten and Goffinet 2009). Petri plates were exposed on days that were both sunny and windy (wind speeds between 3 and 10 km/h; i.e. optimal conditions for drying and explosion of the capsule for propagule release; Glime 2013). After exposition, the Petri plates were covered and placed in germination chambers for six months, under fluorescent light tubes with continuous spectrum Verilux ® (48" and 32 Watt) with a 12 h/12 h light/dark regime. Germination chamber temperature was maintained at 22°C. Petri plates were kept moist by misting with deionized water. When the nutrient agar became too thin it was transferred onto a new Petri plate. Development of bryophyte gametophytes was assessed twice a week to follow germination patterns and to control potential bacterial or fungal contaminations. Minor contaminations were manually removed from the nutrient agar with forceps. In the case of a major contamination (i.e. all of the Petri plate was infected and survival of the protonemata was compromised), protonemata were removed from the plate, bathed in deionised water and transplanted onto a new Petri plate. Three control Petri plates with virgin nutrient agar were placed in the germination chambers every three months for the duration of the 6-month emergence period to identify potential contaminants (air-borne bryophyte propagules). No bryophyte species developed on any of the control plates, indicating that sample plates had not been contaminated during the laboratory growing period. Bryophyte culture with this method was generally successful however, the principal bias is that only the species able to germinate in the Petri plates were accounted for.

All bryophytes were identified in the laboratory following Faubert (2012, 2013, 2014) except for *Sphagnum subtile* (Russ.) Warnst., which follows the nomenclature of the Flora of North America Editorial Committee (2007). Species were classified by taxonomy and growth form (i.e. liverwort, acrocarp, pleurocarp, and *Sphagnum*; Meusel 1935) and by life strategy following During (1992) (Appendix H). Species' reproductive state in the field was also noted (i.e. sterile or fertile with presence of sporophyte or gemmae, Appendix I). Bryophyte species richness and frequency were calculated per plot for the extant community and per group of six Petri plates for the propagule rain (Appendices I and J). The frequency of each species per plot and per group of six Petri plates was defined as the number of microhabitats where a species was found per plot and as the number of Petri plates of the group where a species was recorded. In the Petri plates, one individual refers to a protonema in one Petri plate. While one protonema can generate several stems making it difficult to distinguish individuals, we took monthly photographs of the plates, and used these pictures to identify individuals. Due to the artificial growing conditions in the Petri plates, bryophytes had unusual characteristics, consequently certain specimens were only identified to genus, particularly sphagna and members of the genera *Ditrichum* spp., *Grimmia* spp., *Pohlia* spp., and *Polytrichum* spp. Vouchers are conserved at the University of Québec in Abitibi-Témiscamingue, Qc, Canada.

The roles of temporal, spatial and forest structure variables in explaining patterns of bryophyte dispersal were evaluated (Table 4.1). Temporal variables included time since fire (years), determined from the SOPFEU digital map (2011) and the age of the forest in the residual patch. The minimum stand age of the forest in the residual patches (years) was estimated by coring ten dominant trees in the core of the residual forest patches with an increment corer and counting the number of rings. The age of the oldest tree was established as the minimum stand age. Spatial variables were calculated using ArcGis 10.2 (ESRI 2013) and included residual patch area (ha), distance to the closest residual patch (m), shortest distance to continuous forest (m), and isolation (mean of five distances between the point of interest and all forest sources, i.e. residual forest patch, continuous forest, residual riparian forest; m). Forest structure variables of the residual patches, i.e. canopy openness (%), tree and snag density (number of stems / ha) and stand complexity, were measured in the field during the summer of 2013. Canopy openness was measured using a densiometer, a scored concave mirror, at the level of the bryophyte layer (5 to 10 cm above the forest floor). The measure was taken in three randomly chosen positions in each rectangular plot and averaged. Tree/snag density was calculated in 11.28 m radius (400 m^2) circular plots at the core of each residual patch and with the line intersect method at the edge of each residual patch. All trees and snags with DBH > 9 cm were included. Stand complexity was estimated using the modified Holdridge index (C_{HCL}) (Holdridge *et al.* 1971) computed only on trees with DBH > 9 cm (Lugo *et al.* 1978).

4.4.3 Data analyses

Data analyses of species richness, assemblage and similarity were performed on the extant and propagule rain communities found in the 21 plots where Petri plates had been placed (i.e. core and edge plots in three residual forest patches per fire, and one burned matrix plot per fire) plus two additional burned matrix plots per fire, for a total of 27 plots. The additional burned matrix plots were included for better representation of the extant community in this environment.

R software 3.2.1 (R-Development-Core-Team 2015) was used for statistical analyses with a significance level of $\alpha = 0.05$. Results with *p*-values between 0.1 and 0.05 are also discussed as they suggest trends in the data, which are important to consider in order to identify fine scale biological responses (Murtaugh 2014; de Valpine 2014).

As we used a nested design (plots of residual forests and burned matrix in fires) we tested whether the spatial structure of the sampling influenced the models in the different analyses with a LogLik test (Pinherio & Bates 1995). In cases where the spatial structure did not influence the models, the simpler model without random spatial effects (linear model, lm) was chosen in the spirit of parsimony. When the spatial structure had a significant effect, we used linear mixed models (lme), which are equivalent to lm for a structured dataset.

Comparisons of the composition of extant and propagule rain communities (objective 1) were made using rank abundance curves (Magurran 1988) performed with the package "BiodiversityR" 2.5-3 (Kindt 2015). The overall composition of the two communities was summarised in a detrended correspondence analysis (DCA; Hill & Gauch 1980; Lepš & Šmilauer 2003) *on p*resence-absence data of species occurring more than five times in the entire data-set using the package "vegan" 2.3-0 (Oksanen *et al.* 2015). Specimens identified only to genus and for whom other species of the same genus were present were removed from the DCA analysis as well as from the subsequent analyses of similarity, as the index was calculated from DCA. The subsequent ordination matrix contained 65 species and 48 sites (27 plots of extant community and 21 plots of propagule rain). The significance of the resultant pattern was determined by Multi-Response Permutation Procedure (MRPP) on 2000 permutations.

In order to address the second objective, to determine the relationship between geographic distance and compositional similarity of the propagule rain and extant communities, Jaccard's index of similarity was used. Jaccard's index was chosen because it compares the number of shared species to the total number of species in the combined assemblage while Sørensen's index compares the number of shared species to the mean number of species in a single assemblage; Jost, Chao & Chazdon 2011). Jaccard's index of similarity was calculated between each propagule rain groups (n = 21) and all the extant community plots where Petri plates were placed (n = 21). Similarity between the propagule rain and the extant community was then examined in function of the geographic distance between them. Subsequently, in order to focus on the dispersal into the disturbed matrix, the same analysis was completed considering only the propagule rain of the burned matrix (n = 3) but with all the extant community plots (n = 21). Geographic distances were classified into spatial scales modified from Ross-Davis & Frego (2004): 1. *In situ*, propagules of the extant community in a given sampling point (50 m^2 plot of group of Petri plates); 2. Local, propagules from the closest potential source, i.e. the closest residual patch (650-1100 m); 3. Intra-fire, propagules from all residual patches in a given fire (740-8400 m); 4. Inter-fire, propagules from communities in all residual patches from the other fires (10-130 km). The intra- and inter-fire scales together refer to the regional spatial scale. The spatial structure of the sampling design influenced the results of this analysis, as indicated by the LogLik test, and community similarity among spatial scales was therefore compared using linear mixed models (lme) performed with the package "nlme" 3.1-121 (Pinheiro 2015).

Patterns of individual species in the propagule rain of burned matrices were also examined, to determine from which distance they could have been dispersed. For this comparison, the origin of the species in the propagule rain of the burned matrices (n = 3) was determined in function of the extant community in all the plots, i.e. 42 plots (21 plots where Petri plates were placed plus the 21 additional plots of the linear transect and of the burned matrix; see sampling design for details in

Figure 4.1). The additional plots increased the sampling of the extant community to better represent potential propagule sources in the surrounding landscape. For each record of each species found in the propagule rain of each fire we determined in which extant community plots it was also found. The spatial scale (i.e. *in situ*, local, regional) relative to the record in question was noted. If a species of the propagule rain was encountered at two spatial scales in the extant community, each distance was scored in the analysis. This analysis generated a matrix of species × spatial scale, where the presence or absence of each species at each spatial scale is indicated, which indicates the number of species that potentially dispersed from each spatial scale in each fire, for "total" (all species grouped together, n = 21), "perennial" (n = 9) and "colonist" (n = 10) species groups. The three fires were then averaged to have a mean number of species dispersed per spatial scale. In each group (i.e. total, perennial or colonist) the mean number of species was then divided by the number of plots sampled at each spatial scale in the three fires pooled together (n *in situ* = 3; n closest-RP = 11; n intra fire = 28; n inter fire = 84 i.e. N = 126) in order to take into account the different number of potential propagule sources analysed at each spatial scale. The value obtained was reported as a percent of the total number of species present per plot in the four spatial scales. This actual frequency was then compared to a theoretical expected frequency. Expected frequency was calculated by multiplying the sum of the mean number of species present per plot in each spatial scale by the number of plots that could be potential propagule sources in the target spatial scale and dividing by the total number of potential propagule sources available (N). We therefore obtained an expected frequency specific to each spatial scale weighted by the number of plots participating in the propagule rain at this spatial scale. The difference between actual and expected frequencies for total, perennial and colonist species was then calculated and tested for significance with a Fisher test.

In the third objective we assessed the relative roles of geographic distance and nine environmental variables (divided into temporal, spatial and forest structure classes) in influencing the similarity between extant community where Petri plates were placed (n = 21) and propagule rain community of burned matrix (n = 3) at different spatial scales. Again, Jaccard's index of similarity represented the similarity between the extant and propagule rain communities. In this analysis, we only considered the propagule rain of the burned matrices in order to assess the relative importance of geographic distance compared to environmental variables in bryophyte dispersal after disturbance. We tested the pertinence of including a quadratic relationship between similarity and distance but the inclusion of this term did not result in a significant increase in explanatory power. In the spirit of parsimony, we therefore retained a linear relationship with geographic distance in our models. A model selection procedure using 18 candidate models plus the null model was performed. The first model tested geographic distance (distance between sites) and the nine following models tested each of the variables of the temporal (2 models), the spatial (4 models) and the structure (3 models) classes individually (Appendix K). The eight other models tested biologically relevant combinations of these variables and interaction terms among several variables in each class. The global model combined together eight of the variables of the four different classes plus an interaction term. Conflict between certain variables prevented the use of all 10 variables in the global model, even after algorithm optimization. Here we define the global model as the most complex of the model set. The response variable "similarity", expressed as a proportion follows a normal distribution and was used without transformation in linear mixed models (lme) with random effects, performed with the package "nlme" 3.1-121 (Pinheiro 2015). The explanatory variable dataset was standardised (on columns) to account for the different scales of measurement. Candidate models were ranked based on the Akaike's Information Criterion corrected for small sample size (AICc) (Burnham & Anderson 2002) using the package AICcmodavg 2.0-3 (Mazerolle 2015). Models with a delta AICc (ΔAICc) > 2.0 were considered to have substantially lower empirical support (Burnham & Anderson 2002). The model with the lowest delta AICc was considered as the most parsimonious and indicated the environmental variables that best explained variations in community similarity. In order to illustrate the effect of each explanatory variable of the most parsimonious model, multimodel inference was used. We obtained 95% confidence intervals and model predictions using the modavgpred function of the AICcmodavg 2.0-3 package (Mazerolle 2015). Variables with 95% confidence intervals excluding 0 have a significant effect on the explanatory variable (community similarity) and their predicted values were subsequently plotted against values of the explanatory variable. An estimate of model adjustment was indicated by Spearman's Rho. These analyses were carried out first on all dispersal scales combined to identify a general dispersal pattern and secondly, intra- and inter-fire scales of dispersal were examined individually.

Finally, the influence of geographic distance on similarity was also examined in only the propagule rain, to eliminate the bias associated with the emergence method (objective 4). The 21 plots where Petri plates were placed were again used in the analysis. We calculated Jaccard's similarity index to determine the relationship between the similarity of the propagule rain in different plots and their geographic distance, which was divided into three categories: < 1.5 km (i.e. propagules rain communities at the *in situ* and local scales), between 1.5 and 10 km (i.e. propagule rain communities at intra-fire scale) and > 10 km (i.e. propagule rain communities at inter-fire scale). The spatial structure of the sampling did not influence this analysis, therefore the relationship between geographic distance and community similarity was tested by a linear model (lm), followed by Tukey HSD tests using the package "ade4" 1.7-2 (Dray, Dufour & Thioulouse 2015).

4.5 Results

4.5.1 Compositional similarity between the extant community and the propagule rain

Of the 123 taxa found, 23 were present in both the extant community and the propagule rain. Nineteen species were exclusively found in the propagule rain, and of these 32% were colonist, 37% were perennial and 26% were shuttle (Appendices I and J). In the extant community, 67% of the species sampled were seen fertile at least once and 28% of these fertile species were encountered in the propagule rain (Appendix I). In terms of species richness the extant community was dominated by pleurocarps whereas acrocarps dominated the propagule rain (21 acrocarps: 25 pleurocarps and 20 acrocarps: 12 pleurocarps respectively). In contrast, extant and propagule rain communities were equally divided between perennial and colonist species (40 perennial: 45 colonist and 18 perennial: 18 colonist respectively, Appendices I and J). Five shuttle species were present in each of the communities. Rank abundance curves indicated that the ten most abundant species differed between the extant community and the propagule rain (Figure 4.2a, b). Half of the species were pleurocarps and liverwort species in the extant community whereas in the propagule rain most species were acrocarps. Of the ten most abundant species in the extant community, half were perennials and one species was colonist, while in the propagule rain community, half were colonists and four were perennials (Figure 4.2a, b).

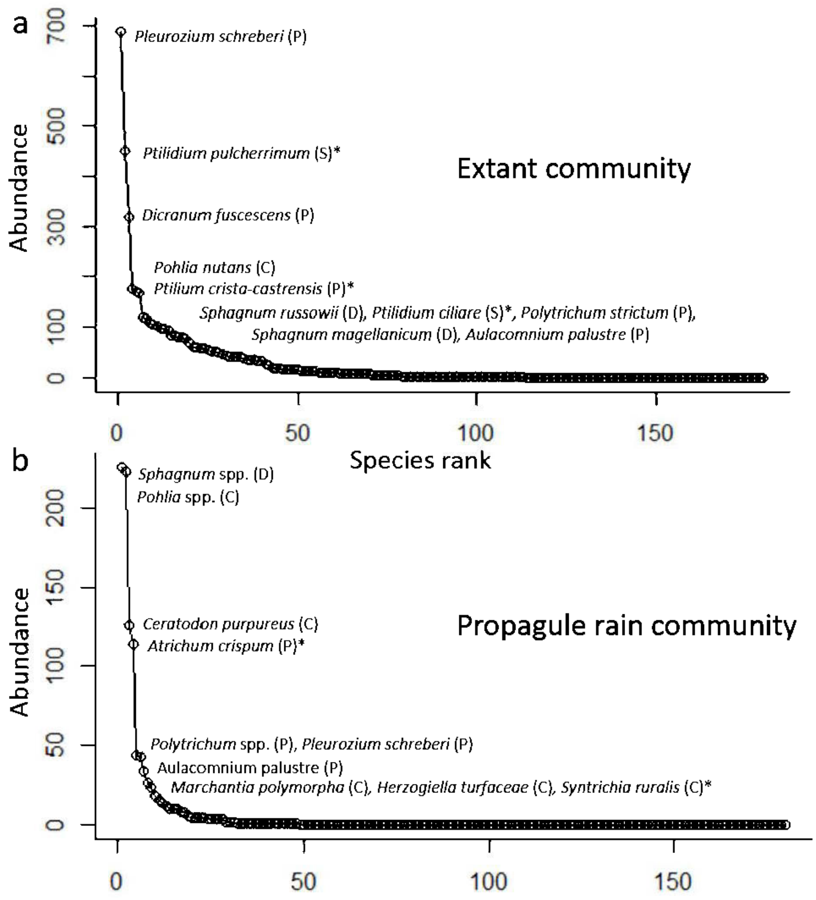

Figure 4.2 Rank abundance curves of the extant (a) and propagule rain communities (b). Only the ten most abundant species are indicated. Letters in brackets behind species names indicate species life strategy: C, colonist; P, perennial; S, shuttle; D, dominant. For more details on species life strategies see Appendix H. *, species exclusive to the community considered.

The DCA indicated that the extant community and the propagule rain differed in overall community composition (MRPP, $P = 0.0004$). The first axis divided the extant community and the propagule rain community, with no overlap in the plots (Eigenvalue = 0.57, gradient length = 3.40 S.D. unit; Figure 4.3). Each community was composed of a specific pool of species and a few common species were shared. The second DCA axis (Eigenvalue = 0.17, gradient length = 2.12 S.D. units) separated the different positions in the residual forest patches (core, edge and burned matrix). This gradient is less obvious in the propagule rain. Even though it was not significant, a trend towards distinct community assemblage among positions within the forest patches is visible (including both extant and propagule rain communities) (MRPP *P* = 0.099; Figure 4.3).

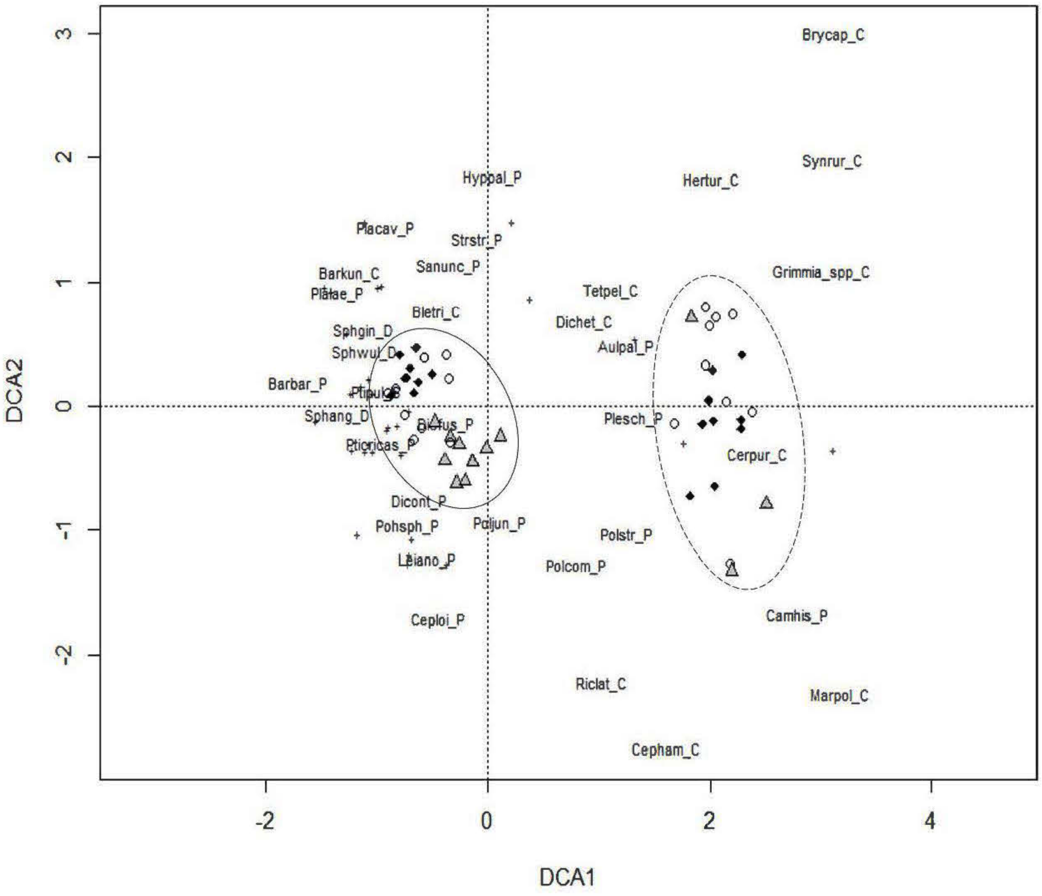

Figure 4.3 Species and site plot of the Detrended Correspondance Analysis of the total matrix of 48 plots including the extant and propagule rain communities. Only the 34 most frequent species are indicated, positions of less frequent species are indicated by +. For complete names see Appendix I. The ellipses indicate community types, the extant community as a solid line, the propagule rain community as a hatched line. Symbols indicate habitat type: core, black diamond; edge, white circle; fire, grey triangle. Letters behind species names indicate species life strategy: C, colonist; P, perennial; S, shuttle; D, dominant. For more details on the species life strategies see Appendix H.

4.5.2 Relationship between geographic distance and community similarity: relative importance of SDD vs LDD

Similarity between the propagule rain and the extant community (considering all plots) and considering only the burned matrix propagule rain (objective 2) was low and varied from 0% to 4% and from 0% to 10.2% respectively (Jaccard's index; data not shown). The degree of similarity between extant and propagule rain communities was not explained by geographic distance (no significant spatial scale was detected; data not shown).

When the potential sources of individual species were examined for the propagule rain of the burned matrix plots (n = 3), the frequency of occurrence of species was independent of the spatial scale of dispersal for both total (P = 0.612) and colonist species (P = 0.868) while a dependence was detected for perennial species (P = 0.048; Figure 4.4). Geographic distance does not influence bryophyte dispersal and potential sources of propagule situated from 0 to 30 km have an equal chance to contribute to the propagule rain. The inter-fire scale was slightly less represented for perennial species and slightly more for colonist species, and *vice versa* for the intra fire scale.

Of the 46 taxa trapped (i.e. 42 species plus 4 taxa only identified to genera and for which species of the same genera have been recorded in the extant community), 19 were not present in the extant community.

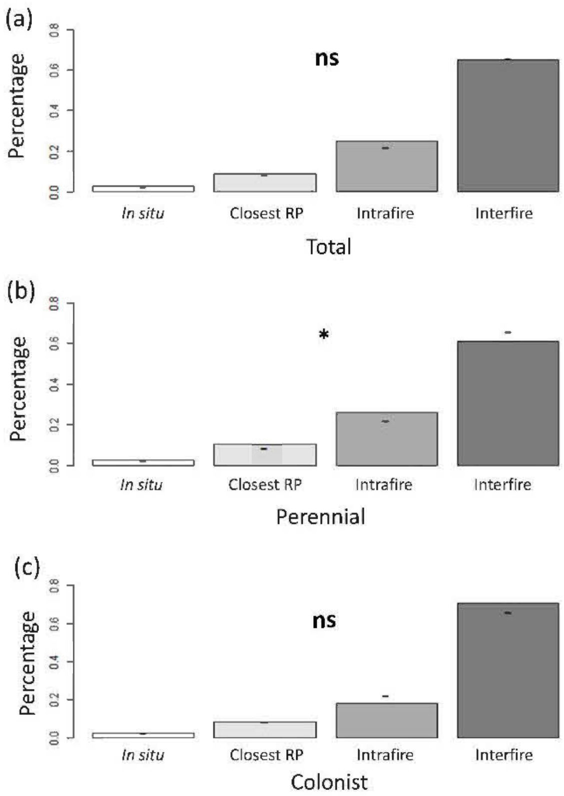

Figure 4.4 Species level comparisons between the propagule rain of burned matrices and the extant community of residual forest patches and burned matrices. Species were grouped in (a) total (n = 21), (b) perennial (n = 9), and (c) colonist (n = 10). Bars represent percentages of occurrence of species per plot and per spatial scale calculated as the mean number of species occurring at one spatial scale divided by the number of plots sampled at this spatial scale in the three fire pooled together (n *in situ* = 3; n closest-RP = 11; n intra fire = 28; n inter fire = 84 i.e. N = 126). This actual frequency was compared, with Fisher tests, to a theoretical expected frequency calculated by multiplying the sum of the mean number of species present per plot in each spatial scale by the total number of plots that could be potential propagule sources in the target spatial scale and dividing by the total number of potential propagule sources available (N). Expected frequencies at each spatial scale are indicated by dashed lines. *In situ*, 1-50 m; Closest-RP: closest residual patch, 650-1100 m; Intra-fire: 640-8400 m; Inter-fire, 12 800 m - 30 km. Significance of the Fisher tests are indicated by the symbols: *, $P < 0.05$; ns, non-significant.

4.5.3 Influence of geographic distance and residual patch characteristics on community similarity

The influence of geographic distance and nine environmental variables on the similarity of the extant community and the propagule rain of the three plots of burned matrix was tested at different spatial scales. When all four spatial scales are pooled together, the model including only temporal predictive variables (forest age and time since fire) was the most parsimonious (i.e. with the lowest ΔAICc value; Table 4.2 and Appendix K). Multimodel inference indicated that community similarity decreased with increasing forest age (confidence interval: -0.022, -0.0067) and time since fire (confidence interval: -5.6383, -1.9653; Figure 4.5a, b).

Table 4.2 Ranking of the models used to assess the role of spatial, temporal and structural variables on similarity between communities based on the ΔAICc*i* value. The response variable, Jaccard's similarity ($Sim_{Jaccard}$), compared the propagule rain in each of the 50 m^2 plot of the burned matrix (n = 3) to each of the 50 m^2 plot of the extant community (n = 21). In situ and local/closest residual patch scales were not analysed because of the small number of replicates. Only the models with a ΔAICc < 2 and the first models with a ΔAICc > 2 are indicated. K_i, number of parameters including the intercept; w_i, Akaike weight; ρ, model adjustment, are only indicated for the best model. See Appendix K for complete model list.

Model °	K_i	$AICc_i$	$\Delta AICc_i$	w_i	ρ
All four dispersal scales pooled					
Mod15 (SimJaccard ~ TSF + AGE)	5	-349.03	0.00	0.82	0.78
Global (SimJaccard ~ DIST + TSF + AGE + ISOL + AREA*ISOL + CANOP +DENS + HOLD)	12	-345.80	3.24	0.16	
Intra-fire scale					
Mod2 (SimJaccard ~ AREA)	4	-81.13	0.00	0.93	0.93
Mod14 (SimJaccard ~ AREA*ISOL)	6	-73.85	7.29	0.02	
Inter-fire scale					
Global (SimJaccard ~ DIST + TSF + AGE + ISOL + AREA*ISOL + CANOP +DENS + HOLD)	11	-235.13	0.00	0.86	0.78
Mod15 (SimJaccard ~ TSF+AGE)	5	-231.48	3.65	0.14	

° AGE, estimated age of forest in residual patch (year); AREA, area (ha); CANOP, canopy openness (%); DENS, trees and snags density (number of stems/ha); DIST, distance among sites (m); DIST CF, distance from closer continuous forest (m); DIST CRP, distance to closest residual patch (m); HOLD, complexity index; ISOL, isolation (m); TSF, time since fire (year).

Note: ~, in function of; +, additive effect; *, interactive effect.

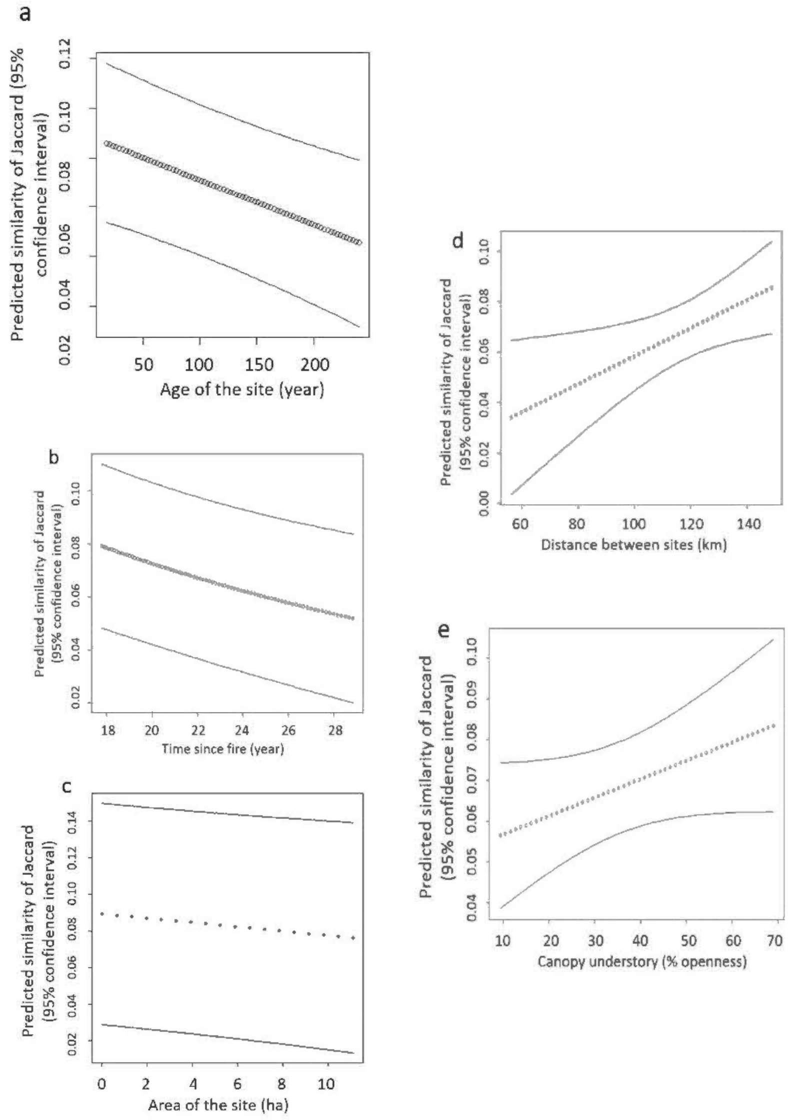

Figure 4.5 Prediction graphs of Jaccard similarity indices between extant and propagule rain communities after multimodel inference of the environmental variables that best explained dispersal patterns observed. (a) and (b) at the global scale (i.e. pool of the four dispersal patterns of bryophyte), (c) at the intra-fire scale, (d) and (e) at the inter-fire scale. Dispersal patterns are indicated by dotted lines, 95% confidence interval is represented by solid lines.

When we only considered the intra-fire scale, the model containing only the predictive spatial variable "patch area" had the lowest AICc (confidence interval: -0.0262, -0,0131; Table 4.2 and Appendix K). Multimodel inference indicated that community similarity decreased with increasing patch size (Figure 4.5c).

At the inter-fire scale, the global model was the most parsimonious and multi-model inference indicated that the variables “patch area” and “forest age” had a significant negative effect on the similarity between the communities (confidence intervals: -0.0203, -0.0052 and -0.0278, -0.0089 respectively, data not shown). In contrast, the variables “canopy understory” and “distance between sites” had a significant positive effect on the similarity between the communities (confidence intervals: 0.0017, 0.0165 and 0.0233, 0.0389 respectively; Figure 4.5d, e).

Overall, environmental characteristics of the residual forest patches and of the landscape (i.e. temporal, physical and structural attributes) had a greater influence on the similarity between communities than geographic distance.

4.5.4 The unimodal relationship between geographic distance and propagule rain community similarity

Similarity among propagule rain communities varied from 25% to 77% for distances from 10 m to 130 km (data not shown). Propagule rain community composition similarity varied significantly with distance ($P = 0.007$) and differed significantly at distances between 1.5 and 10 km ($P = 0.028$; Figure 4.6a) but did not differ significantly at distances < 1.5 km and > 10 km (Figure 4.6a).

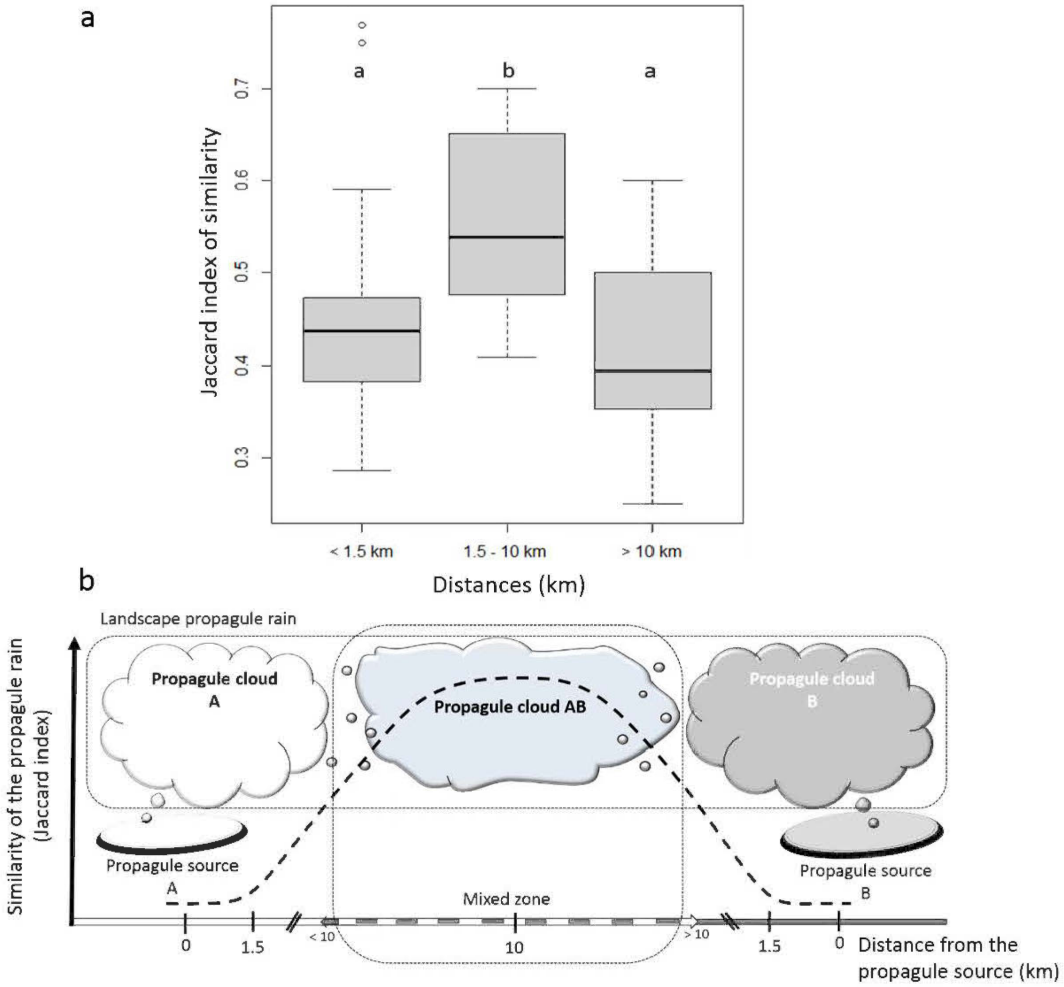

Figure 4.6 Jaccard similarity index among propagule rain communities by distance: < 1.5 km, *in situ* and local/closest residual patch scales; 1.5-10 km, intra-fire scale; > 10 km, inter-fire scale. (a) Results of the linear model (lm) tests, boxplots topped by the same letters are not significantly different as indicated by a Tuckey HSD for a given distance. The horizontal line of the boxplot indicates the median, while the bottom and the top of the box indicate the 25th and the 75th percentiles. The whiskers indicate 2 SD. Points above or below 2 SD are indicated by dots. (b) Schematization of the bryophyte propagule clouds given the distance to the propagule source. Up to 1.5 km radius, the propagule rain was regulated by the propagule cloud of each potential source, generating heterogeneous propagule rain patterns. From 1.5 to 10 km, propagule clouds from each potential propagule source were mixed generating homogenous propagule rain patterns at the regional scale. Beyond 10 km, the propagule rain becomes heterogeneous due to differences in propagule clouds at distant sites. The dashed curve represents the similarity of the propagule rain in the landscape which reaches a maximum at the intra-fire scale (i.e. between 1.5 and 10 km).

4.6 Discussion

The dispersal patterns observed in this study suggest that long distance dispersal is more common than had hitherto been assumed (Jacobson & Peres-Neto 2010), and this for all bryophyte life strategy groups. Some species found in the propagule rain were not encountered in the extant community and the similarity between the communities was positively correlated with geographic distance between the communities. Furthermore, maximal similarity among propagule rain communities was observed at moderate distances (i.e. between 1.5 and 10 km) suggesting a unimodal relationship between community similarity and distance. More than a purely local provider of propagules, the scope of the residual forest patches seems to extend several hundred kilometres, regardless of the life strategy considered.

4.6.1 Extant and propagule rain communities have distinct compositions

As predicted by previous studies (Ross-Davis & Frego 2004; Caners, Macdonald & Belland 2009; Kövendi-Jakó *et al.* 2016), there was little similarity between the extant and propagule rain communities. Colonist and acrocarp species occurred more in the propagule rain while the extant community was dominated by perennial and pleurocarp species. Shuttle species richness did not differ between communities. This pattern could be explained by species' life strategies (During 1992) however, a number of species, including many perennials, were observed in a fertile state and were not found in the propagule rain. The absence of these species in our propagule rain can be explained by the fact that the propagules of these species may not enter the propagule rain (particularly in the case of gemmae), they may be released at temporally distinct moments not covered by our four capture sessions, or they may not germinate in the Petri plates. Alternatively they may be present in the rain at sufficiently low density that they were not captured by our random sample, or may be exclusively dispersed at a hyper-local scale (i.e. surrounding the source colony). Our first hypothesis is therefore rejected as the closest extant community contributes little to the propagule rain. Furthermore, several perennial, colonist and shuttle species found in the propagule rain were not present in the closest extant community or in any of the sampled communities. The question of the origin of these propagules remains unanswered.

4.6.2 Non-linear relationship between community similarity and geographic distance: LDD dominates SDD

The spatial limitation of bryophyte dispersal indicated by numerous studies (Miles & Longton 1992; Laaka-Lindberg, Korpelainen & Pohjamo 2006) suggests that community similarity should decrease with increasing distance. Our study indicates that propagule rain composition is unrelated to distance from a putative propagule source. When we compare the distances travelled by the propagules at the regional scales (both intra- and inter-fire scales; average 21400 m) with the distances travelled at the *in situ* scale (average 25 m), it becomes evident that regional dispersal is common despite a significant handicap. This is true regardless of the species life strategy, although slightly more for colonist than perennial species, which may be justified by their life strategies. Indeed, colonist species are characterized by a high reproductive effort and the production of numerous and light spores (During, 1992). In contrast, perennial species have an overall low sexual reproductive effort (Longton & Schuster 1983; During 1992), and while many of them are commonly fertile there are few sporophytes per colony (Rydgren & Økland 2001; Cronberg 2002). Despite this, Longton & Schuster (1983) have shown that *Hylocomium splendens* may produce large quantities of spores (around 100 000 per capsule) whose relatively small size (14-17 µm in diameter; Hill *et al.* 2007) favours wind dispersal. The tall sporophytes of these species enhance the probability of spore uptake by the wind, and in this way one fertile colony with a few capsules may release large numbers of spores to air layers several kilometers high. Thus these spores can travel long distances due to stochastic wind events (Lönnell, Jonsson & Hylander 2014). Coupled with the large colonies of perennial and dominant species (i.e. sphagna), this may explain the high number of their spores in the propagule rain.

Similarity between propagule rain and extant community was positively correlated with increasing distance, leading to the rejection of our second hypothesis and validating the occurrence of LDD in bryophyte metacommunities. The occurrence of the LDD suggests that dispersal ability alone does not regulate bryophyte colonisation of new areas. At least two non-mutually exclusive filters could also apply to select species: sexual reproductive ability (i.e. quantity and viability of spores), and environmental conditions at the establishment sites (Lönnell, Jonsson & Hylander 2014; Mota de Oliveira & ter Steege 2015). Furthermore, the apparent dominance of regional dispersal events suggests that dispersal mode is not affiliated to the life strategy group but rather depends on species traits. In the context of our second objective, LDD did not appear to be the prerogative of colonist species. The "inverse isolation hypothesis" already advanced by several authors (i.e. Szövényi, Sundberg & Shaw 2012; Sundberg 2013) seems to explain the patterns observed here and bryophyte metacommunity dynamics depends on several dispersal scales, and propagule sources therefore contribute both to local and regional diaspore clouds (Sundberg 2005).

4.6.3 Environmental characteristics of the landscape as main governors of bryophyte metacommunity reassembly

As suggested in our third hypothesis, environmental characteristics of the local habitat also explained the similarity patterns observed between extant and propagule rain communities. Similarity increased with canopy openness, probably due to increased wind speeds and therefore more efficient dispersal in more open stands (Fenton & Bergeron 2006; Sundberg 2013). The pattern of decreasing similarity with increasing time since fire, age and area of the residual forest patches reflects that the oldest and largest patches may better mimic “continuous/undisturbed” forests. They may shelter species with specific microhabitat requirements (i.e. deadwood, canopy enclosure) typical of more advanced stages of succession, increasing the dissimilarity with the propagule rain assemblage composed of species of earliest successional stages. Cronberg (2002) has also suggested that the maintenance of perennial species depends on the age of the patch as sexual reproduction is less common in young patches compared to older patches, which therefore contribute more to propagule clouds. Similarly, Löbel, Snäll & Rydin (2006) demonstrated that many obligate epiphyte bryophytes are affected by patch conditions that are linked to forest stand age. Maintaining old and large sources is therefore critical for the persistence of late seral species that take decades to reappear in a landscape without these refugia (Caners, Macdonald & Belland 2009).

4.6.4 Bryophyte propagule rain over the landscape is homogenised by LDD events

Our results suggest a nonlinear relationship between propagule rain community similarity and distance. The propagule rain at the landscape scale was, as suggested by the fourth hypothesis, composed of various propagule clouds and dispersal within 1.5 km of a focal point (SDD), resulted in little similarity between propagule rain communities (Figure 4.6b). Sundberg (2005) found similar results for sphagna. However, beyond this distance up to 10 km from the focal point (> 1.5 km and < 10 km), similarity among propagule rain communities was at its maximum as the effects of SDD were diluted in a “regional cloud” of LDD contributing to the homogenisation of the propagule rain across the landscape. As suggested by Hylander (2009) and Sundberg (2013), the roles of microsite limitation and/or rapid decline of local availability are masked by a higher regional propagule rain (LDD), which corroborates our species level propagule results that indicated limited local dispersal. Beyond 10 km, the similarity decreased due to the dominance of other propagules clouds from more distant sources. Appropriate meteorological conditions coupled with the absence of physical barriers to the wind in the landscape matrix have been advanced to facilitate the LDD (Sundberg 2013).

Based on the spatial scales used in this study (both in the comparison between extant and propagule rain communities and among propagule rain communities), a working definition of SDD and LDD can be formulated. We might conclude that LDD refers to propagules dispersed from regional sources i.e. from 1.5 to over than 100 km, whereas propagules dispersed from more local sources, under 1.5 km, are included in SDD. However, definitions of LDD and SDD are system and taxon dependent and this definition should only be applied to bryophytes of boreal black spruce-feather moss forests of eastern Canada.

4.6.5 Limitations of the study

Results of this study should be interpreted with some degree of caution as propagules traps cannot discriminate between the absence of a species and its non-detection due to unsuitability of *ex situ* growing conditions (Ross-Davis & Frego 2004). Also, the nutrient medium used to fill Petri plates does not seem suitable for epixylic species such as various liverworts (Caners, Macdonald & Belland 2009). Sterilised and moistened pieces of wood were tried to trap epixylic species (Kimmerer 1991) but they were rapidly contaminated by fungal hyphae.

One other limitation of the emergence method is linked to the timing of six hour-exposure of the Petri plates from the morning to early afternoon. Indeed, propagules are generally released in the morning (Johansson *et al.* 2015) and spores that are released at distant sites may thus be primarily deposited later in the afternoon and the evening because of the extended transportation times. This timing could lead to a bias with an excessive sampling of the propagules from local to very local scales (SDD) compared to propagules from farther distances (LDD). This may have affected our results, but would not lead to a different conclusion, given the evident dominance of LDD. The exposure time may have affected the species trapped and our study may even have minimized the proportion of propagules from distant origins. Indeed, six hours of exposure may lead to less propagules from the regional dispersal scale compared to an entire day of exposure (24 hours).

Finally, the propagule rain varies among seasons and years (Ross-Davis and Frego 2004). Similarly, sporophyte production and diaspore release varies among species (Longton & Greene 1969; Damsholt 2002) and among years with climatic conditions, such as precipitation and air humidity (Johansson *et al.* 2015; Rydgren, Cronberg & Økland 2006). This can affect the pool of propagules potentially available to be trapped. However, our study is based on two trapping sessions in two seasons of two years, capturing spring, summer and fall species. In addition, the climatic conditions of the two years were substantially different (e.g. in temperature, humidity, precipitation) and the compositions of the propagule communities were significantly distinct in 2013 and 2014 (data not shown). Consequently we suggest that a significant part of the natural variability in the propagule rain that is due to seasonality and climate are included in this study. Moreover, considering the extensive sampling design used (i.e. over 10 000 km^2 region in the boreal forest) and the number of taxa recorded (i.e. 123), we estimate that we present a realistic spatial pattern of the propagule rain and extant community.

4.6.6 Implications, conservation and future research

The occurrence of LDD in bryophyte metacommunities explains the Holarctic distribution of several bryophyte species (Vanderpoorten & Goffinet 2009). Furthermore, the preponderance of LDD in all life strategies suggests that the traits used to generate these groups, and especially the size of the spores, do not adequately describe dispersal potential. Timing of propagule release, capsule morphology and climatic events such as wind turbulence and air humidity seem more limiting to bryophyte dispersal than spore size (Johansson *et al.* 2014; Johansson *et al.* 2015). Long distance dispersal capacities associated with species life strategy is therefore put in doubt.

Results of this study compel us to no longer consider bryophyte dispersal patterns as a purely local mechanism but rather as a regional one. More than the specific location of propagule sources, the distribution of sources across the landscape determines bryophyte propagule dispersal and *a fortiori* bryophyte conservation. Moreover, several filters (e.g. sexual organ production, environmental requirements, micro-habitat availability) may be more limiting than dispersal capacity for bryophyte metacommunity assemblages. Future studies should be performed to assess how germination requirements and habitat availability interact with dispersal patterns. Finally, while our results are consistent with those for sphagna, studies in other biomes could inform the generality of these findings.

4.7 Acknowledgements

Funding for this project was provided by the Université du Québec en Abitibi-Témiscamingue (UQAT) and the National Science and Engineering Research Council (NSERC) in partnership with Tembec, Eacom and Resolute Forest Products.

The authors sincerely thank Emilie E. Chavel and Louiza Moussaoui who have provided some of the environmental data used in this paper; Julie Arseneault, Louis Dubois, Philippe Heine, Morgane Higelin, Flora Joubier, and Aurore Lucas for their field and laboratory assistance; Danielle Charron, Pascal Drouin, Philippe Duval, Noémie Graignic, Raynald Julien, Ahmed Koubaa, Danièle Laporte, Marie-Hélène Longpré, Benoit Plante, Michel Poitras and Francine Tremblay for their technical support; Marc J. Mazerolle and Jérémie Alluard for their relevant statistical advices; and Jean Faubert for his precious help in the identification of the most difficult bryophyte samples. The authors also acknowledge the associate editor Peter Vesk

and the editor Mark Rees as well as the anonymous reviewers assigned to the manuscript for their very helpful and constructive comments that have contributed to the obvious improvement of the paper.

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CHAPITRE V

TIME CHANGES EVERYTHING: INTER-ANNUAL VARIATION IN BRYOPHYTE DISPERSAL

Marion Barbé, Nicole J. Fenton, Richard Caners & Yves Bergeron

En préparation pour *Oecologia*

5.1 Abstract

In the current context of global changes that modify species distribution ranges, it is urgent to identify climate variables that impact species dispersal patterns. We investigate patterns of propagule release (sexual and asexual dispersal organels) of boreal bryophyte communities in response to weather. We present the first community level study that also examines the impact of weather on the different phases of bryophyte phenology. Aerial bryophyte propagule rain was trapped during summer and fall 2013 and during spring and fall 2014 and climatic variables were collated for the years 2012, 2013 and 2014. The phases of the phenology and the weather variables that influenced on propagule release one season to two years before it were identified. Propagule release depends on weather conditions at the time of dispersal (i.e. direct weather effects) but also on indirect weather effects during the winter and summer one year preceding dispersal, that influence survival and growth of the mother plant and of fertilization, respectively. We found that propagule release depends on weather conditions occurring from one to several seasons upstream, and especially on humidity, temperature and winter length. Using an original method we provide concrete conclusions about bryophyte dispersal dynamics in response to climate.

Key-words: boreal latitudes, weather conditions, propagule release, phenology, phenophases.

5.2. Résumé

Dans le contexte actuel des changements globaux, responsables de la modification des aires de distribution des espèces, il apparait opportun d’identifier les variables climatiques jouant sur les patrons de dispersion des espèces. Nous étudions les patrons de dispersion des propagules (organelles de dispersion sexuelle et asexuelle) de communautés bryophytiques boréales en réponse au climat. Nous présentons la première étude effectuée à l’échelle de la communauté entière via la division du cycle phénologique des bryophytes en différentes phases. La pluie de propagules aérienne a été interceptée durant l'été et l'automne 2013 et durant le printemps et l'automne 2014, en parallèle de compiler les variables climatiques de la région pour la période 2012 à 2014. Les variables climatiques les plus influentes sur chaque phase du cycle phénologique, une saison à deux ans avant la phase de dispersion, ont été identifiée pour mettre en évidence laquelle de ces phases impacte le plus le relargage des propagules. Le relargage des propagules dépendait de variables climatiques contemporaines à la dispersion (i.e. conditions climatiques directes) mais aussi de conditions climatiques indirectes durant l'hiver et l'été précédent la dispersion, soit, respectivement, durant la survie et croissance de la plante mère et durant la fertilisation. Ainsi, le relargage des propagules semble gouverné par les conditions climatiques d'une à plusieurs saisons en amont et particulièrement par l'humidité, la température et la longueur de l'hiver. À travers cette méthode novatrice, nous fournissons des conclusions concrètes à propos de la dynamique de dispersion des bryophytes en réponse au climat.

Mots-clés : écosystèmes boréaux, conditions climatiques, phénologie, phénophases, relargage des propagules.

5.3. Introduction

How species diversity patterns are influenced by the impacts of environmental factors on organisms' phenology and distribution has often been investigated (Benson-Evans 1961; Dougherty et al. 1994; Xiao et al. 2013). Phenology is the seasonality of events related to reproduction and growth (Stark 2002; c.f. Laaka-Lindberg 2005) and it includes the dispersal phase, which encompasses the production, transport and establishment of propagules (seeds, spores or asexual reproductive units; Bossuyt and Honnay 2006; Johst et al. 2011). Community structure, dynamics and distribution depend on the phenology of species, which is in turn modulated by climate and season (Glime 2013). Consequently, climate changes are expected to influence species' phenology (Hughes 2000; Walther et al.

2002), particularly at northern latitudes where climate change impacts are predicted to be more pronounced (Serreze et al. 2000; Wasley et al. 2006).

Northern ecosystems are dominated by bryophytes, which represent the principal plant biomass, cover and diversity of the understory of boreal forests, bogs, and fens, tundra, and alpine and subpolar fell-fields (Proctor 2011). Bryophytes are poïkylohydric and lack specialized mechanisms for regulating water uptake and loss, which results in their strong dependency on moist microclimates (Löbel and Rydin 2010). This is also true of their phenology, which is composed of the successive phases, [phenophases sensu Stark (2002)], vegetative growth, gametangial initiation, fertilization, sporophyte development and propagule dispersal. Sporophyte development and propagule dispersal depend on the prior phenophases as sporophytes are matrotroph, and consequently represents a cost for the gametophyte (Ehrlén et al. 2000; Bisang and Ehrlén 2002). The phenology of only a few bryophyte species has been investigated (Stark 1997; Laaka-Lindberg 2005; Longton and Greene 1967, 1969). Recently bryophyte phenology has been of interest as bryophytes are used as bio-indicators of climate changes (Gignac 2001; Slack 2011). Studies have shown that mean summer temperature, number of days above 0°C, amount of winter or summer precipitation and humidity are regulators of bryophyte phenology (Sundberg 2002; Johansson et al. 2015). Furthermore, Pohjamo et al. (2006) pointed out the seemingly ambivalent influence of rainy conditions on the liverwort *Anastrophyllum hellerianum*, which enhanced the number of gemmae released but did not affect their dispersal distance patterns. As these studies have all been based on individual bryophyte species, more general patterns remain anecdotal.

We aim to fill this knowledge gap by investigating changes in bryophyte community phenology in response to weather conditions. We trapped aerial propagule rain during two seasons in two consecutive years in boreal black spruce-feather moss forests of eastern Canada, and describe seasonal and annual aerial propagule rain patterns at the scale of the whole bryophyte metacommunity (objective 1). We investigate the 'direct' influence of weather conditions on propagule release, and the 'indirect' effects of the weather conditions on propagule release through their actions on phenophases prior to propagule release (objective 2). To our knowledge, this study is the first performed at the metacommunity scale linking weather variables to each bryophyte phenophase.

We expect that the composition of germinated bryophyte aerial propagule rain will differ among seasons as timing of propagule release varies among species (Hock et al. 2004; Ross-Davis and Frego 2004; Hypothesis 1). In addition, slight variations in abundance or presence of the less frequent species may be found among years, but a same pool of basic species is expected given that the same species make up the extant community (and therefore propagule releasers) among years (Hypothesis 2). Furthermore, we expect that each phenophase of bryophyte phenology will be influenced by specific weather variables (Hypothesis 3), such as water availability during the fertilization phenophase or wind velocity during the dispersal phenophase (Johansson et al. 2014). We therefore expect to highlight which phenophases govern propagule release and identify the weather variables that have the greatest influence on these phenophases.

5.4 Materials and Methods

5.4.1 Study area

The study was conducted within the black spruce (*Picea mariana* Mill., Briton)-feather moss (*Pleurozium schreberi* (Brid.) Mitt.) forest of western Québec, eastern Canada (Appendix L). Stands are dominated by *P. mariana*, but *Pinus banksiana* Lamb., *Populus tremuloides* Michx, *Abies balsamea* (L.) Mill., and *Betula papyrifera* Marshall are secondary species (Saucier et al. 2009). Ericaceous species [e.g. *Rhododendron groenlandicum* (Oeder) Kron & Judd] and bryophyte species dominate the forest understory. In the study area, the average forest age is approximately 140 years (Bergeron et al. 2002).

The topography of the region is flat and altitude varies from 200 to 300 m asl. The climate is subpolar subhumid continental. Average annual temperature and total annual precipitation are respectively 0.2 °C and 995.8 mm (1981 to 2010), recorded at the Chapais 2 weather station, Chapais, Québec (100 to 240 km from our sites; Environment Canada 2015a). The region is characterized by long winters with 312.9 cm of annual snowfall and by a short growing season of 140 to 160 days.

5.4.2 Interception of aerial propagule rains

The aerial propagule rain was sampled by the "emergence method" (Rudolph 1970; Ross-Davis and Frego 2004). In each trapping season 21 groups of six Petri plates (90 mm in diameter) were placed in closed forests and recently burned areas at sampling points spread across the sampling area (50° 56' N, 77° 53' W; 49° 75' N, 76° 29' W; 49° 91' N, 76° 13' W; see Barbé et al. 2016, and Appendix L and M for more details on sites and sampling method). The aerial propagule rain was trapped during four sessions: the 11-Aug and the 16-Aug (summer) and the 4-Sep and the 13-Sep (autumn) of 2013 as well as the 9-Jun and the 11-Jun (spring) and the 14-Sep and 19-Sep (autumn) of 2014. Two days were required for each trapping session due to the distance among the sampling points (average of 128 km). A total of 504 Petri plates were exposed over the four sessions [(6 Petri plates × 21 sampling points) × 4 trapping sessions]. In 2013, all six Petri plate traps were filled with 78.5 cm^2 of nutrient agar made in sterile laboratory conditions [Parker Thompson's basal nutrient medium of Klekowski (1969), described by *C-Fern* Project © (1995-2014)]. In 2014, only three of the Petri plates of the group were filled with nutrient agar whereas the others three Petri plates were filled with pieces of wood collected in the burned matrix of each fire. Wood pieces were sterilized at 60°C for 24h to kill all organisms in the wood without destroying wood structure (A. Koubaa pers. comm.). The sterilized wood was subsequently fragmented into smaller pieces and placed into Petri plates; the wood placed in Petri plates originated from the fire in which it was placed. During each day of aerial propagule rain trapping, Petri plates were deposited in the forest for six hours and then covered and randomly placed in germination chambers for six months, following the protocol described in Barbé et al. (2016). Development of bryophyte gametophytes was assessed twice a week to follow germination patterns and to control potential bacterial or fungal contamination. Three control Petri plates with virgin nutrient agar were placed in the germination chambers every three months for the duration of the 6-month emergence period to identify potential contaminants. No bryophyte species developed on any of the control plates, indicating that sample plates had not been contaminated during the laboratory growing period.

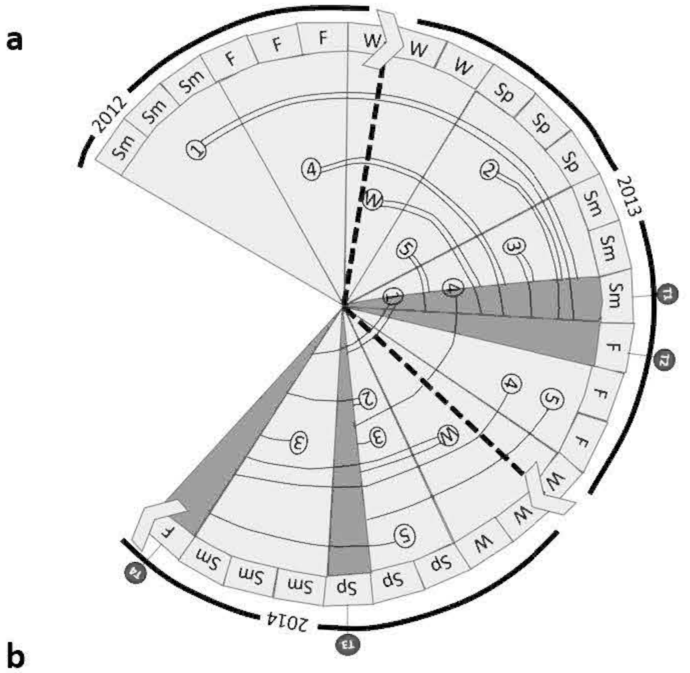
All bryophytes were identified following Faubert (2012-2014). Due to the artificial growing conditions in the Petri plates, bryophytes had unusual characteristics, consequently certain specimens were only identified to genus, particularly sphagna and members of the genera *Ditrichum* spp., *Grimmia* spp., *Pohlia* spp., and *Polytrichum* spp. Vouchers are conserved at the University of Québec in Abitibi-Témiscamingue, Qc, Canada. Species were classified by growth and life forms (i.e. true mosses divided into acrocarps and pleurocarps, liverworts, sphagna) but also by life strategy (i.e. colonist, perennial, shuttle, dominant; During 1992). The dominant life strategy group was composed of only sphagna species; therefore, the taxonomic and life strategy groups are confounded. In the Petri plates, one individual refers to a protonema. While one protonema can generate several stems making it difficult to distinguish individuals, monthly photographs of the plates were taken to follow individual germination events.

5.4.3 Weather variable choice

Weather data were collated from Environment Canada (2015a, 2015b) from the two nearest weather stations Chapais (49° 46' N. 74° 32' O) and Chapais 2 (49° 47' N. 74° 51' O; Appendix L). Weather variables were chosen that are known or supposed to directly (e.g. precipitation, relative humidity, wind speed) or indirectly (e.g. consecutive days without rain as proxy of drought period) influence bryophyte phenological (Hedenäs 2001; Sundberg 2002; Johansson et al. 2015). Of the initial 21 weather variables collated (Appendix N), the 10 uncorrelated variables calculated as monthly values for each year were retained: mean temperature (°C); maximum consecutive days under 0°C; Julian date before exceeding 0°C; mean night/day temperature difference (°C); number of days under 0°C (freezing point of bryophyte cytoplasm is on average 0°C; Longton 1988); mean relative humidity (%); maximum wind speed (km.h^{-1}); number of days with maximum wind speed; number of days under -10°C (estimated temperature of photosynthetic breakdown, Lappalainen et al. 2011); total precipitation (mm); maximum consecutive days without precipitation. Temperature, relative humidity and precipitation in the winter were not considered because bryophytes are generally under constant snow cover and therefore not exposed to ambient air temperatures (Longton and Greene 1967). As there is to date no evidence of gametophyte growth or sporophyte maturation under snow cover in boreal latitudes (Longton 1985), we considered that these phenophases were halted during the winter (Glime 2013). The duration of the winter in boreal latitudes delays the phenology compared to species in more temperate latitudes where winters are milder (Longton and Greene 1969; Imura and Iwatsuki 1989). We therefore also included variables characterizing the winters by their duration: maximum number of consecutive days under 0°C from December to spring and Julian date in the spring at which 0°C is passed.

5.4.4 Relationship between weather and bryophyte phenology

Globally, bryophyte phenology is known for some species (Stark 1997; Laaka-Lindberg 2005; Longton and Greene 1967, 1969) but remains unknown for a substantial number of species. However, in the present study, despite the fact that we are studying the community, a representative cycle was used as many species' cycles are unknown and all species are developing in the same climate. We used the representative phenological cycle described for *Polytrichum* spp. and *Pohlia* spp. from the United States and United Kingdom (adapted from Stark 2002), as these are species that were also found in our study and the study sites were geographically closer to ours than other published cycles. In this 12 month cycle, fertilization occurs in summer, sporophyte maturation occurs during the following spring/summer and spore release occurs from the end of the spring to the end of fall in this second year. Gametophyte growth occurs in fall, spring and summer. Bryophyte phenology was thus divided among the two generations: 1) sporophyte generation, with the phenophases fertilization and maturation-dispersal, and 2) gametophyte generation, with the phenophases winter survival and survival-growth during spring, summer and fall. As we propose that the phenology is spread over two growing years, the sporophyte and the gametangia developments are influenced by the different phenophases spread over the four seasons of the preceding year and the four seasons of the year of spore release (Longton and Greene 1969; Bisang and Ehrlén 2002; Sundberg 2002). Consequently weather conditions in summer and fall 2012, the four seasons in 2013 and in spring and summer 2014 were used to explain the patterns in aerial propagule rain trapped in 2013 and 2014 (Figure 5.1a, b). The 2012 and 2013 weather conditions explain the 2013 patterns, and 2013 and 2014 weather conditions explain 2014 patterns. Weather variables were therefore divided into groups based on the phenophase that they were assumed to impact directly, and by trapping year. For example, the variable "wind speed" was only considered as a direct effect for the phenophase of propagule dispersal, while "mean temperature" may directly influence propagule dispersal, fertilization, sporophyte maturation and gametophyte growth phenophases.



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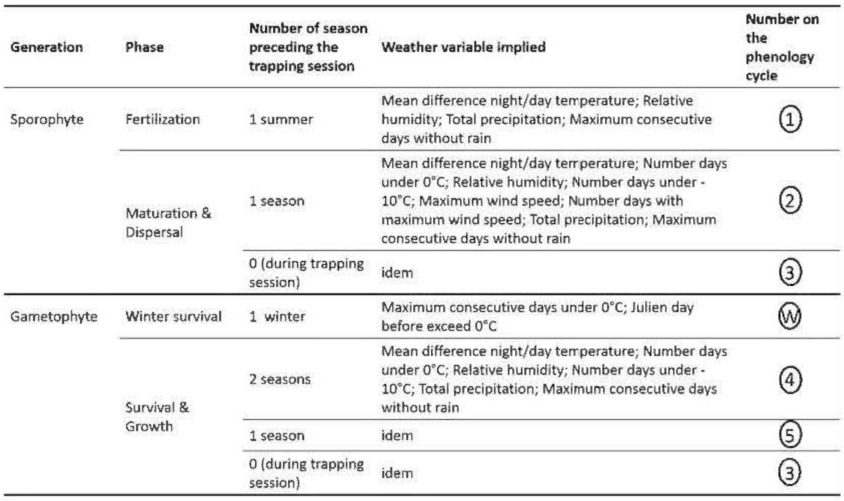

Generation	Phase	Number of season preceding the trapping session	Weather variable implied	Number on the phenology cycle
Sporophyte	Fertilization	1 summer	Mean difference night/day temperature; Relative humidity; Total precipitation; Maximum consecutive days without rain	①
	Maturation & Dispersal	1 season	Mean difference night/day temperature; Number days under 0°C; Relative humidity; Number days under -10°C; Maximum wind speed; Number days with maximum wind speed; Total precipitation; Maximum consecutive days without rain	②
		0 (during trapping session)	idem	③
Gametophyte	Winter survival	1 winter	Maximum consecutive days under 0°C; Julien day before exceed 0°C	Ⓦ
	Survival & Growth	2 seasons	Mean difference night/day temperature; Number days under 0°C; Relative humidity; Number days under -10°C; Total precipitation; Maximum consecutive days without rain	④
		1 season	idem	⑤
		0 (during trapping session)	idem	③

Figure 5.1 Phenology cycle (a) and weather variables (b) used to explain aerial propagule rain patterns trapped in summer 2013 (T1), fall 2013 (T2), spring 2014 (T3) and fall 2014 (T4). Years and seasons (divided into months: F, fall; Sp, spring; Sm, summer; W, winter) are indicated at the exterior of the cycle and bold doted lines separate the years. Trapping sessions (illustrating propagule release) are represented as dark grey pies. Phenology is divided into the sporophyte generation that contains three phenophases: fertilization during the summer of the year preceding the trapping (1), maturation of sporophytes and dispersal of propagules one season preceding the trapping (2) and the season of the trapping (3); and the gametophyte generation that contains five phenophases: winter survival (W), survival and growth of the gametophyte two season preceding the trapping (4), one season preceding the trapping (5) and the season of the trapping (3). Both the phenophases of maturation-dispersal of the sporophyte and of growth-maturation of the gametophyte have the number 3 because concern the same season of trapping but with different environmental variables given the impact on sporophytes/spores or gametophyte. Weather variables impacting each phenophase are indicated in the table. The impact of one phenophase on the one trapping session is materialized by circles with the phenophase number and a line joining the trapping session considered.

5.4.5 Data analyses

Petri plates filled with woody debris were not analyzed because of fungal and bacterial contaminations. Due to the resulting unbalanced design (i.e. 6 Petri plates per plot in 2013 and 3 Petri plates per plot in 2014) and the correlation between the number of plates and species richness/frequency, analyses were made at the Petri plate level for only the plates filled with nutrient agar (n = 378). However, the use of mixed models that take into account the geographic location and reduce the N eliminates the potential pseudoreplication. After identification of individuals grown in Petri plates, we obtained presence/absence data per Petri plate per trapping sessions (n = 4, 1 in spring, 1 in summer, 2 in fall) and per year (n = 2, 2013 and 2014). Species richness and species frequency (number of individuals of each species) were studied per Petri plate in order to obtain mean species richness and mean species frequency per year and season.

5.4.5.1 Aerial propagule rain richness and composition among seasons and between years

R software 3.2.1 (R-Development-Core-Team 2015) was used for statistical analyses with a significance level of $\alpha = 0.05$. The composition of the aerial propagule rain was compared among trapping sessions (objective 1) using rank abundance curves (Magurran 1988) performed with the R package “BiodiversityR” (v. 2.5-3). Total (all bryophyte groups) mean species richness and total mean species frequency of species divided by life form and strategy (During 1992) were compared between years and among seasons (see Models used below). The overall composition was summarized in a Principal Coordinates Analysis (PCoA; Borcard et al. 2011) performed on binary data (i.e. presence/absence data) of all species from all trapping seasons using the R package “vegan” (v. 2.3-0). Jaccard’s dissimilarity index was used as the distance measure because double-presences are not overweighed compared to double-absences (Legendre and Legendre 2012). Double-absences are frequently not considered informative but are relevant in this study because they may be due to various factors such as environmental conditions, species dispersal limitation, random local extinction, historical events or stochastic variation (Legendre and Legendre 2012). The Cailliez correction was performed to correct for the production of several negative eigenvalues by the PCoA, which can affect the representation of objects on the axis (Gower and Legendre 1986). Non-identified protonemata and specimens identified only to genus for whom other species of the same genus were present were removed from the analysis. The subsequent ordination matrix contained 41 species and 338 Petri plates (108 Petri plates in summer 2013, 116 in fall 2013, 57 in spring 2014 and 57 in fall 2014). The remaining 40 Petri plates were empty and therefore removed from the analyses. The significance of the pattern obtained from the PCoA was determined by Multi-Response Permutation Procedure (MRPP) on 9999 permutations.

5.4.5.2 Relationships among weather variables and aerial propagule rain richness and composition

Eleven uncorrelated weather variables were retained from the initial 21 (see Appendix N for details). The mean seasonal values of the retained variables were then compared among years (2012, 2013, 2014) using linear models or generalized models depending on their distributions.

The retained weather variables were passively projected in the Principal Coordinates Analysis (PCoA) to visualize their relative positions on the PCoA ordination axes (Borcard et al. 2011). When a weather variable was hypothesized to influence several phenophases, values for different periods were included. Finally, the influence of the same set of weather variables on aerial propagule rain community composition was assessed using a Multivariate Regression Tree (MRT; De'ath 2002) performed with the R package "mvpart" (v. 1.6-2). Community presence/absence data (41 species and 338 Petri plates) was analyzed to determine which weather variables accounted for the largest proportion of the explained variance in the model, and whether the different years and seasons were discriminated. Trees are described by their fit (i.e. inverse of relative error RE), which varies from 1 (0% of the variance explained by the tree) to 0 (100% of the variance explained by the tree); and their predictive accuracy estimated by the cross-validating error (CVRE), which varies from 1 (poor predictive power) to 0 (good predictive power; De'ath 2002). Locations were included as dummy variables to take into account the spatial structure of the dataset. Subsequently the number of bryophyte species and the weather variables for each leaf (i.e. end group) were calculated. The amount of variation explained by the tree overall and by each branch were also determined.

5.4.5.3 Models used

As our sampling design was spatially nested, we tested whether the spatial structure of the sampling design influenced the models used to explain species richness and frequency with LogLik tests (Pinheiro and Bates 1995). In cases where spatial structure were not influential, the model without random spatial effects (lm, glm) was chosen in the spirit of parsimony. When the spatial structure had a significant effect, we used mixed models (lme, glmer). In cases where the assumptions of normality were met, linear models with or without random effects (lm, lme) were performed with the R package "nlme" (v. 3.1-121). Where the assumption of normality were not met generalized linear mixed models with or without random effects (glm, glmer) were applied with the R package "lme4" (v. 1.1-8), with the appropriate link function. Models were followed by Tukey HSD post-hoc tests performed with the R package "multcomp" (v. 1.4-1). Overdispersion of the generalized models was corrected as needed using Chi-square tests and the c-hat values. The algorithm of non-converging models was optimized via bobyqa function of the glmerControl parameter (Powell 2009). Finally when homoscedasticity assumption was violated, Kruskal-Wallis non-parametric tests equivalent to one-way ANOVA were used, followed by post-hoc multiple comparison tests performed with the R package "pgirmess" (v. 1.6.2).

5.5 Results

5.5.1 Composition of the aerial propagule rain between years and among seasons

In 2014 half the number of petri plates were used compared to 2013, however species richness in 2014 was less than half of that in 2013. A total of 41 taxa were identified during the four trapping sessions: 38 taxa in 2013 (31 in summer, 25 in fall), and 16 in 2014 (14 in spring, 10 in fall; Appendix O). Twelve taxa were shared between years while 25 taxa were found exclusively in 2013, and three exclusively in 2014. One species was only found in the spring, nine species only in the summer and nine only in the fall. The number of protonemata grown was 2740 in 2013 and 756 in 2014. Based on the rank abundance curves, the most abundant taxa were recorded in the different years and seasons, although their order differed: *Atrichum crispum*, *Ceratodon purpureus*, *Pohlia* spp., and *Sphagnum* spp (data not shown). Three additional taxa *Marchantia polymorpha*, *Plagiomnium cuspidatum/drummondii* and *Polytrichum* spp. were mainly found in 2013, while *Aulacomnium palustre*, *Herzogiella turfacea* and *Pleurozium schreberi* were mainly found in 2014.

Mean total species richness and frequency were both significantly higher in 2013 than in 2014 (both $P < 0.0001$; Figure 5.2a, b). Only the mean species richness of perennials differed between years and was significantly greater in 2013 than in 2014 ($P = 0.003$; Figure 5.2a) whereas the mean frequency of acrocarps, liverworts, sphagna/dominants and colonists were significantly higher in 2013 than in 2014 (all $P < 0.001$; Figure 5.2b). In contrast, pleurocarps and perennials were significantly more frequent in 2014 than 2013 (both $P < 0.001$), boosted by the abundance of *Pleurozium schreberi*. In terms of seasons, mean total species richness and frequency were both significantly higher in summer than in spring or fall ($P < 0.001$ and $P = 0.003$ respectively; Figure 5.2c, d). Propagule rain communities did not differ among seasons in any mean species richnesses (Figure 5.2c). However, acrocarps, liverworts, and colonists were significantly more frequent in summer than in the other seasons (all $P < 0.001$; Figure 5.2d). Pleurocarps were also significantly more frequent in the aerial propagule rain community in spring ($P < 0.001$) when sphagna were less frequent ($P < 0.001$).

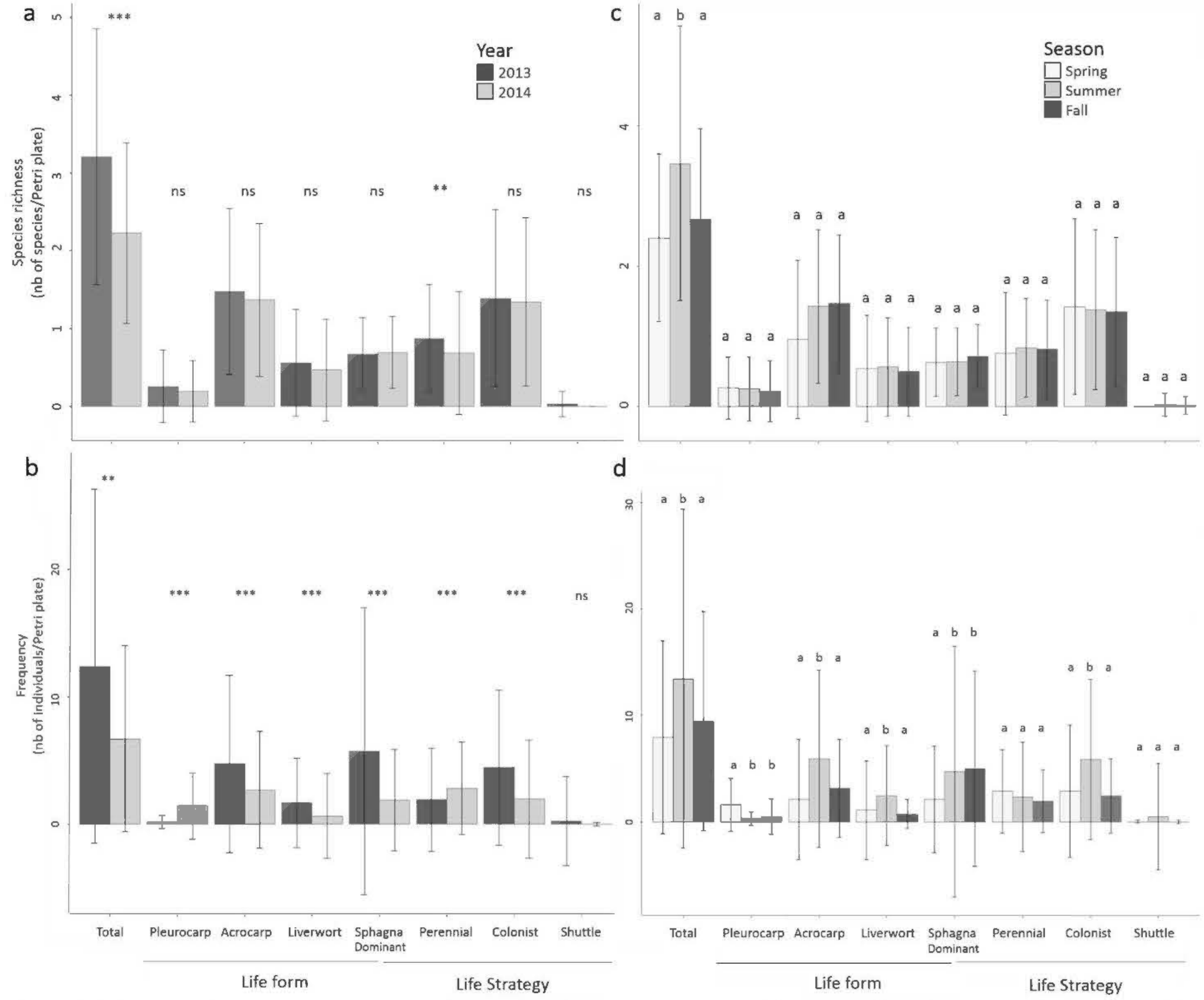

Figure 5.2 Species richness and frequency by year and season for the aerial propagule rain communities trapped in 2013 and 2014, with statistical significance of Kruskall-Wallis tests followed by post-hoc tests. Error bars refers to SD. Levels of significance of the tests are indicated by symbols: **, $P < 0.01$; ***, $P < 0.001$; ns, not significant. Bars topped by different letters are significantly different as indicated by post-hoc tests.

PCoA analysis yielded clear groupings of samples. Aerial propagule rain communities in each year and season were composed of a specific pool of species with relatively few species shared between years (MRPP, $P < 0.001$). The first axis divided aerial propagule rain communities seasonally (Axis 1: 43.46%), with little overlap between seasons in a given year (Figure 5.3a). The second axis divided aerial propagule rain communities annually, with no overlap between years (Axis 2: 40.15%). The aerial propagule rain community of 2013 was more homogeneous among sample sites than in 2014. In 2014, some sites were characterized by a distinct aerial propagule rain community composed of specific species (e.g. *Dicranella heteromalla*, *Pellia neesiana*, *Pleurozium schreberi*).

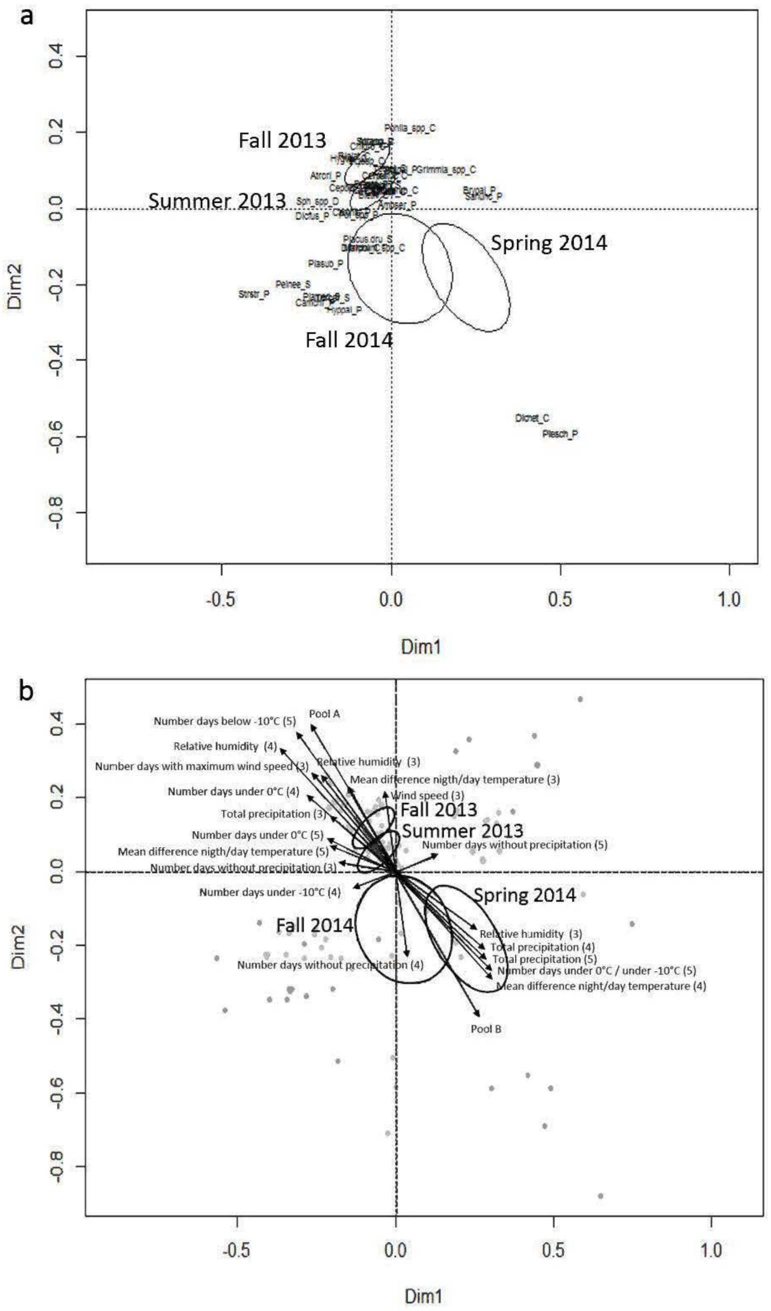

Figure 5.3 Principal correspondence analysis (PCoA) plots of (a) sites with species for the matrix of 338 Petri plates and 41 species by trapping session, and (b) sites with weather variables. The ellipses indicate trapping sessions. Grey dots are sites. Numbers behind weather variables refer to the different phenophases of the bryophyte phenology (see Table 1 for details). Letters behind species names indicate species life strategy of During (1992): C, colonist; D, dominant; P, perennial; S, shuttle. See Appendix O for complete species names.

Note: Pools indicate variables that were superimposed. Pool A groups relative humidity and total precipitation of the phenophase 1; and relative humidity, maximum wind speed, number of days with maximum wind speed, total precipitation, number of days under photosynthetic threshold and maximum consecutive days without rain of the phenophase 2. Pool B groups maximum consecutive days under 0°C, maximum consecutive days without rain and Julien day before exceed 0°C of the phenophase of "winter survival - W"; as well as mean difference night/day temperature of the phenophase 1; mean difference night/day temperature and number of days under 0°C of the phenophase 2.

5.5.2 Weather characteristics of each year and season

Globally, monthly mean temperature and precipitation from 2012 to 2014 coincided with 30-year averages recorded for the study area (1981 to 2010; Appendix P) although March 2012 and 2013 were 5°C warmer and March 2014 was 5°C colder than the 30-year averages. Seasonal weather differed among the years (Table 5.1). Spring 2014 was significantly colder and dryer than springs 2012 and 2013, while spring 2012 was significantly rainier than the springs of 2013 and 2014. Summer 2012 was significantly windier than summer 2014, while the falls 2012 and 2013 did not differ significantly.

Table 5.1 Mean and SD (±) of the 11 weather variables by season in 2012 to 2014. Linear models were used to compare means among years except for underlined values for which generalized models were used. Means followed by the same letter are not significantly different at $P < 0.05$ as indicated by post-hoc tests; letters indicate ranking (i.e: a < b < c).

Weather variables	Seasons									
	Winter		Spring			Summer			Fall	
	2012-2103	2013-2104	2012	2013	2014	2012	2013	2014	2012	2013
Mean temperature (°C)	-14.92a ±3.31	-18.59a ±1.34	2.00a ±7.43	1.12a ±7.50	-2.63a ±11.93	16.07a ±0.66	14.81a ±2.08	15.84a ±0.39	3.72a ±7.16	3.31a ±7.58
Mean night/day temperature difference (°C)	2.48a ±1.92	2.91a ±0.62	4.19a ±0.89	4.14a ±1.29	4.99a ±0.94	4.42a ±0.76	5.09a ±0.92	4.66a ±0.63	2.79a ±1.05	3.02a ±1.30
Maximum consecutive days under -10°C (nb)	50.00a ±0.00	133.00b ±0.00	NA	50.00a ±0.00	133.00b ±0.00	NA	NA	NA	NA	NA
Julian date before exceeding 0°C (date)	63.00a ±0.00	90.00b ±0.00	NA	NA	NA	NA	NA	NA	NA	NA
Number days under 0°C (nb)	0.00 ±0.00	0.00 ±0.00	35.00a ±11.50	42.00a ±12.49	48.00a ±15.00	0.00 ±0.00	0.00 ±0.00	0.00 ±0.00	27.00a ±12.29	33.00a ±12.12
Number days under -10°C (nb)	55.00a ±3.21	77.00a ±2.08	8.00a ±4.61	7.00a ±2.51	23.00b ±13.28	0.00 ±0.00	0.00 ±0.00	0.00 ±0.00	7.00a ±1.15	5.00a ±2.89
Relative humidity (%)	87.45b ±3.95	80.50a ±1.37	66.81a ±5.03	73.82a ±6.10	69.14a ±0.08	75.75a ±8.30	75.18a ±5.80	73.77a ±6.59	88.49a ±1.96	85.98a ±4.01
Maximum wind speed (km/h)	NA	NA	26.00a ±4.04	22.00a ±2.88	19.00a ±1.73	22.00a ±2.51	19ab ±1.15	16b ±1.00	19.00a ±1.15	20.00a ±0.58
Number days with maximum wind speed (km/h)	NA	NA	1.00ab ±1.00	2.00a ±1.00	2.00b ±0.00	1.00a ±1.73	2.00a ±0.58	2.00a ±1.53	3.00a ±0.58	2.00a ±1.00
Total precipitation (mm)	NA	NA	60.80c ±0.00	42.00b ±0.00	25.60a ±0.00	317.20a ±46.96	277.60a ±29.23	319.40a ±31.25	347.70a ±13.25	334.50a ±19.5
Maximum consecutive days without precipitations (nb)	NA	NA	3.00b ±0.00	5.00c ±0.00	2.00a ±0.00	4.00a ±1.15	4.00a ±0.58	6.00a ±1.00	4.00a ±0.50	7.00a ±1.50

5.5.3 Relationships between aerial propagule rain community composition and weather variables

Relationships between weather variables and aerial propagule rain composition, as assessed with their passive insertion in the PCoA, varied from 0.31% to 23.85% for the Axis 1 and from 1.77% to 23.47% for the Axis 2 (data not shown). The variables were clearly divided in two sets: 12 variables mainly correlated with the composition of 2013 and a set of seven variables correlated with the composition of 2014 (Figure 5.3b). Seasonal variation in aerial propagule rain composition did not seem to be correlated with the weather variables.

In the MRT, the weather variables retained explained 7.9% of the variability in the aerial propagule rain with the three-split, four-group model (Figure 5.4). The first split was generated by three variables of four different phenophases and explained 5.9% of the variability. Petri plates influenced by more humid, rainy and cold conditions were found to the right of the split, while Petri plates with influenced by less humid, rainy and cold conditions were to the left. The second and third level splits explained respectively 2.3% and 2.1% of the variability observed and were exclusively generated by weather conditions of the phenophases during the trapping. Several weather variables such as the difference of temperature between night and day, number of days under 0°C, total precipitation, maximum wind speed and number of days with maximum wind speed contributed equally to the splits between groups 1 & 2 and 3 & 4.

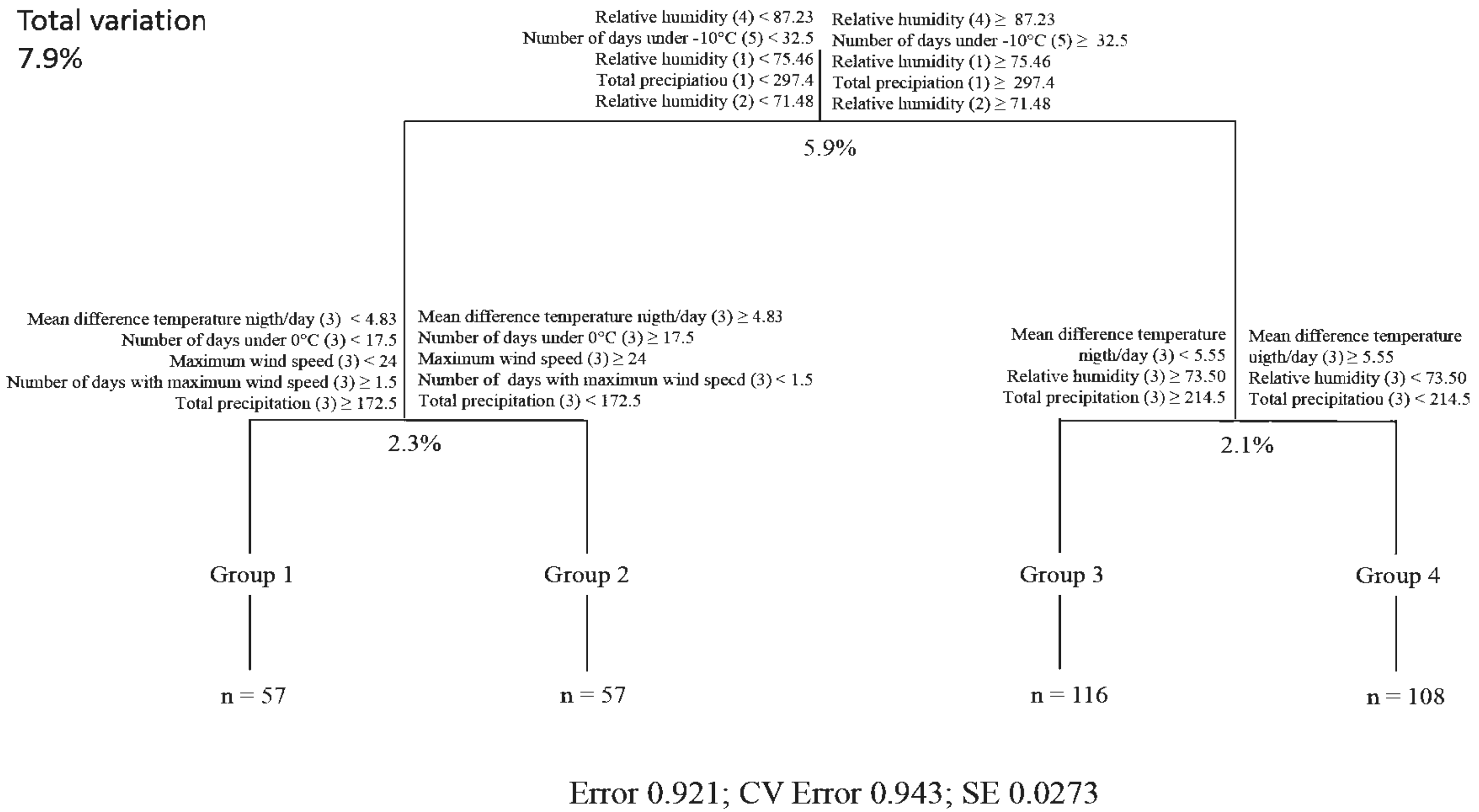

Figure 5.4 Multivariate regression tree (MRT) of the aerial propagule rain community. The three-split, four group model was the best model as selected by parsimony and cross-validated error (CVRE). Factors generating the splits with their mean amounts are listed at each split. The amount of variation explained by the entire tree is the inverse of the error, in this case 7.9%. This total is decomposed into percentage explained by each split. The CV error indicated the potential for the unsuccessful classification of additional samples (i.e. 5.7% chance of successful classification). Each leaf is assigned a group number (indicated beneath the leaf on the graph) and the number of plots within each group or "leaf" is indicated. Numbers behind weather variables refer to phenophases of the phenological cycle, see Figure 5.1 for details.

Influential weather variables varied among the groups with divisions between long and harsh (groups 1 & 2), and short and mild winters (groups 3 & 4), and between groups with less precipitation and lower relative humidity (groups 1 & 2) versus high precipitation and relative humidity (groups 1 & 2; Table 5.2). Groups 1 & 2 were particularly characterized by a high number of days under -0°C and -10°C during the maturation-dispersal phenophase (phenophase 3) and *P. schreberi* was primarily found in these groups (Table 5.3). Groups 3 & 4 represented high-relative humidity groups and were composed of the highest species richness and the greatest species frequency, notably a greater frequency of *Sphagnum* spp., *Aulacomnium palustre, C. purpureus*, *Pohlia* spp. *Polytrichum* spp., and liverwort species (Table 5.3).

Table 5.2 Species composition of the groups determined by multivariate regression tree (MRT). Number are frequency of each species in all Petri plates per group. Bold, liverwort species;*, acrocarp species.

Species	Group 1	Group 2	Group 3	Group 4
Amblystegium serpens	0	0	0	1
*Atrichum angustatum**	0	0	1	0
*Atrichum crispum**	29	20	41	24
Aulacomnium palustre	5	1	10	20
Blepharostoma trichophyllum	0	0	0	1
Brachythecium starkii	0	0	0	1
*Bryum capillare**	0	3	2	1
*Bryum pallescens**	0	4	0	2
Campyliadelphus chrysophyllus	0	3	0	1
Campylium hispidulum	1	0	5	6
Cepphalozia bicuspidata	0	0	0	1
Cephaloziella elachista	0	0	0	5
Cephaloziella hampeana	0	0	1	3
Cephaloziella rubella	0	0	4	8
*Ceratodon purpureus**	9	18	56	44
Chiloscyphus profundus	0	0	1	0
*Dicranum fuscescens**	0	0	2	0
*Dicranella heteromalla**	0	1	0	0
Ditrichum spp.*	0	0	2	1
Grimmia spp.*	0	0	2	6
Herzogiella turfacea	1	1	3	13
Hypnum pallescens	0	0	0	1
Hygroamblystegium varium	0	0	0	3
Marchantia polymorpha	0	3	15	6
Pellia neesiana	1	0	0	0
Plagiomnium cuspidatum/drummondii	0	1	0	1
Plagiomnium medium	0	0	0	1
Platydictya subtilis	0	0	1	3
Platygyrium repens	1	1	0	0
Pleurozium schreberi	16	26	0	1
Pohlia spp.*	24	31	87	80
Polytrichum spp.*	0	0	14	44
Pseudobryum cinclidioides	0	0	0	1
Riccardia latifrons	0	0	1	1
Sanionia uncinata	0	0	0	1
Sphagnum spp.	31	24	90	84
*Splachnum ampullaceum**	0	0	1	0
Straminergon stramineum	0	0	1	0
*Syntrichia ruralis**	0	0	4	11
*Tortula cernua**	0	0	1	0
*Tetraphis pellucida**	0	0	5	5
Total	118	137	350	381

Table 5.3 Weather variables of the groups determined by multivariate regression tree (MRT; Figure 5.4). Values are means of each variable classified by phenophase (see Figure 5.1 for details about numbering) per group.

Weather variables	Group 1	Group 2	Group 3	Group 4
Maximum consecutive days under 0°C	133	133	50	50
Julien day before exceed 0°C	90	90	63	63
Mean difference night/day temperature (1)	5.09	5.09	4.42	4.42
Relative humidity (1)	75.18	75.18	75.75	75.75
Total precipitation (1)	277.6	277.6	317.2	317.2
Maximum consecutive days without rain (1)	4	4	4	4
Mean difference night/day temperature (2)	4.99	4.99	4.14	4.14
Number of days under 0°C (2)	48	48	42	42
Relative humidity (2)	69.14	69.14	73.82	73.82
Maximum wind speed (2)	19	19	22	22
Number days with maximum wind speed (2)	1	1	2	2
Total precipitation (2)	25.60	25.60	42.00	42.00
Number of days under -10°C (2)	23	23	42	42
Maximum consecutive days without rain (2)	2	2	5	5
Mean difference night/day temperature (3)	4.83	4.99	5.09	5.57
Number of days under 0°C (3)	24	48	0	0
Relative humidity (3)	71.45	69.14	75.18	71.83
Maximum wind speed (3)	17.5	19	19	19
Number days with maximum wind speed (3)	1.5	1	2	2
Total precipitation (3)	172.50	25.60	277.60	151.40
Number of days under -10°C (3)	11.5	23	0	0
Maximum consecutive days without rain (3)	4	2	4	4
Mean difference night/day temperature (4)	4.05	5.09	2.79	2.79
Number of days under 0°C (4)	16.5	0	27	27
Relative humidity (4)	80.58	75.18	88.49	88.49
Number of days under -10°C (4)	2.5	0	2	2
Total precipitations (4)	250.30	277.60	231.80	231.80
Maximum consecutive days without rain (4)	5.5	4	4	4
Mean difference night/day temperature (5)	4.00	3.02	4.14	4.14
Number of days under 0°C (5)	40.5	33	42	42
Relative humidity (5)	77.56	85.98	73.82	73.82
Number of days under -10°C (5)	14	5	42	42
Total precipitation (5)	124.30	223.00	42.00	42.00
Maximum consecutive days without rain (5)	4.5	7	5	5

5.6 Discussion

Aerial propagule rain communities differed among seasons and years, and the inter-seasonal and inter-annual variations could be explained by differing inter-annual weather conditions. The division of the bryophyte phenology into phenophases has permitted us to identify that the weather impacts on the gametophyte generation the season before the trapping session and on dispersal are determinant for aerial propagule rain composition. These phenophases are especially influenced by relative humidity and cold temperatures. Nevertheless, the weather variables chosen only explain 7.9% of inter-annual variability in the aerial propagule rain composition, reflecting the complex mechanisms linking bryophyte dispersal patterns to regional weather.

5.6.1 Seasonal aerial propagule rain composition is driven by winter conditions rather than differing species phenologies

Seasonal variations in the aerial propagule rain community have been reported in the past (Hock et al. 2004; Ross-Davis and Frego 2004) and were explained by differential timing in species phenology (Longton and Greene 1969; Longton 1985). In our study, we can use species phenology to explain the greater number of *Sphagnum* propagules trapped at the end of summer and fall. Indeed, certain sphagna species are known as "late dispersers" and wait for the wettest conditions of end of summer and fall for dispersal (Sundberg and Rydin 2002). Similarly, the higher number of liverworts trapped in the hottest and wettest months of summer may be due to their cold and drought sensitivity (Laaka-Lindberg 2005; Pohjamo 2008). However, seasonal aerial propagule rain patterns of the true mosses (acrocarps and pleurocarps) seemed primarily explained by responses to weather conditions, particularly winter length, rather than species phenology. Low acrocarp richness and frequency in 2014 compared to 2013 may be explained by the fact that numerous acrocarps are colonist or shuttle species that have stress tolerant propagules or propagules that enter into dormancy [Pohjamo 2008 based on During (1979)] that permit them to tolerate episodic stresses such as dry and cold conditions. In contrast, pleurocarps, of which many are perennial species (based on During 1979, 1992), tolerate stress as gametophytes and continue to mature under less suitable conditions [e.g. dry and cold periods; Pohjamo 2008 based on During (1979)].

However, we demonstrate that specific weather conditions also explain the seasonality of the aerial propagule rain. Indeed, the lower species richness of spring community compared to summer and fall communities may be linked with harsh winter conditions that can delay some of the phenophases of bryophyte phenology (Longton and Greene 1969; Longton 1985). Gregory (1961) and Crum (2001) report that northernmost latitudes are most “propagule rich” in summer and fall than in mid-spring and early summer, which may be due to the fact that propagules released in the summer and fall beneficiated from two or three maturation seasons (previous fall and spring, and previous fall, spring and summer respectively) whereas propagules released in spring have only beneficiated from the previous fall, before halted sporophyte maturation during the winter (Glime 2013), and the early spring when winter is not too long. This was especially true in 2014 where winter prolonged until the end of April with several weeks under -10°C (compensation point of the photosynthesis is reached, Lappalainen et al. 2011). These conditions could lead to the inhibition of growth/maturation of gametophytes/sporophytes and explained the poor pool of species trapped in 2014. However, keep in mind that our conclusions about seasonality in the aerial propagule rain are biased by the trapping design: spring trapping only occured in 2014 where the winter was harsher and longer than in 2012-2013. Consequently, our first hypothesis cannot be validated as both species phenology and weather conditions explained in part bryophyte propagule rain patterns.

5.6.2 The unexpected inter-annual difference in aerial propagule rain composition

Few species were shared between 2013 and 2014 aerial propagule rain communities and in addition to finding a significant decrease in species richness and abundance in 2014, we observed a marked change in community composition leading to the rejection of our second hypothesis. The inter-annual difference was surprising as most of the species trapped in 2013 were significantly less abundant or absent in 2014. This may in part be explained by the importance of maternal investment in reproduction and the subsequent cost for the female gametophyte (Bisang and Ehrlén 2002). Individuals that have invested in the formation and release of propagules one year may have a reduced sporophyte development and propagule release the next year, as they are energetically limited compared to other individuals.

In this paper we have however focused on a second possibility, suggested by Callaghan et al. (1997) and Slack (2011), that bryophyte development may be impacted by inter-annual climatic variations because of the exposure of the gametophyte to environmental factors. As suggested in our third hypothesis, we underline that specific weather conditions influence directly and indirectly propagule release acting on phenophases prior to and during dispersal. Critical weather conditions influenced both growth and maturation of the gametophyte and maturation and dispersal of the sporophytes that therefore impact on the composition of the aerial propagule rain.

5.6.2.1 The importance of summer conditions

For bryophytes, gametangia development and antherozoid movements are entirely dependent on water availability (Reynolds 1980). We found that precipitation and humidity levels during the fertilization and growth-maturation of the gametophyte dictate the pool of trappable propagules one year later. In accordance with Sundberg (2002) and Proctor (2011), we found that high summer humidity results in a richer trappable species pool the next year. Consequently, propagule release in summer and fall depend on moisture amounts in the previous summer and fall whereas spring propagules depend in part on the conditions of the previous summer. The suitable moisture conditions of 2012 can therefore explain the propagule richness and abundance in 2013.

In addition, weather conditions during dispersal also influenced the trapped species pool. The difference in temperature between night and day was positively associated with species richness and composition, which may be explained by associated changes in humidity that induce spore release (Johansson et al. 2015). Dew formation is higher when there is a greater difference in night and day temperatures and the evaporation of dew in the morning allows spore ejection via drought-rehydratation of the capsule peristome and hygroscopic movements of the elaters (Ingold 1959). Furthermore, heating of the air near the soil in the morning after a cold night causes turbulence as the rises. This, along with strong gusts of wind, could drive long distance dispersal of propagules after their ascension in the air column.

5.6.2.2 The existence of a winter chilling process in bryophytes?

An interesting point raised by our study is the positive impact of low temperatures on aerial propagule rain species richness and frequency. Indeed, one month of cumulative days under -10°C the season before the propagule release resulted in more species trapped. Bryophyte response to low temperatures depends on the season (Rütten and Santarius 1992) and cold periods in the fall may act as signals of winter's arrival and invoke species to allocate energy to gametophyte survival rather than to reproduction and dispersal.

Compared to fall, cold periods during the spring may act as signals of a delayed summer time. In 2014, the long winter until April may have delayed photosynthesis and invoked a "winter chilling process", already known for trees, which prevents budburst at the "wrong period" after warming events in the middle of the winter (Harrington et al. 2010). Applied to bryophytes, we can imagine that the energy allocated to sporophyte and spore production may have been more limited in 2014, resulting in sporophyte abortion (Stark 2002) and may explain the poor diversity of propagules trapped. The need of stimuli to initiate the development of sexual organs has been reported by Glime (2013), who also underlines the poor knowledge about initiation signals on bryophytes but deeper studies are required to confirm whether the "winter chilling process" on bryophytes exists.

5.6.3 Limitations of the study

As stressed in Barbé et al. (2016), both the timing of Petri exposure (morning to early afternoon) and the emergence method used to germinate propagules bring some biases. Indeed, we might have favoured the overrepresentation of local propagules compared to more distant ones that are deposited later in the afternoon (Johansson et al. 2015), together with not differentiating between real absence and a non-germination of one species *ex situ* (Ross-Davis and Frego 2004). We also suspect to have favoured the trapping of sexual *vs* asexual propagules (heavier and mainly used for local dispersal; Kimmerer 1991; Löbel et al. 2006), which certainly influenced on the patterns detected. Furthermore, the use of same representative phenology for all bryophyte species as well as the non-consideration of the species sexual investment are over-simplification of our system, however forced by the lack of knowledge on the phenology of the majority of the species. Finally, keep in mind that this study is a "snap shot" of propagule rain patterns and that we have used of weather variables and trapping data of two years, while the chances of identifying spurious patterns are higher than a long term study.

5.6.4 Conclusions

The understanding of bryophyte phenology in response to weather conditions is crucial, especially in the contemporary context of climate changes and in the use of bryophytes as bio-indicator species. This study is the first trying to disentangle the influence of weather variables on the phenology of bryophyte metacommunities dissected into phenophases. We report that propagule release depends on the weather conditions during dispersal but also during survival and growth of the mother gametophyte, particularly winter, and during the fertilization phenophase. Consequently, propagule release seems governed by indirect and direct effects of humidity and temperature one to several preceding seasons. Further modelisation studies, involving long term trapping and weather variables will offer clearer and stronger answers about bryophyte dispersal patterns in response to regional climate, but this work offers new avenues to address this complex subject.

5.7 Acknowledgements

Funding: This project was funded by the Université du Québec en Abitibi-Témiscamingue (UQAT) and the National Science and Engineering Research Council (NSERC) in partnership with Tembec, Eacom and Resolute Forest Products.

The authors sincerely thank Julie Arseneault, Joëlle Castonguay, Louis Dubois, Morgane Higelin, and Aurore Lucas for their field and laboratory assistance; Pascal Drouin, Noémie Graignic, Ahmed Koubaa, Danièle Laporte, Marie-Hélène Longpré, Benoit Plante and Francine Tremblay for their technical support, and Jean Faubert for his precious help in the identification of the most difficult bryophyte samples.

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CHAPITRE VI

CONCLUSION GÉNÉRALE

Après avoir sillonné le sud d'Eeyou Istchee Baie James, sélectionné 30 îlots résiduels dans six feux différents et récolté plus d'un million de spécimens de bryophytes sur une surface équivalente à près de 48 terrains de tennis (9300 m^2), nos conclusions viennent ébranler plusieurs des stéréotypes à la fois sur les rôles des îlots résiduels, mais aussi concernant la dynamique des populations bryophytiques. À des fins d'aménagement écosystémique, cette thèse visait à estimer les rôles de refuge et de source de propagules des îlots résiduels post-feu tout en estimant les effets de bordure sur les communautés bryophytiques. Conjointement, nous souhaitions éclaircir les patrons de dispersion, les réponses aux conditions climatiques et la distribution des bryophytes en pessière noire à mousses.

Pour commencer, nos travaux réfutent le rôle de refuge des îlots résiduels pour les bryophytes étant donné l'absence de certaines caractéristiques environnementales, mais aussi de plusieurs espèces, dont principalement des hépatiques forestières, dans les îlots résiduels post-feu comparé aux forêts non perturbées. Cependant, la richesse moyenne des bryophytes supérieure dans les îlots résiduels et la présence de quatre espèces rares pour la province du Québec aboutit à les qualifier d'« habitats de haute qualité » pour les bryophytes. De plus, certaines caractéristiques spatiales et structurelles des îlots résiduels conduisent à une composition des communautés de bryophytes plus similaire à celles retrouvées dans les forêts non perturbées, fournissant des guides pour l'aménagement des îlots de rétention dans les parterres de coupes.

De sucroit, il apparaît que les îlots résiduels post-feu en forêt boréale soient dépourvus d'habitat de cœur, où la composition de la communauté bryophytique serait similaire à celle retrouvée dans les forêts non perturbées. Cette différence en termes de composition en espèces est imputable à l'effet de bordure, ressenti même dans les îlots résiduels les plus larges (de 3 à 11 ha) dans lesquels des espèces inféodées aux vieilles forêts non perturbées sont absentes. Cette étude fournit alors un contrôle de la réponse naturelle des bryophytes à l'effet de bordure, jusque là falsifiée par des interprétations issues d'études réalisées dans des paysages perturbés anthropiquement.

Conjointement à ces conclusions, nous corroborons le rôle de sources de propagules des îlots résiduels post-feu qui participent à la recolonisation de la matrice brûlée, non pas uniquement à l'échelle locale, mais aussi à l'échelle régionale. Ces conclusions renversent simultanément le paradigme d'une capacité de dispersion limitée des bryophytes. En effet, nous rapportons l'occurrence de la dispersion à longue distance (de 650 m à 30 km ; échelle régionale) et ce, quelle que soit la stratégie de vie des bryophytes. La topographie et les vents dominants de la région pourraient expliquer les distances accrues parcourues par les propagules bryophytiques en pessière noire.

À des fins purement bryologiques, nous rapportons l'existence d'une variabilité interannuelle de la pluie de propagules aérienne des bryophytes en réponse aux conditions climatiques. Après division du cycle phénologique des bryophytes en différentes phases, nous démontrons que les conditions climatiques concomitantes, mais aussi en amont de la dispersion des propagules gouvernent la composition de la pluie de propagules. Ainsi, la fertilisation durant l'été, un an avant la dispersion des propagules, mais aussi la croissance et la maturation du gamétophyte les saisons précédant la libération des propagules, déterminent la pluie de propagules disponible la saison voire l'année suivante. Le taux d'humidité, mais aussi la température sont les conditions les plus influentes sur le cycle phénologique des bryophytes. De plus, sous les latitudes nordiques, la longueur et la rudesse de la saison hivernale sont de premières importances pour le déroulement du cycle phénologique des bryophytes. Cependant, ce travail de type « capture d'écran » necessite d'être complémenté par des études à plus long terme pour en asseoir les conclusions.

La question du transport externe des bryophytes par des agents biotiques, les micromammifères, est abordée dans l'annexe 1 ci-après. Spéculée par les bryologues à maintes reprises (Carey, 2003 ; Kimmerer, 1994 ; Rydgren *et al.*, 2007), cette étude est la première à directement prouver cette interaction. À l'issue d'un travail collaboratif entre mammalogistes et bryologues, ayant allié les compétences respectives de chacun en trappe et brossage de mammifères et en culture *in vitro* et identification de bryophytes, nous mettons en évidence le transport de six taxa bryophytiques par cinq espèces de micromammifères en pessière noire à mousses. Ce travail, bien qu'il puisse paraître anecdotique, rapporte une interaction journalière entre deux groupes d'organismes cosmopolites de la forêt boréale et qui pourraient avoir une portée plus conséquente qu'attendue sur la dynamique des populations bryophytiques. Les micromammifères représentent alors des « liens mobiles » (Couvreur *et al.*, 2004) pleinement impliqués dans la dynamique métapopulationnelle des bryophytes.

Finalement, cette thèse a permis le recensement de 168 espèces de bryophytes dans la région d'étude. Le sud du Nord-du-Québec et l'Abitibi-Témiscamingue sont qualifiés de « trous noirs » des connaissances en bryologie (comm. pers. J. Faubert, 2015). Au terme d'un an et demi d'identification, nous rapportons, en annexe 2, l'extension d'aire de 35 espèces, dont 20 nouvelles pour la région d'étude et étendons leurs aires de distribution vers le nord. Ce doctorat contribue alors à l'actualisation du portrait bryologique préindustriel de la pessière noire à mousses nord-américaine.

6.1 Limitations

Pour commencer, bien que chacune des identifications bryologiques fut vérifiée par la Dre Nicole Fenton et que les spécimens les plus récalcitrants furent envoyés pour analyse au bryologue québécois, Mr Jean Faubert, l'étude des bryophytes force à l'humilité et je tiens à souligner que les erreurs d'identification, particulièrement concernant les spécimens germés en laboratoire, m'incombent intégralement.

Outre ce point fondamental, chacun des chapitres présentés ici jouit de ses limites respectives, spécifiées durant ledit chapitre. C'est ainsi que les méthodes d'interception, de collecte et de culture des propagules amènent chacune leurs lots de biais.

D'aucuns noteront la variance limitée expliquée par les modèles présentés. Nous souhaitons souligner qu'une telle variance reste néanmoins conséquente dans le cadre de l'étude de processus biologiques à si fine échelle. C'est pourquoi, bien que cela ne fasse pas l'unanimité dans la communauté scientifique, nous discutons des résultats au-dessus du seuil de significativité arbitrairement fixé à 0.05 (*i.e.*, $0.05 < \alpha < 0.1$; Murtaugh, 2014 ; de Valpine, 2014). Les résultats de ce doctorat concordent donc avec les conclusions de Fenton et Bergeron (2013) et Huntley *et al.* (2010) rapportant l'invalidité d'utiliser une « photographie instantanée et ponctuelle » des conditions de l'habitat pour modéliser les patrons de distribution et dispersion des espèces, dans notre cas des bryophytes. La stochasticité neutre ou encore les effets fondateurs impliquant que la composition d'une communauté dépendent de l'identité des espèces la composant avant la perturbation, mais aussi de l'ordre d'arrivée des espèces (Herben, 1995 ; Vellend *et al.*, 2014) sont des processus pouvant justifier la faible variance expliquée par nos modèles, et devront être intégrés dans de futures études traitant de problématiques similaires.

Pour finir, bien que cette thèse traite de processus généraux (patrons de dispersion, réponses aux effets de bordure et aux conditions climatiques), les résultats rapportés ici demeurent effectifs pour les communautés bryophytiques en pessière noire à mousses du Québec et c'est avec beaucoup de circonspection que nous proposerons de les étendre à d'autres écosystèmes. Néanmoins, nous offrons des pistes de réflexion solides et des méthodes reproductibles dans le cadre de futures études dans d'autres écosystèmes et, pourquoi pas même, portant sur d'autres organismes.

6.2 Recommandations pour l'aménagement forestier écosystémique

L'aménagement forestier écosystémique ambitionne la poursuite de l'exploitation forestière en parallèle du maintien de la biodiversité et de la fonctionnalité des écosystèmes en s'inspirant des patrons de perturbations naturelles (Bergeron et Harvey, 1997). Ce projet s'inscrit pleinement dans ce contexte en rapportant le rôle des îlots résiduels post-feu dans la dynamique de régénération forestière. En nous penchant à une nouvelle échelle, celle des bryophytes, nous offrons un canevas à très fines mailles pour l'aménagement forestier. Les attributs des îlots résiduels mis en exergue comme d'intérêt dans la dynamique des populations bryophytiques devront être considérés lors de l'élaboration des bouquets et îlots de rétention dans les parterres de coupes. En effet, les caractéristiques des îlots résiduels post-feu, qu'elles soient spatiales (*e.g.*, aire et forme, isolement), temporelles (âge, temps depuis la perturbation) ou structurelles (*e.g.*, densité du peuplement, complexité) font influencer à la fois la survie, la dispersion et la recolonisation des bryophytes, elles-mêmes garantes de la résilience de l'écosystème suite à la perturbation.

Nous rapportons ainsi, à l'issue du chapitre II, l'importance des caractéristiques temporelles, spatiales et structurelles des îlots résiduels pour la richesse spécifique et la composition des communautés bryophytiques. Les îlots résiduels contenant un peuplement forestier de plus de 56 ans pour une surface excédant 0.20 ha et une structure horizontale et verticale modérée (*i.e.*, < 8 m de hauteur moyenne, 550 tiges/ha en moyenne et moins de 10 m^3/ha de bois mort au sol en début de décomposition) contiennent une communauté bryophytique plus similaire à celle des forêts non perturbées. De tels îlots résiduels participent au maintien des espèces les plus sensibles à la perturbation telles que de nombreuses hépatiques forestières non retrouvées dans la matrice perturbée. Bien que ces caractéristiques contribuent à la persistance d'espèces sensibles, l'absence de plusieurs autres taxa dans les îlots résiduels souligne la nécessité de 1/ conserver des peuplements forestiers continus et matures aux abords des zones de coupes, et de 2/ conserver des îlots de rétention plus représentatifs de la compostion de la matrice pré-coupe. La conception d'îlots résiduels selon les critères cités ci-dessus, cumulée à la conservation de peuplements non perturbés sont les clefs du maintien de la bryo-diversité dans les paysages perturbés que cela soit naturellement ou de façon anthropique.

Ajoutés à ces caractéristiques, les résultats du chapitre III attestent de l'absence de cœur même dans les îlots résiduels de plus de trois hectares. De plus, certaines espèces retrouvées dans les forêts non perturbées demeurent absentes de l'intérieur des îlots résiduels excédant 11 ha. Cela suggère que la fragmentation du paysage suite à la perturbation engendre des conditions d'habitats distinctes entre les îlots résiduels et les forêts non perturbées. Cet effet est cependant atténué dans les bordures orientées au nord, qui contiennent davantage d'espèces inféodées aux forêts non perturbées, comparées aux bordures orientées au sud. Cette conclusion offre des perspectives intéressantes sur le plan de l'orientation des îlots de rétention. De plus, ce travail souligne que les îlots de rétention ne pourront en aucun cas être utilisés comme substituts des forêts non perturbées en vue de maintenir les espèces sensibles à la création de bordures. Les conclusions des chapitres II et III renforcent de surcroit l'inadéquation de maintenir des bouquets et des îlots forestiers de trop petites superficies (< 3 ha) dans les parterres de coupes.

Outre ces conclusions, le chapitre IV rapporte le rôle des îlots résiduels comme sources de propagules à l'échelle locale, mais aussi, et principalement, à l'échelle régionale. La dynamique des populations bryophytiques est donc influencée par des sources de propagules *i.e.*, des îlots résiduels, distants de plus de 30 km.

Ainsi, en se focalisant sur les bryophytes, cette étude suggère d'élargir notre angle de vue pour concevoir un aménagement forestier à double échelle :

(i) locale pour une conception individualisée des bouquets et îlots de rétention ciblée sur l'âge, la taille et la structure des peuplements conservés dans les parterres de coupes ;

(ii) du paysage pour un agencement spatial optimal des bouquets et îlots de rétention dans les unités d'aménagement et des unités d'aménagement elles-mêmes.

Les unités d'aménagement forestier sont divisées, par le Ministère des Forêts, de la Faune, et des Parcs (MFFP) en compartiments d'organisation spatiale (COS) de 30 à 150 km² (Nappi, 2013 ; MFPP, 2015). Dans les Plans d'Aménagement Forestier Intégré (PAFI) de la pessière noire à mousses, un minimum de 30% de la superficie productive des COS doit être maintenu en forêts résiduelles d'au moins 7 m de hauteur (Nappi, 2013 ; MFPP, 2015). Aussi, dans les territoires certifiés FSC (Forest Stewardship Council) 10% de la superficie productive des COS devra être conservés sous forme de forêts matures (> 90 ans ; Dallaire & Légaré 2016). Bien que les conclusions de cette thèse ne permettent pas de statuer sur la proportion de forêts résiduelles à conserver au sein des COS, elles permettent d'étayer les connaissances sur le design local (*i.e.*, âge, superficie, structure) des îlots de rétention à maintenir en vue d'optimiser la régénération forestière. Étant donné nos résultats sur les distances potentiellement parcourues par les propagules bryophytiques en forêt perturbée naturellement, la superficie minimale et l'agencement des COS ainsi que l'agencement des forêts résiduelles à l'échelle du paysage semblent des points fondamentaux. Aussi, une proportion donnée du territoire devra être maintenue sous forme de forêts non perturbées. En effet, les peuplements forestiers non perturbés considérés dans cette étude contribuent dans leur ensemble au maintien d'espèces bryophytiques qui auraient sinon disparu du territoire suite au feu. Ajoutée aux échelles spatiales locale et du paysage, l'échelle temporelle devra donc être considérée. Il apparaît nécessaire de maintenir, au sein de chaque COS, des vieux peuplements forestiers permanents non aménagés. Nous entendons ici conserver des peuplements vieux au sens de l'âge de l'arbre vétéran du peuplement, mais aussi de l'âge dont origine le peuplement lui-même. On parle du temps depuis la dernière perturbation majeure encourue, qui peut considérablement excéder celui de l'arbre le plus vieux (Arsenault, 2003 ; Campbell & Fredeen, 2004). Dans cette étude certains peuplements originent de feu de plus de 3000 ans, pour des arbres vétérans agés de 150 à 200 ans. De tels peuplements sont indispensables pour les organismes sensibles aux perturbations et requérant des conditions microclimatiques stables ainsi que des quantités et qualités de legs biologiques données (*e.g.*, bois mort en stade avancé de décomposition ; Siitonen, 2001), comme c'est le cas des bryophytes (Humphrey *et al.*, 2002 ; Lesica *et al.*, 1991 ; Rambo, 2001). Ces peuplements ne pourront en aucun cas être substitués par les îlots de rétention dans les unités d'aménagements ; de leur pérennité dépend celle des bryophytes les plus sensibles et, *a fortiori,* la résilience de l'écosystème.

6.3 Perspectives en termes de conservation de la bryoflore

Dans ces travaux l'approche de « filtre brut » a été préférée à celle de « filtre fin » en vue de focaliser sur la communauté bryophytique dans son ensemble et non sur des espèces individuelles (Lindenmayer *et al.*, 2000 ; Noss, 1987). Les bryophytes sont utilisées comme espèces bio-indicatrices et sont traitées en termes de richesse spécifique et de composition des communautés ce qui permet de tirer des conclusions générales de leurs patrons de dispersion, colonisation et distribution. Nous espérons que cette thèse contribuera à une gestion plus réfléchie des écosystèmes forestiers en vue de maintenir leurs fonctionnalités et résiliences, mais aussi, à la protection des bryophytes, patrimoine végétal remarquable et fragile des forêts boréales canadiennes.

Au regard des conclusions du chapitre IV et de l'annexe I, nous rapportons l'importance de l'échelle régionale pour la dispersion et recolonisation du paysage par les bryophytes. Cela suggérerait une moindre limitation des bryophytes par leurs capacités de dispersion que par les conditions de l'environnement et la qualité des microhabitats (Lönnell *et al.*, 2014 ; Mota de Oliveira et ter Steege, 2015). De plus, en parallèle de la conservation des bryophytes, il faudra veiller à préserver les interactions entre d'autres organismes tels que les micromammifères, eux aussi menacés par la fragmentation du territoire engendrée par l'exploitation forestière (*c.f.* Fisher et Wilkinson, 2005).

Les conclusions issues du chapitre V et de l'annexe II démontrent de la pertinence d'utiliser les bryophytes, à l'instar des lichens (Perhans *et al.*, 2009), des micromammifères (Pearce & Venier, 2005) ou encore des coléoptères (Bouget *et al.*, 2014), comme sentinelles de l'environnement et indicatrices de l'effet des perturbations naturelles et anthropiques sur l'écosystème. Slack (2011) qualifie les bryophytes de « Canaries dans une mine de charbon » étant donné leur sensibilité aux changements des conditions environnementales. Cependant, leur utilisation comme espèces bio-indicatrices requiert des connaissances fondamentales de leurs aires de distributions, prérequis aussi indispensable à leur protection. À ce titre, l'actualisation du portrait bryologique préindustriel de la pessière noire à mousses du sud du Nord-du-Québec présenté en annexe II ci-après est une des fiertés de ce doctorat. Les extensions d'aires et les occurrences de nouvelles espèces dans la région soulignent qu'un travail conséquent demeure quant à la compréhension de la dynamique des bryophytes, mais aussi, et en premier lieu, quant à leur distribution.

Bien que cette thèse vienne étayer les recommandations du MFFP en termes d'aménagement forestier et les connaissances de la dynamique des bryophytes, il soulève surtout un nombre conséquent de nouvelles questions : la croissance des bryophytes diffère-t-elle dans les îlots résiduels et les forêts non perturbées ? Les communautés bryophytiques sont-elles similaires entre les îlots résiduels post-feu et les îlots de rétention post-coupe ? À quelle proportion de la dispersion participent les agents biotiques ? Quelle part de la variabilité dans les patrons observés est expliquée par la stochasticité et les effets fondateurs ? Quelle est l'aire de distribution réelle des espèces de bryophytes en forêt boréale ?

L'étude des bryophytes permet d'affiner nos connaissances de la dynamique forestière naturelle en vue de maintenir la capacité de l'écosystème à faire face aux perturbations futures, qu'il s'agisse de l'exploitation forestière comme des changements climatiques. Ainsi, le vieil adage nippon disait vrai : « qui cherche la source du fleuve, la trouvera en regardant les gouttes d'eau sur la mousse »…

ANNEXE I

DISPERSAL OF BRYOPHYTES AND FERNS IS FACILITATED BY SMALL MAMMALS IN THE BOREAL FOREST

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Ecoscience, **DOI: 10.1080/11956860.2016.1235917**

A1.1 Abstract

Bryophytes and pteridophytes are important contributors to ecosystem services in boreal regions. Abiotic agents are considered their main dispersers, but recent studies suggest that biotic agents including invertebrates, birds, and large mammals might also be efficient dispersal agents. Dispersal of cryptogams by ground-dwelling small mammals is often assumed to occur, but has yet to be demonstrated. In this study, we present the first evidence of boreal cryptogam species being dispersed by ground-dwelling small mammals. In 2013 and 2014, we recorded bryophyte cover and fern presence in 35 sites in black spruce forest. We also collected diaspores by brushing the fur of 99 ground-dwelling small mammals live-trapped in the same sites. Diaspores were then germinated on nutrient agar for six months. Viable diaspores of five bryophyte species and one fern species were successfully grown. No association was found between the cryptogam community sampled on site and the diaspore community grown on artificial substrate. Unlike abiotic agents that randomly disperse cryptogams, small mammals are more likely to transport diaspores to suitable substrates where microhabitat requirements for germination are met. Our results highlight the need to consider a broad spectrum of dispersal agents when focusing on the community dynamics of cryptogams.

Key-words: boreal forest, cryptogams, microhabitat requirements, medium-range dispersal, rodents

A1.2 Résumé

Les cryptogames (bryophytes et pteridophytes) représentent une composante fondamentale des régions boréales, et leur dispersion à moyenne et longue distance dépend principalement d'agents abiotiques. Des études récentes suggèrent pourtant l'importance d'agents biotiques tels que les invertébrés, les oiseaux et les grands mammifères comme vecteur de dispersion. La dispersion des cryptogames par les micromammifères est régulièrement admise mais n'a encore jamais été formellement examinée. Dans cette étude, nous présentons la première preuve tangible du transport des cryptogames boréaux par des micromammifères. Au cours des étés 2013 et 2014, nous avons estimé le couvert des bryophytes et la présence des fougères (communauté *in situ*) dans 35 sites en pessière noire à mousses. Conjointement, nous avons brossé le pelage de 99 micromammifères de cinq espèces différentes capturés vivants dans les mêmes sites. Le matériel végétal collecté a été disposé durant six mois sur un gel nutritif d'agar afin d'étudier la germination. Nous avons observé la germination de cinq espèces de bryophytes et d'une espèce de fougère. Nous n'avons trouvé aucune association entre la communauté de cryptogames *in situ* présente dans les sites et la communauté germée sur un substrat artificiel. Contrairement à la dispersion aléatoire par des agents abiotiques, la dispersion par les micromammifères est plus susceptible de transporter les diaspores vers des substrats propices à leur germination. Nos résultats soulignent l'importance de considérer la dispersion par les micromammifères dans l'étude des dynamiques des communautés de cryptogames.

Mots-clef : cryptogames, dispersion à moyenne distance, exigences de microhabitat, forêt boréale, rongeurs

A1.3 Introduction

Bryophytes [i.e., true mosses, liverworts and sphagna, following Crum (2001)] and ferns play important roles in the functioning of the boreal forest. They provide many organisms with shelter and food (Davidson et al. 1990; Haines & Renwick 2009), and they contribute to numerous ecosystem services. For instance bryophytes and ferns are implied in water filtration, nutrient retention, nitrogen fixation (through the association of some bryophytes and aquatic ferns with cyanobacteria), and they also provide germination substrates for tree seeds (Baker et al. 2003; Bay et al. 2013; Clark et al. 2005; DeLuca et al. 2007; George & Bazzaz 1999; Turetsky et al. 2012). The dispersal capacities of bryophytes and ferns remains a controversial topic, as some studies have reported dispersal distances of only a few meters for bryophytes and ferns (Söderström 1987; Tájek et al. 2011), whereas other studies have demonstrated their ability to travel between 20 and 100 km and beyond (De Groot et al. 2012; Hylander 2009; Sundberg 2013). Both bryophytes and ferns reproduce sexually and asexually, although vegetative reproduction is less common among ferns than bryophytes. Although still debated, it is assumed that the sexual "dust-like spores" of bryophytes are effective dispersal agents contributing to long distance dispersal. In contrast, vegetative propagation by asexual agents such as gemmae and specialized brood-leaves or by vegetative fragments of leaves and stems mainly supports short-distance dispersal and local population maintenance (c.f. Boch et al. 2013; Eckert 2002; Löbel & Rydin 2009; Muñoz et al. 2004; Pohjamo et al. 2006). Fragments of mature individuals can also grow into new individuals (Benscoter 2006; Mälson & Rydin 2007; Rochefort et al. 2003). Bryophytes and ferns are believed to disperse mainly through abiotic agents, such as water and wind (Johansson et al. 2014; Muñoz et al. 2004). Dispersal by biotic agents also occurs, with evidence of transport by birds (Davison 1976; Lewis et al. 2014; Osorio-Zuñiga 2014), large mammals and bats (Heinken et al. 2001; Parsons et al. 2007, Pauliuk et al. 2011), as well as invertebrates (Kimmerer & Young 1995; Marino et al. 2009; Rudolphi 2009). Such transport may be exozoochorous (i.e., external attachment on animal) or endozoochorous (i.e., internal, passing through the digestive tracts), and consumption of both bryophytes and pteridophytes has been shown (Arosa et al. 2010; Boch et al. 2013). Although one study has indirectly linked bryophyte abundance to the dynamics of small mammal populations (Rydgren et al. 2007), and some authors have speculated that small mammals transport bryophytes (Carey 2003; Kimmerer 1994), to our knowledge, external dispersal of bryophytes and ferns by ground-dwelling small mammals (a form of mammiochory) has yet to be demonstrated. As boreal ground-dwelling small mammals are in continuous contact with the cryptogam layer during their daily activities, we hypothesize that dispersal of cryptogam species by small mammals is likely to occur. We predict 1) that cryptogam diaspores are frequently dispersed by all species of small mammals without any exclusive species-specific associations, 2) that the cryptogam species found on small mammal fur may reflect the extant cryptogam community found on sites, and 3) that distinct life traits (e.g., formation of large carpets, production of copious quantities of diaspores) may render some cryptogam species more susceptible to be dispersed by small mammals than other cryptogam species.

A1.4 Materials and methods

A1.4.1 Study area and sampling

The study area covers a total of 8325 km^2 (79°29’W, 49°00’N – 75°39’W, 50°22’N) in the western black spruce (*Picea mariana*)-feather moss (*Pleurozium schreberi*) forest of Québec eastern Canada (Grondin 1996). This boreal region is characterized by a subpolar continental climate. Average annual temperature and precipitation are respectively 1 °C and 927.8 mm (1981 to 2010), recorded at the nearest weather station, Lebel-sur-Quévillon, Québec (Environment Canada 2015). The main tree species are black spruce (*P. mariana*), jack pine (*Pinus banksiana*) and balsam fir (*Abies balsamea*), along with occasional broadleaf species such as white birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*). The understory is primarily composed of ericaceous species (e.g., *Rhododendron groenlandicum*). True mosses form a dense carpet and are slowly replaced by *Sphagnum* species as drainage conditions deteriorate due to paludification with time since fire (Fenton & Bergeron 2006). The region is also characterized by large, recurrent and severe wildfires (8000 ha on average; Bergeron et al. 2004), although fire is increasingly being replaced by forest management practices as the primary agent of disturbance (Imbeau et al. 2015).

We selected a total of 35 sites distributed among old undisturbed forest stands (over 100 years old), post-fire remnant patches (3.9 ha [range: 0.4 - 11.1]) left after wildfires that occurred over 20 years ago, green tree retention patches (0.7 ha [range: 0.1 - 1.3]) left after recent clear-cutting (< 10 years), and linear cutblock separators (60-100 m large, connected to old-growth forests) that separate clearcut areas. Sites were at least 500 m apart, based on the average movement distance of the most mobile species (Larsen & Boutin 1994), to ensure that any two sites were independent. Live-trapping was conducted between July 23rd and August 15th in 2013 and between June 1st and August 21st in 2014, with both Tomahawk live-traps (8.0 x 8.0 x 41.0 cm - Tomahawk Live Trap llc ®) and Sherman live-traps (7.5 x 9.0 x 23.0 cm - H.B. Sherman Traps, Inc. ®). Tomahawk live-traps were used to trap arboreal mammalian species such as American red squirrels (*Tamiasciurus hudsonicus*) and northern flying squirrels (*Glaucomys sabrinus*). Sherman live-traps enabled us to trap smaller ground-dwelling mammals such as southern red-backed voles (*Myodes gapperi*). All traps were baited with peanut butter and apple pieces, which provide water and food to the trapped individuals. Cotton batting was also added to each trap to provide shelter and insulation in order to ensure better survival. We established one transect of six Tomahawk live-traps per site with a distance of 10 m between traps. Transects were 50 m long in order to accommodate our smallest sites. Then we established a 15 m square trapping grid of 16 Sherman live-traps centred on the transect line with traps spaced at 5 m intervals (Figure A1.1). We trapped during 72 consecutive hours, checking the traps twice a day (early morning and late afternoon). Each site was monitored with this trapping regime during one trapping session in 2013 (three nights). In 2014, three trapping sessions were completed (three nights in each of June, July, and August). Toothbrushes were used to collect the potential diaspores (i.e., spores, gemmae, vegetative fragments) on the fur of the trapped small mammals. Each small mammal was gently brushed on their back, belly and paws with a new toothbrush for two minutes. We then sealed each toothbrush in a new labelled plastic bag. All individuals were released after brushing. Diaspores were visible neither on the mammalian fur nor used toothbrushes. All manipulations adhered to the Canadian Council on Animal Care Guidelines and were approved by the Institutional Animal Care Review Committee at the Université du Québec en Abitibi-Témiscamingue (UQAT, permit no. 2013-04-02). The extant bryophyte and fern community composition of the 35 sites was estimated using three 1-m^2 (1 x 1 m) quadrats placed randomly within the Sherman trapping grid. Percent cover of each bryophyte species present was visually estimated. Species represented by only one individual were noted as trace (i.e., less than 1% of cover of the 1 m^2 quadrat). Only the presence/absence of fern species was recorded.

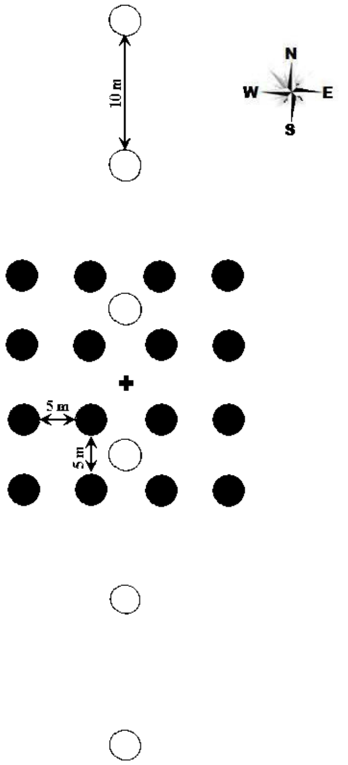

Figure A1.1 Representation of the trapping station at each site. The filled cross (✚) represents the trapping station centre, empty circles (○) represent one Tomahawk live-trap, filled circles (●) represent one Sherman live-trap.

We germinated the diaspores collected on an agar substrate following the "emergence method" used by Ross-Davis & Frego (2004). In the laboratory, we washed each toothbrush with deionized water over a Petri plate 90 mm in diameter to extract potential diaspores. Each Petri plate contained 78.5 cm^2 of nutrient agar prepared in sterile laboratory conditions [Parker Thompson's basal nutrient medium of Klekowski (1969), described by *C-Fern* Project © (1995–2014)]. After the extraction, Petri plates were covered and placed randomly in germination chambers for six months (from September 2013 to March 2014 after the 2013 trapping session and from September 2014 to March 2015 after the 2014 trapping session), under continuous spectrum Verilux ® (48" and 32 Watt) fluorescent light tubes with a 12 h/12 h light/dark regime. Petri plates were misted with deionized water as needed to prevent them from drying out. Germination chamber temperature was maintained at 22 °C. When the nutrient agar became too thin, the entire content of the Petri plate was transferred to a new Petri plate with fresh nutrient medium. When the growing bryophytes and ferns were too tall for Petri plates to contain they were placed in individual transparent plastic pots. Development of bryophyte gametophytes was assessed twice a week following germination. Minor contamination by fungus or algae was manually removed from the nutrient agar with forceps. In the case of a major contamination, where the Petri plate was entirely covered by fungus or algae and survival of the protonemata was compromised, protonema were removed from the plate, bathed in deionized water and transplanted in a new Petri plate. Three control Petri plates with virgin nutrient agar were placed in the germination chambers every three months for the duration of the 6-month emergence period to identify potential contaminants (air-borne diaspores). No species developed on any of the control plates, indicating that sample plates had not been contaminated during the laboratory growing period. Cryptogam culture with this method was generally successful, even though it introduces a bias towards cryptogam species able to germinate in artificial conditions.

All individuals were identified in the laboratory following Faubert (2013, 2014) for bryophytes. Ferns were identified following Martineau (2014). Due to the artificial growing conditions in Petri plates, bryophytes lacked some critical features for species identification, which is why some specimens were only identified to genus, in particular sphagna and members of the genera *Pohlia* sp. and *Polytrichum* sp.

A1.4.2 Statistical analyses

Data from 2013 and 2014 were pooled for analyses. Furthermore, we made no distinction among the types of sites where small mammals were trapped due to the low sample size in each site type (old-growth forests, post-fire remnant patches, green-tree retention patches and linear cut-block separators). We consequently pooled data for all small mammals. We conducted analyses according to cryptogam species taxonomic groups and life forms: liverworts, sphagna, and true mosses, divided into acrocarpous and pleurocarpous groups. No distinction was made between individuals germinated from spores or gemmae because we could not distinguish among these two forms of diaspores on Petri plates. Vegetative fragments (i.e., stem and leaf fragments) deposited on Petri plates were also considered. To avoid overestimating the number of dispersed diaspores, cryptogam individuals were counted using the number of individual protonema and vegetative fragments instead of the number of stems produced, given that a single protonema can generate several stems in one Petri plate. As it is difficult to distinguish protonema once the plant is fully developed, monthly photographs of the plates were used to identify individual protonema. We counted the number of protonema germinated from spores/gemmae as well as the number of vegetative fragments in each Petri plate. Species abundance was calculated as the number of individual of each species per Petri plate. The extant community present on each site was described using the mean percent cover of each bryophyte species recorded in three 1-m^2 quadrats. Ferns were considered present if observed in at least one of the three 1-m^2 quadrats per site.

We compared the composition of the extant community and the diaspore community grown in Petri plates using Kendall rank correlations (Legendre & Legendre 2012). The individuals identified to genus in the Petri plates were compared to the species from the same genus in the extant community (e.g., *Polytrichum* sp. from Petri plates were compared to *Polytrichum commune* sampled on site). As there was no linear pattern between the two variables and because some variables included outliers, the Kendall rank correlation was more appropriate than the Pearson product-moment correlation to quantify the association between the abundance of species grown in Petri plates and percent cover of species in the extant community. Similarly, to assess whether the abundance of species grown in Petri plates was linked to their presence onsite, we used a second Kendall rank correlation on the abundance of the cryptogam species grown in Petri plates and their cover in small mammal trapping grids. We obtained the p-value of each Kendall rank correlation coefficient by randomization after 1000 iterations. This approach consisted of permuting the original data for each variable to break the pairwise structure of the data in agreement with the null hypothesis of no correlation and computing the test statistic at each iteration. All analyses were conducted in R 3.0.1 statistical software (R Core Team 2015).

A1.5 Results

A total of 99 small mammals were trapped and brushed, including southern red-backed voles (*Myodes gapperi*), American red squirrels (*Tamiasciurus hudsonicus*), deer mice (*Peromyscus maniculatus*), northern flying squirrels (*Glaucomys sabrinus*) and common heather voles (*Phenacomys ungava*) (Table A1.1). Approximately half of the trapped individuals carried viable bryophyte and pteridophyte diaspores that germinated within six months (i.e., 50.5%; Table A1.1).

Table A1.1 Number of Petri plates incubated with material brushed from five small mammal species trapped in the boreal forest. A separate Petri plate was used for each small mammal individual and represents the number of small mammals carrying viable diaspores.

Mammal species	Total Petri plates incubated (n)	Petri plates with germination (n)	Petri plates with germination (%)
Glaucomys sabrinus / northern flying squirrel	11	6	54.5
Tamiasciurus hudsonicus / American red squirrel	28	14	50.0
Myodes gapperi / red-backed vole	40	20	50.0
Peromyscus maniculatus / deer mouse	18	8	44.4
Phenacomys ungava / common heather vole	2	2	100.0
Total	99	50	50.5

We counted a total of 172 individuals on Petri plates, germinated from spores/gemmae or identified as vegetative fragments such as leaf or stem pieces.

Six bryophyte species (*Ceratodon purpureus*, *Platygyrium repens*, *Pleurozium schreberi*, *Pohlia* sp., *Polytrichum* sp. and *Sphagnum* sp.) and one pteridophyte species (*Dryopteris* cf. *carthusiana)* were recorded, along with 11 unidentifiable protonema (Figure A1.2 and Table A1.2). Sphagna represented 68.6% of the identified bryophyte protonemata. Three acrocarpous and two pleurocarpous species were encountered consisting of 22.1% and 9.3% of the identified protonemata, respectively. No liverworts developed on the Petri plates.

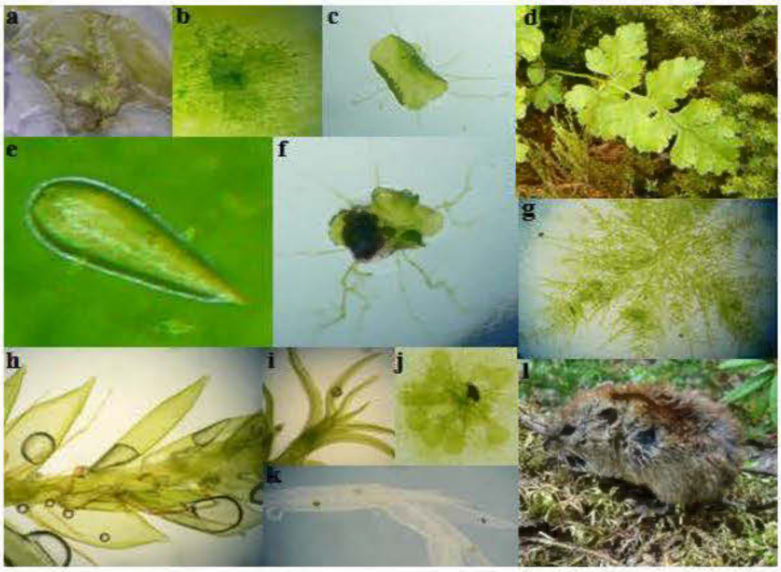

Figure A1.2 Photography of cryptogam species grown ex situ (a–k) and of one Southern red-backed vole found in situ in Pleurozium schreberi (l). Protonemata (a–c, f–g and j); Juvenile *Dryopteris* cf. *carthusiana* (d); Leaf and branch of Sphagnum sp. (e and k); Stem of *P. schreberi* (h); Stem of *Polytrichum* sp. (i); Southern red-backed vole (*Myodes gapperi*) (l). Photo credits: M. Barbé (a–k); D. Fauteux (l).

The number of mammalian species transporting a given bryophyte or fern species ranged from one to all five small mammal species (Table A1.2). Mammalian species transported from eight to 64 diaspores from two to five different bryophyte or fern species. We found no association between bryophyte species and mammalian species. However, the one fern species was exclusively found on the fur of American red squirrels.

Table A1.2 List of bryophyte and fern species brushed from five small mammal species trapped in boreal forests (n = 99 individuals trapped). Values refer to the number of bryophyte individuals grown in Petri plates counted as number of protonemata germinated from spores/gemmae or as number of vegetative fragment. As one Petri plate may contain several protonema, the values in brackets represent the number of Petri plates in which the cryptogam species were found. In species richness of bryophytes and ferns protonemata of Sphagnum sp. and Sphagnum leaves were grouped together and unidentified protonemata and unidentified stems/leaves were omitted because we could not determine if they were new species or not. [a], Acrocarp; [b], Pleurocarp; [c], Fern.

Bryophyte species	*Glaucomys sabrinus* / northern flying squirrel	*Tamiasciurus hudsonicus* / American red squirrel	*Myodes gapperi* / southern red-backed vole	*Peromyscus maniculatus* / deer mouse	*Phenacomys ungava* / common heather vole	Sum of diaspores	Number of species as dispersal agents
Ceratodon purpureus [a]	0	1 (1)	0	3 (1)	0	4	2
Platygyrium repens [b]	2 (1)	0	0	0	0	2	1
Pleurozium schreberi [b]	0	10 (2)	1 (1)	0	0	11	2
Pohlia spp.[a]	0	0	11 (1)	8 (2)	0	19	2
Polytrichum spp.[a]	1 (1)	1 (1)	3 (2)	1 (1)	2 (1)	8	5
Sphagnum spp.	6 (5)	19 (10)	18 (11)	47 (4)	6 (1)	96	5
Protonemata unidentified	2 (4)	3 (1)	5 (4)	1 (1)	0	11	4
Dryopteris cf. *carthusiana* [c]	0	2 (2)	0	0	0	2	1
Sphagnum sp. leaves*	2 (2)	4 (1)	6 (5)	4 (2)	0	16	4
Stems/Leaves unidentified*	0	1 (1)	2 (1)	0	0	3	2
Sum of individuals germinated from spores/gemmae + vegetative fragments	11+2	36+5	38+8	60+4	8		
Cryptogam species richness per small mammal species	3	5	4	4	2		

"*" agents referring to vegetative fragment.

In the extant community, we found 16 bryophyte taxa: five pleurocarpous, seven acrocarpous and two liverwort species (Figure A1.3). This value represents the minimum species richness of the sites, true species richness was probably much higher. Two bryophyte species found in Petri plates were not encountered in the extant community: *C. purpureus* and *P. repens*. Sphagna were present in all sites. Various ferns were present as isolated individuals. Sphagna dominated both the pool of diaspores collected and the species cover on site. However, there was no association between the species composition of bryophytes and ferns on site and the species composition grown in Petri plates (Kendall tau = 0.05, *p*-value = 0.752, Figure A1.3). Similarly, we found no association between the abundance of bryophyte and fern species grown in Petri plates and their cover on site (Kendall tau = 0.69, *p*-value = 0.078).

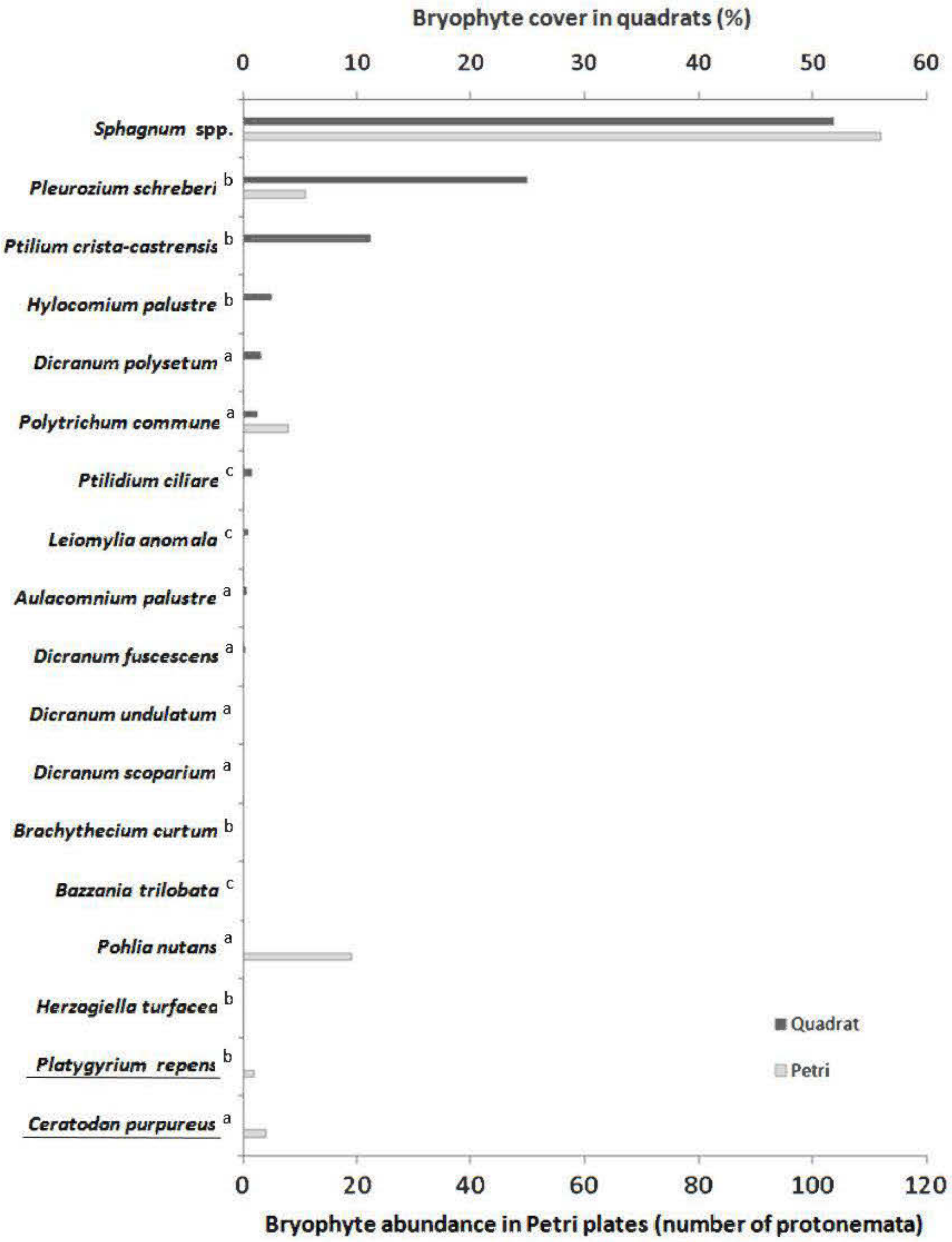

Figure A1.3 Comparison of bryophyte cover sampled onsite and bryophyte abundance in Petri plates. Dark grey bars, mean bryophyte cover (%) per 1-m^2 quadrats; light grey bars, bryophyte abundance in Petri plates (number of protonemata from spores/gemmae + number of vegetative fragments in the case of *Sphagnum* sp.). Species are ranked by percent cover on site; species reported on site but with no apparent bars on the graph were present as less than 1% of cover and are noted as trace (Tr), except for the underlined species that were not recorded on site. [a], Acrocarp; [b], Pleurocarp; [c], Liverwort.

The fern *Dryopteris* cf. *carthusiana* is not displayed on the graph because only the presence/absence of fern was recorded on site without consideration of their percent cover.

A1.6 Discussion

Southern red-backed voles, American red squirrels, and deer mice were the most abundant mammal species in our study sites. We found that these three species along with northern flying squirrels and common heather voles were dispersal agents for true mosses, sphagna and ferns. We also found that small mammals can transport several species of bryophytes and in some cases, a copious amount of viable diaspores of individual bryophyte species. Our results demonstrate that ground-dwelling small mammals are not occasional dispersal agents but instead represent important dispersers of bryophytes and ferns. Furthermore, ground-dwelling small mammals are in direct contact with the cryptogam layer and this may enhance the dispersal of cryptogams that rarely produce spores or that are poorly dispersed by the wind.

Mammalian species transported a fraction of species from the pool of bryophyte genera available on sites. Keeping in mind that some of the taxa that germinated were not identified to species due to germinating constraints, the pool of species found in Petri plates only represented 20% of the species encountered on site. This represents less than half of what was found by Pauliuk et al. (2011) who collected 40% of the bryophytes species found in European dry grassland ecosystems on large mammals. One factor explaining the low percent transported may be that none of the species collected are known to have developed features on their diaspores to actively rely on zoochory for dispersal (e.g., spore ornamentation, colorful spores, and sticky or odorous secretion to attract animal species; Demidova & Filin 1994; Ignatov & Ignatova 2001; Rudolphi 2009). Alternatively, if the main agent transported was spores, species phenology may have impacted our results, as not all cryptogam species produced dispersal agents during our trapping sessions. For instance, the over-abundance of sphagna diaspores may be explained by the coincidence of diaspore release and our experiment (Sundberg & Rydin 2002).

In contrast, two species germinated in Petri plates that were not found in the extant community, namely *Ceratodon purpureus and Platygyrium repens*. These species may have become attached to the fur of the small mammals when they dig in the moss layer and mineral soil searching for food such as seeds and insects (Merritt 1981). This activity may result in some spores present in the soil propagule bank becoming attached to their fur.

The only species of fern transported by a small mammal, *D.* cf *carthusiana,* is common in the boreal forest and produces large amounts of spores easily dispersed by wind (Rünk et al. 2012). However, ferns also reproduce by vegetative fragments and alternative diaspores (c.f. Boch et al. 2013), which may be brushed off by passing animals. In the present study, American red squirrels are the largest species trapped on our study sites and the only one that carried fern spores. Despite this, we found no apparent exclusive association between cryptogams and small mammals, which can possibly be explained by the low number of individuals trapped for some mammalian species.

Small mammal transport offers two main advantages over wind transport. First, as small mammals and bryophytes share the same types of microhabitats (Fauteux et al. 2012; Lõhmus et al. 2007; Mills & Macdonald 2004) small mammals offer oriented dispersal of the diaspores over the landscape. In contrast, during wind dispersal all diaspores are randomly deposited in microhabitats up to several kilometres away during wind dispersal (Lönnell 2011; van Zanten & Gradstein 1988). Secondly, ground-dwelling small mammals can transport species that are not efficient at wind dispersal, due to either low sporophyte production or sporophyte morphology. Ground-dwelling small mammals can transport cryptogam diaspores within their home range (from several meters for deer mice, up to 3.5 km for red squirrels; Bowman et al. 2002; Larsen & Boutin 1994, 1995; Wells-Gosling & Heaney 1984). Cryptogams could also be transported beyond small mammal home ranges during mammalian species dispersal and establishment of new home ranges. As a possible example, we brushed one individual that was carrying *C. purpureus,* 80 m away from the closest *C. purpureus* colony found in a concurrent study performed on the same study sites (Barbé et al. 2016).

We showed that ground-dwelling small mammals disperse bryophytes and ferns. However, additional species could be identified. Indeed, some species do not germinate on the agar substrate and others may have germinated after 6 months. However, as a concomitant study performed with the same protocol yielded the germination of 46 bryophyte species (Barbé et al. 2016). We argue that the reduced pool of species from this study is not due to the germination protocol. The composition of the bryophyte aerial propagule rain will differ among seasons with species phenology (Hock et al. 2004; Ross-Davis & Frego 2004; Stark 2002). Moreover, weather conditions such as relative humidity, night temperatures and rainfall might also have influenced cryptogam phenology via spore release (Glime 2014; Johansson et al. 2015), small mammal activity (Wróbel & Bogdziewicz 2015) and diaspore adherence to fur. In addition, other constraints associated with the sampling methods could have affected the results such as the use of cotton balls for the small mammal trapping in which diaspores might have been deposited during the many hours spent by the animals in the traps. In the future, we recommend to also collect the cotton balls provided in the traps. Finally, it may be important to consider the effectiveness of toothbrushes at removing diaspores that are electrostatically charged. Alternative collection methods on the fur might yield different species, and this topic could be explored in future studies.

To our knowledge, we provide the first direct evidence of epizoochory involving bryophytes and ferns and ground-dwelling small mammals in boreal forest ecosystems. The daily interaction between small mammals and the cryptogam layer could contribute to the directed transport of bryophyte and fern diaspores over medium distances and towards suitable substrates. Persistence of bryophyte and fern metapopulations depends on dispersal across the forest matrix and small mammals are identified as “mobile link organisms” (sensu Couvreur et al. 2004) that may participate in connecting fragmented bryophyte and fern populations. Our results open the door for a timely revision of bryophyte and fern dispersal mechanisms, extending the notion of epizoochory by ground-dwelling small mammals to other cryptogams such as horsetail, lichen or liverwort species.

A1.7 Acknowldgements

We thank Pierre Martineau for confirming fern identifications, and Dominique Fauteux for lending photographs of small mammals. The authors thank all the field and lab assistants who provided logistical support, and helped in collecting the samples, growing the bryophytes and taking photos.

The work was supported by the Fonds de Recherche du Quebec–Nature et Technologies (FRQNT) under the grant 2013-FM-170582; and the Natural Sciences and Engineering Research Council of Canada (NSERC) under the grant NSERC CRD 428686-11 Bergeron.

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ANNEXE II

DISTRIBUTION RANGE EXTENSION OF 35 BRYOPHYTE SPECIES FROM SAMPLING IN THE NEGLECTED SOUTH OF NORTHERN-QUÉBEC (CANADA)

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En préparation pour *Canadian Field Naturalist*

A2.1 Abstract

While the North American bryoflora is relatively well-known, some territories as the south of the Northern-Québec administrative region (between 49 and 51°N and 74 and 79°W) remain under sampled. We report the presence of 168 bryophyte taxa for this region, of which 35 (14 true mosses, 20 liverworts, 1 sphagna) represent noteworthy records. Occurrences of some taxa already known in the region but previously under sampled were actualized, whereas 20 taxa are news for the region. These inventories contribute both to actualize the status of occurrences and to extend the distribution ranges of these taxa toward the north. Disjunct distribution ranges of some taxa are linked together and their microhabitat preferences are documented. This work is a substantial input to the Flora of the bryophytes of Québec-Labrador and can be used to redefine protection priority ranks of species in North America.

Keywords: range extension; black spruce-feather moss forest; bryoflora; bryo-geography; boreal; liverwort; true moss; sphagna.

A2.2 Résumé

Malgré une globale bonne connaissance de la bryoflore nord-américaine, certaines régions telles que le Nord-du-Québec, et particulièrement le sud entre le 49^{e} et le 51^{e} parallèle nord, demeurent sous-échantillonnées. Nous rapportons ici la présence de 168 taxons bryophytiques, dont 35 taxa (14 mousses, 20 hépatiques et 1 sphaigne) représentent des ajouts substantiels à la flore de la région. Certains de ces taxons étaient déjà connus au Québec et 20 sont nouveaux pour le territoire considéré. Ces récoltes permettent d'actualiser les statuts d'occurrences et d'étendre l'aire de répartition de ces espèces vers le nord. Les aires de répartition de plusieurs taxons considérées disjointes à ce jour sont ralliées et leurs préférences en termes de microhabitats sont renseignées.

Ce travail représente un apport conséquent à aux connaissances de la flore des bryophytes du Québec-Labrador et permettra de redéfinir les rangs de priorité de conservation des espèces à l'échelle de l'Amérique du Nord.

Mots-clés : aire de répartition ; bryoflore ; forêt boréale ; hépatiques ; mousses ; pessière noire ; Québec ; sphaignes.

A2.3 Introduction

Bryophytes (*i.e.* true mosses, liverworts and sphagna), jointly with lichens, represent the most conspicuous components of the vegetation of the northern latitudes (Turetsky *et al.* 2012). They form a continuous carpet of several centimeters thick in coniferous boreal forests, represent a major element in net primary productivity, understory biomass and in biodiversity (Bisbee *et al.* 2001; Proctor 2011). This is especially true in the bioclimatic subdomain of the boreal black spruce feather-moss forest, which is characterized by shady, humid, chemically poor and acidic conditions favouring a copious diversity of bryophyte species, particularly *Sphagnum* spp. in poorly drained habitats (Fenton and Bergeron 2006; Vile *et al.* 2011).

Bryophytes represent 25% of the plant diversity of Québec (Faubert *et al.* 2010). In 2016, the database of the bryophytes of Québec-Labrador listed 582 mosses, 231 liverworts and 62 sphagna species (Faubert *et al.* 2014+). However, the distribution range of some species remains partially defined and even unknown in certain areas (Faubert and Gagnon 2013). This is the case in the administrative regions of Abitibi-Témiscamingue and the southern portion of the Northern-Québec, which are under sampled compared to various other regions. However, knowledge of the real distribution ranges of bryophytes is an elementary step in establishing conservation plans and in orientating forest management practices in these regions where boreal forests are disturbed both by natural wildfires and forest harvest. The addition of cumulative disturbances to the landscape jeopardizes the resilience of the ecosystem (Gauthier *et al.* 2008) and threatens species ill-adapted to anthropogenic environments, including many bryophyte species (Fenton and Frego 2005; Hylander *et al.* 2005; Caners *et al.* 2013).

Over the last decade, with the publication of the "Catalogue des bryophytes du Québec et du Labrador" (Faubert 2007), the list of bryophyte species continues to grow (Gauthier 2011; Moisan and Pellerin 2011; Faubert *et al.* 2012; Faubert and Gagnon 2013) and new species mentions are continuously compiled in the online database of the bryophyte of the Québec-Labrador (Faubert *et al.* 2014+) contributing to the constant updating of the bryophyte flora (Faubert 2012-2014). Benefiting from the intensive sampling performed for related studies, this paper provides an update of the Quebec bryophyte flora and an increased understanding of bryophyte distribution ranges in North America. This paper also improved knowledge about bryophyte microhabitat preferences in the black spruce forest ecosystem together with providing a preindustrial portrait of this ecosystem to better plan forest management practices and bryophyte conservation.

A2.4 Methods

A2.4.1 Study area

The study area covers a total of 73 197 km^2 (79°69' W, 50°71' N - 74°50' W, 50°71' N - 79°69' W, 48°83' N - 74°50' W, 48°83' N) in western Québec (Canada) (Figure A2.1a). It is located in the southern portion of the Northern-Québec administrative region. After the retreat of the Laurentide Ice Sheet between 12,000 and 7,000 RCYBP (Andrews 1973), the area was covered by the proglacial lake Barlow-Ojibway until 11,500 and 7,900 RCYBP (Vincent and Hardy 1977). Sedimentation in the lake generated a thick layer of clay (10-60 m) that forms the soils of the "Clay Belt" of northeastern Ontario and northwestern Québec. The relief of the region is plane and altitude varies from 200 to 300 m above sea level.

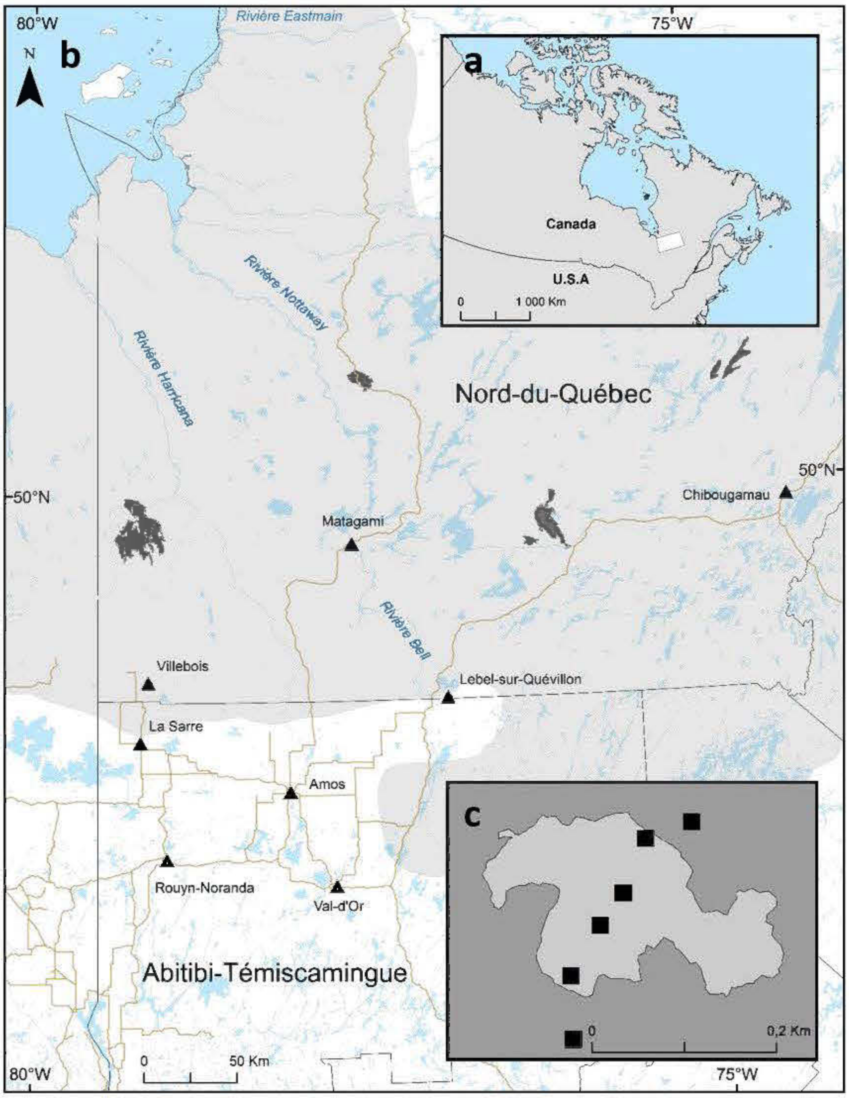


Figure A2.1 a) Location of the study area in northwestern Québec, Canada. d) The six wildfires sampled (dark grey shapes) in black spruce-feather moss forest bioclimatic domain (light gray zone; adapted from Payette and Bouchard 2001). c) Example of the sampling design used in a residual patch (light grey) surrounded by a wildfire burned matrix (dark grey). Sample plots (black squares) of 50 m² are located along a transect crossing the residual. Squares in the dark grey area correspond to fire plots, squares at the limits of the residual patch are edge plots, and the two plots in the center are core plots (only 1 in residual patch < 1 ha).

The study area is a part of the black spruce-feather moss forest bioclimatic domain, which extends over 154 184 km² in Québec (Figure A2.1b). Stands are dominated by *Picea mariana* Mill. Briton in addition with *Pinus banksiana* Lamb., *Populus tremuloides* Michx, *Abies balsamea* (L.) Mill., and *Betula papyrifera* Marshall. The understory is characterized by ericaceous shrubs [*e.g. Rhododendron groenlandicum* (Oeder) Kron & Judd] on a ground cover of bryophytes (Saucier *et al.* 2009). Average annual temperatures and precipitations are respectively 1°C and 928 mm (1981 to 2010) (Lebel-sur-Quévillon weather station; Environment Canada 2015). The region is characterized by long winters with 313 cm of annual snowfall and by a short growing season (140 to 160 days). The natural dynamics of the forests in the study area are primarily driven by stand replacing wildfires. The fire cycle was estimated at 398 years since 1920 (Bergeron *et al.* 2004), consequently, the average age of the forest is in excess of 150 years.

A2.4.2 Bryophyte sampling

Bryophytes were sampled according to a modified form of the "floristic habitat sampling" of Newmaster *et al.* (2005). In the original method, all the habitats are searched for species with no specific reference to area. Here the sampling was restricted to 50 m^2 rectangular plots where bryophytes were recorded in all the microhabitats present (*e.g.* coarse woody debris, tree bases, peat mounds, waterholes). We did not select habitats of interest for sampling certain taxa or the maximum of species, but rather all species in all microhabitats within a specific area.

Bryophytes were sampled in six wildfires varying in age, size and origin (Table A2.1). Within each wildfire, we identified five residual patches and three burned matrix areas for a total of 30 residual patches from 36 to 3400 years (time since the last wildfire) and 18 burned matrices from 10 to 44 years (time since the last wildfire). This sampling was designed in such a way because benefiting from related studies (Barbé et al. 2016, refers to Chapter IV; Barbé et al. in revision, refers to Chapter II) included in a thesis project focusing in the role of post-fire residual patches in bryophyte community reassembly after disturbance. All the residual patches were chosen based on the criteria of the dominance of black spruce, accessibility (< 600 m from a road) and a flat topography. Patches varied in size

(0.05-11.1 ha), age (36 to 3400 years) and forest structure (e.g. 7.41 to 108.8 m^3/ha of coarse woody debris; Barbé *et al.* 2016; Moussaoui *et al.* 2016). From June to September 2013, bryophytes were sampled in 5 × 10 m rectangular plots (50 m^2) in all patches. Within each patches, a north-south transect was designed to cross the patch from edge to edge (Figure A2.1c). For patches smaller than 1 ha, five plots at least 10 m apart were placed, two in the surrounding burned matrix, two straddling the edges of the patch and one in the centre of the patch. For patches larger than 1 ha, two plots were placed in the centre of the patch for a total of six plots. Three positions were subsequently defined: fire, edge and centre. In each wildfire, three additional 50 m^2 plots of burned matrix (n = 18) were placed as far as possible from all residual forest patches (from 200 to 8500 m) to ensure that as much of the bryophyte diversity of the burned matrix was sampled as possible. In total, the bryophyte community was sampled in 9 300 m^2 corresponding to 186 rectangular plots (*i.e.* 60 at the edges, 48 in the centres and 60 in the fire of the patches, and 78 in the burned matrix). The four corners of each plot were geolocalized using Garmin® GPS GSPmap 62. Bryophyte species present in all microhabitats of the 50 m^2 plot were sampled and then placed in individually marked paper bags.

Table A2.1 Wildfire zones of bryophyte sampling spatial and physical characteristics [data from SOPFEU digital map of the fires in Québec (2011)].

Fire	N° Feu	GPS Coordinates	Ecological Region*	Area (ha)	Date	Origin
MAT	249	50° 56' N, 77° 53' W	6a	6915,39	1997	Lighting
CASA	7104	49° 79' N 79° 26' W	6a	25516,81	1976	Human
SEL	283	49° 85' N, 79° 14' W	6a	18166,70	1997	Lighting
OH	7088	49° 91' N, 76° 13' W	6a	18764,04	1986	Human
MOH	232	49° 75' N, 76° 29' W	6a	2536,66	1997	Lighting
CHAP	D13-38	50° 57' N, 74° 69' W	6d	9877,33	1971 + 2005	NA

*Refers to Blouin and Berger (2004, 2005).

In total, bryophytes were sampled in 11 036 microhabitats, each of them containing four species on average (from 0 to 20) for a total of 1 318 163 specimens. All samples were dried and stored until identification to the species level in laboratory using a stereomicroscope and a microscope. Damaged, senescent or too young specimens were only identified to genus. Vouchers are store at the Université du Québec en Abitibi-Témiscamingue (Québec, Canada). Nomenclature follows Faubert (2012-2014) except for *Sphagnum subtile* (Russ.) Warnst., which follows the nomenclature of the Flora of North America Editorial Committee (2007). Microhabitats where species were recorded were qualitatively compared with data from the Flora of the bryophyte of the Québec-Labrador (Faubert 2012-2014) in order to underline potential specificities of the species to one microhabitat in the study area.

A2.4.3 Species cartography

Distribution maps were produced only for species that present changes compared to their original distributional range for the study area. New occurrences were compared with those presented in the published Flora and online database of the bryophytes of the Québec-Labrador (Faubert 2012-2014; Faubert *et al.* 2014+). Documented occurrences of the species corresponds to GPS locations and were used with the permission of the open access and participative online database of the bryophytes of the Québec-Labrador currently updated with independent botanists' records (Faubert *et al.* 2014+). Maps were generated using the geographic information system ArcGis 10.3.1 (ESRI 2015). Original map layers come from the GéoIndex+ platform of the Geographic and Statistic Information Center (GéoStat Center) of the Université Laval created with data from Statistics Canada, geographic division, DMTI Spatial Inc., and ESRI. The projection used for all maps was NAD83 CSRS MTM 10.

A2.4.4 Data analyses

Species were classified as rare (< 5 occurrences; Faubert *et al.* 2014+), infrequent (5 to 10 occurrences), uncommon (10 to 30 occurrences), and common (> 30 occurrences). Rare, infrequent and uncommon species were mapped as dots, whereas common species were mapped as shaded zones. Current status of occurrence of certain species were re-estimated by comparison between documented and new occurrences.

Microhabitats where species were found in the study area were compared with those previously documented (Faubert 2012-2014). Microhabitats were classified as humus (T - terricolous species living on soil and litter), bog (B - species living among sphagna, in fens and bogs), dead wood (DW - facultative or obligate epixylics), epiphyte (EP - strictly epiphyte or corticolous species living at the base of trees) and rock (R - saxicolous species). Species inhabiting constantly humid habitats (*i.e.* old dead wood totally collapsed, oozing rocks, water holes or edges of creeks) were classified in the humus group but identified with a "W". At a finer scale, dead wood was categorized using Thomas *et al.*'s (1979) decay classification system for snags and dead wood: classes 1 and 2 were grouped and correspond to "recently" fallen dead trees with bark and branches intact; class 3 refers to dead wood without bark or branches and with softening wood; and classes 4 and 5 were grouped and refer to dead woods with a collapsed shape. Burned wood was also noted. Finally, the host tree species was recorded

A2.5 Results

A.2.5.1 Reworked status of occurrences and maps

The sampling effort was equivalent at each plot with an average of 32 bags recorded per plot regardless of the localization (edge, centre, fire, burned matrice). The area curves of the bryophyte species by life form generally plateaued, testifying to the quality of the sampled design used (Figure A2.2). This is particularly true for sphagna species for which the jackknife estimate approximates the actual number of species if all species were found by sub-sampling the data set (19 species estimated: 18 species found). On the other hand, for true mosses and liverworts further sampling would be expected to reveal additional species (96 estimated: 88 found and 69 estimated: 62 found respectively). While it is difficult to exhaustively describe the entire bryophyte community, the "microhabitat method" used for bryophyte sampling is suitable to reach a substantial level of bryophyte richness.

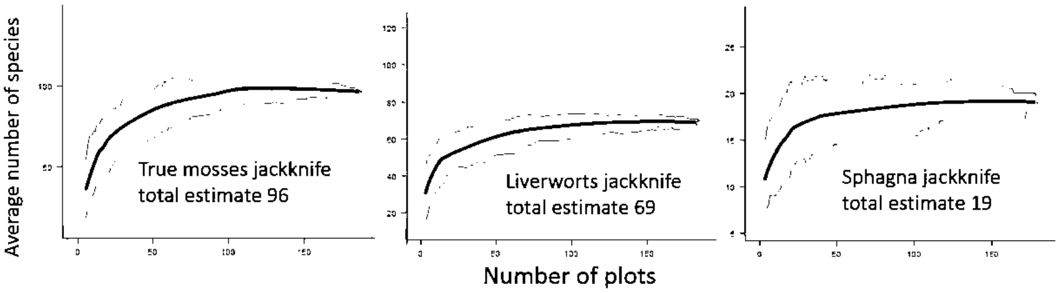


Figure A2.2 Species area curves (black thick lines) with confidence intervals (grey thin lines) by bryophyte life form. First-order jackknife estimates are included for each curve and approximate the actual number of species if all species were found by sub-sampling the data set.

A total of 168 species (88 mosses, 62 liverworts and 18 sphagna) were identified. The bryophyte community sampled was composed at 70% of common species (118 species) that are ubiquitous for the Québec-Labrador and for the boreal black spruce forest (mapped as shaded zones). Post-fire residual patches were dominated by the feather mosses *Hylocomium splendens*, *Pleurozium schreberi*, and *Ptilium crista-castrensis* with frequent records of the acrocarp species *Dicranum fuscescens* and *Polytrichum commune*, and of the liverworts *Lophozia ventricosa*, *Ptilidium ciliare*, and *Ptilidium pulcherrimum*. The wettest sites also supported *Aulacomnium palustre*, *Sanionia uncinata* and *Warnstorfia fluitans*, whereas disturbed sites (*i.e.* burned stands) included *Ceratodon purpureus*, *Polytrichum juniperinum* and *Pohlia nutans*. Furthermore, the presence of deep mats of sphagna was expected as many of our sites were paludified or in paludification process (*Sphagnum capillifolium*, *S. fallax*, *S. magellanicum*; Fenton *et al.* 2005). In contrast, 37% of the most common species in the coniferous boreal forest of Québec province were underrepresented (≤ 15 occurrences) in the study area (*Barbilophozia hatcheri*, *Bryum capillare*, *Sphagnum cuspidatum*, *Tomenthypnum nitens*).

Thirty five other species (14 true mosses, 20 liverworts, and one sphagna) represent noteworthy records (Table A2.2). Of which, four species (group 1) were uncommon or infrequent but were expected to be found because already recorded within 25 km from the study area: *Calypogeia sphagnicola*, *Fuscocephaloziopsis pleniceps*, *Lophozia guttulata*, and *Sphenolobus hellerianus* (Figure A2.3). Ten other species (group 2), four true mosses: *Brachythecium erythrorrhizon*, *Brachythecium starkii*, *Isopterygiopsis muelleriana*, and *Polytrichum commune* var. *perigoniale* and six liverworts: *Cephaloziella hampeana*, *Kurzia pauciflora*, *Lophozia ascendens*, *Lophozia bicrenata*, *Odontoschisma francisci*, and *Schistochylopsis laxa* were common to rare for the province and already recorded near the study area but sporadically (1 to 3 occurrences from 20 to 115 km; Figure A2.4).

Table A2.2 List of the 35 species with a distribution range extension for the south of the Northern-territories of Québec, Canada. Species are classified by life form. The number of documented and new occurrences, the status, the type of correction applied to their distribution, the distance to the closer documented occurrence, and details about microhabitat preferences of the species are indicated.

Species	Documented occurrences*	New occur-rences	Status on Quebec-Labrador from documented to new occurrences (→)	Type of correction of the distribution range	Closer documented occurrence (km)	Brief description	Documented microhabitats*	New microhabitats
Moss								
Brachythecium erythrorrhizon	25	4	Unusual	Enlargement	~ 115	Basiphilous	T/R	DW/W
Brachythecium starkii[†]	13	92	Unusual → Common	Enlargement	~ 110	Id confusion[1]	T/W	DW/EP/T/W
Campylium protensum	19	19	Rare → Unusual	Boundaries pushed to the West	~ 605	Id confusion	W	DW/EP/W
Dicranum fulvum	Grey zone	3	Common	Boundaries pushed to the North	~ 135	Acidiphilous	R	DW/W
Helodium blandowii var. *blandowii*	Grey zone	3	Common	Boundaries pushed to the West	~ 325	Basiphilous	B/W	EP/T
Hypnum curvifolium	Grey zone	2	Common	Boundaries pushed to the West	~ 270		NA	DW
Hypnum fauriei	-	1	Q°	Enlargement		Id confusion	DW/EP/R,/T	EP
Isopterygiopsis muelleriana	32	9	Common	Enlargement	~ 100		R	DW/R/W
Isopterygiopsis pulchella	48	3	Common	Boundaries pushed to the West	~ 550		DW/EP/R/T	EP/T/W
Pohlia elongata var. *elongata*	20	2	Unusual	Boundaries pushed to the West	~ 260		NA	T
Pohlia sphagnicola[†]	18	634	Unusual → Common	Enlargement	~ 300	Id confusion	B	B/DW/EP/T/ W
Polytrichum commune var. *perigoniale*	25	12	Unusual	Boundaries pushed to the West	~ 60		T	DW/T
Thuidium recognitum	Grey zone	5	Common	Boundaries pushed to the North	~ 75	Basiphilous	DW/EP/R/W	DW
Ulota crispa	Grey zone	16	Common	Enlargement	~ 165		EP	DW/EP/T

Liverwort								
Calypogeia sphagnicola†	12	151	Unusual → Common	Enlargement→ BBSF?	~ 25		B	B/DW/EP/R/T/W
Calypogeia suecica	15	6	Unusual	Boundaries pushed to the West	~ 300	< 2 mm	DW	DW/W
Cephaloziella elachista	10	20	Infrequent → Unusual	Enlargement	~ 365	< 0,5 mm US§	B	B/DW/EP/T/W
Cephaloziella hampeana	16	56	Unusual → Common	Enlargement	~ 20	US	B/DW/R	DW/EP/T
Cephaloziella spinigera	10	10	Infrequent	Enlargement	~ 360	US	B	DW/EP/T
Chiloscyphus coadunatus var. *rivularis*	17	29	Rare → Unusual	Enlargement	~ 550		R/W	DW/EP/W
Fuscocephaloziopsis loitlesbergeri†	10	100	Infrequent → Common	Enlargement	~ 490	0,6-0,8 mm US	B	B/DW/EP/T
Fuscocephaloziopsis pleniceps†	29	219	Unusual → Common	Enlargement → BBSF?	~ 25		B/DW/W	B/DW/EP/R/W
Kurzia pauciflora	18	3	Unusual	Enlargement	~ 65	US	B	DW/T
Leiocolea rutheana	15	1	Unusual	Enlargement	~ 450	3-5 mm	B	W
Lophozia ascendens	30	20	Unusual	Enlargement	~ 35	0,8-1,3 mm	DW/W	DW/EP
Lophozia bicrenata	25	14	Unusual	Enlargement	~ 45	US	T	DW/R/T/W
Lophozia gnttulata†	21	82	Unusual → Common	Enlargement → BBSF?	~ 27	1-1,8 mm	B/DW	B/DW/EP/R/T/W
Lophozia silvicola	3	77	Infrequent → Common	Boundaries pushed to the West	~ 350	Acidiphilous ID confusion	DW/R/W	B/DW/EP/T
Mesoptychia heterocolpos var. *heterocolpos*	67	2	Common	Enlargement	~ 670	Basiphilous	DW/R	W
Odontoschisma francisci	18	19	Rare → Unusual	Elargement	~ 80	Acidiphilous	W	DW/EP/W
Scapania apiculata	6	3	Infrequent	Boundaries pushed to the West	~ 360		DW	B/DW
Scapania uliginosa	9	1	Infrequent	Boundaries pushed to the West	~ 465	< 4 mm	R/W	R/W
Schistochilopsis laxa	3	2	Rare	Enlargement	~ 35	1,5 -2 mm	B	B/T
Sphenolobus hellerianus†	38	92	Unusual → Common	Enlargement → BBSF?	~ 26	< 1 mm US	DW/W	DW/EP/W
Sphagnum								
Sphagnum tenerum	7	29	Infrequent → Unusual	Enlargement	~ 350	ID confusion	NA	B/DW/R/T

*, refers to Faubert *et al.* 2014+

Acronyms: B, bog; DW, dead wood; EP, epiphytic or corticolous; NA, non-specified; R, rock; T, terricolous; W, wet habitats.

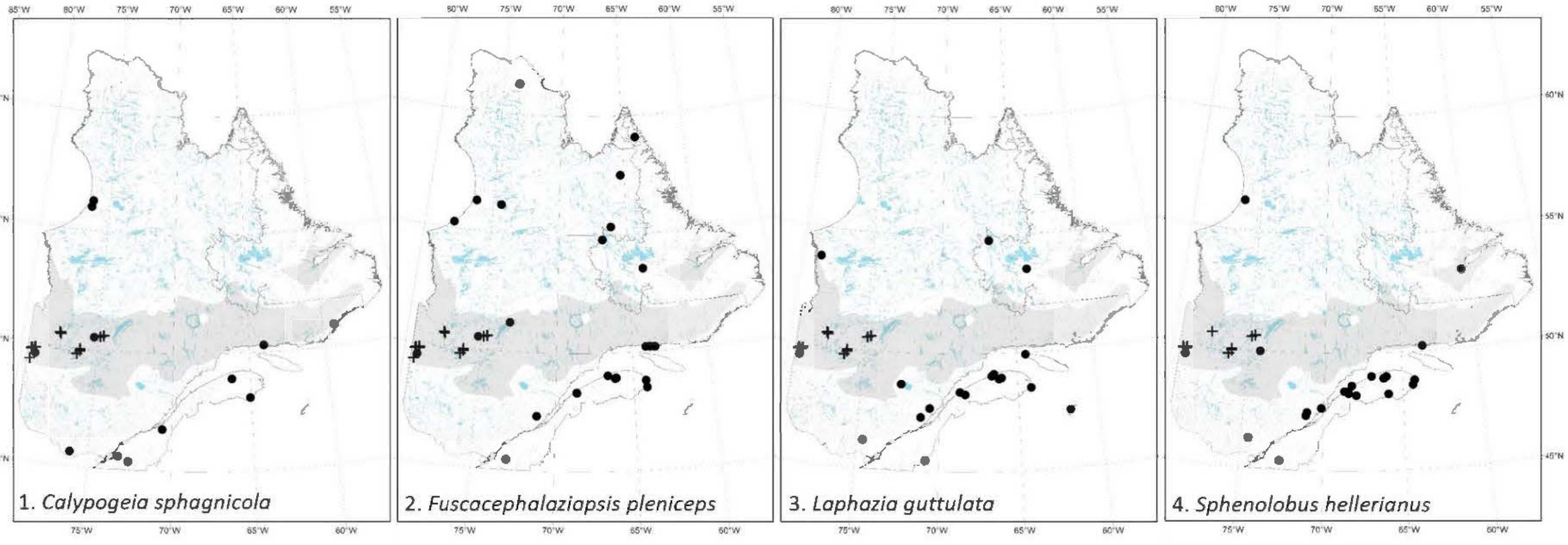
ǀ, identification confusion, species for which identification can be difficult due to a lack in diagnostic characters to discriminate among species of the same genera.

§, US, under sampled species, their minute size probably generates an underestimation of their real occurrences and distributions.

†, significant addition to the Flora.

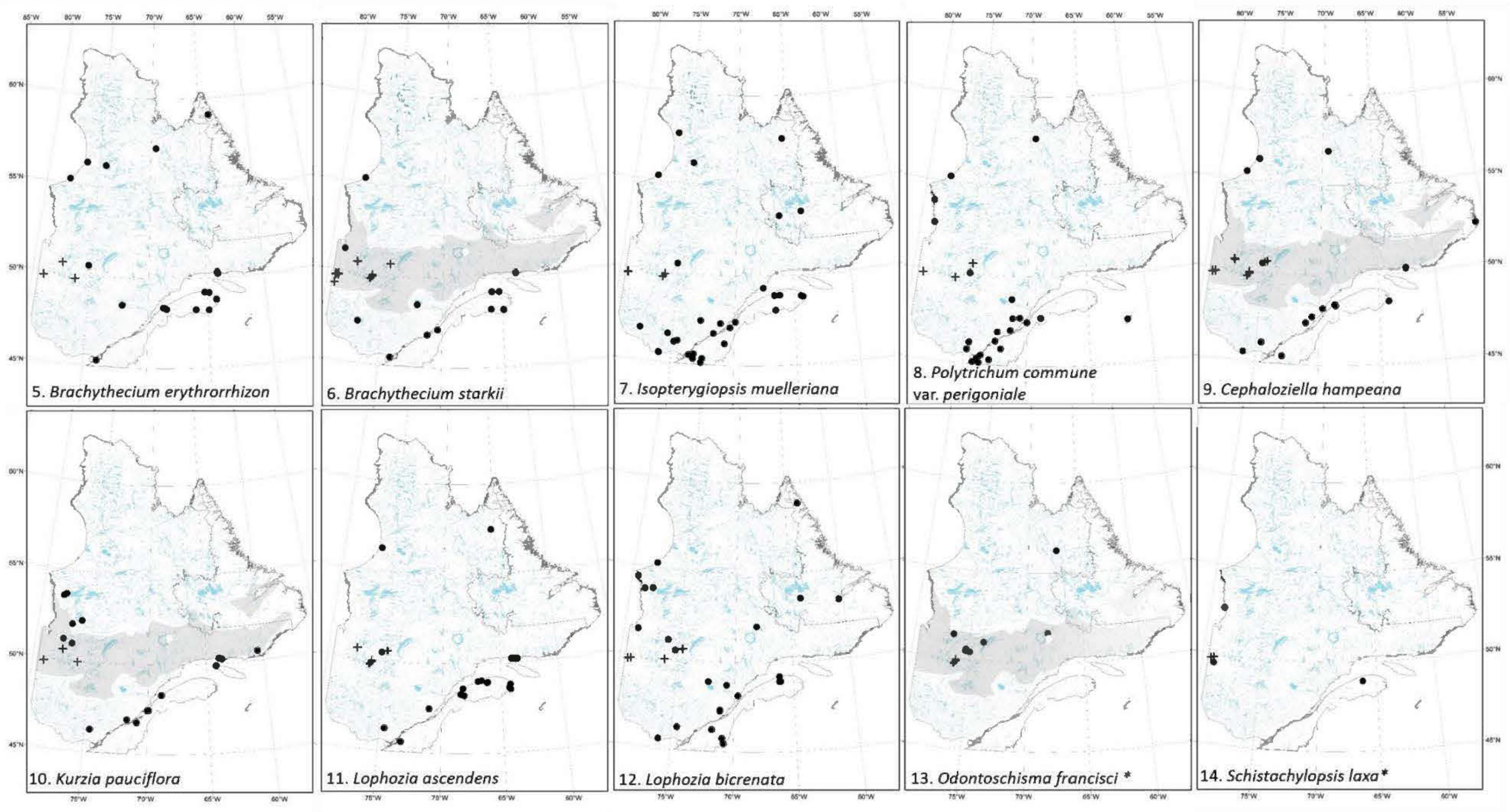
BBSF?, questionable extension at the whole boreal black spruce forest bioclimatic domain [based on vegetation zones defined by Payette and Bouchard (2001)].

Q°, the species was confounded with *Hypnum fertile*. Therefore, presenting a map is impossible without a previous revision of the herbarium specimens.



1. *Calypogeia sphagnicola* 2. *Fuscacephalaziapsis pleniceps* 3. *Lophazia guttulata* 4. *Sphenolobus hellerianus*

Figure A2.3 Maps of the distribution range of the four species of the group 1. These species are uncommon or infrequent in the province but already recorded from 26 km to 32 km of the study area. Dots, documented occurrences; Plus, new occurrences. The shaded zone represents the boreal black spruce-feather moss forest and is used to describe continuous distribution areas where species should occur even the shaded zone cover enclaves where the taxon has not yet been found but where its presence is deemed probable.

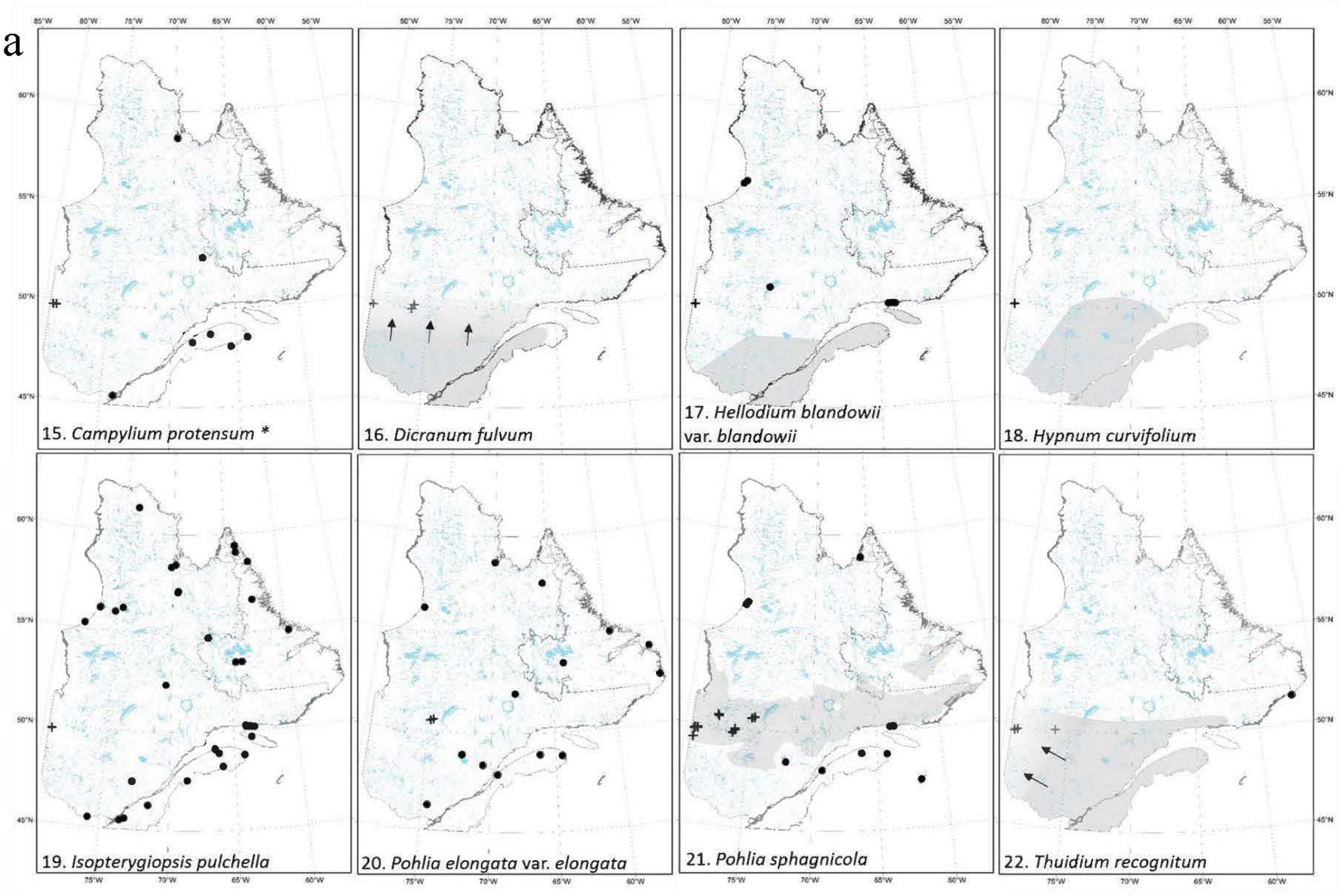


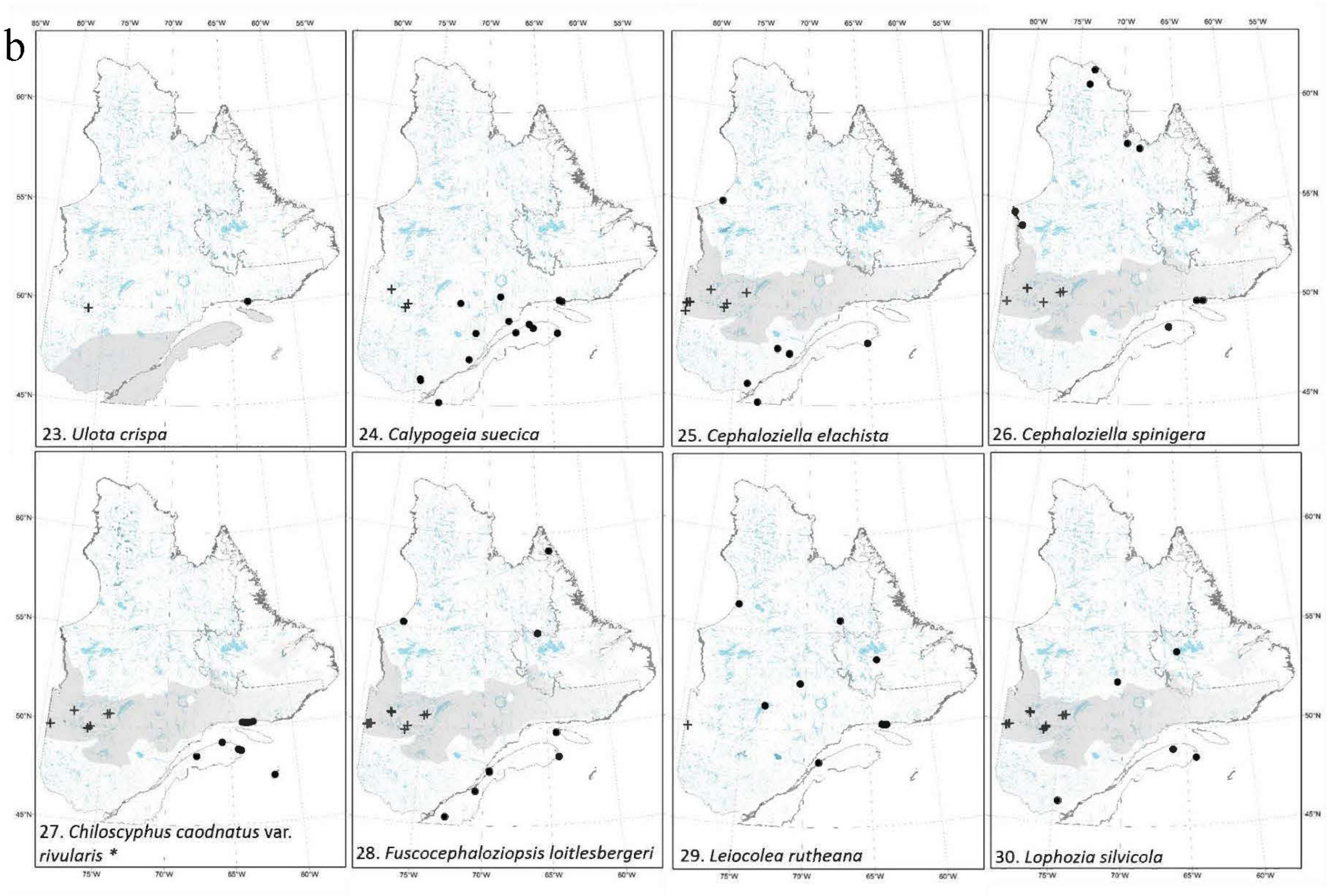
5. *Brachythecium erythrorrhizon*
6. *Brachythecium starkii*
7. *Isopterygiopsis muelleriana*
8. *Polytrichum commune* var. *perigoniale*
9. *Cephaloziella hampeana*
10. *Kurzia pauciflora*
11. *Lophozia ascendens*
12. *Lophozia bicrenata*
13. *Odontoschisma francisci* *
14. *Schistachylopsis laxa**

Figure A2.4 Maps of the distribution range of the 10 species of the group 2. These species are common to rare in the province and have been already sporadically recorded in the study area. Their presence in the study area was confirmed with the numerous new occurrences reported. Dots, occurrences of reference; Plus, new occurrences. The shaded zone represents the boreal black spruce-feather moss forest. "*" rare species for the province (based on Faubert *et al.* 2014+).

Finally, 20 species (group 3) are new records for the study area with distribution range extensions from 75 km to more than 670 km. Distribution ranges of the nine true mosses: *Campylium protensum*, *Dicranum fulvum*, *Hellodium blandowii* var. *blandowii*, *Hypnum curvifolium*, *Isopterygiopsis pulchella*, *Pohlia elongata* var. *elongata*, *Pohlia sphagnicola*, *Thuidium recognitum*, and *Ulota crispa*, of the 10 liverworts: *Calypogeia suecica*, *Cephaloziella elachista*, *Cephaloziella spinigera*, *Chiloscyphus coadnatus* var. *rivularis*, *Fuscocephaloziopsis loitlesbergeri*, *Leiocolea rutheana*, *Lophozia silvicola*, *Mesoptychia heterocolpos* var. *heterocolpos*, *Scapania apiculata*, and *Scapania uliginosa*, and of the sphagna *Sphagnum tenerum* were extended to include the study area (Figure A2.5a, b and c).

Hypnum fauriei was sampled a single time in the study area. The species is presented for information purposes only given the uncertainties about its distribution in Québec-Labrador (Faubert 2012-2014).


a
15. *Campylium protensum* *
16. *Dicranum fulvum*
17. *Hellodium blandowii* var. *blandowii*
18. *Hypnum curvifolium*
19. *Isopterygiopsis pulchella*
20. *Pohlia elongata* var. *elongata*
21. *Pohlia sphagnicola*
22. *Thuidium recognitum*



23. *Ulota crispa*

24. *Calypogeia suecica*

25. *Cephaloziella elachista*

26. *Cephaloziella spinigera*

27. *Chiloscyphus caodnatus* var. *rivularis* *

28. *Fuscocephaloziopsis loitlesbergeri*

29. *Leiocolea rutheana*

30. *Lophozia silvicola*

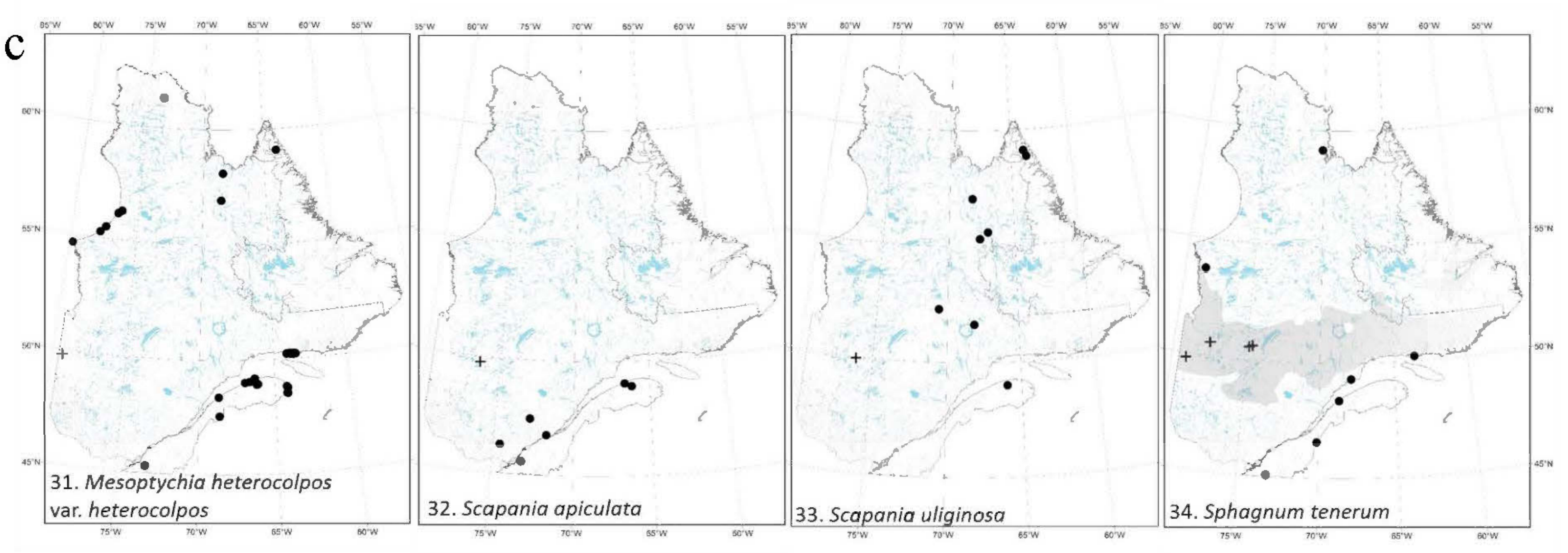


Figure A2.5a, b and c Maps of the distribution range of the 20 species of the group 3. These species are new records for the study area with distribution ranges extension from 77 km to more than 650 km of their closer documented occurrence. Dots, documented occurrences; Plus, new occurrences. The shaded zone represents the boreal black spruce-feather moss forest. Maps with shaded zones presented as a gradient of greys illustrate that the species distribution at the whole black spruce forest is uncertain given the few records reported in the lighter grey areas. Arrows suggest the extension of the distribution range of the species toward the area pointed. "*" rare species for the province (based on Faubert *et al.* 2014+)..

A.2.5.2 Bryophyte preferences in terms of microhabitats

The microhabitat preferences of the 35 species discussed above, no marked differences were found compared to the Flora of the bryophytes of the Québec-Labrador (Table A2.2 and Figure A2.6 a, b), except for *P. sphagnicola* and *C. sphagnicola* as well as several liverworts, which are found in a copious variety of substrates in the study area compared to restricted to bogs and ferns in the Flora. Eighteen species were recorded at the base of tree trunks (Table A2.2 and Figure A2.7) and were generally associated with only one tree species, however multiple host trees were also identified for some bryophyte species (*e.g. P. sphagnicola, B. starkei, C. elachista*). Similarly, numerous species were found on dead wood (Table A2.2 and Figure A2.8) whereas this microhabitat preference was not reported in the Flora (*e.g. B. erythrorrizon, D. fulvum*). No affinities between a bryophyte species and one of the dead wood decay classes was found even liverwort species were preferentially found on dead wood in most advanced decay classes (classes 3, 4 & 5; Figure A2.8).

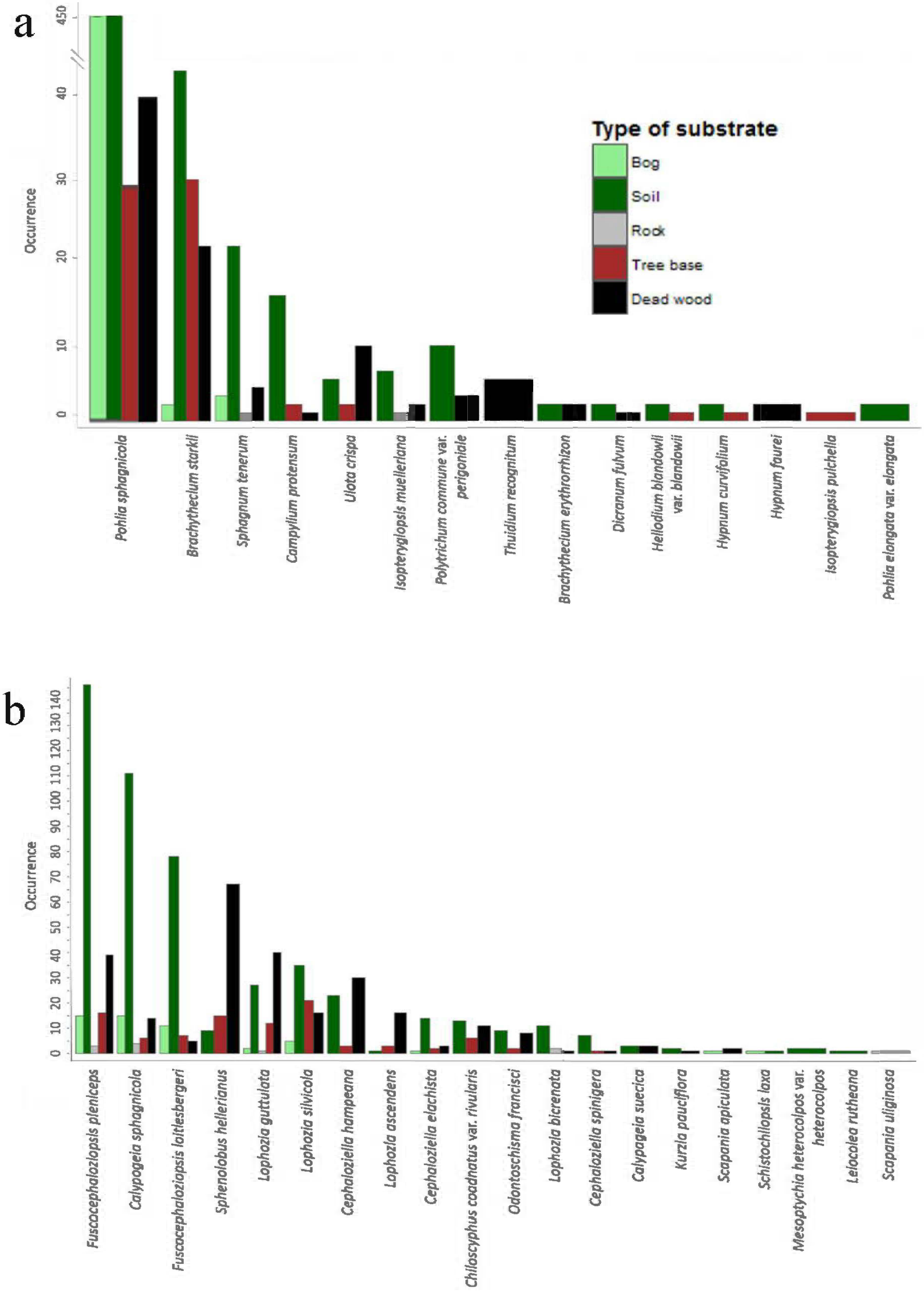


Figure A2.7 Occurrences of the true mosses (a) and of the liverworts (b) per substrate types in the study area.

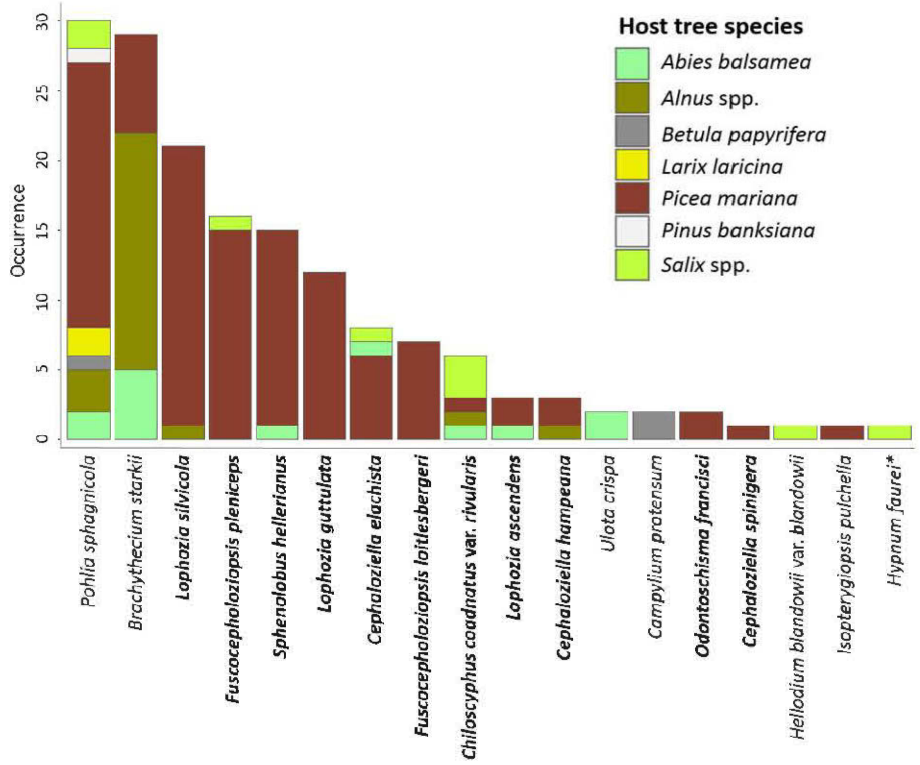


Figure A2.8 Occurrences of the epiphytes and corticolous species by host tree species. Liverworts are indicated in bold. "*", species exclusively sampled on tree trunks and not recorded in other types of microhabitat.

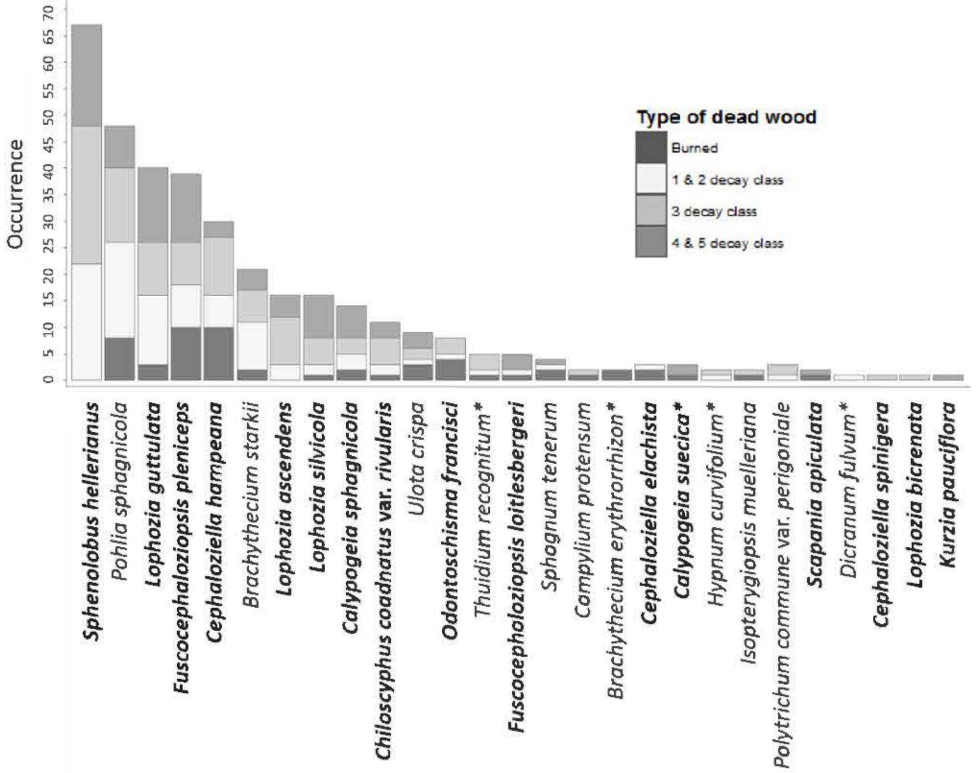


Figure A2.9 Occurrences of the epixylic species on dead wood classified with Thomas *et al.*'s (1979) decay classification system (see method for details) and given their burned status. Liverworts are indicated in bold. "*", species exclusively sampled on dead wood and not recorded in other types of microhabitat.

A2.6 Discussion

We have documented 20 new species for the study area and delimited new distribution ranges of 15 others. The distribution range and the occurrence of each of these species is extended towards the study area. Our results suggest that these species may be more common than expected in the Québec-Labrador and especially in the bioclimatic domain of the black spruce-feather moss forest.

A2.6.1 Distribution range extended at the whole boreal black spruce forest

Even though already documented in the study area, we increase the comprehension of the distribution of four liverworts *C. sphagnicola*, *F. pleniceps*, *L. guttulata* and *S. hellerianus* with 82 to more than 200 new records. These new records, together with the records already documented from eastern Québec suggest the extension of the distribution ranges of these species at the whole black spruce forest. Furthermore, the dispersed and numerous locations of these species sustain that they are common but under sampled in the province. Extension of their distributions to all of Québec-Labrador is possible but more sampling, especially focusing on boggy habitats are needed to determine the true distribution of these liverworts, which represent significant components of the black spruce forest.

Extensions of the liverworts *C. elachista, C. hampeana, C. spinigera, C. coadnatus* var. *rivularis, F. loitlesbergeri, K. pauciflora* and *O. franscici* and of the true mosses *B. starkii* and *P. sphagnicola* to black spruce forest domain are also proposed. However, some of these species (*C. elachista, C. spinigera, C. coadnatus* var. *rivularis, F. loitlesbergeri, L. silvicola* and *O. franscici*) were rarely or even not recorded in the east of the Québec, which suggests to be careful with their extensions to the whole black spruce forest in the province. In light of the 92 and 56 new records of *B. starkii* and *C. hampaena* respectively, as well as of the 634 new records of *P. sphagnicola,* we suggest to change the status of these species from uncommon to common in the province. Liverworts and especially Cephaloziellaceae and *K. pauciflora* are minute taxa (less than 1 mm wide shoots) especially difficult to detect that has led to an under estimation of their occurrences and distributions. Directed sampling campaigns focusing on these taxa may distinguish between a lack of sampling and real rarity. In regards of the two true mosses *B. starkii* and *P. sphagnicola* their distribution ranges have suffered from difficulties in identification (Faubert 2012-2014). Indeed, the lack of marked diagnostic characters to discriminate among the species of the same genera has led to currently identified *B. starkii* as *B. curtum* and *P. sphagnicola* as *P. nutans*, and v*ice versa*. As suggested in the Flora, study of herbarium specimens and especially inattention in the identification of these confounding taxa are probably responsible of the diminished understanding of the real distribution of these species (Faubert 2012-2014). The same observation is made for the sphagna *S. tenerum*, currently identified as *S. capillifolium*.

The case of *L. bicrenata* needs to be discussed. This unusual and minute sized species is typical of disturbed landscapes and present in dispersed locations across the whole province. The question of the generalization of this distribution in the Québec is therefore raised and further sampling campaigns could permit distinguish between this real unusual status and this ubiquity but under sampling in the Québec.

A2.6.2 Distribution range extended toward the north

In parallel, and while few new occurrences of *D. fulvum* and *T. recognitum* were reported (3 and 5 respectively), we propose to extend the distribution of *D. fulvum* of 135 km toward the north and to extend the distribution of *T. recognitum* of 75 km toward the west. These species are common in the province but were not recorded before in the study area. *H. blandowii* var. *blandowii, H. curvifolium*, and *U. crispa* are also common and were presented as shaded zones in the Flora. However, we are not comfortable to extend their distribution toward the north given the unique new occurrence recorded in the study area together with the important distance from their original distributions (325 km, 270 km, and 165 km respectively).

Finally, both the few documented and new occurrences (generally less than 10 occurrences) of the remaining 14 species sampled in the study area did not permit to map their distribution as shaded zones. However, the new records of *B. erythrorrhizon, I. muelleriana, P. commune* var. *perigoniale, L. ascendens* and *L. bicrenata* enable us to link their disjunct distribution ranges between southern and northern Québec. Furthermore, the records of *C. protensum, I. pulchella, P. elongata* var. *elongata, C. suecica, L. rutheana, M. heterocolpos* var. *heterocolpos, S. apiculata,* and *S. uliginosa* contribute to document their presence in the north of the Québec, from 260 km to 670 km of their previously documented occurrences.

We conclude by highlighting the noteworthy records of the rare true mosses *C. protensum* and *H. fauriei* and of the rare liverworts *C. coadnatus* var. *rivularis, O. franscisci,* and *S. laxa,* which confirm the importance to improve bryophyte sampling campaigns in the neglected regions of the Québec-Labrador.

A2.6.3 Implications for management and conservation

This study suggests that numerous bryophytes may be more common than expected in Québec-Labrador. We present a substantially revised and updated list of the bryoflora of the south of the Northern-Québec as well as to provide a bryological preindustrial portrait of the boreal black spruce forest. Furthermore, these actualizations of bryophyte distributions can be used to redefine protection priority ranks of the species but also to model their responses to forest harvest and global changes. Naturally, keep in mind that this work not provide an exhaustive and static portrait of the bryophyte flora in the study area and that the maps presented will be updated as result of new sampling campaigns. The records of uncommon, infrequent, and rare species sustain that black spruce feather-moss forest is a bryo-diversity hotspot that require particular conservation attentions.

The south of the Northern-Québec is qualified of « black hole » of the knowledge about bryoflora, which better suggests the paucity of the sampling campaigns in the region rather than the species absence. Substantial works remain to be done to map the real bryophyte distributions in the province, and especially in the boreal feather-moss forest where looking for a bryophyte is like looking for a needle in a haystack!

A2.7 Acknowledgements

Funding for this study was provided by fellowships from the Fonds de Recherche du Quebec–Nature et Technologies (FRQNT), the *Natural Sciences and Engineering Research Council* of Canada (NSERC) and the University of Quebec in Abitibi-Témiscamingue (UQAT). The authors thank Louis Dubois, Philippe Heine and Flora Joubier for their help in collecting bryophyte samples.

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APPENDIX A

Temporal, severity, spatial and structural variables measured at each of the undisturbed forests, residual forest patches and burned matrices sampled in the study. Variables were measured in three 50 m^2 plots in undisturbed forests and in three or four 50 m^2 plots in residual forest patches (< 1 ha or > 1 ha). Values were given as means ± standard errors, absence of standard errors means that the value was measured at only one plot. Several letters for the water hole variable refers to the values measured at each of the plot per site, one letter means the different plots have the same value. For more details on the sampling design see Figure 2.1. "*", spatial variables consisted of proxies of site area and shape, see Methods for details.

Wild-fire	Habitat type[1]	Temporal variable	Severity variable	Spatial variables*		Forest structure variables							
		Estimated age of forest (yr)	Fire severity[2]	Buffer zone width (m)	Shape (m)	Tree & snag density (stems/ha)	Number of tree species	Mean height (m)	CWD-1&2 (m^3/ha)	CWD-3 (m^3/ha)	CWD-4&5 (m^3/ha)	Number of micro-habitats	Water hole[3]
LQY	BM7	16	HS	0	0	0	3	0	0	56.06	3.87	8.5±2.12	W
LQY	RP7	191	HS	108.6	21.99	900±565.68	3±0.81	18.09	34.65±10.51	11.53±16.31	5.39±3.07	6.75±0.95	W
CAZ	BM1	37	LS	0	0	200	3	0	8.59	50.96	6.32	6.5±0.57	W, T
CAZ	RP1	525	LS	142.02	73.63	1837.5±1325.82	2.5±0.58	13.11	3.56±2.72	11.76±10.54	2.19±2.71	6.5±0.7	W
CAZ	BM3	37	LS	0	0	167	2	0	2.86	21.91	3.34	8.5±0.7	T
CAZ	RP3	140	NA	33.54	19.69	2400±848.53	2.66±1.15	11.75	0.76±0.05	1.12±0.65	3.90±2.69	8±2	T
MAT	BM28	15	HS	0	0	500	5	0	0	10.85	0.38	8.5±2.12	W
MAT	RP28	216	HS	66.54	38.6	1162.5±512.65	3.5±0.58	16.37	25.13±12.77	10.28±5.58	29.52±40.8	7.5±2.38	T
SEL	BM13	17	HS	0	0	500	3	0	7.52	9.64	1.57	8±0	W
SEL	RP13	157	LS	112.26	70.15	1612.5±512.65	2.25±0.96	14.22	9.14±7.32	5.62±7.95	0.36±0.38	6.5±0.58	W
LQO	BM16	27	HS	0	0	100	4	0	0	7.46	1.09	8±1.41	W, T
LQO	RP16	155	LS	105.2	37.92	1700±1484.92	3±0.81	15.16	7.62±10.77	2.11±0.23	0.10±0.15	7.75±0.96	W, T
LQO	BM17	27	HS	0	0	600	6	0	47.99	33.43	5.08	8±1.41	W, T
LQO	RP17	85	HS	25.02	11.91	1475±813.17	4.33±0.57	16.91	21.62±13.93	33.75±18	2.11±0.74	7.66±1.52	T
LQO	BM18	27	HS	0	0	300	4	0	0	5.82	4.95	7±1.41	W
LQO	RP18	80	HS	23.92	12.93	1625±813.17	3±1	13.16	3.8±5.37	7.76±0.14	0.8±0.61	7.33±1.53	W
LQY	BM9	16	HS	0	0	300	5	0	0	0	1.09	8±0	W
LQY	RP9	240	LS	172.16	108.83	1162±300.52	2.75±0.95	18.47	18.48±1.06	18.64±4.09	2.4±0.87	6.25±0.95	W, T
LQY	BM8	17	HS	0	0	600	4	0	35.71	11.97	3.4	7.5±2.12	T
LQY	RP8	140	HS	106.7	49.03	1312.5±300.52	3±0	14.92	41.32±10.25	16.49±20.2	0.47±0.36	7.25±1.5	W
LQO	BM20	27	HS	0	0	0	2	0	14.02	58.77	1.78	7.5±0.7	W
LQO	RP20	171	LS	70.35	7.41	1562.5±441.91	3.25±0.5	15.6	11.34±6.04	11.74±11.75	2.71±1.2	6.75±0.95	W, T
MAT	BM30	15	HS	0	0	100	3	0	0	0	0	8±0	W
MAT	RP30	77	HS	22.04	13.98	762.5±371.23	3..33±0.5	9.18	4.16±5.89	1.47±2.08	0.17±0.22	8±1	W, T

MAT	BM27	15	HS	0	0	400	3	0	0	19.12	2.5	9.5±0.7	W
MAT	RP27	127	LS	26.88	19.67	1662.5±371.23	3.66±1.15	14.03	4.18±3.90	3.64±5.15	1.36±0.23	9±1	T
CAZ	BM2	29	LS	0	0	100	3	0	0	7.33	1.72	8.5±2.12	W, T
CAZ	RP2	70	LS	63.12	49.22	1300±424.26	2±0	14.61	3.86±5.45	9.95±10.93	0.77±0.4	6.33±0.58	W, T
LQY	BM10	16	HS	0	0	700	4	0	57.48	34.55	2.86	10±1.41	W
LQY	RP10	173	HS	127.54	102.74	1162.5±229.81	3.5±0.58	14.65	38.6±7.65	27.63±18.43	1.97±0.19	7.75±0.5	W, T
SEL	BM14	16	HS	0	0	600	2	0	6.18	10.72	1.61	7.5±0.7	W
SEL	RP14	246	NA	61.48	27.11	3300±141.42	2±0.81	8	0.1±0.14	0	0.1±0.14	5.25±0.5	W, T
LQO	BM19	27	HS	0	0	200	4	0	0	0	0.28	6.5±2.12	W
LQO	RP19	80	HS	54.12	28.62	2700±848.52	3±1	14.71	1.98±1.58	4.02±0.62	0.43±0.15	7.33±1.15	W
MAT	BM MAT	15	HS	0	0	280	4±0	0	0	8.74	0.77	8.33±1.53	W, W, T
LQY	BM LQY	15	HS	0	0	380	3±1.73	0	18.63	21.08	4.46	8.33±1.53	W
LQO	BM LQO	27	HS	0	0	240	3.33±0.58	0	12.40	21.09	2.63	7.66±2.51	W
MAT	BM29	15	HS	0	0	0	3	0	0	3.66	0.14	9±4.24	T
MAT	RP29	70	HS	62.36	56.83	900±989.95	4±1.41	12.46	1.10±1.56	1.16±1.65	0.13±0.03	8±0.81	T
CAZ	BM4	37	LS	0	0	200	4	0	0	7.46	1.98	7.5±0.7	W, T
CAZ	RP4	3400	LS	166.76	68.94	1013.5±511.23	3.25±0.96	13.33	6.67±9.43	7.26±7	0.52±0.33	6.25±0.5	W, T
CAZ	BM5	37	LS	0	0	167	4	13.68	2.86	21.91	3.34	6.5±0.7	W, T
CAZ	RP5	305	NA	118.74	30.69	488.88±0	2.25±1.26	7.8	0	0	0	6.25±0.95	W
SEL	BM15	17	HS	0	0	600	2	0	6.18	10.72	1.61	8±1.41	W
SEL	RP15	129	NA	24.66	7.18	4600±1414.21	2±0	10	0.8±0.48	1.02±0.76	0.2±0.28	6.66±0.58	W, T
MAT	BM26	15	HS	0	0	200	4	0	0	10.07	0.85	4.5±0.7	W, T
MAT	RP26	100	LS	32.18	14.46	1287.5±1396.53	3±0	14.62	6.07±4.61	1.11±1.57	0.46±0.56	6.66±1.15	W
LQY	BM6	16	HS	0	0	300	3	0	0	2.85	11.12	8.5±0.7	W, T
LQY	RP6	99	HS	41.78	5.49	1087.5±53.03	2.66±1.15	19.28	49.88±11.86	53.90±19.92	1.64±1.26	6.66±0.57	W
CAZ	BM CAZ	37	LS	0	0	167	4±1.73	0	2.86	21.91	3.34	7.66±1.15	T, W, T
SEL	BM SEL	17	HS	0	0	600	4.33±0.58	0	6.18	10.72	1.61	5.33±1.53	W
SEL	BM12	17	HS	0	0	400	4	0	4.99	1.54	1.54	6.5±2.12	W
SEL	RP12	135	HS	39.16	5.86	937.5±194.45	2.25±0.5	9.08	5.97±0.41	0	0.48±0.68	5.75±1.5	W
CHA	BMCHA	8	HS	0	0	360	4±1	0	5.84	28.51	2.91	7.66±2.51	W, W, T
CHA	BM21	8	HS	0	0	200	4	0	6.23	88.47	0	6.5±0.7	T
CHA	RP21	163	HS	116.32	49.55	1437.5±1537.96	2.5±0.58	15.9	12.59±17.81	4.13±4.46	0.34±0.48	6.75±1.26	W, T
CHA	BM24	42	HS	0	0	600	4	0	6	2.07	0	7.5±0.7	W
CHA	RP24	148	HS	119.54	68.59	1262.5±17.68	3.5±0.58	13.32	22.06±0.08	17.66±17.61	2.13±2.89	6.75±0.5	T

CHA	BM25	8	HS	0	0	400	4	0	0	45.73	7.78	8.5±2.12	W
CHA	RP25	172	HS	70.12	37.43	1687.5±689.43	3±1.41	13.11	37.49±0.29	9.19±5.36	1.19±1.14	8.5±3.11	W
CHA	BM23	183	HS	0	0	0	4	0	17	6.31	3.06	4.5±0.7	W
CHA	RP23	183	HS	23.95	7.08	2100±919.24	3±1.73	12.35	5.76±2.58	7.71±1.56	0.16±0.06	8.33±2.31	T
CHA	BM22	8	HS	0	0	600	6	0	0	0	3.73	6±0.00	W
CHA	RP22	178	HS	108.14	58.66	1987.5±17.68	3.25±1.89	15.7	20.06±28.38	0	0.76±0.25	6.25±0.96	W
SEL	BM11	17	HS	0	0	900	2	0	6.04	21	1.72	4±2.83	W
SEL	RP11	36	HS	21.52	7.2	587.5±123.74	1.33±0.58	10.11	6.7±0	10.58±3.60	0.16±0.18	8.66±0.58	W, T
CAZ	UF1	1300	HS	532.4	489.40	1075	3	12.5	29.99	28.27	28.41	4.66±2.31	T, W, T
CAZ	UF3	186	HS	584.58	438.90	1725	3	13.25	13.21	3.84	2.17	3.66±1.53	T
SEL	UF9	182	LS	675.58	656.70	1700	5	16.5	47.62	29.91	10.42	3.33±1.53	T, W, T
SEL	UF11	179	HS	1132.3	732.90	1050	4	13.5	47.48	22.04	5.14	5.66±1.53	T, T, W
SEL	UF13	171	LS	782.74	505.50	1350	3	13.25	14.27	34.77	15.41	5.66±1.53	T
SEL	UF14	3120	LS	110.5	51.58	1300	1	12.5	17.33	10.18	0	6.33±1.53	W, T, T
SEL	UF32	172	HS	655.22	332.30	1025	4	18.25	45.15	87.79	44.92	8±2.64	W, T, W
SEL	UF37	170	HS	235.68	87.55	1000	4	15.75	47.17	27.98	10.27	5.33±0.58	W
MAT	UF39	145	HS	683.86	434.36	1625	5	17.5	39.04	48.05	48.4	7±2.00	T
SEL	UF43	150	LS	938.22	680.83	1325	6	17.5	47.83	20.21	6.8	7.66±0.58	NA
CAZ	UF48	168	LS	2406.4	1212.7	775	11	11.25	13.49	13.26	2.18	3.66±1.53	W, T, T
CAZ	UF52	130	LS	401.34	369.87	1125	4	12.5	7.83	1.66	0	5.66±1.53	T
CAZ	UF56	110	HS	231.16	70.07	1625	3	14.75	4.36	1.66	0	2.66±0.58	W, W, T
SEL	UF60	390	LS	977.34	635.94	775	8	13.75	2.69	20.21	11.08	5.66±1.15	T
CAZ	UF61	108	LS	481.38	240.35	975	1	11.5	3.84	7.32	5.65	5.66±1.15	W, T, T
SEL	UF63	126	LS	215.2	117.41	475	2	9.6	8.19	2.69	0	5±1.73	W, T, W
CAZ	UF68	3840	LS	649.36	388.51	25	3	NA	0	0	0	4.66±1.15	W, T, W
CAZ	UF72	3630	LS	475	319.73	200	6	NA	0	0	0	4.66±1.53	W
MAT	UF76	910	LS	620.4	417.71	425	9	8.75	7.32	6.95	3.47	3.66±0.58	W, T, T
SEL	UF77	110	LS	814.12	708.46	875	4	11.9	7.57	5.14	0	6.66±2.51	T, W, W
MAT	UF86	1960	LS	2068	1072.5	0	1	0	0	0	0	5±3.46	T

LQY	UF105	125	HS	839.4	942.52	2200	4	14.9	12.5	2.96	0	3.33±1.53	W, W, T
LQO	UF109	460	LS	793.04	485.55	1000	2	14.4	23.35	25.49	11.51	7.66±1.53	W
MAT	UF121	250	LS	208.6	82.37	1050	5	16.75	82.57	12.33	8.55	3±1.00	W, T, T
LQO	UF130	156	LS	476.4	187.33	675	8	14.9	24.18	6.74	50.65	6±1.73	T, W, T
LQO	UF131	980	LS	1650.8	902.5	600	1	14.2	13.48	29.77	16.77	7.33±1.53	W, T, T
LQO	UF132	2560	LS	1923.5	1547.6	1025	6	14.4	47.86	66.12	34.87	9±1.73	W, W, T
LQO	UF134	96	HS	866.4	616.97	2400	7	16	15.95	7.07	19.41	4.33±0.58	W, W, T
LQY	UF136	190	HS	926.66	1087.7	550	8	17.7	89.15	79.61	63.65	6±1.00	T, T, W
LQY	UF138	200	LS	802.6	548.67	500	4	12.3	4.11	0	0	4.33±1.53	W
LQY	UF139	99	HS	468	392.99	1600	4	13.25	2.63	2.63	0	7.33±1.15	T, T, W
LQY	UF142	163	HS	470.8	389.39	925	4	15.5	66.61	22.04	48.35	4.33±1.53	W
LQY	UF143	270	LS	1208.8	743.19	575	8	14.4	62.99	18.91	38.65	4±1.00	W, T, T
LQO	UF145	80	HS	283.8	147.01	2025	9	13.7	4.11	0	13.32	4±0.00	W, T, T
LQO	UF150	220	LS	1021.2	850.38	1375	4	11.4	10.36	5.26	5.92	5.5±1.15	W
LQO	UF153	104	LS	1222.8	791.72	2650	5	13.9	8.55	1.48	0	6.33±2.51	T
LQO	UF156	280	LS	1820.8	1011.7	350	9	15.8	12.33	5.26	15.5	4.66±1.53	T
LQO	UF158	187	LS	620.2	198.02	0	1	9.5	2.96	2.96	16.44	3±0.00	W, T, W
LQO	UF159	109	LS	1663.7	1244.9	0	3	0	17.6	3.81	32.32	4.66±0.58	W

[1] BM, burned matrix; RP, residual forest patch; UF, undisturbed forest.

[2] HS, high severity; LS, low severity; NA, non-available.

[3] T, True – presence of water holes; W, Wrong – absence of water holes, NA, non-available.

APPENDIX B

Number of bryophyte taxa found at each habitat type: undisturbed forest, residual forest patch and burned matrix in boreal black spruce feather-moss forest after wildfire in western Québec region. Nomenclature follows Faubert (2012-2014) except for *Sphagnum subtile* which follows the Flora of North America Editorial Committee (2007). Species are presented by life forms. ‡, infrequent (≤ 5 occurrences in all dataset); †, restricted to the habitat type. Species in bold are rare for the Québec province (Faubert et al. 2014+). N refers to the number of plots sampled where the species is present. Codes of species names used in the analyses are given.

Taxon	Species code	Undisturbed forest	Residual forest patch	Burned matrix
N		117	108	78
TRUE MOSSES				
Amblystegium serpens	Ambser	3	2	2
Aulacomnium palustre	Aulpal	37	70	65
Blindia acuta‡	Bliacu	1†	0	0
Brachythecium acutum‡	Braacu	3†	0	0
Brachythecium campestre	Bracam	6	6	11
Brachythecium curtum	Bracur	4	31	21
Brachythecium erythrorrhizon‡	Braery	0	2	1
Brachythecium plumosum‡	Braplu	0	0	1†
Brachythecium populeum‡	Brapop	0	2	1
Brachythecium reflexum	Braref	2	13	11
Brachythecium rutabulum	Brarut	1	4	4
Brachythecium spp.		1	3	3
Brachythecium starkii	Brasta	20	23	9
Brachythecium velutinum	Bravel	3	11	5
Breidleria pratensis	Brapra	4	3	1
Brotherella recurvans	Brorec	5	6	2
Bryhnia graminicolor‡	Brygra	3†	0	0
Bryum capillare‡	Brycap	0	0	1†
Callicladium haldanianum	Calhal	5	5	0
Calliergon cordifolium‡	Calcor	3	1	1
Calliergon giganteum‡	Calgig	1†	0	0
Calliergon richardsonii‡	Calric	0	3	1
Campyliadelphus chrysophyllus	Camchr	5	2	3
Campylium protensum‡	Campro	0	2	2
Campylium stellatum	Camste	3	2	1

Campylophyllum hispidulum	Camhis	6	6	2
Ceratodon purpureus	Cerpur	3	14	40
Dicranella heteromalla	Dichet	1	2	7
Dicranum flagellare	Dicfla	7	19	8
Dicranum fragilifolium[‡]	Dicfra	0	2[†]	0
Dicranum fulvum[‡]	Dicful	0	1	2
Dicranum fuscescens	Dicfus	99	100	46
Dicranum montanum	Dicmon	14	14	5
Dicranum ontariense	Dicont	14	38	35
Dicranum polysetum	Dicpol	30	87	60
Dicranum scoparium sensu lato	Dicsco	17	18	12
Dicranum spp.		0	14	4
Dicranum spurium[‡]	Dicspu	0	1	1
Dicranum undulatum	Dicund	57	43	58
Drepanocladus aduncus	Dreadu	5	7	2
Fissidens osmundoides[‡]	Fisosm	1	1	1
Hamatocaulis vernicosus[‡]	Hamver	2[†]	0	0
Helodium blandowii[‡]	Helbla	0	0	2[†]
Herzogiella striatella[‡]	Herstr	0	2[†]	0
Herzogiella turfacea	Hertur	19	34	12
Hygroamblystegium varium	Hygvar	0	4	4
Hylocomium splendens	Hylspl	9	52	8
Hypnum curvifolium	Hypcur	7	1	1
Hypnum fauriei[‡]	Hypfau	0	1[†]	0
Hypnum imponens	Hypimp	8	5	7
Hypnum pallescens	Hyppal	4	26	19
Hypnum spp.		1	3	1
Isopterygiopsis muelleriana	Isomue	0	4	3
Isopterigiopsis pulchella[‡]	Isopul	0	2	1
Leptobryum pyriforme[‡]	Leppyr	0	0	1[†]
Leptodictyum riparium	Leprip	1	5	2
Meesia triquetra[‡]	Meetri	1[†]	0	0
Mnium spinulosum	Mnispi	3	2	1
Oncophorus wahlenbergii	Oncwah	8	18	5
Orthotrichum ohioense[‡]	Ortohi	1[†]	0	0
Orthotrichum speciosum[‡]	Ortspe	0	1[†]	0
Paludella squarrosa[‡]	Palsqu	1[†]	0	0
Plagiomnium cuspidatum[‡]	Placus	1	2	1
Plagiomnium medium[‡]	Plamed	0	2[†]	0
Plagiothecium cavifolium	Placav	31	32	9
Plagiothecium denticulatum	Pladen	13	14	3
Plagiothecium laetum	Plalae	59	63	24

Plagiothecium spp.		2	1	1
Platydictya subtilis[‡]	Plasub	2[†]	0	0
Platygyrium repens	Plarep	2	9	3
Pleurozium schreberi	Plesch	98	108	78
Pogonatum dentatum[‡]	Pogden	0	0	3[†]
Pohlia cruda[‡]	Pohcru	0	2[†]	0
Pohlia elongata[‡]	Pohelo	0	2[†]	0
Pohlia filum[‡]	Pohfil	0	0	3[†]
Pohlia nutans	Pohnut	84	84	75
Pohlia sphagnicola	Pohsph	1	64	60
Pohlia spp.		0	1	0
Polytrichum commune	Polcom	1	29	42
Polytrichym commune var. *perigoniale*[‡]	Polcom_per	0	2	2
Polytrichum juniperinum	Poljun	0	19	55
Polytrichum longisetum[‡]	Pollon	0	1[†]	0
Polytrichum pallidisetum[‡]	Polpal	0	3[†]	0
Polytrichum piliferum	Polpil	0	0	16[†]
Polytrichum spp.		0	1	2
Polytrichum strictum	Polstr	10	26	69
Pseudobryum cinclidioides[‡]	Psecin	0	2[†]	0
Ptilium crista-castrensis	Pticricas	43	95	62
Pylaisia polyantha[‡]	Pylpol	1[†]	0	0
Rhizomnium pseudopunctatum	Rhipse	19	11	3
Rhizomnium punctatum	Rhipun	7	6	1
Rhynchostegium serrulatum[‡]	Rhyser	0	1	1
Rhytidiadelphus triquetrus[‡]	Rhytri	0	2[†]	0
Sanionia uncinata	Sanunc	41	43	22
Sarmentypnum exannulatum	Sarexa	7	3	3
Splachnum ampullaceum[‡]	Splamp	0	1[†]	0
Straminergon stramineum	Strstr	12	35	4
Tetraphis pellucida Hedw.	Tepel	61	63	24
Tetraplodon angustatus[‡]	Tetang	1	1	0
Thuidium recognitum[‡]	Thurec	0	2	1
Tomentypnum falcifolium	Tomfal	0	12	7
Tomentypnum nitens	Tomnit	7	4	4
Trematodon ambiguus	Treamb	0	0	2[†]
Ulota coarctata[‡]	Ulocoa	1[†]	0	0
Ulota crispa[‡]	Ulocri	0	2	2
Warnstorfia fluitans	Warflu	7	37	19
SPHAGNA				
Sphagnum angustifolium	Sphang	35	85	44
Sphagnum capillifolium	Sphcap	69	69	66

Sphagnum cuspidatum‡	Sphcus	4	0	1
Sphagnum fallax	Sphfal	50	38	31
Sphagnum fuscum	Sphfus	17	38	47
Sphagnum girgensohnii	Sphgir	7	49	10
Sphagnum magellanicum	Sphmag	30	62	34
Sphagnum pulchrum‡	Sphpul	0	2	3
Sphagnum quinquefarium‡	Sphqui	0	3	1
Sphagnum riparium‡	Sphrip	0	0	2†
Sphagnum rubellum	Sphrub	23	19	34
Sphagnum russowii	Sphrus	54	98	60
Sphagnum squarrosum	Sphsqu	4	4	5
Sphagnum subtile	Sphsub	1	14	7
Sphagnum tenellum‡	Sphtenellum	0	0	1†
Sphagnum tenerum	Sphtenerum	0	5	9
Sphagnum warnstorfii	Sphwar	4	12	14
Sphagnum wulfianum	Sphwul	2	16	6
Sphagnum spp.		14	48	44
LIVERWORT				
Anastrophyllum hellerianum	Anahel	24	36	3
Anastrophyllum michauxii	Anamic	2	4	0
Anastrophyllum minutum	Anamin	4	5	2
Anastrophyllum spp.		0	0	1
Barbilophozia attenuata	Baratt	8	16	1
Barbilophozia barbata	Barbar	20	23	1
Barbilophozia floerkei‡	Barflo	2†	0	0
Barbilophozia hatcheri‡	Barhat	0	2†	0
Barbilophozia kunzeana	Barkun	13	41	9
Barbilophozia spp.		0	1	0
Bazzania tricrenata‡	Baztric	5†	0	0
Bazzania trilobata‡	Baztril	0	3†	0
Blepharostoma trichophyllum	Bletri	45	50	12
Calypogeia integristipula	Calint	1	3	3
Calypogeia muelleriana	Calmue	44	35	20
Calypogeia neesiana	Calnee	14	10	12
Calypogeia sphagnicola	Calsph	21	22	33
Calypogeia spp.		2	3	6
Calypogeia suecica‡	Calsue	1	2	2
Cephalozia bicuspidata	Cepbic	16	18	12
Cephalozia catenulata‡	Cepcat	3†	0	0
Cephalozia connivens	Cepcon	66	66	36
Cephalozia loitlesbergeri	Ceploi	2	15	21
Cephalozia lunulifolia	Ceplun	73	58	30

Cephalozia macrostachya‡	Cepmac	3†	0	0
Cephalozia pleniceps	Cepple	55	59	37
Cephalozia spp.		0	4	8
Cephaloziella divaricata‡	Cepdiv	1	2	1
Cephaloziella elachista	Cepela	1	5	9
Cephaloziella hampeana	Cepham	9	6	22
Cephaloziella rubella	Ceprub	39	33	52
Cephaloziella spinigera	Cepspi	4	4	4
Cephaloziella spp.		6	8	16
Chiloscyphus coadunatus var. *rivularis*	Chicoa_riv	8	9	4
Chiloscyphus pallescens‡	Chipal	1†	0	0
Chiloscyphus polyanthos‡	Chipol	1†	0	0
Chiloscyphus profundus	Chipro	11	27	8
Cladopodiella fluitans	Claflu	7	0	3
Cladopodiella francisci‡	Clafra	0	1	3
Frullania eboracensis‡	Fruebo	0	2	1
Frullania oakesiana‡	Fruoak	1	2	0
Geocalyx graveolens	Geogra	14	23	10
Gymnocolea inflata subsp. *inflata*	Gyminf_inf	6	5	1
Jamesoniella autumnalis	Jamaut	49	55	20
Jungermannia gracillima‡	Jungra	0	0	1†
Jungermannia leiantha	Junlei	11	11	4
Kurzia pauciflora‡	Kurpau	0	0	3†
Leiocolea heterocolpos‡	Leihet	1	0	1
Leiocolea rutheana‡	Leirut	2	1	0
Leiomylia anomala	Leiano	34	30	48
Lepidozia reptans	Leprep	74	67	15
Lophozia ascendens	Lopasc	5	10	2
Lophozia bicrenata	Locbic	0	0	8†
Lophozia guttulata	Lopgut	5	36	15
Lophozia longidens	Loplon	8	22	5
Lophozia obtusa‡	Lopobt	2†	0	0
Lophozia silvicola	Lopsil	5	30	11
Lophozia ventricosa	Lopven	97	86	31
Lophozia spp.		5	22	11
Marchantia polymorpha‡	Marpol	0	0	1†
Mylia taylorii‡	Myltay	2†	0	0
Nowellia curvifolia	Nowcur	11	20	5
Odotonschisma denudatum‡	Ododen	0	1	1
Pallavicinia lyellii‡	Pallye	0	0	2†
Plagiochila porelloides	Plapor	3	3	2
Ptilidium ciliare	Pticil	79	99	38

Ptilidium pulcherrimum	Ptipul	76	107	45
Riccardia latifrons	Riclat	33	12	10
Riccardia palmata[‡]	Ricpal	4[†]	0	0
Riccardia spp.		0	0	1
Scapania apiculata[‡]	Scaapi	1	1	1
Scapania irrigua	Scairr	17	16	7
Scapania mucronata[‡]	Scamuc	1[†]	0	0
Scapania paludicola[‡]	Scapal	3	1	0
Scapania uliginosa[‡]	Scauli	0	0	1[†]
Scapania spp.		0	1	2
Schistochilopsis capitata[‡]	Schcap	1[†]	0	0
Schistochilopsis grandiretis[‡]	Schgra	1[†]	0	0
Schistochilopsis incisa[‡]	Schinc	4	1	0
Schistochilopsis laxa[‡]	Schax	1	2	0
Schistochilopsis spp.		0	3	1
Tritomaria exsectiformis	Triexs	20	19	2
Tritomaria quinquedentata[‡]	Triqui	1[†]	0	0

APPENDIX C

Correlation coefficients among 12 environmental variables. Numerical variables relationships were assessed with Spearman rank correlations (ρ), numerical and categorical variables relationships were graphically assessed with boxplots (not shown; NC, not correlated). Values with *P*-values < 0.05 are bolded.

Environmental variable		1	2	3	4	5	6	7	8	9	10	11	12
Temporal													
Age	1	1.00											
Of severity													
Severity (LS/HS)*	2	NC	1.00										
Spatial													
Area (m)	3	**0.27**	NC	1.00									
Shape (SD unit)	4	**0.26**	NC	**0.95**	1.00								
Structural													
Tree & snag density (nb/ha)	5	**0.28**	NC	0.00	0.04	1.00							
Number of tree species	6	0.01	NC	**0.42**	**0.42**	**-0.03**	1.00						
Mean tree height (m)	7	**0.12**	NC	**0.38**	**0.39**	0.50	0.13	1.00					
CWD-1&2 (m^3/ha)	8	**0.30**	NC	**0.23**	**0.30**	**0.32**	**0.22**	0.30	1.00				
CWD-3 (m^3/ha)	9	-0.05	NC	0.12	**0.19**	-0.14	**0.15**	**0.06**	**0.50**	1.00			
CWD-4&5 (m^3/ha)	10	**0.12**	NC	**0.35**	**0.41**	-0.08	**0.28**	**0.27**	**0.48**	**0.58**	1.00		
Number of microhabitats	11	**-0.35**	NC	**-0.35**	**-0.31**	-0.07	-0.09	-0.20	-0.11	0.13	-0.11	1.00	
Water hole (Y/N)*	12	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	1.00

CWD, coarse woody debris by decay class (1 to 5) from Thomas et al. (1979), see methods for details.
"*" For categorical variables: Y, presence of water hole; N, absence of water hole; LS, low severity; HS, high severity.

APPENDIX D

Mean and SD of continuous environmental variables per habitat type (A); values corresponds to the number of plots with the character between parentheses for categorical environmental variables (B). Generalized linear mixed models were used to compare means/values among habitat types excepted for variable followed by ‡ for which linear mixed model were performed. Means/values followed by different letters are significantly different as indicated by post-hoc tests equivalent to Tukey HSD for mixed models.

Variable	Undisturbed forest (n = 117)		Residual forest patch (n = 108)		Burned matrix (n = 78)	
A-Continuous	Mean	SD	Mean	SD	Mean	SD
Temporal						
Age	618.19a	1009.27	194.81b	515.19	22.99c	20.74
Spatial						
Area (m^2)	829.87a	534.80	86.26b	44.57	0	0
Shape (SD unit)	561.11a	361.48	42.19b	29.20	0	0
Structural						
Tree & snag density (nb/ha)‡	1024.36a	651.94	1518.84b	966.85	335.24c	217.99
Number of tree species	4.72a	2.56	2.90b	1.01	3.47b	1.10
Mean tree height (m)	13.17a	3.89	13.76a	2.86	0.47b	2.39
CWD-1&2 (m^3/ha)	23.22a	23.57	13.99b	15.30	7.65c	12.80
CWD-3 (m^3/ha)	17.03a	21.31	9.89b	13.57	18.68a	19.13
CWD-4&5 (m^3/ha)	14.62a	17.49	2.22b	7.89	2.62b	2.24
Number of microhabitats‡	5.20a	2.00	7.06b	1.41	7.45b	1.8
*B-Categorical**						
Severity						
Severity (LS/HS)	78/39a		33/61b		13/65c	
Structural						
Water hole (Y/N)	61/53a		44/64a		18/60b	

CWD, coarse woody debris by decay class (1 to 5) from Thomas et al. (1979), see methods for details.

"*" For categorical variables: Y, presence of water hole; N, absence of water hole; LS, low severity; HS, high severity.

APPENDIX E

Environmental variables classified in five categories (temporal, severity, spatial and structural at coarse and fine scales) and the protocol used in sampling (as noted below) in undisturbed cores, residual cores and edges sampled in the study area. "*", values measured at the forest stand scale; "†", values measured in a 400 m² plot at the center of each forest stand; "‡", values measured in 50 m² plot. For the variables measured at the plot level, values are means ± standard errors, absence of standard errors means that the value was measured at only one plot. Several letters for the water hole variable refers to the values measured at each plot per site, one letter means the different plots have the same value or the value was measured at only one plot. For more details on the sampling design see Figure 3.1.

			Temporal variables		Severity variable	Spatial variables				Stand structure At coarse scale										Stand structure At fine scale			
Wildfire	Forest stand^{1}	Position	Age of forest (yr)†	Time since fire (yr)*	Fire severity^{2}†	Area (ha)*	Shape (m)*	Buffer zone width (m)*	Isolation (m)*	Tree & snag density (stems/ha)†	Number of tree species‡	Mean tree height (m)†	CWD-Total (m^3/ha)†	CWD-1&2 (m^3/ha)†	CWD-3 (m^3/ha)†	CWD-4&5 (m^3/ha)†	Holdridge complexity index (C_{HCL})†	Canopy closure (%)^{3}†	Number of different micro-habitats‡	Saturation of the microhabitats (%)‡	Water hole^{4}‡	Temperature (°C)‡	Relative humidity (%)‡
CAZ	RP1	Core	525	37	PS	5.51	73.63	142.02	299.2	2775	2±0	13.11	19.8	5.49	4.31	0.27	303.48±0	C	6.5±0.70	0.88±0.04	W	16.1	91.68
CAZ	RP1	Edge	525	37	PS	5.51	73.63	142.02	144.6	900	3±0	13.11	87.575	1.64	19.22	4.11	59.73±0	C	6.5±0.70	1±0	W	NA	NA
LQY	RP10	Core	173	16	S	2.69	102.74	127.54	245.2	1325	3.5±0.70	14.65	115.34	33.19	14.6	1.84	171.13±34.5	D	7.5±0.70	0.73	W	14.43	90.44
LQY	RP10	Edge	173	16	S	2.69	102.74	127.54	73	1000	3.5±0.70	14.65	118.86	44.02	40.67	2.105	106.95±21.6	D	8±0	0.82±0.08	W, T	NA	NA
SEL	RP11	Core	36	16	S	0.15	7.2	21.52	561.6	675	1	10.11	21.17	6.7	13.13	0.03	4.25	D	9	0.64	W	NA	NA
SEL	RP11	Edge	36	16	S	0.15	7.2	21.52	562.6	500	1.5±0.70	10.11	19.42	6.705	8.04	0.29	3.28±1.54	C	8.5±0.70	0.48±0.11	W, T	NA	NA
SEL	RP12	Core	135	16	S	0.49	5.86	39.16	310	1075	2.5±0.70	9.08	5.68	5.68	0	0	24.10±6.81	D	6.5±2.12	0.77±0.01	W	NA	NA
SEL	RP12	Edge	135	16	S	0.49	5.86	39.16	269.4	800	2±0	9.08	21.865	6.26	0	0.96	11.67±0	D	5±0	0.61±0.07	W	NA	NA

SEL	RP13	Core	157	16	PS	3.97	70.15	112.26	735.6	1975	2±1.41	14.22	7.27	3.96	0	0.09	162.72±115	D	6.5±0.70	0.90±0.04	W	NA	NA
SEL	RP13	Edge	157	16	PS	3.97	70.15	112.26	665.4	1250	2.5±0.70	14.22	35.95	14.32	11.245	0.635	62.92±17.79	D	6.5±0.70	0.74±0.04	W	NA	NA
SEL	RP14	Core	246	16	NA	1.25	27.11	61.48	192.4	3200	1.5±0.70	11	0.2	0.2	0	0	NA	C	5.5±0.70	0.74±0	T	NA	NA
SEL	RP14	Edge	246	16	NA	1.25	27.11	61.48	108.2	3400	2.5±0.70	8	0.2	0	0	0.2	NA	C	5±0	0.62±0.06	W	NA	NA
SEL	RP15	Core	129	16	NA	0.19	7.18	24.66	2513.4	3600	2	13	1.88	0.46	1.56	0.4	NA	E	6	0.76	T	NA	NA
SEL	RP15	Edge	129	16	NA	0.19	7.18	24.66	2315.4	5600	2±0	10	1.63	1.15	0.48	0	NA	D	7±0	0.63±0	W	NA	NA
LQO	RP16	Core	155	27	PS	4.24	37.92	105.2	333.8	2750	3±0	15.16	17.19	15.24	1.95	0	587.57±0	E	8±1.41	0.86±0.01	T	14.42	90.87
LQO	RP16	Edge	155	27	PS	4.24	37.92	105.2	192	650	3±1.41	15.16	5.68	0	2.28	0.21	25±11.78	E	7.5±0.70	0.79±0.13	W, T	14.7	92.92
LQO	RP17	Core	85	27	S	0.23	11.91	25.026	276.2	2050	4	16.91	90.84	11.77	21.02	1.58	703.43	D	9	0.89	T	NA	NA
LQO	RP17	Edge	85	27	S	0.23	11.91	25.026	278.2	900	4.5±0.70	16.91	120.725	31.47	46.485	2.635	115.63±18.1	E	7±1.41	0.72±0.26	T	NA	NA
LQO	RP18	Core	80	27	S	0.05	12.93	23.92	114.6	2200	4	13.16	28.81	7.6	7.66	0.37	329.82	E	9	1	W	14.87	85.03
LQO	RP18	Edge	80	27	S	0.05	12.93	23.92	104	1050	2.5±0.70	13.16	27.82	0	7.86	1.23	51.92±14.68	D	6.5±0.70	0.43±0.01	W	NA	NA
LQO	RP19	Core	80	27	S	0.75	28.62	54.12	356.8	3300	3	14.71	19.23	3.1	4.46	0.32	762.22	E	8	0.90	W	NA	NA
LQO	RP19	Edge	80	27	S	0.75	28.62	54.12	300.2	2100	3±1.41	14.71	13.27	0.865	3.585	0.54	255.31±120	E	7±1.41	0.79±0.29	W	NA	NA
CAZ	RP2	Core	70	37	PS	0.93	49.22	63.12	332.6	1600	2	14.61	27.94	7.72	2.22	0.49	159.61	D	7	0.96	T	15.4	94.74
CAZ	RP2	Edge	70	37	PS	0.93	49.22	63.12	271.6	1000	2±0	14.61	34.925	0	17.69	1.06	50.90±0	D	6±0	0.85±0.06	W, T	NA	NA
LQO	RP20	Core	171	27	PS	2.2	7.41	70.35	376.6	1875	3.5±0.70	15.6	78.44	7.07	3.43	1.86	509.41±103	D	7.5±0.70	0.85±0.05	W	14.095	96.27
LQO	RP20	Edge	171	27	PS	2.2	7.41	70.35	284.8	1250	3±0	15.6	93.315	15.615	20.05	3.555	183.42±0	D	6±0	0.88±0.03	W, T	15.12	91.18
CHAP	RP21	Core	163	8	S	5.23	49.55	116.32	998.62	2525	2±0	15.9	50.37	25.19	0.98	0.69	439.13±0	D	6±1.41	0.88±0.07	T	NA	NA
CHAP	RP21	Edge	163	8	S	5.23	49.55	116.32	950.7	350	3±0	15.9	0	0	7.285	0	6.36±0	C	7.5±0.70	0.71±0.01	W, T	NA	NA

CHAP	RP22	Core	178	8	S	2.79	58.66	108.14	320.3	1975	2±0	15.7	22.81	0	0	0.59	262.07±0	D	6±1.41	0.83±0.01	W	NA	NA
CHAP	RP22	Edge	178	8	S	2.79	58.66	108.14	308.1	2000	4.5±2.12	15.7	62.745	40.135	0	0.945	671.38±316	D	6.5±0.70	0.62±0.30	W	NA	NA
CHAP	RP23	Core	183	8	S	0.19	7.08	23.95	494	2750	2	12.35	15.17	3.94	6.61	0.12	231.76	D	7	0.76	T	NA	NA
CHAP	RP23	Edge	183	8	S	0.19	7.08	23.95	495.3	1450	3.5±2.12	12.35	19.805	7.585	8.815	0.21	125.50±76.0	C	9±2.82	0.71±0.23	T	NA	NA
CHAP	RP24	Core	148	42	S	3.33	68.59	119.542	534.9	1275	3.5±0.70	13.32	55.55	22.12	30.12	0.09	234.61±47.3	D	7±0	0.86±0	T	NA	NA
CHAP	RP24	Edge	148	42	S	3.33	68.59	119.542	555.1	1250	3.5±0.70	13.32	95.025	22	5.215	4.18	170.48±34.4	D	6.5±0.70	0.84±0.03	T	NA	NA
CHAP	RP25	Core	172	42	S	1.37	37.43	70.12	413.6	2175	2.5±0.70	13.11	57.22	37.29	5.4	0.39	221.69±62.7	D	7.5±0.70	0.72±0.01	W	NA	NA
CHAP	RP25	Edge	172	42	S	1.37	37.43	70.12	361.2	1200	3.5±2.12	13.11	83.255	37.7	12.99	2.005	130.52±79.1	D	9.5±4.94	0.77±0.11	W	NA	NA
MAT	RP26	Core	100	16	PS	0.38	14.46	32.18	937	2575	3	14.62	40.97	9.34	0	0.86	540.07	E	6	0.96	W	NA	NA
MAT	RP26	Edge	100	16	PS	0.38	14.46	32.18	898	600	3±0	14.62	6.135	2.81	2.22	0.07	16.96	D	7±1.41	0.82±0.11	W	NA	NA
MAT	RP27	Core	127	16	PS	0.17	19.67	26.88	879.8	1925	3	14.03	57.55	1.42	0	1.53	286.98	E	9	1	T	14.08	88.42
MAT	RP27	Edge	127	16	PS	0.17	19.67	26.88	841.8	1400	4±1.41	14.03	33.77	6.94	7.29	1.205	123.27±43.58	C	9±1.41	0.57±0.17	T	14.45	94.61
MAT	RP28	Core	216	16	S	1.36	38.6	66.54	651.4	1525	3.5±0.70	16.37	106.8	34.16	14.23	58.41	257.66±52.05	D	6.5±0.70	0.62±0.01	T	14.48	95.94
MAT	RP28	Edge	216	16	S	1.36	38.6	66.54	561.8	800	3.5±0.70	16.37	32.6	16.1	6.33	0.625	47.39±9.57	D	8.5±3.53	0.68±0.11	T	NA	NA
MAT	RP29	Core	70	16	S	0.93	56.83	62.36	767.4	1600	3.5±0.70	12.46	8.26	2.21	0	0.16	151.34±30.57	E	8.5±0.70	0.91±0.06	T	NA	NA
MAT	RP29	Edge	70	16	S	0.93	56.83	62.36	673.4	800	4.5±2.12	12.46	4.21	0	2.335	0.115	26.74±29.41	D	7.5±0.70	0.54±0.31	T	NA	NA
CAZ	RP3	Core	140	37	NA	0.28	19.69	33.54	1244.76	3000	2	13.5	7.1902	0.72	0.656	5.8142	NA	E	6	0.86	T	NA	NA
CAZ	RP3	Edge	140	37	NA	0.28	19.69	33.54	1260	1800	3±1.41	10	4.38	0.8	1.58	2	NA	D	9±1.41	0.83±0.04	T	NA	NA
MAT	RP30	Core	77	16	S	0.15	13.98	22.04	645.8	1025	3	9.18	0.68	0	0	0.02	28	D	8±	0.73	T	15.13	85.59
MAT	RP30	Edge	77	16	S	0.15	13.98	22.04	618.4	500	3.5±0.70	9.18	16.67	8.33	2.95	0.33	7.14±1.44	D	8±1.41	0.27±0.17	W, T	NA	NA

CAZ	RP4	Core	3400	37	PS	7.82	68.94	166.76	660	1375	3±1.41	13.33	43.45	13.34	2.31	0.76	176.17±83	D	6±0	0.83±0.10	W, T	15.47	91.78
CAZ	RP4	Edge	3400	37	PS	7.82	68.94	166.76	446.2	652	3.5±0.70	13.33	16.975	0	12.215	0.29	26.63±5.38	B	6.5±0.70	0.85±0.01	W, T	15.07	89.02
CAZ	RP5	Core	305	37	NA	3.78	30.69	118.74	748.2	488.88	1.5±0.70	7.8	0	0	0	0	13.23±6.23	D	7±0	0.62±0.06	W	NA	NA
CAZ	RP5	Edge	305	37	NA	3.78	30.69	118.74	598.8	488.88	3±1.41	7.8	0	0	0	0	26.47±12.47	D	5.5±0.70	0.47±0.20	W	NA	NA
LQY	RP6	Core	99	16	S	0.62	5.49	41.78	361.2	1125	2	19.28	125.68	58.27	39.82	0.75	119.81	E	7	0.75	W	NA	NA
LQY	RP6	Edge	99	16	S	0.62	5.49	41.78	312.6	1050	3±1.41	19.28	150.595	41.49	67.99	2.535	101.51±47.8	D	6.5±0.70	0.54±0.071	W	NA	NA
LQY	RP7	Core	191	16	S	3.92	21.99	108.6	391.8	1300	3±0	18.09	160.08	42.08	0	3.22	295.67±0	D	7±1.41	0.97±0	W	NA	NA
LQY	RP7	Edge	191	16	S	3.92	21.99	108.6	226	500	3±1.41	18.09	172.845	27.215	23.07	7.56	12.88±6.07	D	6.5±0.70	0.90±0.10	W	NA	NA
LQY	RP8	Core	140	16	S	3.69	49.03	106.7	209.4	1525	3±0	14.92	58.88	48.57	2.21	0.22	210.71±0	C	8.5±0.70	0.84±0.03	W	14.73	96.57
LQY	RP8	Edge	140	16	S	3.69	49.03	106.7	86.2	1100	3±0	14.92	76.74	34.07	30.78	0.73	99.99±0	C	6±0	0.84±0.03	W	NA	NA
LQY	RP9	Core	240	16	PS	11.11	108.83	172.16	765.6	1375	2±0	18.47	95.94	17.73	15.75	1.71	144.04±0	D	5.5±0.70	0.97±0	T	15.3	92
LQY	RP9	Edge	240	16	PS	11.11	108.83	172.16	555.6	950	3.5±0.70	18.47	90.91	19.23	21.54	3.09	110.66±22.3	D	7±0	0.75±0.02	W	16	86.8
CAZ	UF1	-	1300	NA	S	18.94	489.46	532.4	0	1075	3	12.5	86.69	29.99	28.27	28.41	80.62	C	4.66±2.3	0.85±0.09	T,W,T	15.4	92.87
LQY	UF105	-	125	NA	S	21.66	942.52	839.4	0	2200	4	14.9	15.46	12.5	2.96	0	432.6	D	3.33±1.5	0.93±0.02	W,W,T	NA	NA
LQO	UF109	-	460	NA	PS	24.05	485.55	793.04	0	1000	2	14.4	60.37	23.35	25.49	11.51	46.08	C	7.66±1.5	0.88±0.11	W	NA	NA
SEL	UF11	-	179	NA	S	22.53	732.9	1132.38	0	1050	4	13.5	75.66	47.48	22.04	5.14	79.38	C	4.66±1.5	1±0	T,T,W	15.54	88.37
MAT	UF121	-	250	NA	PS	19.66	82.37	208.6	0	1050	5	16.75	103.46	82.57	12.33	8.55	149.49	C	3±1	0.92±0.01	W,T,T	NA	NA
SEL	UF13	-	171	NA	PS	25.55	505.53	782.74	0	1350	3	13.25	64.46	14.27	34.77	15.41	91.22	C	4.66±1.5	0.96±0.06	T	NA	NA
LQO	UF130	-	156	NA	PS	21.31	187.33	476.4	0	675	8	14.9	81.59	24.18	6.74	50.65	136.78	B	6±1.73	0.80±0.14	T,W,T	NA	NA
LQO	UF131	-	980	NA	PS	41.31	902.5	1650.8	0	600	1	14.2	60.04	13.48	29.77	16.77	14.484	B	7.33±1.5	0.97±0.04	W,T,T	NA	NA

LQO	UF132	-	2560	NA	PS	23.58	1547.68	1923.52	0	1025	6	14.4	148.86	47.86	66.12	34.87	221.4	C	9±1.73	1±0	W,W,T	NA	NA
LQO	UF134	-	96	NA	S	23.4	616.97	866.4	0	2400	7	16	42.44	15.95	7.07	19.41	967.68	D	4.33±0.5	1±0	W,W,T	NA	NA
LQY	UF136	-	190	NA	S	33.11	1087.79	926.66	0	550	8	17.7	232.43	89.15	79.61	63.65	140.18	C	6±1	0.89±0.09	T,T,W	14.94	90.6
LQY	UF138	-	200	NA	PS	15.93	548.67	802.6	0	500	4	12.3	4.11	4.11	0	0	27.06	B	4.33±1.52	0.89±0.01	W	NA	NA
LQY	UF139	-	99	NA	S	38.06	392.99	468	0	1600	4	13.25	5.26	2.63	2.63	0	262.88	C	7.33±1.1	0.95±0.04	T,T,W	14.52	92.94
SEL	UF14	-	3120	NA	PS	11.98	51.58	110.5	0	1300	1	12.5	27.51	17.33	10.18	0	32.5	C	6.33±1.5	0.97±0.04	W,T,T	NA	NA
LQY	UF142	-	163	NA	S	25.5	389.39	470.8	0	925	4	15.5	137.02	66.61	22.04	48.35	86.02	C	4.33±1.52	0.94±0.06	W	NA	NA
LQY	UF143	-	270	NA	PS	58.58	743.19	1208.88	0	575	8	14.4	120.57	62.99	18.91	38.65	152.35	C	4±1	0.93±0.06	W,T,T	NA	NA
LQO	UF145	-	80	NA	S	39.68	147.01	283.8	0	2025	9	13.7	17.43	4.11	0	13.32	1023.69	D	4±0	0.87±0.05	W,T,T	NA	NA
LQO	UF150	-	220	NA	PS	10.95	850.38	1021.24	0	1375	4	11.4	21.55	10.36	5.26	5.92	100.32	C	5.66±1.15	0.84±0.11	W	NA	NA
LQO	UF153	-	104	NA	PS	40.16	791.72	1222.8	0	2650	5	13.9	10.03	8.55	1.48	0	791.95	D	6.33±2.51	NA	T	NA	NA
LQO	UF156	-	280	NA	PS	16.58	1011.71	1820.8	0	350	9	15.8	33.1	12.33	5.26	15.5	59.724	B	4.66±1.52	NA	T	NA	NA
LQO	UF158	-	187	NA	PS	91.36	198.02	620.2	0	0	1	9.5	22.37	2.96	2.96	16.44	0	B	3±0	NA	W,T,W	NA	NA
LQO	UF159	-	109	NA	PS	111.56	1244.92	1663.78	0	0	3	0	53.74	17.6	3.81	32.32	0	A	4.33±0.57	NA	W	NA	NA
CAZ	UF3	-	186	NA	S	10.69	438.99	584.58	0	1725	3	13.25	19.24	13.21	3.84	2.17	219.42	D	3.66±1.52	0.90±0.01	T	NA	NA
SEL	UF32	-	172	NA	S	41.87	332.27	655.22	0	1025	4	18.25	177.88	45.15	87.79	44.92	164.615	D	8±2.64	0.62±0.11	W,T,W	NA	NA
SEL	UF37	-	170	NA	S	15.23	87.55	235.68	0	1000	4	15.75	85.43	47.17	27.98	10.27	176.4	C	5.33±0.57	0.98±0.03	W	NA	NA
MAT	UF39	-	145	NA	S	10.3	434.36	683.86	0	1625	5	17.5	135.5	39.04	48.05	48.4	227.5	D	7±2	0.59±0.51	T	NA	NA
SEL	UF43	-	150	NA	PS	37.55	680.83	938.22	0	1325	6	17.5	74.84	47.83	20.21	6.8	486.9375	D	7.66±0.57	0.38±0.16	NA	NA	NA
CAZ	UF48	-	168	NA	PS	12.29	1212.75	2406.4	0	775	11	11.25	23.93	13.49	13.26	2.18	326.08125	C	3.66±1.52	1±0	W,T,T	NA	NA

CAZ	UF52	-	130	NA	PS	42.89	369.87	401.34	0	1125	4	12.5	9.5	7.83	1.66	0	118.125	C	5.66±1.52	0.5±0.07	T	NA	NA
CAZ	UF56	-	110	NA	S	25.72	70.07	231.16	0	1625	3	14.75	6.02	4.36	1.66	0	151.003125	D	2.66±0.57	0.91±0.01	W,W,T	NA	NA
SEL	UF60	-	390	NA	PS	31.58	635.94	977.34	0	775	8	13.75	33.99	2.69	20.21	11.08	289.85	C	5.66±1.15	0.9±0	T	NA	NA
CAZ	UF61	-	108	NA	PS	6.61	240.35	481.38	0	975	1	11.5	16.82	3.84	7.32	5.65	22.425	C	5.66±1.15	0.86±0.09	W,T,T	NA	NA
SEL	UF63	-	126	NA	PS	3.1	117.41	215.2	0	475	2	9.6	10.89	8.19	2.69	0	13.68	B	5±1.73	0.92±0.07	W,T,W	NA	NA
CAZ	UF68	-	3840	NA	PS	436.93	388.51	649.36	0	25	3	NA	0	0	0	0	NA	C	4.66±1.15	0.08±0.02	W,T,W	NA	NA
CAZ	UF72	-	3630	NA	PS	738	319.73	475	0	200	6	NA	0	0	0	0	NA	B	4.66±1.52	0.88±0.11	W	NA	NA
MAT	UF76	-	910	NA	PS	26.79	417.71	620.4	0	425	9	8.75	17.74	7.32	6.95	3.47	46.85625	B	3.66±0.57	0.77±0.12	W,T,T	NA	NA
SEL	UF77	-	110	NA	PS	479.76	708.46	814.12	0	875	4	11.9	12.7	7.57	5.14	0	99.96	C	6.66±2.51	0.92±0.07	T,W,W	NA	NA
MAT	UF86	-	1960	NA	PS	1820.47	1072.51	2068	0	0	3	0	0	0	0	0	0	B	5±3.46	0.93±0.02	T	NA	NA
SEL	UF9	-	182	NA	PS	17.64	656.7	675.58	0	1700	5	16.5	87.96	47.62	29.91	10.42	448.8	C	3.33±1.52	0.79±0.16	T,W,T	NA	NA

[1] RP, residual forest patch; UF, undisturbed forest.

[2] HS, high severity; LS, low severity; NA, non-available.

[3] A, 20-30%; B, 31-50%; C, 51-60%; D, 61-80%; E > 80%

[4] T, True – presence of water holes; W, Wrong – absence of water holes, NA, non-available.

APPENDIX F

Mean and SD of continuous (A) and categorical (B) environmental variables per forest type and results of Kruskal-Wallis tests used to compare them (see note below). For categorical variables, values correspond to the number of plots with the character between parentheses. N, number of sites; n, number of plots per forest type. Means between square parentheses refers to the values for north-facing (N) and south-facing (S) edges. Kruskal-Wallis tests followed by multiple comparison tests were used to compare means/values among undisturbed cores and residual cores and edges. Means/values followed by different letters are significantly different ($\alpha < 0.05$). A second analysis was made to compare residual north- and south-facing edges; small letters as indices report the significant level for this comparison. "*", marginal significance of the test ($0.1 < \alpha < 0.5$).

Environmental variable	Undisturbed core (N = 39)		Residual patch (N = 30)			
	(n = 117)		Core (n = 48)		Edge (n = 60, 30 north & 30 south)	
A-Continuous	Mean	SD	Mean	SD	Mean	SD
Temporal						
Age (year)	618.00A*	1009.00	308.00A*	658.00	*id*	*id*
Time since fire (year)	NA	NA	22.43	10.72	*id*	*id*
Spatial						
Area (ha)	105.10A	275.00	2.82B	2.66	*id*	*id*
Shape proxy (SD unit)	561.11A	361.48	42.19B	29.20	*id*	*id*
Buffer zone width (m)	829.87A	534.80	86.26B	44.47	*id*	*id*
Forest influence (m)	0	0	554.70B	386.91	510.62B	441.04
Coarse scale structure						
Tree & snag density (number/ha)	1024.36A	651.94	1876.10B	757.15	1233.03A	1025.53
Number of tree species	4.72A‡	2.56	2.62B	0.87	3.11B	1.07
					N[3.26]a	[1.26]
					S[2.96]a	[0.85]
Mean tree height (m)	13.17A	3.89	13.96A	2.69	13.61A	2.99
CWD-total (m^3/ha)	54.78A	54.86	46.74A	43.63	48.26A	48.50
CWD-1&2 (m^3/ha)	23.22A	23.57	15.37AB	15.98	12.88B	14.77
CWD-3 (m^3/ha)	17.03A	21.31	5.99B	9.10	13.00A	15.68
CWD-4&5 (m^3/ha)	14.62A	17.49	3.18B	11.69	1.45B	1.69
Holdrige complexity index	207.79A	249.70	261.26B	185.23	97.43C	139.24
					N[107.65]a	[169.30]
					S[87.22]a	[103.15]
Fine scale structure						
Number of microhabitats	5.20A	2.00	7.04B	1.20	7.08B	1.56
					N[7.00]a	[1.68]
					S[7.16]a	[1.46]
Saturation (%)	0.85A	0.21	0.83A	0.11	0.70B	0.19
					N[0.69]a	[0.20]
					S[0.72]a	[0.18]
Relative humidity (%)	91.19A	1.97	92.05A	3.43	90.90A	2.91
Temperature (°C)	15.10A	0.42	14.89A	0.63	15.07A	0.55

B-Categorical			
Severity			
Severity (LS/HS)!	78/39A	15/27B	18/34B
Structural at coarse scale			
Canopy closure (%) (A<B<C<D<E)!	3/27/60/27/0A	1/0/3/30/14B	0/2/13/33/12C
Structural at fine scale			
Water hole (Y/N)!	61/53A	22/26A	22/38A

id, variable was measured at the scale of the whole patch and is the same for cores and edges.
!, LS, low severity; HS, high severity; A, 20-30% of closure; B, 30-50%, C, 50-60%; D, 60-80%; E, > 80%; Y, presence of water holes; N, absence of water holes.

APPENDIX G

Number of occurrences of each bryophyte taxa found in each forest type: undisturbed core, residual core and residual north-facing and south-facing edges in boreal black spruce feather-moss forest after wildfire in western Québec. Nomenclature follows Faubert (2012-2014) except for *Sphagnum subtile* which follows the Flora of North America Editorial Committee (2007). Species are presented by life forms. ‡, infrequent (≤ 5 occurrences in all dataset); †, restricted to the habitat type; *, over represented in the habitat type. A species can be over represented in two forest types due to the pair of comparison considered i.e. undisturbed core vs residual core, residual core vs residual edge, and residual north vs south edge. When this occurred the species was not considered as an indicator species (except if the species is over represented in both edge orientations). A "*" for residual patch north-facing and south-facing edge indicates the dominance of the species in edges without dominance for one of the two orientations. N refers to the number of plots sampled where the species is present. Codes of species names used in the analyses are indicated.

Taxon	Species code	Undisturbed core	Residual core	Residual edge	
				North	South
N		117	48	30	30
TRUE MOSSES					
Amblystegium serpens‡	Ambser	3	1	0	1
Aulacomnium palustre	Aulpal	37	29	23	18
Blindia acuta‡	Bliacu	1†	0	0	0
Brachythecium acutum‡	Braacu	3†	0	0	0
Brachythecium campestre	Bracam	6	1	4	1
Brachythecium curtum	Bracur	4	13	9	9
Brachythecium erythrorrhizon‡	Braery	0	1	1	0
Brachythecium populeum‡	Brapop	0	1	1	0
Brachythecium reflexum	Braref	2	4	8*	1*
Brachythecium rutabulum‡	Brarut	1	1	2	1
Brachythecium spp.		1	5	2	1
Brachythecium starkei	Brasta	20	6	11*	6
Brachythecium velutinum	Bravel	3	4	3	4
Breidleria pratensis	Brapra	4	0	3	0
Brotherella recurvans	Brorec	5	3	3	0
Bryhnia graminicolor‡	Brygra	3†	0	0	0
Callicladium haldanianum	Calhal	5	0	2	3
Calliergon cordifolium‡	Calcor	3	0	1	0
Calliergon giganteum‡	Calgig	1†	0	0	0

Calliergon richardsonii[‡]	Calric	0	2	0	1
Campyliadelphus chrysophyllus	Camchr	5	0	2	0
Campylium protensum[‡]	Campro	0	1	1	0
Campylium stellatum[‡]	Camste	3	1	1	0
Campylophyllum hispidulum	Camhis	6	3	2	1
Ceratodon purpureus	Cerpur	3	0	7*	7*
Dicranella heteromalla[‡]	Dichet	1	1	1	0
Dicranum flagellare	Dicfla	7	10	4	5
Dicranum fragilifolium[‡]	Dicfra	0	1	1	0
Dicranum fulvum[‡]	Dicful	0	0	0	1[†]
Dicranum fuscescens	Dicfus	99	46	27	27
Dicranum montanum	Dicmon	14	9	1	4
Dicranum ontariense	Dicont	14	17	10	11
Dicranum polysetum	Dicpol	30	35	24	28
Dicranum scoparium sensu lato	Dicsco	17	5	8*	5
Dicranum spp.		0	5	4	5
Dicranum spurium[‡]	Dicspu	0	0	0	1[†]
Dicranum undulatum	Dicund	57	14	13	16
Drepanocladus aduncus	Dreadu	5	1	4	2
Fissidens osmundoides[‡]	Fisosm	1	0	1	0
Hamatocaulis vernicosus[‡]	Hamver	2[†]	0	0	0
Herzogiella striatella[‡]	Herstr	0	1	1	0
Herzogiella turfacea	Hertur	19	13	15	6
Hygroamblystegium varium[‡]	Hygvar	0	3	1	0
Hylocomium splendens	Hylspl	9	27	12	13
Hypnum curvifolium	Hypcur	7	0	1	0
Hypnum fauriei[‡]	Hypfau	0	1[†]	0	0
Hypnum imponens	Hypimp	8*	2	1	2
Hypnum pallescens	Hyppal	4	9	9	8
Hypnum spp.		1	2	1	0
Isopterygiopsis muelleriana[‡]	Isomue	0	2	1	1
Isopterigiopsis pulchella[‡]	Isopul	0	1	1	0
Leptodictyum riparium	Leprip	1	3	1	1
Meesia triquetra[‡]	Meetri	1[†]	0	0	0
Mnium spinulosum[‡]	Mnispi	3	0	2	0
Oncophorus wahlenbergii	Oncwah	8	7	10	1
Orthotrichum ohioense[‡]	Ortohi	1[†]	0	0	0
Orthotrichum speciosum[‡]	Ortspe	0	0	0	1[†]
Paludella squarrosa[‡]	Palsqu	1[†]	0	0	0
Plagiomnium cuspidatum[‡]	Placus	1	1	1	0
Plagiomnium medium[‡]	Plamed	0	0	2[†]	0
Plagiothecium cavifolium	Placav	31	17	10*	5

Plagiothecium denticulatum	Pladen	13	4	9*	1
Plagiothecium laetum	Plalae	59	31	15	17
Plagiothecium spp.		2	0	0	1
Platydictya subtilis[‡]	Plasub	2[†]	0	0	0
Platygyrium repens	Plarep	2	2	4	3
Pleurozium schreberi	Plesch	98	48	30	30
Pohlia cruda[‡]	Pohcru	0	1	1	0
Pohlia elongata[‡]	Pohelo	0	0	0	2[†]
Pohlia nutans	Pohnut	84	32	28	24
Pohlia sphagnicola	Pohsph	1	26	19	19
Pohlia spp.		0	0	1	0
Polytrichum commune	Polcom	1	10	12	7
Polytrichym commune var. *perigoniale*[‡]	Polcom_per	0	0	2[†]	0
Polytrichum juniperinum	Poljun	0	2	7*	10*
Polytrichum longisetum[‡]	Pollon	0	0	1[†]	0
Polytrichum pallidisetum[‡]	Polpal	0	1	1	1
Polytrichum spp.		0	0	0	1
Polytrichum strictum	Polstr	10	2	8	16
Pseudobryum cinclidioides[‡]	Psecin	0	1	1	0
Ptilium crista-castrensis	Pticricas	43	44	26	25
Pylaisia polyantha[‡]	Pylpol	1[†]	0	0	0
Rhizomnium pseudopunctatum	Rhipse	19*	4	5	2
Rhizomnium punctatum	Rhipun	7	3	3	0
Rhynchostegium serrulatum[‡]	Rhyser	0	1[†]	0	0
Rhytidiadelphus triquetrus[‡]	Rhytri	0	1	1	0
Sanionia uncinata	Sanunc	41	18	14	11
Sarmentypnum exannulatum	Sarexa	7	1	0	2
Splachnum ampullaceum[‡]	Splamp	0	0	1[†]	0
Straminergon stramineum	Strstr	12	17	10	8
Tetraphis pellucida Hedw.	Tepel	61	33	16	14
Tetraplodon angustatus[‡]	Tetang	1	0	1	0
Thuidium recognitum[‡]	Thurec	0	1	1	0
Tomentypnum falcifolium	Tomfal	0	4	5*	3*
Tomentypnum nitens	Tomnit	7*	1	3	0
Ulota coarctata[‡]	Ulocoa	1[†]	0	0	0
Ulota crispa[‡]	Ulocri	0	1	0	1
Warnstorfia fluitans	Warflu	7	17	12	8
SPHAGNA					
Sphagnum angustifolium	Sphang	35	39	23	23
Sphagnum capillifolium	Sphcap	69	29	18	22
Sphagnum cuspidatum[‡]	Sphcus	4[†]	0	0	0

Sphagnum fallax	Sphfal	50	15	13	10
Sphagnum fuscum	Sphfus	17	12	11	15
Sphagnum girgensohnii	Sphgir	7	25	14	10
Sphagnum magellanicum	Sphmag	30	27	18	17
Sphagnum pulchrum[‡]	Sphpul	0	2[†]	0	0
Sphagnum quinquefarium[‡]	Sphqui	0	1	1	1
Sphagnum rubellum	Sphrub	23	4	7	8
Sphagnum russowii	Sphrus	54	44	28	26
Sphagnum squarrosum	Sphsqu	4	2	0	2
Sphagnum subtile	Sphsub	1	7	4	3
Sphagnum tenerum[‡]	Sphtenerum	0	1	2	2
Sphagnum warnstorfii	Sphwar	4	6	5	1
Sphagnum wulfianum	Sphwul	2	6	4	6*
Sphagnum spp.		14	24	12	12
LIVERWORT					
Anastrophyllum hellerianum	Anahel	24	16	9	11
Anastrophyllum michauxii	Anamic	2	1	1	2
Anastrophyllum minutum	Anamin	4	2	2	1
Barbilophozia attenuata	Baratt	8	8	6	2
Barbilophozia barbata	Barbar	20	13	4	6
Barbilophozia floerkei[‡]	Barflo	2[†]	0	0	0
Barbilophozia hatcheri[‡]	Barhat	0	0	1[†]	1[†]
Barbilophozia kunzeana	Barkun	13	20	12	9
Barbilophozia spp.		0	2	1	0
Bazzania tricrenata[‡]	Baztric	5[†]	0	0	0
Bazzania trilobata[‡]	Baztril	0	3[†]	0	0
Blepharostoma trichophyllum	Bletri	45	26	14	10
Calypogeia integristipula[‡]	Calint	1	1	1	1
Calypogeia muelleriana	Calmue	44	18	11*	6
Calypogeia neesiana	Calnee	14	5	4	1
Calypogeia sphagnicola	Calsph	21	9	7	6
Calypogeia spp.		2	3	0	0
Calypogeia suecica[‡]	Calsue	1	1	1	0
Cephalozia bicuspidata	Cepbic	16	11	5	2
Cephalozia catenulata[‡]	Cepcat	3[†]	0	0	0
Cephalozia connivens	Cepcon	66	30	22*	14
Cephalozia loitlesbergeri	Ceploi	2	7	4	4
Cephalozia lunulifolia	Ceplun	73	28	15	15
Cephalozia macrostachya[‡]	Cepmac	3[†]	0	0	0
Cephalozia pleniceps	Cepple	55	26	17	13
Cephalozia spp.		0	1	2	1
Cephaloziella divaricata[‡]	Cepdiv	1	0	1	1

Cephaloziella elachista	Cepela	1	1	2	2
Cephaloziella hampeana	Cepham	9*	1	1	4
Cephaloziella rubella	Ceprub	39	11	11*	11*
Cephaloziella spinigera	Cepspi	4	0	0	4
Cephaloziella spp.		6	4	2	2
Chiloscyphus coadunatus var. *rivularis*	Chicoa_riv	8	5	3	1
Chiloscyphus pallescens‡	Chipal	1†	0	0	0
Chiloscyphus polyanthos‡	Chipol	1†	0	0	0
Chiloscyphus profundus	Chipro	11	11	9	7
Cladopodiella fluitans	Claflu	7†	0	0	0
Cladopodiella francisci‡	Clafra	0	0	1†	0
Frullania eboracensis‡	Fruebo	0	0	2†	0
Frullania oakesiana‡	Fruoak	1	0	1	1
Geocalyx graveolens	Geogra	14	12	7	4
Gymnocolea inflata subsp. *inflata*	Gyminf_inf	6	3	1	1
Jamesoniella autumnalis	Jamaut	49	29	16*	10
Jungermannia leiantha	Junlei	11	4	4	3
Leiocolea heterocolpos‡	Leihet	1†	0	0	0
Leiocolea rutheana‡	Leirut	2	1	0	0
Leiomylia anomala	Leiano	34	8	12	10
Lepidozia reptans	Leprep	74	34	15	18
Lophozia ascendens	Lopasc	5	5	3	2
Lophozia guttulata	Lopgut	5	12	12	12
Lophozia longidens	Loplon	8	9	6	7
Lophozia obtusa‡	Lopobt	2†	0	0	0
Lophozia silvicola	Lopsil	5	15	9	6
Lophozia ventricosa	Lopven	97	37	27	22
Lophozia spp.		5	12	12	8
Mylia taylorii‡	Myltay	2†	0	0	0
Nowellia curvifolia	Nowcur	11	9	7	4
Odotonschisma denudatum‡	Ododen	0	1†	0	0
Plagiochila porelloides	Plapor	3	1	2	0
Ptilidium ciliare	Pticil	79	45	26	28
Ptilidium pulcherrimum	Ptipul	76	48	29	30
Riccardia latifrons	Riclat	33*	6	4	2
Riccardia palmata‡	Ricpal	4†	0	0	0
Scapania apiculata‡	Scaapi	1	1	0	0
Scapania irrigua	Scairr	17	7	6	3
Scapania mucronata‡	Scamuc	1†	0	0	0
Scapania paludicola‡	Scapal	3	0	1	0
Scapania spp.		0	1	0	0

Schistochilopsis capitata[‡]	Schcap	1[†]	0	0	0
Schistochilopsis grandiretis[‡]	Schgra	1[†]	0	0	0
Schistochilopsis incisa[‡]	Schinc	4	1	0	0
Schistochilopsis laxa[‡]	Schax	1	0	2	0
Schistochilopsis spp.		0	1	1	1
Tritomaria exsectiformis	Triexs	20	9	5	5
Tritomaria quinquedentata[‡]	Triqui	1[†]	0	0	0

APPENDIX H

Classification of bryophyte species based on life strategy (adapted from During 1992).

Life-history strategies	Life span	Reproduction	Spore	Ecology
Perennials (P)	10 years or more	Very low sexual reproduction effort i.e. few capsules	< 20 µm and very numerous	Stable habitat where the variation is tolerated: peatlands, forest floor
Colonists and pioneer colonists (C)	< 5 years	High vegetative and sexual reproduction effort i.e. many capsules	< 20 µm and very numerous	Ephemeral substrates, their recurrence is unpredictable; ability to colonize harsh environments like the early stages of primary succession
Shuttle (S)	> 5 years (except *Ptilidium pulcherrimum* < 5 years)	Generally high vegetative and sexual reproduction effort i.e. many capsules	> 20 µm and very numerous	Substrates of long period like tree branches
Dominants (D)	10 years or more	Very low sexual reproduction effort i.e. few capsules	> 20 µm	Sphagna

APPENDIX I

Total number of bryophyte taxa found in extant community and propagule rain by position (i.e. edge and core of the residual forest patches and burned matrix areas - BM) in boreal black spruce feather-moss forest after natural fire in western Québec. Nomenclature follows Faubert (2012, 2013, 2014) except for *Sphagnum subtile* which follows the Flora of North America Editorial Committee (2007). Species are divided by taxonomy (Meusel 1935) and life strategy (adapted from During (1992), see Appendix H for more details). SL: Surrounding Landscape, refers to the extra plots of the extant community. +, species present within the surrounding landscape; - absent from the surrounding landscape and subsequently exclusive to the propagule rain; ( ) presence of the genus, not necessarily the species. Fertile state of collected samples is indicated by (!) for presence of sporophytes and (Φ) for presence of gemmae. Six letters code used to name species in the analyses is given.

Taxon	Life strategy	Extant community			Propagule rain			SL	Fertile state	Species code
		Edge	Core	BM	Edge	Core	BM			
N		9	9	9	9	9	3			
ACROCARP										
Acrocarp spp.		0	0	0	1	0	0			
Atrichum angustatum	P	0	0	0	0	0	1	-		Atrang
Atrichum crispum	P	0	0	0	9	9	3	-		Atrcri
Aulacomnium palustre	P	7	7	9	6	6	2	+		Aulpal
Bryum capillare	C	0	0	0	4	2	0	-		Brycap
Bryum pallescens	P	0	0	0	1	1	2	-		Brypal
Ceratodon purpureus	C	2	0	4	9	9	3	+	!	Cerpur
Dicranella heteromalla	C	1	0	3	1	0	0	+	!	Dichet
Dicranum flagellare	C	1	2	1	0	0	0		!	Dicfla
Dicranum fulvum	P	0	0	1	0	0	0			Dicful
Dicranum fuscescens	P	8	9	5	1	1	0	(+)	!	Dicfus
Dicranum montanum	P	0	0	1	0	0	0			Dicmon
Dicranum ontariense	P	2	2	5	0	0	0		!	Dicont
Dicranum polysetum	P	8	6	8	0	0	0		!	Dicpol
Dicranum scoparium sensu lato	P	0	1	1	0	0	0		!	Dicsco
Dicranum undulatum	S	3	2	6	0	0	0		!	Dicund
Dicranum spp.		1	2	0	0	0	0			
Ditrichum spp.	C	0	0	0	1	1	0	-		Ditrichum_spp
Grimmia spp.	C	0	0	0	1	4	1	-		Grimmia_spp
Oncophorus wahlenbergii	P	2	1	0	0	0	0		!	Onwah
ACROCARP										
Plagiomnium cuspidatum / drummondii [‡]	S	0	0	0	1	0	0	(+)		Placus/dru
Plagiomnium medium	S	0	0	0	0	1	0	(+)	!	Plamed

Pogonatum dentatum	P	0	0	1	0	0	0		!	Pogden
Pohlia nutans	C	8	8	9	0	0	0		!	Pohnut
Pohlia sphagnicola	P	4	4	7	0	0	0		!	Pohsph
Pohlia spp.	P*	0	0	0	9	9	3	(+)		
Polytrichum commune	P	3	2	6	1	2	0	(+)	!	Polcom
Polytrichum juniperinum	P	3	0	8	1	0	0	(+)	!	Poljun
Polytrichum piliferum	P	0	0	1	0	0	0		!	Polpil
Polytrichum strictum	P	3	0	9	2	5	0	(+)	!	Polstr
Polytrichum spp.	P*	0	0	0	8	7	2	(+)		
Pseudobryum cinclidioides	S	0	0	0	0	1	0	-		Psecin
Rhizomnium pseudopunctatum	S	1	0	0	0	0	0		!	Rhipse
Splachnum ampullaceum	C	0	0	0	1	0	0	+		Splamp
Syntrichia ruralis	C	0	0	0	6	3	1	-		Synrur
Tetraphis pellucida	C	5	8	4	5	3	1	+	! Φ	Tetpel
Tortula cernua	S	0	0	0	1	0	0	-		Torcer
PLEUROCARP										
Pleurocarp spp.		2	2	0	1	2	0			
Amblystegium serpens	P	0	0	0	1	0	0	(-)	!	Ambser
Brachythecium campestre	P	1	0	0	0	0	0			Bracam
Brachythecium curtum	P	3	5	3	0	0	0			Bracur
Brachythecium reflexum	P	3	2	1	0	0	0		!	Braref
Brachythecium rutabulum	P	0	1	0	0	0	0		!	Brarut
Brachythecium starkii	P	2	1	0	1	0	0	(+)	!	Brasta
Brachythecium velutinum	C	1	1	1	0	0	0		!	Bravel
Brotherella recurvans	P	1	0	0	0	0	0		!	Brorec
Campyliadelphus chrysophyllus	P	0	0	0	2	1	1	(+)	!	Camchr
Campylophyllum hispidulum	P	0	1	0	4	4	1	(+)	!	Camhis
Herzogiella striatella	P	0	1	0	0	0	0		!	Herstr
Herzogiella turfacea	C	3	2	0	6	5	1	(+)	!	Hertur
Hygroamblystegium varium	C	0	0	1	1	2	0	+	!	Hygvar
Hylocomium splendens	P	2	7	0	0	0	0		!	Hylspl
Hypnum fauriei	C	0	1	0	0	0	0		!	Hypfau
Hypnum imponens	P	0	0	1	0	0	0		!	Hypimp
Hypnum pallescens	P	2	4	0	1	0	0	(+)	!	Hyppal
Hypnum spp.		0	2	0	0	0	0			
Leptodictyum riparium	C	1	1	0	0	0	0		!	Leprip
Plagiothecium cavifolium	P	2	4	1	0	0	0		!	Placav
PLEUROCARP										
Plagiothecium denticulatum	P	3	0	0	0	0	0		!	Pladen
Plagiothecium laetum	P	6	9	1	0	0	0		!	Plalae
Platydictya subtilis	P	0	0	0	3	1	0		!	Plasub

Platygyrium repens	P	0	0	0	1	1	0	+	!	Plarep
Pleurozium schreberi	P	9	9	9	8	9	2	+	!	Plesch
Ptilium crista-castrensis	P	8	9	9	0	0	0		!	Pticricas
Sanionia uncinata	P	6	4	2	0	0	1		!	Sanunc
Straminergon stramineum	P	4	4	0	1	0	0	+	!	Strastr
Tomentypnum falcifolium	P	1	2	0	0	0	0			Tomfal
Warnstorfia fluitans	P	4	5	3	0	0	0		!	Warflu
SPHAGNUM										
Sphagnum spp.	D	4	7	5	9	9	3	(+)	!	
Sphagnum angustifolium	D	7	9	2	0	0	0		!	Sphang
Sphagnum capillifolium	D	5	5	9	0	0	0		!	Sphcap
Sphagnum fallax sensu lato	D	4	6	5	0	0	0			Sphfal
Sphagnum fuscum	D	2	0	8	0	0	0		!	Sphfus
Sphagnum girgensohnii	D	5	7	4	0	0	0			Sphgir
Sphagnum magellanicum	D	8	5	2	0	0	0		!	Sphmag
Sphagnum pulchrum	D	0	1	0	0	0	0			Sphpul
Sphagnum rubellum	D	3	0	3	0	0	0		!	Sphrub
Sphagnum russowii	D	8	9	7	0	0	0		!	Sphrus
Sphagnum squarrosum	D	1	1	1	0	0	0			Sphsqu
Sphagnum subtile	D	0	1	0	0	0	0		!	Sphsub
Sphagnum tenellum	D	0	0	0	2	1	0	(-)		Sphten
Sphagnum warnstorfii	D	0	0	2	0	0	0		!	Sphwar
Sphagnum wulfianum	D	3	2	1	0	0	0			Sphwul
LIVERWORT										
Anastrophyllum hellerianum	C	3	3	0	0	0	0		Φ	Anahel
Barbilophozia attenuata	C	0	1	0	0	0	0		Φ	Baratt
Barbilophozia barbata	P	3	3	0	0	0	0			Barbar
Barbilophozia kunzeana	C	4	5	1	0	0	0		Φ	Barkun
Blepharostoma trichophyllum	C	2	5	1	1	0	0	+	!	Bletri
Calypogeia integristipula	C	0	0	1	0	0	0			Calint
Calypogeia muelleriana	C	1	2	4	0	0	0		!	Calmue
Calypogeia neesiana	C	2	2	2	0	0	0			Calnee
Calypogeia sphagnicola	P	2	2	8	0	0	0			Calsph
Calypogeia suecica	C	1	1	0	0	0	0			Calsue
Calypogeia spp.		0	0	1	0	0	0			
Cephalozia bicuspidata	C	0	2	3	1	0	0	(+)		Cepbic
Cephalozia connivens	P	6	8	6	0	0	0		!	Cepcon
LIVERWORT										
Cephalozia loitlesbergeri	P	0	0	6	0	0	0		!	Ceploi
Cephalozia lunulifolia	C	4	7	5	0	0	0		!	Ceplun
Cephalozia pleniceps	C	7	4	7	0	0	0		!	Cepple

Cephalozia spp.		0	0	2	0	0	0			
Cephaloziella elachista	C	0	0	2	1	2	0	(+)	!	Cepela
Cephaloziella hampeana	C	0	0	4	2	1	1	(+)	!	Cepham
Cephaloziella rubella	C	3	0	9	5	2	1	(+)	!	Ceprub
Cephaloziella spinigera	C	1	0	0	0	0	0		!	Cepspi
Cephaloziella spp.	C*	1	1	2	5	1	1	(+)		
Chiloscyphus coadunatus	C	0	1	0	0	0	0			Chicoa
Chiloscyphus profundus	C	3	3	0	0	1	0	(+)	!	Chipro
Cladopodiella francisci	C	0	0	2	0	0	0		Φ	Clafra
Frullania oakesiana	S	1	0	0	0	0	0		!	Fruoak
Geocalyx graveolens	C	1	2	0	0	0	0		!	Geogra
Jamesoniella autumnalis	C	3	5	1	0	0	0		!	Jamaut
Kurzia pauciflora	C	0	0	1	0	0	0			Kurpau
Leiomylia anomala	P	3	1	8	0	0	0		Φ	Leioano
Lepidozia reptans	C	4	9	1	0	0	0		!	Leprep
Lophozia ascendens	C	1	1	0	0	0	0		! Φ	Lopasc
Lophozia bicrenata	C	0	0	1	0	0	0		Φ	Lopbic
Lophozia guttulata	C	2	2	4	0	0	0		! Φ	Lopgut
Lophozia longidens	C	0	4	0	0	0	0		Φ	Loplon
Lophozia silvicola	C	4	1	3	0	0	0		Φ	Lopsil
Lophozia ventricosa	C	8	8	4	0	0	0		! Φ	Lopven
Lophozia spp.		3	4	0	0	0	0			
Marchantia polymorpha	C	0	0	0	5	6	2	-		Marpol
Nowellia curvifolia	C	2	0	0	0	0	0		!	Nowcur
Odotonschisma denudatum	C	0	1	0	0	0	0		Φ	Ododen
Pellia neesiana	S	0	0	0	1	0	0	-		Pelnee
Ptilidium ciliare	S	7	8	3	0	0	0		!	Pticil
Ptilidium pulcherrimum	S	9	9	6	0	0	0		!	Ptipul
Riccardia latifrons	C	1	1	3	0	1	1	(+)	Φ	Riclat
Scapania irrigua	C	2	0	2	0	0	0		Φ	Scairr
Scapania paludicola	P	0	1	0	0	0	0			Scapal
Scapania uliginosa	C	0	0	1	0	0	0			Scauli
Scapania spp.		0	2	1	0	0	0			
Schistochilopsis incisa	C	0	1	0	0	0	0		Φ	Schinc
Tritomaria exsectiformis	C	1	2	0	0	0	0		Φ	Triexs
Prothalle spp.		0	0	0	8	4	3			

C, colonist; D, dominant; P, perennial; S, shuttle.

‡ Impossible to distinguish between the two species given the lack (i.e. fertile phase) or modification of diagnostic characters because of their growth in laboratory conditions.

*A life strategy was affiliated to the taxa only identified to genus and present in the propagule rain community based on the dominant life strategy of the other species of the genera.

APPENDIX J

Species richness, species frequency and number of plots with the presence of the different bryophyte taxonomic groups and life strategies sampled in boreal black spruce feather-moss forest after natural fire in western Québec. Species are classified by their community affiliation (EC, extant community; PR, propagule rain community or both). See Appendix H for more details about species life strategies. Species frequency are calculated on 27 plots for the extant community (i.e. 21 plots where Petri plates were placed in residual forest patches and burned matrix areas plus 6 additional plots of burned matrix), and in 21 plots for the propagule rain community. Number in parentheses refers to proportions of presence in plots.

	Taxonomic group				Life strategy			
	Acrocarp	Pleurocarp	Liverwort	Sphagnum	Colonist	Perennial	Shuttle	Dominant
Species common to Extant Community (EC) and Propagule Rain (PR)								
Number of species (n = 23)	8	8	7	0	12	11	0	0
Frequency total	155	110	62	-	143	195	-	-
Frequency in EC	106	63	42	-	75	136	-	-
Frequency in PR	49	47	20	-	68	59	-	-
Number of plots with positive records in EC	27 (1)	27 (1)	21 (0.77)	-	25 (0.92)	27 (1)	-	-
Number of plots with positive records in PR	21 (1)	21 (1)	14 (0.66)	-	21 (1)	21 (1)	-	-
Species exclusive to Extant Community (EC)								
Number of species (n = 80)	13	17	37	13	33	29	5	13
Frequency	96	113	252	136	188	210	55	136
Number of plots with positive records	27 (1)	27 (1)	27 (1)	27 (1)	27 (1)	27 (1)	26 (0.96)	27 (1)
Species exclusive to Propagule Rain (PR)								
Number of species (n = 19)	12	4	2	1	6	7	5	1
Frequency	55	11	14	3	38	37	5	3
Number of plots with positive records	21 (1)	9 (0.43)	13 (0.62)	3 (0.14)	18 (0.86)	21 (1)	3 (0.14)	3 (0.14)

APPENDIX K

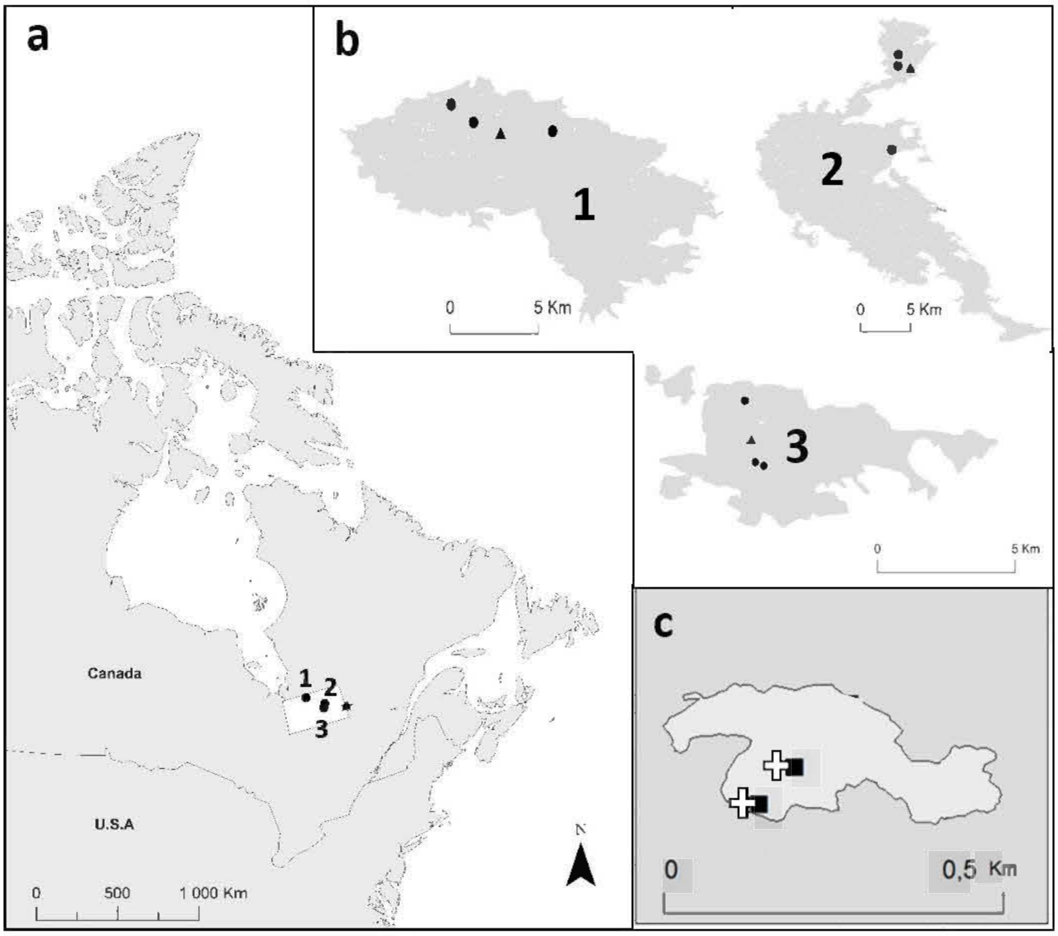
Candidate models used to assess the role of distance between sites and environmental variables on the similarity among communities. The response variable, Jaccard's similarity, was calculated in each of the three 50 m² plots of fire and compared with the 18 plots of 50 m² of extent communities. +, additive effect; *, interactive effect.

Candidate n	Distance a sites (m)	Environmental variables		
		Temporal	Spatial	Forest structure
Mod1	+DIST			
Mod2			+AREA	
Mod3			+DIST CF	
Mod4			+ISOL	
Mod5			+DIST CRP	
Mod6		+TSF		
Mod7		+AGE		
Mod8				+CANOP
Mod9				+DENS
Mod10				+HOLD
Mod11				+CANOP+DENS
Mod12				+CANOP*HOLD
Mod13			+AREA+DIST CF+ISOL+DIST	
Mod14			+AREA*ISOL	
Mod15		+TSF+AGE		
Mod16			+DIST CF+DIST CRP	
Mod17			+ISOL+DIST CF+DIST CRP	
Global	+DIST	+TSF+AGE	+ ISOL+AREA*ISOL	+CANOP +DENS+HC
Null model				

AGE, estimated age of forest in residual patch (year); AREA, area (ha); CANOP, canopy openness (%); DENS, trees and snags density (number of stems/ha); DIST, distance among sites (m); DIST CF, distance from closer continuous forest (m); DIST CRP, distance to closest residual patch (m); HOLD, complexity index; ISOL, isolation (m); TSF, time since fire (year).

APPENDIX L

Location of the study area, studied fires and illustration of the sampling design used for the trapping of the aerial propagule rain in the boreal black spruce-feather moss forest. (a) Location of the study area in the province of Québec, Canada. Large dots and numbers refer to fires; stars represent weather stations. (b) Zoom on the three fires studied, small dots, residual forest patches (3 per fire); triangles, burned matrix areas (1 per fire – materialized as a 50 m² plot). (c) Focus on one residual forest patch (light grey shape) surrounded by the burned matrix (dark grey shape). Squares, 50 m² plots of edge and core used to trap the aerial propagule rain; white crosses represent groups of six Petri plates.



APPENDIX M

Temporal, spatial and structural variables measured in each of the residual forest patch and burned matrix in three natural fires in boreal black spruce forest of Northern Québec. Isolation and canopy openness are means ± standard errors, all other variables are absolute values.

			Temporal variables		Spatial variables				Forest structure variables		
Fire	Sites[1]	Position	Time since fire (year)	Estimated age of forest (year)	Area (ha)	Distance from closer continuous forest (m)	Distance to closest residual patch (m)	Isolation (m)	Canopy openness (%)	Trees and snags density (number of stems/ha)	Holdridge complexity indices of the stand
LQY	RP8	Edge	18	140	3.69	1360	174	86.2±121.3	44.10±5.14	1100	99.99
LQY	RP8	Centre	18	140	3.69	1389	157	209.4±108.2	45.14±13.55	1525	210.78
LQY	RP9	Edge	18	240	11.11	557	1943	555.6±136.5	48.96±17.77	950	94.85
LQY	RP9	Centre	18	240	11.11	496	2000	765.6±264.8	29.86±4.21	1375	144.04
LQY	RP10	Edge	18	173	2.69	1209	114	73±86.8	15.28±5.24	1000	122.24
LQY	RP10	Centre	18	173	2.69	1134	214	245.2±104.9	29.17±6.83	1325	146.69
LQY	B1	Fire	18	18	0.015	984	658	634±210.1	59.72±22.88	314.3	0
LQO	RP16	Edge	29	82	4.24	829	110	192±248.1	9.72±9.68	650	33.34
LQO	RP16	Centre	29	82	4.24	883	165	333.8±208.5	15.63±13.78	2750	587.58
LQO	RP18	Edge	29	80	0.05	555	90	104±52.7	47.92±17.77	1050	62.30
LQO	RP18	Centre	29	80	0.05	554	91	114.6±52.7	12.85±6.69	2200	329.82
LQO	RP20	Edge	29	171	2.2	868	535	284.8±139.4	36.46±18.52	1250	183.45
LQO	RP20	Centre	29	171	2.2	949	479	376.6±141.6	26.74±6.61	1875	582.19
LQO	B1	Fire	29	29	0.015	1550	717	186.4±35.1	37.85±7.31	212.5	0
MAT	RP27	Edge	18	183	0.17	1591	100	841.8±479.8	52.08±29.70	1400	92.45
MAT	RP27	Centre	18	183	0.17	1561	113	879.8±473.2	16.67±8.13	1925	286.98
MAT	RP28	Edge	18	216	1.36	770	230	561.8±774.5	14.93±9.68	800	40.62
MAT	RP28	Centre	18	216	1.36	835	198	651.4±775.4	27.08±1.04	1525	294.48
MAT	RP30	Edge	18	79	0.15	1672	93	618.4±415.2	34.72±5.74	500	8.17
MAT	RP30	Centre	18	79	0.15	1678	101	645.8±411.3	21.18±6.77	1025	28.00
MAT	B1	Fire	18	18	0.015	1772	1054	1303.2±360.9	55.55±35.62	240	0

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[1] B, burned matrix; RP, residual forest patch.

APPENDIX N

Spearman rank correlation among weather variables measured as mean values per month per year (n = 31) from spring 2012 to summer 2014. Values < - 0.70 or > 0.70 were considered as correlated. Significant *P*-value (*P* < 0.05) are indicated in bold. *, variables retained.

Weather variables[1]		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Mean maximum temperature (°C)	1	-																				
Mean minimum temperature (°C)	2	**0.99**	-																			
Mean temperature (°C)*	3	**1.00**	**1.00**	-																		
Maximum consecutive days under 0°C (nb)*	4	**-0.77**	-0.44	-0.58	-																	
Julian date before exceeding 0°C (date)*	5	**-0.77**	-0.44	-0.58	**1.00**	-																
Extreme maximum temperature (°C)	6	**0.97**	0.95	0.96	-0.30	-0.30	-															
Extreme minimum temperature (°C)	7	**0.97**	**0.99**	**0.98**	-0.31	-0.31	**0.94**	-														
Mean nocturnal temperature (°C)	8	**0.99**	**1.00**	**1.00**	-0.63	-0.63	**0.96**	**0.98**	-													
Mean diurnal temperature (°C)	9	**1.00**	**1.00**	**1.00**	-0.53	-0.53	**0.96**	**0.98**	**1.00**	-												
Mean night/day temperature difference (°C)*	10	**0.58**	**0.53**	**0.56**	0.34	0.34	**0.60**	**0.50**	**0.51**	**0.58**	-											
Nb days under 0°C (nb)*	11	-0.31	-0.28	-0.28	0.07	0.07	-0.26	-0.33	-0.28	-0.28	-0.16	-										
Maximum relative humidity (%)	12	0.56	**0.56**	**0.56**	**-0.80**	**-0.80**	**0.48**	**0.58**	**0.58**	**0.54**	0.03	-0.27	-									
Minimum relative humidity (%)	13	-0.67	**-0.67**	**-0.67**	-0.49	-0.49	**-0.72**	**-0.65**	**-0.64**	**-0.68**	**-0.69**	0.01	-0.01	-								
Mean relative humidity (%)*	14	-0.33	-0.30	-0.31	-0.60	-0.60	**-0.39**	-0.26	-0.27	-0.32	**-0.71**	-0.06	0.13	**0.73**	-							
Mean wind speed (km/h)	15	-0.16	-0.15	-0.15	-0.06	-0.06	-0.09	-0.16	-0.14	-0.16	-0.31	**0.43**	-0.07	-0.04	**-0.08**	-						
Maximum wind speed (km/h)*	16	-0.17	-0.19	-0.19	1.00	1.00	-0.04	-0.16	-0.18	-0.19	-0.12	0.10	-0.06	-0.06	**-0.01**	**0.57**	-					
Nb days with maximum wind speed (nb)*	17	0.21	0.18	0.20	-1.00	-1.00	0.23	0.19	0.19	0.19	0.11	-0.14	0.09	-0.13	-0.18	-0.04	**-0.46**	-				
Nb days under -10°C (nb)*	18	**-0.88**	**-0.90**	**-0.90**	**0.74**	**0.74**	**-0.83**	**-0.87**	**-0.90**	**-0.89**	**-0.40**	-0.01	**-0.63**	**0.60**	0.24	-0.10	0.06	-0.12	-			
Total precipitation (mm)*	19	-0.03	0.22	0.16	NA	NA	-0.07	0.27	0.28	0.13	**-0.54**	0.25	NA	**0.44**	0.55	0.01	-0.09	0.18	NA	-		
Mean precipitation (mm)	20	-0.07	-0.08	0.04	NA	NA	-0.30	0.07	0.13	0.01	**-0.48**	0.31	NA	0.43	0.56	-0.22	-0.28	0.10	NA	**0.85**	-	
Nb days without precipitation (nb)	21	0.32	0.26	0.28	NA	NA	**0.56**	0.36	0.25	0.28	0.24	0.04	NA	-0.38	-0.39	0.30	0.09	0.46	NA	0.13	-0.28	-
Maximum consecutive days without precipitation (nb)*	22	-0.12	-0.13	-0.11	NA	NA	-0.12	-0.04	-0.11	-0.09	0.05	**0.54**	NA	0.12	0.11	0.02	-0.34	**0.54**	NA	0.14	-0.01	**0.54**

[1] Weather variables were collated from Environment Canada (2015a, 2015b)

APPENDIX O

Number of bryophyte individuals found in propagule rain by trapping session (i.e. summer and fall 2013 and spring and fall 2014) in boreal black spruce feather-moss forest after natural fire in western Québec. Only the frequency of the species in the Petri plates filled with nutrient agar are given. The number N of Petri plate per trapping session is indicated. Nomenclature follows Faubert (2012-2014). Species are presented by growth form and life strategy (adapted from During 1992). ‡, only found in the year; †, only found both in the year and in the season. Six letters code used to name species in the analyses is given.

Taxon	Life strategy	2013		2014		Species code
		Summer	Fall	Spring	Fall	
N		126	126	63	63	
ACROCARP						
Acrocarp spp.		0	1†	0	0	
Atrichum angustatum	P	0	1†	0	0	Atrang
Atrichum crispum	P	23	42	20	29	Atrcri
Aulacomnium palustre	P	16	14	1	5	Aulpal
Bryum capillare	C	1	2	3	0	Brycap
Bryum pallescens	P	2	0	4	0	Brypal
Ceratodon purpureus	C	49	51	18	9	Cerpur
Dicranella heteromalla	C	0	0	1†	0	Dichet
Dicranum fuscescens	P	0	1†	0	0	Dicfus
Ditrichum spp.	C	1‡	2‡	0	0	Ditrichum_spp
Grimmia spp.	C	7‡	1‡	0	0	Grimmia_spp
Plagiomnium cuspidatum / drummondii *	S	1	0	1	0	Placus/dru
Plagiomnium medium	S	1†	0	0	0	Plamed
Pohlia spp.		80	87	31	24	
Polytrichum spp.		43‡	15‡	0	0	
Pseudobryum cinclidioides	S	1†	0	0	0	Psecin
Splachnum ampullaceum	C	0	1†	0	0	Splamp
Syntrichia ruralis	C	10‡	5‡	0	0	Synrur
Tetraphis pellucida	C	3‡	7‡	0	0	Tetpel
Tortula cernua	S	0	1†	0	0	Torcer
PLEUROCARP						
Amblystegium serpens	P	1†	0	0	0	Ambser
Brachythecium starkii	P	1†	0	0	0	Brasta
Campyliadelphus chrysophyllus	P	1	0	3	0	Camchr
Campylium hispidulum	P	5	4	0	1	Camhis
Herzogiella turfacea	C	14	2	1	1	Hertur
Hygroamblystegium varium	C	3†	0	0	0	Hygvar

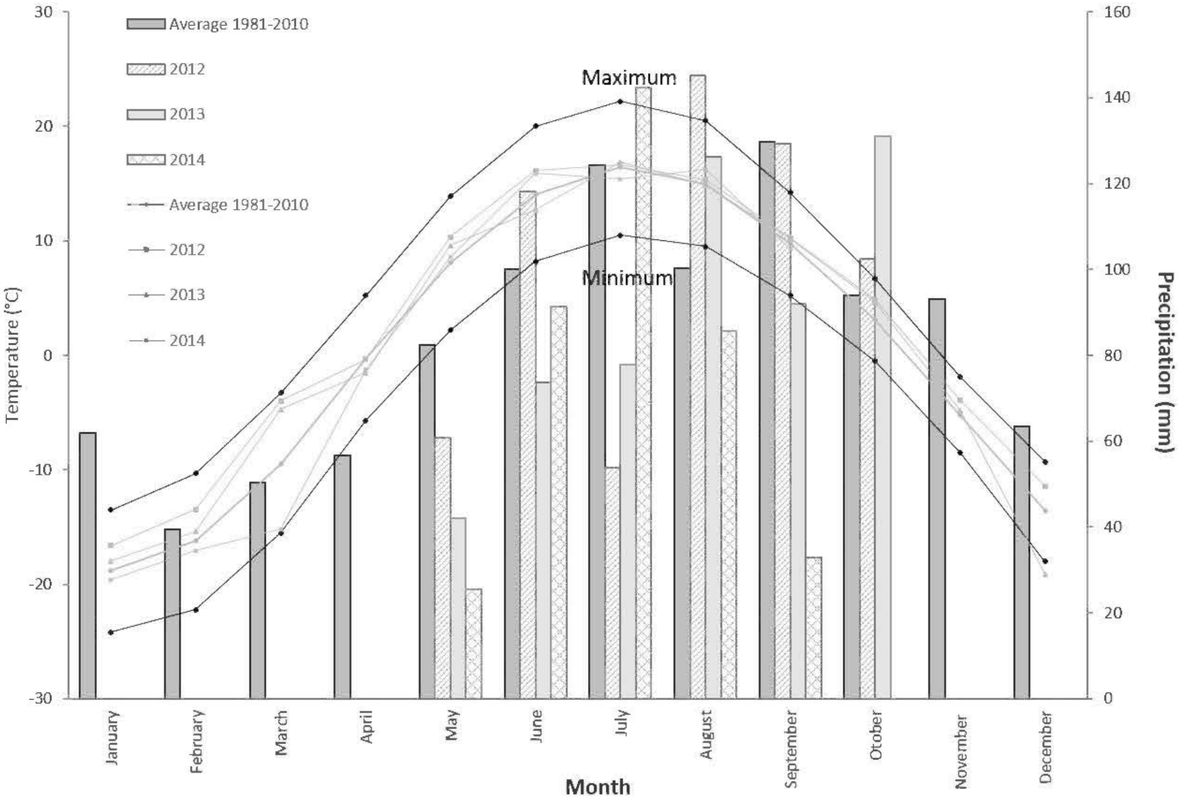
Hypnum pallescens	P	1†	0	0	0	Hyppal
Pleurocarp spp.		1	1	1	0	
Platydictya subtilis	P	3‡	1‡	0	0	Plasub
Platygyrium repens	P	0	0	1‡	1‡	Plarep
Pleurozium schreberi	P	1	0	26	16	Plesch
Sanionia uncinata	P	0	1†	0	0	Sanunc
Straminergon stramineum	P	0	1†	0	0	Strastr
SPHAGNUM						
Sphagnum spp.	D	83	91	24	31	
LIVERWORT						
Blepharostoma trichophyllum	C	1†	0	0	0	Bletri
Cephalozia bicuspidata	C	1†	0	0	0	Cepbic
Cephaloziella elachista	C	5†	0	0	0	Cepela
Cephaloziella hampeana	C	3‡	1‡	0	0	Cepham
Cephaloziella rubella	C	11‡	1‡	0	0	Ceprub
Cephaloziella spp.		5‡	2‡	0	0	
Chiloscyphus profundus	C	0	1†	0	0	Chipro
Marchantia polymorpha	C	6	15	3	0	Marpol
Pellia neesiana	S	0	0	0	1†	Pelnee
Riccardia latifrons	C	1‡	1‡	0	0	Riclat
UNIDENTIFIED PROTHALLES		4	3	6	9	

C, colonist; D, dominant; P, perennial; S, shuttle.

* Impossible to distinguish between the two species given the lack (i.e. fertile phase) or modification of diagnostic characters because of their growth in laboratory conditions.

APPENDIX P

Thirty year average (from 1981 to 2010) and 2012-2014 monthly mean temperatures and precipitations recorded at the study area's nearest weather station (automated Chapais 2, Environment Canada 2015a, b). Monthly mean temperatures are indicated in grey, bold line indicates the 30-year average and lights lines the values for 2012 to 2014. Monthly mean maximum and minimum temperatures during 30-year average are indicated by black lines. Precipitation are indicated by bars, precipitations from November to April in 2012, 2013 and 2014 were not included as it does not impact bryophytes beneath the snow cover.



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