Abondance et diversité des lichens au Nunavik en contexte de changements climatiques

Mémoire

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Résumé

Les lichens constituent une composante importante de la biodiversité en milieu arctique et subarctique et y jouent plusieurs rôles écologiques. En raison de leur métabolisme poïkilohydrique et de leur croissance lente, les lichens apparaissent toutefois comme étant vulnérables dans le présent contexte de changement climatique. Afin de mieux comprendre les conséquences des changements climatiques sur les lichens, nous avons identifié les patrons et déterminants de l'abondance et de la diversité des lichens le long d'un gradient latitudinal au Nunavik et évalué l'impact du couvert arbustif sur les communautés lichéniques.

Nos résultats révèlent que les types de formation végétale, qui influencent les interactions compétitives entre les espèces, et la latitude, qui agit comme indicateur du climat régional, sont les principaux déterminants de l'abondance, de la diversité et de la composition des communautés lichéniques à l'échelle du gradient. À l'échelle locale, le couvert arbustif et graminoïde réduit l'abondance et la diversité, ce qui témoigne de la faible compétitivité des lichens. La comparaison des communautés lichéniques en milieu ouvert et sous arbuste révèle un déclin du couvert lichénique de plus de 50% sous la canopée. De plus, les arbustes engendrent une réduction de la diversité lichénique qui augmente avec le temps, et modifient la composition des communautés en excluant les espèces nécessitant les conditions environnementales spécifiques aux milieux ouverts.

En combinant deux approches distinctes, nous avons démontré l'importance de l'impact de la végétation vasculaire sur les lichens. Nos résultats laissent présager une restructuration majeure des communautés lichéniques, alors que les changements climatiques favorisent un déplacement des zones de végétation vers le nord ainsi qu'une expansion croissante des arbustes. En permettant une meilleure compréhension des facteurs environnementaux influençant les lichens, ce projet s'inscrit dans un effort visant à comprendre la dynamique des écosystèmes nordiques, en vue de mieux prédire les changements de végétation futurs.

Abstract

Lichens are a key component of arctic and subarctic ecosystems, as they constitute an important part of biodiversity and are involved in many ecological processes. However, lichens appear vulnerable in the present context of climate change because of their poikilohydric metabolism and their slow growth rate. In order to understand the implications of climate change on lichens, we identified patterns and determinants of lichen abundance and diversity along a latitudinal gradient in Nunavik and evaluated the impact of shrubs on lichen communities.

Our results reveal that vegetation types, which influence competitive interactions, and latitude, which is used as a proxy of regional climate, are the main factors involved in driving lichen abundance, diversity and community composition at the gradient scale. At the local scale, shrub and graminoid cover induces a lower lichen cover and diversity, highlighting the low competitive abilities of lichens. When comparing lichen communities in open area and under shrubs, we observe a decline of lichen cover of more than 50% under shrub canopy. Shrubs also induce a decline of lichen diversity that seems to intensify with time, and modify community composition by excluding species that require the open environment conditions.

By combining two distinct methods, we highlighted the predominance of vascular plants in profiling lichen communities. As climate change is promoting further shrub expansion and a northward shift of vegetation zones, a major restructuration of lichen communities is likely to be observed in the next decades. By identifying environmental drivers of lichen communities at different spatial scales, this project takes part in a global effort towards a better understanding of northern ecosystems dynamics that aims to improve our ability to predict future changes in vegetation.

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Simplement pour souligner
la force de ces mots

« Il est un temps où le courage et l'audace tranquilles
deviennent pour un peuple, aux moments clés de son existence,
la seule forme de prudence convenable.
S'il n'accepte pas alors le risque calculé des grandes étapes,
il peut manquer sa carrière à tout jamais,
exactement comme l'homme qui a peur de la vie. »

- René Lévesque

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Avant-propos

Le présent mémoire avait pour objectifs d'identifier les patrons et déterminants de l'abondance et la diversité des communautés lichéniques sur un gradient latitudinal au Nunavik, Québec, Canada, en plus d'évaluer l'impact des arbustes sur les lichens. Nous avons été en mesure de répondre à ces objectifs par la caractérisation des communautés lichéniques dans divers types de milieux dans six régions d'études au Nunavik. Ce mémoire présente dans un premier temps le cadre théorique général du projet sous forme d'une introduction générale. Suivent deux chapitres sous forme d'articles scientifiques en anglais qui présentent les résultats liés aux objectifs du projet. Une conclusion générale permettant une synthèse des principaux résultats ainsi qu'une ouverture vers des perspectives de recherche clôt le présent mémoire.

Le premier chapitre s'intéresse aux patrons et déterminants de l'abondance et de la diversité des lichens à différentes échelles spatiales sur un gradient latitudinal au Nunavik. Ce chapitre est présenté sous forme d'un article intitulé *Patterns and determinants of lichen abundance and diversity over a latitudinal gradient in Nunavik (Québec, Canada)* et a été soumis à *Journal of Biogeography* en date du 6 juillet 2020. Le deuxième chapitre porte sur l'influence de la canopée arbustive sur l'abondance et la diversité des communautés de lichens. Cet article, intitulé *Shrub canopy induces a decline of lichen abundance and diversity in Nunavik (Québec, Canada)*, est présenté tel qu'il a été publié dans le journal *Arctic, Antarctic and Alpine Research* en novembre 2019.

Les auteurs du premier chapitre sont dans l'ordre sont Catherine Chagnon, Martin Simard et Stéphane Boudreau. Les auteurs du deuxième chapitre sont Catherine Chagnon et Stéphane Boudreau. Je siège comme première auteure de ces deux articles en raison de mon implication active dans toutes les étapes du projet, de l'élaboration du projet à la rédaction. Martin Simard siège comme auteur du premier chapitre en raison de son implication au cours de la rédaction. Mon directeur de recherche, Stéphane Boudreau, s'est également impliqué dans l'entièreté du processus menant à la réalisation des deux articles et m'a guidé au moment de la rédaction.

L'ensemble des spécimens lichéniques récoltés pour identification seront déposé à l'Herbier Louis-Marie suivant le dépôt de ce mémoire.

Introduction

Lichens et rôles écosystémiques

Les lichens sont des organismes résultant de la symbiose entre un fongus (généralement un ascomycète; le mycobionte) et une algue verte et/ou une cyanobactérie (le photobionte). Leurs morphologies variées leur permettent de coloniser divers types de substrat dans des habitats très diversifiés (Nash 2008). Les lichens sont généralement retrouvés dans des environnements extrêmes (Grime 1979) et sont peu abondants dans les environnements où les conditions favorables engendrent une compétition accrue avec les plantes vasculaires. À l'échelle planétaire, ils dominent environ 8% des écosystèmes terrestres, mais leur répartition est majoritairement concentrée dans les écosystèmes de haute latitude ou de haute altitude (Nash 2008).

À l’échelle circumpolaire, les espèces lichéniques constituent une portion importante de la biodiversité. En fait, leur richesse spécifique en milieux arctiques est parfois supérieure à celle des espèces vasculaires (Longton 1988, Matveyava and Chernov 2000). Leurs divers rôles fonctionnels contribuent à maintenir l'intégrité des écosystèmes en milieu arctique. Par exemple, environ 10% des espèces de lichens sont composées d’un symbionte cyanobactérien capable de fixer l’azote atmosphérique qui devient disponible pour l’écosytème suite à la décomposition du thalle, ce qui leur permet de participer au budget azoté de l’écosystème (Darnajoux et al. 2014, Zhang et al. 2016). Les lichens absorbent également les nutriments d’origine allochtone présents dans l’air et dans les précipitations, ce qui constitue un intrant nutritionnel pour l’écosystème (Asplund et Wardle 2017). Ces organismes pionniers peuvent aussi coloniser le substrat rocheux et en désagréger la couche superficielle, ce qui permet la mise en circulation des nutriments. Ce faisant, les lichens contribuent aux premières étapes de la pédogénèse et facilitent l’établissement des plantes vasculaires, initiant ainsi la succession végétale (Chen et al. 2000). La présence des espèces lichéniques peut également influencer la composition de la communauté végétale vasculaire en favorisant ou inhibant la germination des graines (Houle and Filion 2003, Asplund and Wardle 2017). Par ailleurs, certaines espèces de lichens sont étroitement associées au caribou migrateur dont la diète hivernale est composée principalement de lichens (Heggberget et al.

2002, Ophof et al. 2013). Finalement, les lichens jouent un rôle dans la régulation du climat global puisque les surfaces terrestres qu'ils dominent possèdent un albédo élevé, réfléchissant une partie importante du rayonnement solaire du fait de leur couleur claire (Beringer et al. 2005, Bernier et al. 2011)

En raison de leurs caractéristiques physiologiques, les lichens sont très sensibles à la modification de leur environnement immédiat. En effet, les lichens ne possèdent pas de tissus spécialisés dans la régulation de leur contenu en eau et ne sont physiologiquement actifs que lorsqu'hydratés (Green et al. 2008). Un tel métabolisme poïkilohydrique leur permet de coloniser des substrats pour lesquels la disponibilité en eau est limitée (Kappen and Valladares 2007). Par conséquent, leur contenu en eau s'équilibre avec celui de l'environnement, ce qui affecte directement leur capacité photosynthétique (Kappen and Valladares 2007), se traduit par une faible croissance annuelle variant d'imperceptible à quelques millimètres (Nash 2008) et leur octroie une faible compétitivité. La température agit également sur la croissance et la physiologie des lichens (Hamada 1983, Pisani et al. 2007). Par exemple, la température optimale pour la photosynthèse des lichens arctiques est relativement basse, variant entre 5 et 25°C selon les espèces (Longton 1988). La capacité photosynthétique de certaines espèces semble ainsi particulièrement vulnérable à des températures plus élevées (Kershaw and Smith 1978, Kershaw 1985); leur performance pourrait donc être affectée négativement par les changements climatiques actuels. Par conséquent, la répartition des habitats propices aux lichens devrait diminuer au cours des prochaines décennies (Rubio-Salcedo et al. 2017).

Changements majeurs en Arctique

Changements climatiques

Au cours des dernières décennies, les changements climatiques ont induit un réchauffement particulièrement important en Arctique, où le taux d'augmentation des températures est près de deux fois plus élevé qu'à l'échelle planétaire (Arctic Climate Impact Assessment 2004, Winton 2006). Cette augmentation rapide des températures en milieux arctique et subarctique devrait se poursuivre dans les prochaines décennies (IPCC 2014) et engendrer d'importantes modifications des écosystèmes arctiques, tant au niveau de leur productivité que de leur structure. Des changements majeurs sont déjà perceptibles en Arctique, que ce soit la diminution du couvert et de l'épaisseur de la banquise, la fonte des nappes glaciaires ou la dégradation du pergélisol (IPCC 2014). Ces changements ont également des répercussions à l'échelle planétaire en induisant, par exemple, la libération de gaz à effet de serre dans l'atmosphère en raison d'une respiration microbienne accrue suite à la fonte du pergélisol (Tamocai et al. 2009), ou encore, en affectant le niveau et la salinité des océans, ce qui pourrait avoir un impact sur la circulation thermohaline (McGuire et al. 2006). Des changements marqués du couvert et de la composition de la végétation sont également notables (Arctic Climate Impact Assessment 2004, Tape et al. 2006) et suggèrent qu'une restructuration des communautés végétales est en cours.

Le phénomène d'arbustation

Parallèlement à l'augmentation rapide des températures en milieu nordique, une augmentation de l'indice de végétation par différence normalisée (NDVI; *Normalized Difference Vegetation Index*), un indicateur de productivité primaire, est observée à l'échelle circumpolaire (Forbes et al. 2010, McManus et al. 2012, Ju and Masek 2016). Selon des analyses de photographies aériennes, cette augmentation de productivité primaire résulte d'une augmentation quasi-généralisée du couvert arbustif (Sturm et al. 2000a, Ropars and Boudreau 2012, Tremblay et al. 2012, Fraser et al. 2014, Moffat et al. 2016). Dans les écosystèmes de hautes latitudes, l'augmentation des températures de l'air et des sols résulte en une disponibilité accrue des nutriments et allonge la saison de croissance (ACIA 2004), ce qui semble favoriser les espèces arbustives. Dans ces régions, une augmentation rapide de l'abondance de ces espèces a d'ailleurs été démontrée au cours d'études expérimentales simulant le réchauffement climatique et l'augmentation de la disponibilité des nutriments (Chapin et al. 1995, Chapin and Shaver 1996, Zamin and Grogan 2012).

Selon les scénarios de changements climatiques considérés, certaines études prévoient une augmentation de l'étendue du couvert arbustif atteignant entre 50% et 70% dans les écosystèmes nordiques d'ici 2050 (Pearson et al. 2013, Lemay et al. 2018). Or, le phénomène d'arbustation observé à l'échelle circumpolaire a un impact considérable sur le système climatique planétaire. La présence accrue des espèces ligneuses favorise notamment la dégradation du pergélisol (Lawrence and Swenson 2011, Bonfils et al. 2012) et augmente les taux d’évapotranspiration, ce qui accroît la présence de vapeur d’eau dans l’atmosphère et pourrait engendrer une rétroaction positive sur le réchauffement atmosphérique (Swann et al. 2009). De plus, l’augmentation du couvert arbustif diminue généralement l’albédo des surfaces terrestres et augmente l’épaisseur du couvert nival, ce qui maintient la température des sols plus élevée en hiver. Une température des sols accrue durant l’hiver pourrait soutenir une augmentation de l’activité des microorganismes de la décomposition et augmenter la disponibilité des nutriments, ce qui pourrait engendrer une rétroaction positive sur l’avancée des espèces arbustives (Figure 1, Sturm et al. 2001, 2005).

À l’échelle locale, le développement d’un couvert arbustif modifie la structure verticale de la végétation et influence les communautés végétales sous-jacentes. En effet, les arbustes réduisent la quantité de lumière atteignant le sol, que ce soit via la création d’une voûte arbustive relativement fermée ou encore par une abondante production de litière. Dans certains cas, la présence des arbustes peut avoir un rôle facilitateur et favoriser l’établissement de certaines espèces en fournissant une protection contre les conditions environnementales difficiles (Ballantyne and Pickering 2015) et contre l’herbivorie (Pajunen et al. 2011). L’impact du développement d’un couvert arbustif sur les autres espèces végétales varie toutefois en fonction des habiletés compétitives de ces dernières (Schöb et al. 2013). Dans les milieux nordiques, les stratégies adoptées par une majorité d'espèces végétales sont associées aux stress imposés par les conditions environnementales difficiles. En contrepartie, ces espèces possèdent bien souvent une faible compétitivité, ce qui diminue leur capacité à rivaliser avec les arbustes pour l’acquisition de ressources sous des conditions climatiques améliorées (Bret-Harte et al. 2008, Myers-Smith et al. 2011).

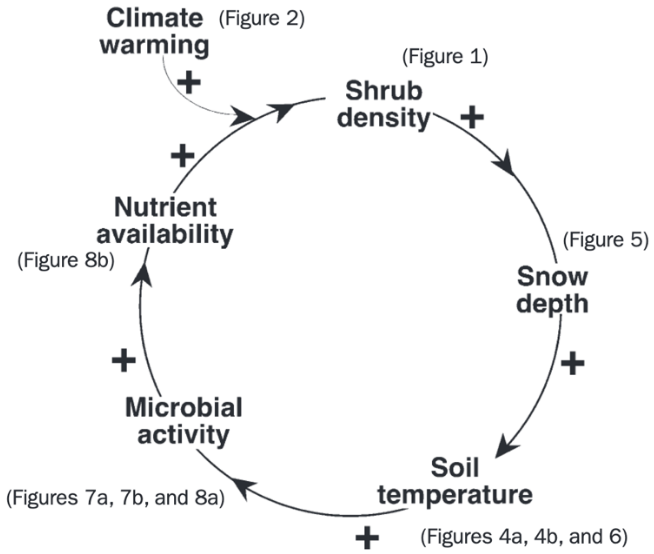

Figure 1. Boucle de rétroaction positive entre l'arbustation, l'augmentation du couvert de neige et la disponibilité des nutriments dans le sol. Tiré de Sturm et al. (2005b).

Recul des lichens

Une diminution importante du couvert lichénique a été notée dans les dernières décennies via différentes analyses de photographies aériennes et semble résulter de l'avancée des espèces arbustives (Ropars and Boudreau 2012, Tremblay et al. 2012, Provencher-Nolet et al. 2014, Moffat et al. 2016). Au Québec subarctique, Provencher-Nolet et al. (2014b) ont démontré une diminution de la superficie des zones dominées par les lichens de 42,8 hectares dans la région d'Umiujaq entre 1994 et 2010, dont 41,6 ha (97%) ont été remplacés par une végétation à dominance arbustive. Dans le nord-ouest du Canada, les photographies aériennes montrent une diminution du couvert lichénique pour 96% des sites étudiés entre 1980 et 2013, alors qu'une augmentation du couvert arbustif est visible dans 97% des cas (Fraser et al. 2014). Ces auteurs notent d'ailleurs que de larges zones dominées par les lichens fréquemment observables par avion ou lors des campagnes de terrain dans les années 1980 ont presque complètement disparues aujourd'hui. Ces observations suggèrent que le changement climatique agit de manière indirecte sur les lichens en favorisant la croissance et l'établissement des espèces vasculaires, qui induisent un déclin des espèces lichéniques par exclusion compétitive (Cornelissen et al. 2001, Alatalo et al. 2017).

Ces observations à l'échelle du paysage sont également appuyées par des études expérimentales simulant les effets des changements climatiques. En effet, un déclin de la biomasse des lichens a d'abord été notée au cours d'une étude expérimentale d'augmentation des températures et de fertilisation et à long terme (Chapin et al. 1995), suggérant un déclin de ce groupe sous l'effet du changement climatique. Une diminution semblable de l'abondance des lichens a été obtenue au cours d'expériences subséquentes en milieux nordiques, tant en Europe qu'en Amérique du Nord (Elmendorf et al. 2012, Zamin et al. 2014, Alatalo et al. 2017). Une diminution de la richesse spécifique des lichens a également été notée suivant un réchauffement expérimental (Lang et al. 2012, Alatalo et al. 2017) et confirme la vulnérabilité de ce groupe vis-à-vis des changements climatiques.

Déterminants environnementaux de l'abondance et de la diversité des lichens

Outre les interactions compétitives avec les plantes vasculaires, plusieurs facteurs environnementaux influencent l'abondance et la diversité des espèces lichéniques. Les études se concentrant sur les relations entre les lichens et les caractéristiques du milieu demeurent toutefois peu abondantes, et témoignent d'une variation spatiale des facteurs environnementaux régulant l'abondance et la diversité des lichens. Par exemple, Giordani et al. (2014) ont conclu que la disponibilité de l'eau, de la lumière et de différents types de substrats étaient les principaux facteurs déterminant la composition des communautés de lichens en région Méditerranéenne. Nelson et al. (2015a) ont pour leur part conclu que le pH du sol et l'altitude étaient les facteurs déterminants dans le parc national Denali, en Alaska.

Au cours des dernières années, une augmentation du nombre d'études évaluant l'association entre les lichens et les variables environnementales est toutefois notable. Plusieurs de ces études utilisent les traits fonctionnels des espèces lichéniques (Giordani et al. 2014, Matos et al. 2015, Nelson et al. 2015a, 2015b, Bässler et al. 2016, Benítez et al. 2017), bien que leur utilisation pour ce groupe demeure largement inférieure à l'utilisation qui en est faite pour les plantes vasculaires (Martin and Mallik 2017). L'étude des traits fonctionnels permet de mieux comprendre les exigences environnementales des organismes, les interactions entre les organismes et leur milieu ainsi que les interactions compétitives entre les espèces (Cadotte et al. 2011). Un trait fonctionnel se définit comme une caractéristique mesurable qui agit sur la performance d'un organisme en influençant la réponse de cet organisme aux conditions environnementales ou encore qui détermine l'effet de cet organisme sur son milieu. La variation des traits fonctionnels au sein d'une communauté, c'est-à-dire la diversité fonctionnelle, permet de comprendre comment la diversité est reliée aux caractéristiques d'un milieu, et comment cette diversité répondra en cas de perturbation ou de changement environnemental (Suding et al. 2008, Lavergne et al. 2010). De plus, puisque les écosystèmes sont souvent caractérisés par une redondance fonctionnelle, la diversité fonctionnelle peut permettre de déceler des changements majeurs au sein de la composition d'une communauté et de ses rôles écosystémiques, qui pourraient autrement passer inaperçus si seule la richesse spécifique était considérée (Cadotte et al. 2011).

L'analyse des traits fonctionnels a également été utilisée pour évaluer les changements futurs au sein des communautés lichéniques en réponse à divers scénarios de changements climatiques (Ellis 2013, Allen and Lendemer 2016, Rubio-Salcedo et al. 2017). La forme de croissance, la nature du photobionte et la stratégie reproductive apparaissent comme de bons indicateurs de la stratégie adaptative d'une espèce aux caractéristiques de son milieu, puisque ces traits influencent la réponse des espèces aux conditions environnementales (Tableau 1). En fonction de la relation entre les traits fonctionnels spécifiques et les caractéristiques du milieu, il a également été possible de calculer la vulnérabilité des espèces lichéniques face à différents scénarios de changements climatiques pour la péninsule ibérique, et même d'évaluer leur répartition future en fonction de la disponibilité de leur habitat en 2080 (Rubio-Salcedo et al. 2017). Ces auteurs indiquent une perte d'habitat pour 75% des espèces étudiées et une vulnérabilité plus importante pour les espèces sensibles à la dessiccation, soit les espèces à thalle de grandes dimensions et les cyanolichens, en raison de la diminution prévue des précipitations en Méditerranée au cours des prochaines décennies. L'étude des traits fonctionnels s'avère donc un outil puissant pour étudier la vulnérabilité des espèces en réponse aux changements climatiques.

Tableau 1. Traits fonctionnels des lichens et leur influence sur la réponse des organismes vis-à-vis des conditions environnementales

Trait fonctionnel	Attributs possibles	Impacts sur la répartition en fonction des conditions environnementales
Forme de croissance	Fruticuleux Foliacé – érigé Foliacé – prostré Squamuleux Crustacé Lépreux Gélatineux	La forme de croissance est intimement liée au rapport surface/volume qui détermine la vitesse à laquelle l'eau est absorbée et la vitesse d'évapotranspiration du thalle (Lakatos et al 2006, Gaussla 2014, Asplund et Wardle 2017). Le contenu en eau affecte directement l'efficacité de la photosynthèse (Pardow et al. 2010). Les espèces ayant un grand rapport surface/volume (e.g. fruticuleuses) sont plus compétitives (Rogers 1990), contrairement aux espèces ayant un plus faible rapport (e.g. crustacées) qui sont plus résistantes à la dessiccation (Green et al. 1980).
Photobionte	Algue verte Cyanobactérie Tripartite	Le type de photobionte influence les besoins d'une espèce en lumière, température et eau (Lange et al. 1986, Marini et al. 2011) affectant directement l'efficacité de la photosynthèse. Les cyanolichens nécessitent un apport en eau liquide et sont restreints aux milieux plus humides (Lange et al. 1986) alors que les espèces ayant une algue verte comme photobionte sont moins sensibles et supportent davantage un milieu plus sec (Lange et al. 1986).
Mode de reproduction	Spores – sexuée Sorédies – asexuée Isidies – asexuée Lobules – asexuée	La reproduction par spores permet une dispersion sur de grandes distances en raison de leur petite taille, contrairement aux propagules végétatives qui sont dispersées sur de plus petites distances de par leur plus grande taille (Ellis 2012). Les lichens se reproduisant par le biais de propagules de grande taille sont plus compétitifs, alors que ceux utilisant de plus petites propagules sont plus résistants au stress (Rogers 1990). Certains lichens du genre *Cladonia* se reproduisent principalement par fragmentation du thalle, notamment via le piétinement des caribous, ce qui restreint leur dispersion sur de petites distances (Nelson et al. 2015a).

Contexte de l'étude

Aire d'étude

Le Nunavik, territoire situé au nord du 55^{e} parallèle au Québec, a subi un réchauffement particulièrement important des températures moyennes depuis le début des années 1990 (Allard et al. 2007). Cette région présente l'un des taux d'augmentation du NDVI les plus élevés sur le continent nord-américain au cours des dernières décennies (Ju and Masek 2016). De même, une augmentation du NDVI a été observée pour 30% des 260 000 km^2 analysés par imagerie satellitaire Landsat le long d'un gradient latitudinal au Nunavik (McManus et al. 2012). À plus fine échelle, les observations permettent de relier le taux élevé d'augmentation du NDVI au phénomène d'arbustation qui est bien documenté dans les régions d'Umiujaq (Provencher-Nolet et al. 2014), de Kangiqsualujjuaq (Tremblay et al. 2012) et de la rivière Boniface (Ropars et al. 2015a). L'avancée des espèces arbustives au

Nunavik semble majoritairement associée au bouleau glanduleux, *Betula glandulosa* Michx., une espèce arbustive à feuillage caduc qui répond rapidement à l'amélioration des conditions environnementales (Ropars and Boudreau 2012, Tremblay et al. 2012, Ropars et al. 2015b).

Un récent rapport du consortium en climatologie régionale Ouranos (2015) fait état des connaissances quant à l'évolution du climat au Québec et évalue l'ampleur des changements à venir d'ici 2100. Comparativement à l'ensemble de la province, ce rapport projette une augmentation plus importante des températures dans le Nord du Québec, augmentation pouvant atteindre jusqu'à 10°C selon les scénarios d'émissions de gaz à effet de serre les plus pessimistes. Selon ces prédictions, les changements de température les plus importants se produiraient au cours de la saison hivernale et induiraient une réduction du nombre annuel de jours de gel. De même, la durée de la saison de croissance, qui s'accroît depuis les années 1970, devrait augmenter d'une vingtaine de jours d'ici 2050. Alors qu'une augmentation des précipitations annuelles a été observée pour Kuujjuaq au cours des dernières décennies, les modèles de projections s'accordent sur une augmentation des précipitations estivales et automnales dans le Nord du Québec d'ici 2100 (Ouranos 2015). Les changements à venir en termes de température et de précipitation sont donc susceptibles de favoriser l'avancée du couvert arbustif dans les années à venir, et ainsi avoir un impact négatif sur les communautés lichéniques au Nunavik.

Contexte théorique

Bien que l'impact de l'arbustation sur l'abondance des lichens ait été évalué à large échelle dans certaines régions du Nunavik, son effet sur l'abondance et la diversité des lichens à plus fine échelle demeure peu documenté. Très peu de données sont disponibles quant à la diversité des lichens au Nunavik, ceux-ci étant généralement traités comme un unique groupe fonctionnel regroupant l'ensemble des espèces. Ainsi, de nouvelles mentions d'espèces de lichens pour le territoire canadien ou même pour l'Amérique du Nord sont régulièrement rapportées lors de campagnes de terrain menées dans ce territoire (Gagnon 2016). Selon le *Consortium of North American Lichen Herbaria* (CNALH), 464 espèces de lichens ont été identifiées au nord du 55^{e} parallèle dans la province de Québec, alors que le nombre d'espèces de lichens en milieu arctique à l'échelle planétaire est évalué à ~ 1750 (Meltofte et al. 2013). Les facteurs déterminants l'abondance et la diversité des lichens au Nunavik demeurent également peu documentés. Or, une meilleure compréhension des déterminants environnementaux agissant sur la composition des communautés, de même qu'une connaissance des patrons actuels de l'abondance et de la diversité des lichens, sont nécessaires en vue d'évaluer les changements de végétation à venir dans le présent contexte de changements climatiques.

Objectifs et hypothèses

L'objectif de cette étude est de caractériser, à différentes échelles spatiales, l'abondance et la diversité des lichens le long d'un gradient latitudinal au Nunavik, qui s'étend de l'écotone forêt-toundra à la toundra prostrée, en vue d'évaluer l'influence du milieu et les implications des changements climatiques pour ces organismes. Notre hypothèse de recherche suppose que l'abondance et la diversité des lichens varieront le long de ce gradient latitudinal en fonction des caractéristiques abiotiques du milieu et de la composition de la communauté végétale, en fonction de l'hétérogénéité du milieu à l'échelle locale et des gradients macroclimatiques à l'échelle du gradient latitudinal.

Plus précisément, les objectifs de cette étude sont (1) d'évaluer le couvert, la richesse spécifique et la diversité fonctionnelle des macrolichens (espèces pouvant être identifiées à l'aide de structures macroscopiques) à l'échelle du gradient latitudinal et à l'échelle locale, (2) de déterminer les caractéristiques du milieu qui affectent la composition des communautés à l'échelle du gradient latitudinal et à l'échelle locale, et finalement, (3) d'évaluer l'influence de l'avancée du couvert arbustif sur l'abondance, la richesse spécifique et la diversité fonctionnelle des communautés de macrolichens.

En ce qui a trait au premier objectif, nous prévoyons que le couvert lichénique diminuera en fonction de la latitude. En effet, la végétation au sud du gradient latitudinal est caractérisée par la présence de forêts ouvertes dont le sol est recouvert d'un tapis lichénique dense (Payette et al. 2001) alors que les régions plus au nord du gradient présenteront un couvert lichénique plus éparse et moins homogène. La richesse spécifique et l'équitabilité seront plus élevées dans la portion centrale du gradient latitudinal. La toundra est abondante dans les latitudes intermédiaires et constitue un milieu hétérogène, susceptible de contenir un plus grand nombre d'espèces lichéniques. De plus, les zones au centre du gradient latitudinal devraient avoir une productivité intermédiaire par rapport aux extrémités nord et sud du gradient, ce qui devrait favoriser une plus grande richesse spécifique lichénique (Virtanen et al. 2013). Finalement, la diversité fonctionnelle des communautés lichéniques sera corrélée à la richesse spécifique et sera plus élevée à une latitude intermédiaire, en raison de l'hétérogénéité du milieu. La structure fonctionnelle des communautés sera variable à l'échelle du gradient latitudinal et à l'échelle locale et sera influencée par les caractéristiques biotiques et abiotiques spécifiques à chacun des milieux.

Pour ce qui est du deuxième objectif, les caractéristiques abiotiques et biotiques des milieux affecteront la composition des communautés lichéniques en termes d'espèces et de traits fonctionnels (Marini et al. 2011, Giordani et al. 2014, Bässler et al. 2016, Matos et al. 2017). Les caractéristiques locales du milieu, telles que l'exposition, l'indice topographique, les substrats disponibles, la quantité de matière organique au sol, le pH du sol, le couvert des autres groupes fonctionnels de végétation, etc. sont susceptibles d'affecter les espèces et les traits fonctionnels caractérisant la communauté localement. À l'échelle du gradient, les caractéristiques macroclimatiques telles que les températures moyennes annuelles, les précipitations moyennes annuelles et l'altitude affecteront la composition des communautés.

Pour le troisième objectif, nous sommes d'avis que le couvert, la richesse spécifique, et l'équitabilité des macrolichens diminueront en présence d'un couvert arbustif (Cornelissen et al. 2001, Lang et al. 2012, Alatalo et al. 2017) par rapport au milieu ouvert. Les arbustes modifieront les caractéristiques environnementales du milieu et augmenteront la compétition entre les espèces, ce qui sera délétère pour la majorité des espèces lichéniques. Généralement, les espèces lichéniques présentes à proximité ou sous un couvert arbustif devraient être mieux adaptées à un milieu plus humide et moins lumineux.

1. Patterns and determinants of lichen abundance and diversity across a latitudinal gradient in Nunavik (Québec, Canada)

1.1. Résumé

Les lichens constituent un élément clé des écosystèmes nordiques, mais apparaissent vulnérables face aux changements climatiques en raison de leurs caractéristiques physiologiques. Pour mieux comprendre l'impact des changements climatiques sur les écosystèmes nordiques, nous avons caractérisé les communautés lichéniques et leurs déterminants environnementaux sur un gradient latitudinal. Les types de végétation et la latitude profilent l'abondance et la diversité des lichens à l'échelle du gradient et mènent à une différenciation des communautés suivant les domaines bioclimatiques. La richesse spécifique est promue par la diversité des types de végétation à l'échelle du gradient et par la diversité des substrats à l'échelle locale. À travers le gradient, la végétation réduit l'abondance et la diversité, soulignant la faible compétitivité des lichens, mais affecte peu la diversité fonctionnelle. En favorisant les plantes vasculaires, les changements climatiques sont susceptibles de diminuer l'abondance et la diversité des lichens, sans toutefois compromettre leur contribution aux fonctions écosystémiques.

1.2. Abstract

Lichens constitute a major part of northern ecosystems' biodiversity and are involved in many ecological processes. However, they appear vulnerable in the present context of climate change, as they suffer from increased competition with vascular plants and may be affected by warmer temperatures. To predict future changes in northern ecosystems, a better understanding of the determinants of lichen abundance and diversity across spatial scales is needed. We characterized lichen communities across a latitudinal gradient ranging from subarctic (56°N) to arctic (62°N) Nunavik (Québec, Canada) and investigated the patterns and drivers of lichen abundance and diversity. Model selections revealed that vegetation types and latitude were the main determinants of lichen abundance and diversity, which was also supported by a differentiation of lichen communities that followed Québec's bioclimatic zones. Regional species richness was promoted by the diversity of co-occurring vegetation types, while local species richness benefited from the diversity of available substrate. Lichen cover and species richness decreased poleward, which may result from local edaphic characteristics or past disturbances. Throughout the gradient, vascular plant abundance had a negative impact on lichen cover and species richness and highlights the low competitive ability of lichens. However, we found little influence of vascular plants on functional diversity. Thereby, if the increased competition with vascular plants promoted by climate change may induce a decline in lichen cover and species richness, lichens' contribution to ecosystem functions may be only slightly affected.

1.3. Introduction

As the rate of climate warming in the Arctic is twice that observed in any other region on the planet (Arctic Climate Impact Assessment 2004), arctic vegetation is currently undergoing major changes. Since the beginning of the 1980s, a substantial increase in the normalized difference vegetation index (NDVI) is observed at the circumpolar scale and reveals increasing primary productivity (Forbes et al. 2010, McManus et al. 2012, Fraser et al. 2014, Ju and Masek 2016). In many regions, this greening trend is mainly associated with the expansion of shrubs (Ropars and Boudreau 2012, Tremblay et al. 2012, Fraser et al. 2014, Moffat et al. 2016). This restructuring of vegetation communities increases soil temperatures during winter by trapping snow and triggers permafrost degradation (Lawrence and Swenson 2011, Bonfils et al. 2012). The warmer and enriched soils are thereby likely to benefit further shrub expansion and to induce positive feedbacks on the ongoing climate warming (Sturm et al. 2000a, 2005). By increasing competition for resources, shrub expansion also impacts less competitive organisms such as lichens, which cover has declined over the last decades to the benefit of shrub species (Ropars and Boudreau 2012, Tremblay et al. 2012, Provencher-Nolet et al. 2014, Moffat et al. 2016).

Lichens constitute a major component of Arctic biodiversity, with species richness often greater than that of vascular plants (Longton 1988, Matveyava and Chernov 2000). Lichens play important roles in northern ecosystem functioning: they influence seedling establishment (Houle and Filion 2003, Asplund and Wardle 2017), contribute to pedogenesis (Chen et al. 2000), and increase nutrient availability through absorption of nutrients from the air and precipitation (Asplund and Wardle 2017). About 10% of lichen species contain nitrogen-fixing bacteria and contribute to increasing nitrogen availability (Nash 2008, Zhang et al. 2016). Moreover, lichen-dominated areas have a high albedo (Beringer et al. 2005, Bernier et al. 2011), reflecting a substantial portion of the incoming solar radiation. Therefore, lichens are also involved in global climate regulation and permafrost preservation (Jorgenson et al. 2010, Porada et al. 2016).

Resulting from a symbiosis between a fungus, usually an ascomycete (the mycobiont), and a green alga and/or a cyanobacterium (the photobionts), lichens show diverse growth forms that allow them to colonize various habitats, including extreme habitats characterized by harsh climatic conditions (Nash 2008). However, their slow growth rate, ranging from imperceptible to a few millimeters per year (Nash 2008), gives them low competitive abilities (Grime 1979). As poikilohydric organisms, lichens need a constant water supply from their environment to be metabolically active (Kappen and Valladares 2007). Once hydrated, their photosynthesis rate is a function of the temperature (Green et al. 2008), with an optimum temperature usually ranging from 5°C to 25°C for arctic lichens (Longton 1988). Moreover, net photosynthesis decline was observed for some species when exposed to higher temperatures (Kershaw and Smith 1978, Kershaw 1985), suggesting that they might be vulnerable to warming. Therefore, lichens in northern ecosystems are likely to be affected by climate change as the loss of suitable habitat for some species may arise in the coming years (Rubio-Salcedo et al. 2017).

To evaluate modifications in lichen communities associated with current and future climate change, a better understanding of the environmental factors influencing lichen abundance and diversity is needed. The association between environmental characteristics and lichens remains unclear and only a few studies have investigated lichen community responses based on data at the species level (Lang et al. 2012, Nelson et al. 2015a, 2015b, Alatalo et al. 2017). Similarly, the study and use of functional traits of lichens is still incomplete when compared to vascular plants (Martin and Mallik 2017, Roos et al. 2019). Using community species composition as well as community functional traits may reveal associations with abiotic and biotic factors that will be altered by climate change (Giordani et al. 2014, Matos et al. 2015, Nelson et al. 2015b, Koch et al. 2018, Roos et al. 2019), paving the way to enhanced projections of future lichen diversity (Rubio-Salcedo et al. 2017). Concurrently, functional diversity is well suited for evaluating the response of ecosystems to climate change as it is directly related to ecosystem functioning (Webb et al. 2010).

In this study, we characterized lichen communities focusing on functional traits at the species level across a latitudinal gradient and multiple spatial scales. Considering the ecological relevance of lichens, we aim to identify patterns and determinants of lichen abundance and diversity in order to evaluate future changes in northern ecosystems. Our study covers a latitudinal gradient across Nunavik, a vast territory located north of the 55th parallel in Québec province, Canada (Figure 1.1). Nunavik is experiencing extensive warming since the

1990s (Allard et al. 2007), a trend that is predicted to continue over the next decades as mean annual temperature for the region is expected to increase by 2.4 to 9.6°C by the end of the century (Ouranos 2015). As major shifts in vegetation are expected under such climatic scenarios (Arctic Climate Impact Assessment 2004), lichens are likely to be significantly affected. Our specific objectives were therefore 1) to evaluate macrolichen cover, species richness, functional diversity, community composition among the dominant vegetation types and across a latitudinal gradient in Nunavik and 2) to identify the environmental determinants of lichen communities at different spatial scales.

1.4. Methods

1.4.1. Latitudinal gradient

Sampling was carried-out in six regions distributed along a latitudinal gradient of *ca.* 640 km in Nunavik (Québec, Canada). From south to north, we visited Clearwater Lake (56°20'N, 74°27'W), Boniface River (57°45'N, 76°10'W), Le Roy Lake (58°29'N, 75°28'W), Payne Lake (59°32’N, 74°63'W), Chukotat River (61°18'N, 75°55'W) and Deception Bay (62°05'N, 74°16'W, Figure 1.1). The southernmost region of the gradient, Clearwater Lake, is located about 190 km south of the treeline in the discontinuous permafrost zone. The climate in this area is subarctic with a mean annual temperature of -4.5°C and mean annual precipitation of *ca*. 800 mm (1981-2010; Charron, 2015). The northernmost region, Deception Bay, is located at the northern tip of Ungava Peninsula, on the coast of the Hudson Strait. It is located in the continuous permafrost zone and is characterized by an arctic climate with a mean annual temperature of -8.5°C and mean annual precipitation of *ca*. 475 mm (1981-2010; Charron 2015).

For each of the studied regions, the most dominant vegetation types were identified according to their land surface cover, based on the Québec Northern Vegetation Map produced by the Ministère des Forêts, de la Faune et des Parcs (MFFP 2018) of the Government of Québec. Using ArcGIS (version 10.5), three sites of each of the dominant vegetation types were randomly selected in a radius of five kilometers around each region’s research station prior to fieldwork. Minimal distance between sampling sites was set to 250 meters. For each vegetation polygon of the vegetation map, a 250 m-wide buffer zone was excluded to ensure that sampling was conducted in the central section of the polygon. In order to eliminate the fact that the vegetation type nomenclature included a latitudinal effect, i.e., two similar vegetation types would have different names if present at different latitudes, we simplified the vegetation nomenclature (Table S1). During fieldwork, we observed that the distinction between prostrate tundra and herbaceous tundra in Chukotat River and Deception Bay was unclear. Thereby, we pooled those vegetation types as herbaceous tundra, as both were dominated by graminoid and forb species. In Deception Bay, patches of shrub tundra were sampled instead of prostrate tundra.

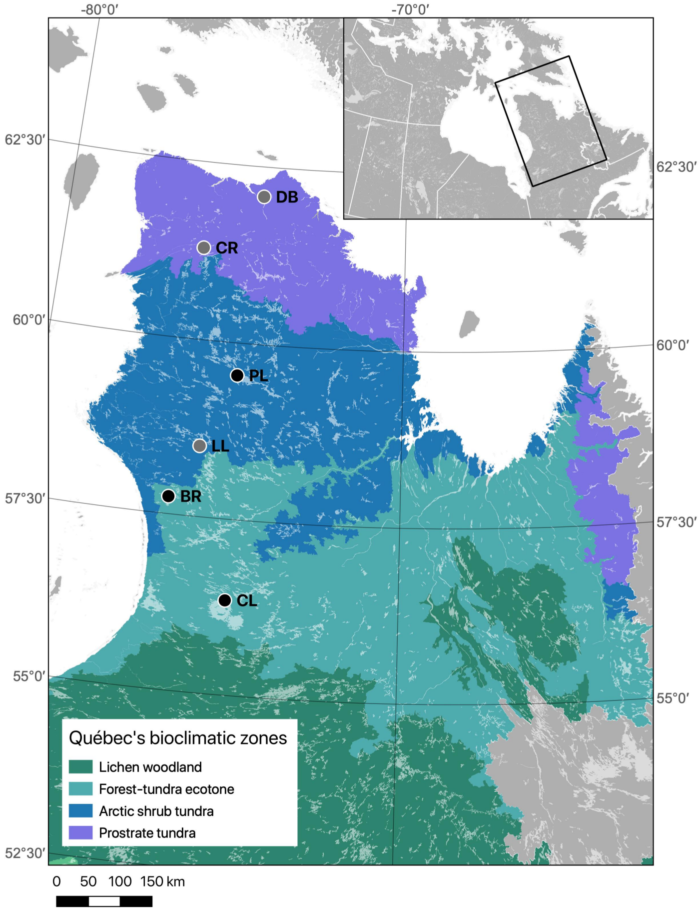

Figure 1.1. Location of the six regions sampled in August 2018 (black dots) and 2019 (grey dots) in Nunavik, Québec, Canada: Clearwater Lake (CL, 56°20’N), Boniface River (BR, 57°45'N), Le Roy Lake (LL, 58°29'N), Payne Lake (PL, 59°32'N), Chukotat River (CR, 61°18'N) and Deception Bay (DB, 62°05'N), and Québec’s bioclimatic zones (Ministère des Forêts, de la Faune et des Parcs, 2020).

1.4.2. Field sampling

For each of the sampled site, a 30 m x 40 m quadrat was positioned in a representative portion of the site. Twenty 1 m-long linear surveys were randomly positioned along parallel transects placed every two meters along the largest (40 m) side of the quadrat. Cover of terricolous and saxicolous lichens, i.e. growing on soil and rocks respectively, was recorded by species to the nearest centimeter for each 10 cm segment along every 1 m-long linear surveys. Species for which cover was < 1 cm were assigned a cover of 0.5 cm. Vegetation cover was also evaluated for each of the following vascular plant functional groups (erect shrubs (> 15 cm), prostrate shrubs (< 15 cm), graminoids, forbs and bryophytes).

For each survey, macrolichens (fruticose, foliose and squamulose lichens) were identified to the species level according to the floras of Thomson (1984), Brodo et al. (2001), Hinds and Hinds (2007) and Thell and Moberg (2011). *Cladonia arbuscula* Wallr. and *Cladonia mitis* Sandst. were both identified as *C. mitis*, since the PD (phenylethylenediamine) spot test necessary to distinguish both species was not performed during fieldwork. *Cladonia sulphurina* Michx. and *Cladonia deformis* Hoffm. were also recorded together as *C. sulphurina*, since the distinction between these two species is mainly based on the presence of squamatic acid revealed by UV light, which was not used during fieldwork. *Cladonia borealis* Stenroos and *Cladonia coccifera* Willd. were both identified as *C. borealis* because they are morphologically very similar. For the same reason, *Cladonia stygia* Ruoss and *Cladonia rangiferina* Wigg. were pooled. *Cladonia trassii* Ahti and *Cladonia stricta* Nyl. were also pooled because taxonomic distinction between the two species is still unclear. Finally, *Stereocaulon* species were only identified to the genus level due to the unclear taxonomy of the genus (Lavoie et al. 2020). Other specimens that could not be identified directly in the field were collected and brought back at the Louis-Marie Herbarium (Laval University, Québec, Canada) for further identification using dissecting microscopes and chemical spot tests. The cover of primary thallus of *Cladonia* species was measured but all specimens were recorded as *Cladonia* spp. and were therefore not included in species richness analyses. Crustose lichens cover was also measured but species were not identified, so they were only included in abundance analyses.

For each 1 m-long survey transect, we measured the height and evaluated canopy closure of erect shrubs, using the following cover classes: 0-25%, 25-50%, 50-75%, and 75-100%. Soil organic layer thickness was measured at the center of every survey transect and a total of 5 soil samples were collected systematically at every site to measure soil pH in the laboratory. Soil pH was evaluated by suspending soil material in distilled water and using a pH-meter (Eckert and Sims 1995).

1.4.3. Lichens functional traits

Three functional traits were chosen to assess lichen functional diversity: 1) photobiont: green algae, cyanobacteria, or tripartite association (green algae and cyanobacteria) 2) thallus growth form: fruticose (branched, cladoniiform, or filamentous), foliose (three-dimensional (3D), broad or appressed), squamulose or crustose and 3) asexual reproduction propagules: isidia, soredia or lobules (Table S2). The chosen traits have been widely used in the literature as they are informative on the ability of lichens to cope with environmental stresses (Giordani et al. 2014, Matos et al. 2015, Nelson et al. 2015b, Bässler et al. 2016, Prieto et al. 2017, Rubio-Salcedo et al. 2017). For example, lichens having cyanobacteria as photobiont (cyanolichens) are more sensitive to low humidity availability than lichens with green algae as photobiont (chlorolichens) (Lange et al. 1986). On the other hand, cyanobacterial photobionts may be able to cope better with low nutrient availability as they are able to fix atmospheric nitrogen (Palmqvist 2000). Lichen thallus growth form has implications for water uptake and evaporation rate (Lakatos et al. 2006, Asplund and Wardle 2014), two features that influence thallus water content and, therefore, metabolic activity (Pardow et al. 2010). Species having a higher surface/volume ratio (e.g. fruticose species) are thus likely to be more competitive while species having a lower ratio (e.g. crustose species) show higher resistance to desiccation. Lastly, reproduction strategies influence the dispersion ability of the species (Ellis 2012), propagules' competitive ability and stress tolerance (Rogers 1990). We compiled functional traits for all identified species based on floras used for identification.

1.4.4. Environmental variables

We identified the environmental variables that were likely to affect lichen cover and diversity across the different sites. For every sampled site, elevation was obtained using the Canadian

Digital Elevation Model (CDEM) with a 30-m spatial resolution. Slope, aspect, and topographic position index (TPI) were derived from the CDEM using ArcGIS. Surficial deposits were obtained from the northern Québec surficial deposit map (Ministère des Forêts, de la Faune et des Parcs, 2018). Climate variables were modelled at a 50-km spatial resolution by the Ouranos Consortium (2015) for the 1981-2000 period. We also selected relevant climate variables modelled by Ouranos (2015) for the 1981-2000 period: mean annual temperature and total annual precipitation, which are directly related to photosynthesis rates (Longton, 1988), the number of days during which a thaw-freeze event occurred, which may induce severe photobiont damage (Bjerke, 2011), the duration of the snow cover period, which affects the length of the growing season, and the maximum depth of the snow cover, which may induce greater decomposition of lichen thallus (Wahren et al. 2005, Bidussi et al. 2016).

1.4.5. Statistical analyses

Observed abundance and diversity across the gradient

To characterize macrolichen communities along the latitudinal gradient, we computed total species richness per region, Simpson's dissimilarity index, mean lichen cover at each site, and functional diversity (Rao's Q).

Simpson's dissimilarity index (β_{sim}, equation 1) was computed for pairs of adjacent regions to measure species turnover within the latitudinal gradient:

$$\beta_{sim} = \frac{\min(b,c)}{a+\min(b,c)} \quad (1)$$

where a is the number of species common at both sites, b is the number of species only observed in the first site, and c is the number of species only observed in the second site. Simpson's dissimilarity index was computed using the package "betapart" (Baselga and L. Orme 2012) in R environment (R Core Team 2013).

Rao’s quadratic entropy (equation 2, Botta-Dukát 2005) was calculated to evaluate multidimensional functional diversity among the sampled sites, using the function “dbFD” of the package “FD” (Laliberte and Legendre 2010):

$$FD_Q = \sum_{i=1}^{S-1} \sum_{j=i+1}^{S} d_{ij} p_i p_j \qquad (2)$$

where S is the number of species in a community, d_{ij} is the dissimilarity of species i and j according to their traits, p_i the abundance of the i^{th} species and p_j the abundance of the j^{th} species in the community. This functional diversity index estimates the dispersion of communities in trait space considering species abundance and is little affected by species richness (Laliberte and Legendre 2010).

We looked for latitudinal trends (either linear or quadratic) for each of the following variables using generalized linear models: species richness, cover, and functional diversity. We also compared lichen cover and species richness between regions with Tukey’s Honestly Significant Difference (HSD) posthoc test.

Determinants of abundance, species richness, and functional diversity

Model selection was used to identify environmental factors influencing lichen communities in terms of cover, species richness, and functional diversity at different spatial scales. Candidate models were chosen a priori based on ecologically relevant hypotheses (Table 1.1). All variables were checked for collinearity prior to being added into the models and all assumptions of normality and homogeneity of variances were carefully checked. Whenever model selection could not identify a unique model explaining the observed data (AIC weights < 0.90), model averaging was used to evaluate the effect of the parameters included in the best models. Models were fitted using the package “nmle” (Pinheiro et al. 2018) and model selection and model averaging were performed with AICc weights using AICcmodavg (Mazerolle 2015).

At the gradient scale, all climate variables showed collinearity ($r > 0.75$, Figure S1) and were strongly correlated to latitude, which was thereby the only variable included in the models. We performed mixed models using the sites as the sampling unit and the region as a random effect to assess the impact of vegetation type, aspect, topographic position index (TPI), surficial deposit, slope, elevation, and latitude (either as linear or quadratic, based on previous results).

At the local scale, we used the 1 m-long surveys as the sampling unit. Explanatory variables were shrub cover, graminoid cover, rock cover, soil pH, and soil organic layer thickness, which were all obtained from field sampling. Bryophyte cover was not included in the models, as bryophytes and lichens share a similar ecological niche in the vegetation structure. Indeed, ground layer vegetation is usually occupied by either lichens or bryophytes, resulting in typically negatively correlated abundances of the two groups.

Changes in community composition

To compare community composition between regions and vegetation types, non-metric multidimensional scaling (NMDS) was performed on individual site communities using the function "metaMDS" of the package "vegan" (Oksanen et al. 2018). Rare species occurring in only one site were removed prior to the analysis. A first NMDS was implemented on a site × species matrix using the Bray-Curtis dissimilarity index. To test for differences in the functional composition of the communities, community-level weighted mean (CWM) of trait values were calculated using the function "dbFD" of the "FD" package. As traits were nominal, CWMs were computed as the abundance of each class for a given trait. We performed a second NMDS on a site × CWM matrix, using again a Bray-Curtis index to visualize the functional community composition.

We also performed a variance partitioning analysis to assess the relative influence of the significant determinants identified by model selection on community composition using the function "varpart" of the package "vegan". Pairwise-PERMANOVA was performed on both species and traits NMDS to check for variability in community composition between regions using the package "pairwiseAdonis" (Martinez Arbizu 2019). P-values obtained through pairwise PERMANOVA were corrected for multiple testing using the Bonferroni correction. When differences were found, we used beta dispersion analyses to complement PERMANOVAs as it provides information on differences in beta dispersion (mean distance between the site and the polygon's centroid) while PERMANOVAs indicate a difference that can be explained by either beta dispersion or community composition (location of the polygon in multidimensional space). Beta dispersion analyses were implemented using function “betadisper” of the package “vegan” and computed on both species and trait distances to evaluate differences between regions and vegetation types.

Table 1.1. Models and variables included in the model selections for each spatial scale to determine drivers of lichen abundance, species richness and functional diversity across a latitudinal gradient in Nunavik, Québec, Canada.

Scale	Variables	Models
Gradient	- Latitude - Vegetation type - Aspect - Topographic position index (TPI) - Surficial deposit - Slope - Elevation	- Null model - Latitude* - Latitude + Vegetation type - Latitude + Aspect + TPI + Surficial deposit + Slope + Elevation - Global model
Local	- Shrub cover - Graminoid cover - Rock cover - Soil pH - Soil organic layer thickness	- Null model - Soil organic layer thickness + soil pH + rock cover - Shrub cover + graminoid cover - Global model

* We tested either latitude or latitude^2 depending on the latitudinal trend previously identified for each of cover, species richness and functional diversity.

Functional trait relationships with environmental variables and community composition

To better understand drivers of community composition, the correlation between CWMs and the species ordination was assessed using the function “envfit” of the package “vegan” and added to the NMDS plot. Environmental variables that were found to influence lichen richness, cover and functional diversity in previous models were also tested for correlation with the ordination and plotted when significant. We tested for relationships between CWMs and environmental variables significantly correlated with the ordination using linear models. Associations of CWM with regions and vegetation types were assessed using Pearson’s point biserial correlation coefficient (equation 3; De Caceres and Legendre 2009) using the function “multipatt” of the package “indicspecies” (De Cáceres 2013):

$$r_{pb} = \frac{\mathrm{N} \times a_p - a \times N_p}{\sqrt{(N \times l^2 - a^2) \times (N \times N_p - N_p^2)}} \qquad (3)$$

where N is the total number of sites, N_p the number of sites belonging to the target sites group, a is the sum of the abundance values of the species across all sites, a_p is the sum of the abundance values of the species within the target sites group and l is the norm of the vector abundances for the species. All statistical analyses were performed in R version 3.5.2 (R Core Team 2013).

1.5. Results

1.5.1. Lichen abundance and diversity across the gradient

A total of 94 macrolichen species were recorded across the gradient (Table S3). Total regional diversity varied from 38 species at Chukotat River to 59 species at Boniface River (Figure 1.2a). Mean species richness by site showed a quadratic relationship with latitude ($p = 0.005$, $R^2 = 0.29$; Figure 1.2a) and peaked at intermediate latitudes (~ 59°N). Mean richness was lower in Chukotat River (CR) compared to Le Roy Lake (LL; $p = 0.022$) and Payne Lake (PL; $p = 0.008$) and in Deception Bay (DB) compared to Le Roy Lake ($p = 0.022$). Species turnover was the lowest between Clearwater Lake (CL) and Boniface River (BR; $\beta_{sim} = 0.11$) and the greatest between Payne Lake and Chukotat River ($\beta_{sim} = 0.42$, Figure 1.2b). Lichen cover per site (mean ± SE) was found to be the lowest at Deception Bay (7.75 ± 1.57%) and the highest at Boniface River (35.33 ± 7.45%, Figure 1.2c). Cover decreased with increasing latitude ($p < 0.001$, $R^2 = 0.34$; Figure 1.2c) and was lower in Chukotat River compared to Clearwater Lake ($p = 0.028$) and Boniface River ($p = 0.022$) and in Deception Bay compared to Clearwater Lake ($p = 0.020$) and Boniface River ($p = 0.016$). Functional diversity (Rao's Q) increased with latitude ($p < 0.001$, $R^2 = 0.35$, Figure 1.2d) and ranged from 0.08 at Clearwater Lake to 0.18 at Deception Bay (Figure 1.2d).

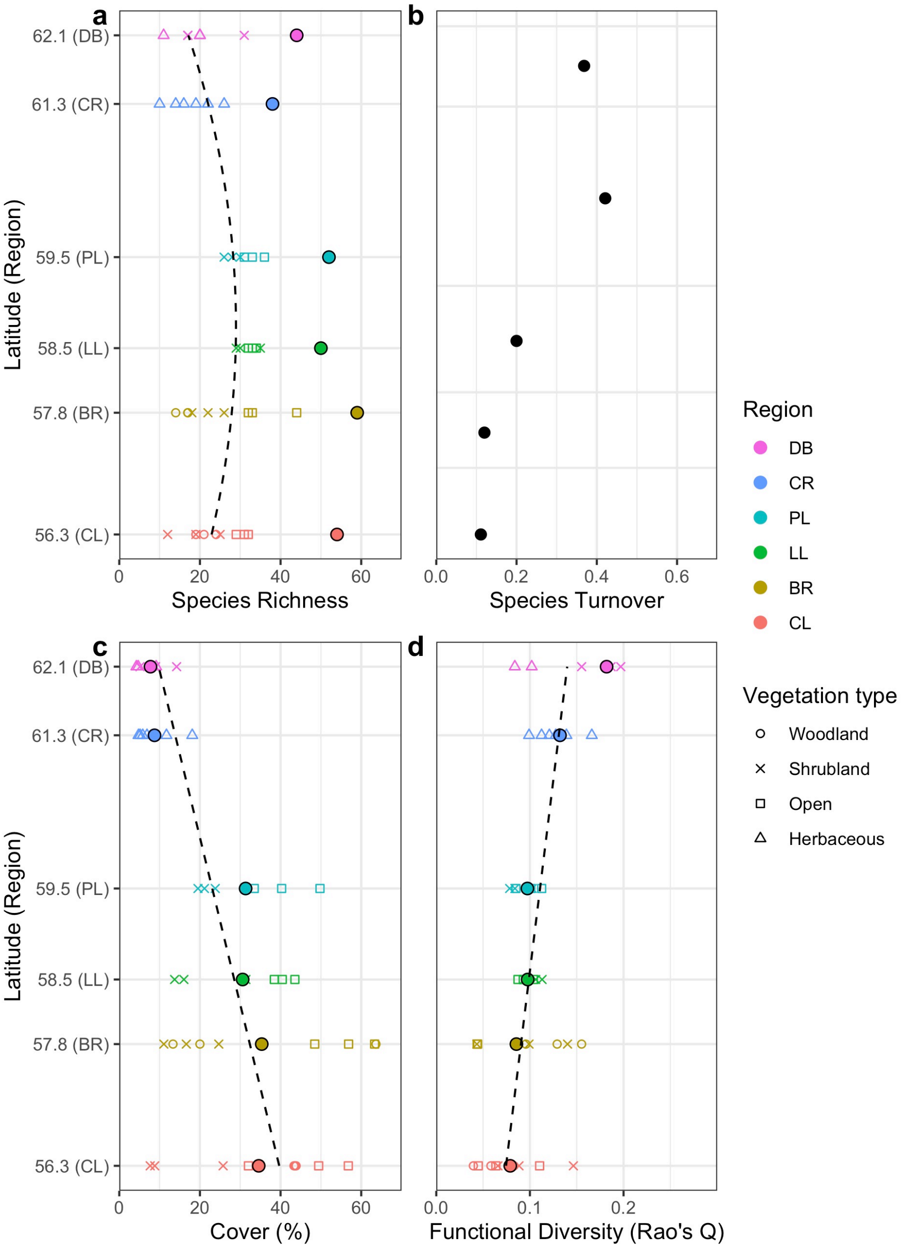

Figure 1.2. a) Lichen species richness, b) species turnover between adjacent regions (Simpson dissimilarity index), c) lichen cover as the percentage of the surveyed ground covered by lichens, and d) functional diversity (Rao's Q) across the latitudinal gradient. Large colored dots with a black outline represent the regional total species richness on panel a, the mean regional lichen cover on panel c, and the regional functional diversity on panel d. Small colored symbols represent the 42 sampled sites. Dashed lines represent significant latitudinal trends. Lichens were surveyed in the dominant vegetation types along a latitudinal gradient, from south to north: Clearwater Lake (CL, 56°20'N), Boniface River (BR, 57°45'N), Le Roy Lake (LL, 58°29'N) Payne Lake (PL, 59°32'N), Chukotat River (CR, 61°18'N) and Deception Bay (DB, 62°05'N).

1.5.2. Determinants of abundance, species richness, and functional diversity

At the gradient scale, i.e. considering the 42 sites as the sampling units, global models were the most plausible ones for cover and species richness with AIC weights of 1.00 (Table 1.2). Lichen species richness was affected by vegetation type ($p < 0.001$, Figure 1.3), surficial deposit ($p < 0.001$), latitude ($p = 0.011$), and elevation ($p = 0.013$). Species richness in shrublands was lower than that of open vegetation ($p < 0.001$) and higher than that of herbaceous tundra ($p = 0.019$). Shrublands and woodlands showed no difference in terms of species richness. Glacial and fluvioglacial surficial deposits were associated with a higher species richness compared to marine deposits ($p < 0.001$) and rocky substrates ($p = 0.006$). Species richness showed a negative quadratic association with latitude and was negatively associated with elevation. TPI, aspect and slope had no effect on lichen species richness. Lichen cover was affected by vegetation type ($p < 0.001$, Figure 1.3), latitude ($p = 0.016$), and marginally affected by surficial deposit ($p < 0.079$). Lichen cover was lower in shrubland and herbaceous tundra, compared to woodlands and open vegetation ($p < 0.001$). Elevation, TPI, and aspect showed no effect on lichen cover. Functional diversity was only positively associated with latitude ($p < 0.001$, Figure 1.3) as revealed by model averaging. Model selection revealed that the model including only the latitude was the most plausible one according to our model selection ($AICw = 0.77$), followed by the model including both latitude and vegetation type ($AICw = 0.22$), the latter having no effect on functional diversity. No other considered variables impacted functional diversity at the gradient scale.

At the local scale, *i.e.* within a site and when considering the 1-m survey transects as the sampling unit, model selection indicated that the global models were the most plausible ones for cover and species richness ($AICw = 1.00$ for both variables). Species richness was negatively influenced by shrub ($p < 0.001$) and graminoid ($p < 0.001$) covers and by soil pH ($p = 0.003$). Species richness also decreased with increasing organic layer thickness ($p = 0.048$) but was not affected by rock cover. On the other hand, lichen cover was positively affected by rock cover ($p < 0.001$) and negatively affected by shrub ($p < 0.001$) and graminoid ($p = 0.002$) covers as well as by soil pH ($p = 0.003$). Organic layer thickness had no effect. Functional diversity was best explained by the model including only graminoid and shrub cover, with an AIC weight of 0.93. Functional diversity was negatively associated with shrub cover ($p = 0.005$), while graminoid cover had no effect.

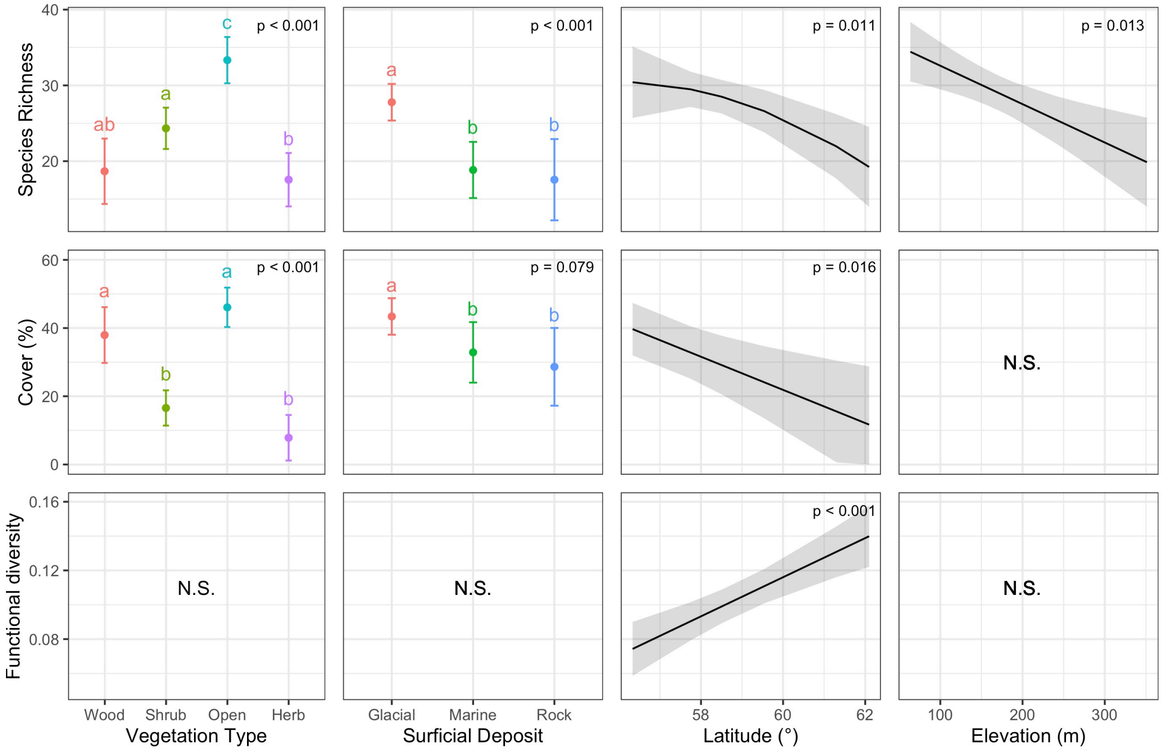

Figure 1.3. Lichen species richness (top row), lichen cover as the percentage of the surveyed ground covered by lichens (middle row), and functional diversity (Rao's Q; bottom row) ± 95% CI, as a function of the dominant vegetation types (first column), the surficial deposits (second column), the latitude (third column) and the elevation (fourth column) in Nunavik, Québec, Canada. Forty-two (42) sites were sampled in 6 regions along a latitudinal gradient: Clearwater Lake (CL, 56°20'N), Boniface River (BR, 57°45'N), Le Roy Lake (LR, 58°29'N) Payne Lake (PL, 59°32'N), Chukotat River (CR, 61°18'N) and Deception Bay (DB, 62°05'N). N.S. panels reflect non-significant relationships.

Table 1.2. AIC model selection to determine drivers of lichen abundance, species richness and functional diversity across a latitudinal gradient in Nunavik, Québec, Canada. The first column indicates the spatial scale at which the models were performed. When global, models were performed on the 42 sites distributed along a latitudinal gradient and using a random effect for the regions. When local, models were performed on the 20 1-m-surveys carried in every site, using a nested random effect for Region/Site. The R^2 represent the variance explained by the fixed effects.

Scale	Models	AIC	Δ AIC	AIC Wt	R^2
Gradient	**Species Richness**				
	Global model	235.74	0.00	1.00	0.86
	$Latitude^2$ + Aspect + TPI + Surficial deposit + Slope + Elevation	256.32	20.58	0.00	0.62
	$Latitude^2$ + Vegetation type	269.39	33.65	0.00	0.65
	$Latitude^2$	291.28	55.54	0.00	0.27
	Null model	293.68	57.94	0.00	0.00
	Cover				
	Global model	511.08	0.00	1.00	0.84
	Latitude + Aspect + TPI + Surficial deposit + Slope + Elevation	530.10	19.01	0.00	0.62
	Latitude + Vegetation type	574.49	63.40	0.00	0.75
	Latitude	605.90	94.82	0.00	0.34
	Null model	613.93	102.84	0.00	0.00
	Functional diversity				
	Latitude	-161.86	0.00	0.77	0.35
	Latitude + Vegetation type	-159.35	2.52	0.22	0.43
	Null model	-152.61	9.25	0.01	0.00
	Latitude + Aspect + TPI + Surficial deposit + Slope + Elevation	-126.86	35.00	0.00	0.50
	Global model	-122.92	38.94	0.00	0.57
Local	**Species Richness**				
	Global model	1037.29	0.00	1.00	0.38
	Shrub cover + graminoid cover	1066.46	29.17	0.00	0.28
	Soil organic layer thickness + soil pH + rock cover	1087.90	50.61	0.00	0.08
	Null Model	1119.86	82.57	0.00	0.00
	Cover				
	Global model	1672.47	0.00	1.00	0.42
	Soil organic layer thickness + soil pH + rock cover	1695.75	23.27	0.00	0.25
	Shrub cover + graminoid cover	1780.97	108.50	0.00	0.13
	Null Model	1804.50	132.03	0.00	0.00
	Functional Diversity				
	Shrub cover + graminoid cover	-660.25	0.00	0.93	0.06
	Null Model	-654.91	5.33	0.07	0.00
	Global model	-641.06	19.18	0.00	0.10
	Soil organic layer thickness + soil pH + rock cover	-637.15	23.10	0.00	0.05

1.5.3. Community composition

Among the previously identified environmental determinants at the gradient scale, the vegetation types explained the greatest part of the variance in community composition (Figure 1.4, $R^2 = 0.34$), followed by latitude ($R^2 = 0.20$), surficial deposits ($R^2 = 0.07$) and elevation ($R^2 = 0.04$). Overall, environmental factors explained 51% of the observed variance in lichen community composition.

The ordination mapping of lichen communities also presents distinct clusters associated with regions. For both species composition and functional composition, a first cluster included the lichen communities from the two southernmost regions, Clearwater Lake and Boniface River, while a second one included communities from Le Roy and Payne Lakes, which are at the middle of the gradient (Figure 1.4a, b). These two clusters are supported by pairwise PERMANOVA analyses (Figure 1.4a, b; Table S5). Moreover, the spatial proximity of the sites belonging to the second cluster (LL and PL) reflects the lower beta dispersion observed for this region. Communities from Chukotat River and Deception Bay appear as two distinct clusters based on the pairwise PERMANOVA analysis considering species composition (Figure 1.4a, Table S5), but do not differ when considering functional composition (Figure 1.4b, Table S5). These communities are more scattered in the multidimensional space, which reflects their greater beta dispersion and functional diversity.

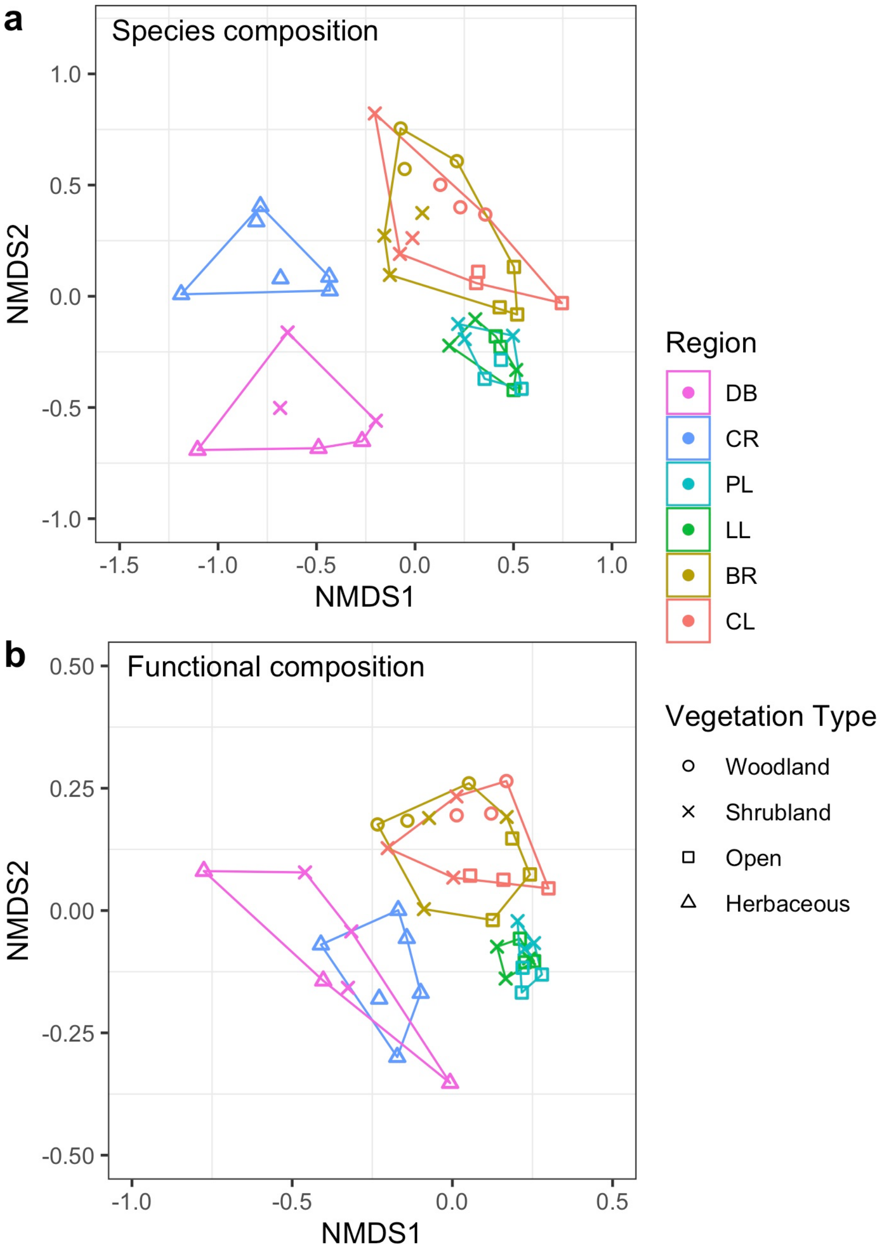

Figure 1.4. Ordination plot showing a two-dimensional non-metric multidimensional scaling (NMDS) analysis for a) species composition (stress = 0.176) and b) functional composition using traits community weighted-means (stress = 0.104). Both NMDS were computed using adjusted Bray-Curtis indices. Sampling was done in 42 sites in the dominant vegetation types (represented by the different symbols) in six regions (polygons) along a latitudinal gradient in Nunavik, Québec, Canada, from south to north: Clearwater Lake (CL, 56°20’N), Boniface River (BR, 57°45'N), Le Roy Lake (LL, 58°29'N) Payne Lake (PL, 59°32'N), Chukotat River (CR, 61°18'N) and Deception Bay (DB, 62°05'N).

1.5.4. Functional trait relationships with environmental variables and community composition

Functional traits showed significant correlations with community composition. Functional traits showed associations with the three clusters identified in an earlier analysis, as indicated by point biserial correlation coefficients (Figure 1.5, Table S4). Branched fruticose lichens were associated to the Clearwater Lake and Boniface River regions. Fruticose filamentous, appressed foliose and crustose growth forms were associated to Le Roy and Payne Lakes, as well as lichens with isidias as asexual propagules. Cladoniiform lichens were associated with Chukotat River and Deception Bay. However, 3D foliose lichens were associated only with Chukotat River while cyanolichens, tripartite, and broad foliose lichens were associated with Deception Bay.

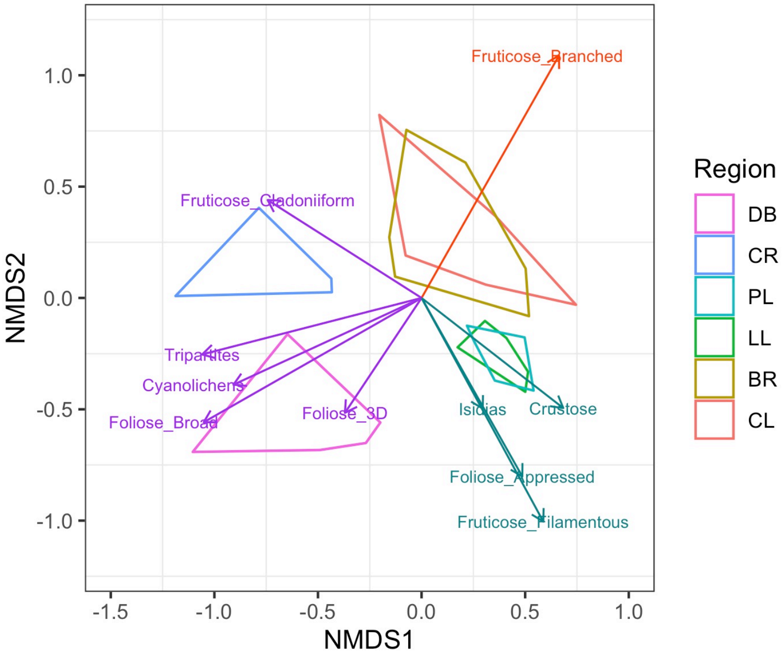

Figure 1.5. Functional traits correlated to ordination (NMDS) of lichen community composition. Color of the vectors represent their association with the sampled regions: the orange vector was associated with Clearwater Lake (CL) and Boniface River (BR), turquoise vectors were associated with Le Roy Lake (LL) and Payne Lake (PL), and purple vectors were associated with Chukotat River (CR) and/or Deception Bay (BD).

1.6. Discussion

1.6.1. Pattern and determinants of lichen communities

By characterizing lichen communities across a latitudinal gradient in Nunavik, we found that lichen cover, diversity and community composition were influenced by multiple factors acting across different spatial scales. Vegetation types and latitude were found to have the greatest influence on lichen communities among the tested variables whereas topography, surficial deposits, and soil conditions appeared to have lesser importance. Therefore, competitive interactions with vascular plants that differ between vegetation types and regional climate appear as the most important drivers of this complex dynamic.

Throughout the gradient and on a multi-scale basis, vegetation had a significant impact on lichen cover and diversity. At the gradient scale, vegetation communities dominated by woody, *i.e.* woodland and shrubland, or herb species (herbaceous tundra) had lower lichen species richness and cover than open environments. At the local scale, we found that both lichen cover and species richness were negatively associated with shrub and graminoid cover, corroborating the results of a previous study (Chagnon and Boudreau 2019). This negative response of lichen species to vascular plant cover reflects their low competitive ability. Indeed, lichens are vulnerable to the increased competition for light induced by vascular plant cover and litter production (Chapin et al. 1995, Cornelissen et al. 2001, Joly et al. 2009, Pajunen et al. 2011, Lang et al. 2012). Vascular plants are also likely to increase nutrient availability (Sturm et al. 2005), a phenomenon that may affect lichens that perform better in less competitive, nutrient-poor habitats. An increased snow cover depth under shrubs (Sturm et al. 2000b, Paradis et al. 2016) may also negatively impact lichens by increasing chlorophyll degradation and thallus decomposition (Bidussi et al. 2016).

Our results also report a differentiation of lichen communities that follows Québec's bioclimatic zones (Ministère des Forêts de la Faune et des Parcs 2020). As climate and vegetation types are used to define bioclimatic zones, this result supports the importance of latitude and vegetation types in profiling lichen communities. Indeed, we identified, from south to north, three groups of lichen communities associated respectively with the forest-tundra (CL and BR), the erect shrub tundra (LL and PL), and the prostrate tundra zones (CR and DB). We found that the co-occurrence of highly distinct vegetation types in the forest-tundra zone (Clearwater Lake and Boniface River) supported the highest regional species richness. On the other hand, site species richness appeared to be related to the diversity of available substratum, as suggested by previous studies (Holt 2007, Nelson et al. 2015b). Indeed, extensive rock cover in the erect shrub tundra zone (Le Roy and Payne Lakes) likely promoted the presence of saxicolous taxa and increased the local (i.e. site) species richness. Further north, an important decline of lichen cover was observed in the prostrate tundra zone (Chukotat River and Deception Bay). This region was also characterized by its distinct community composition, lower species richness and higher functional diversity when compared to the other two zones.

Across the latitudinal gradient, our results reveal a decline in lichen abundance and diversity towards northern latitudes, a result that contrasts with previous studies in the Canadian High Arctic that have shown an increase in lichen abundance and diversity with latitude (Vonlanthen et al. 2008, Epstein et al. 2008). Lichens thrive in harsher climatic conditions because they experience less competition with vascular plants in those environments (Grime 1977, Vonlanthen et al. 2008). Nevertheless, extreme conditions can also be detrimental for lichens (Nelson et al. 2015a), which depend on temperature and water availability for photosynthesis (Longton 1988). Evidence of temperature-limited growth was found for lichens in cold environments (Longton 1988) and is in line with the decline of lichen richness towards polar deserts (Matveyava and Chernov 2000). Thereby, lichen abundance and diversity are likely to peak at an intermediate latitude in northern ecosystems, as lichens are limited by competition with vascular plants in the south and by extreme conditions in the north. As the climate is still relatively mild in the northern portion of our latitudinal gradient, it should not limit lichen growth, suggesting that other factors are likely responsible for the observed lichen decline. However, the non-inclusion of crustose lichens in our richness analysis certainly contributes to the decreasing species richness poleward.

The low abundance and diversity of lichens observed in the northernmost regions are likely to arise from site-specific factors, a result similar to the one found along a latitudinal gradient in Eurasia, where differences in lichen communities were attributed to local soil material and disturbances (Virtanen et al. 2006). In this study, the soils of the northernmost sites were less acidic and may indicate greater nutrient availability (Gough et al. 2000) likely to impact lichens through increased competition (Gould and Walker 1999, Roland et al. 2017). Moreover, both Chukotat River and Deception Bay are located within the summer calving grounds of the Leaf River caribou herd. As lichens are very sensitive to heavy trampling during the summer (Oksanen 1978, Joly et al. 2009), the high densities of caribou observed at the beginning of the 2000s (Taillon et al. 2016) could have had severe impacts on lichen communities. Because of their slow growth, lichen recovery from caribou disturbances is a slow process (Haapasaari 1988) and can take up to 50 years (Moser et al. 1979). Lastly, coastal influence in Deception Bay could also be involved in shaping lichen communities, as revealed by the high occurrence of cyanolichens that are restricted to wetter habitats (Lange et al. 1986). Wetter conditions may also promote the abundance of vascular plants and increase competition that may affect lichen communities. Other factors such as microtopography (Holt 2007, Giordani et al. 2014), soil texture (Holt 2007) and soil moisture (Roland et al. 2017) may also influence lichen communities but were not included in this study.

A contrasting pattern of functional diversity and species richness was also found across the gradient, as functional diversity peaked at high latitudes, while species richness decreased. This pattern contrasts with the habitat filtering theory, which states that stressful environments should promote lesser functional diversity (Cornwell et al. 2006). Functional diversity is thereby expected to decrease along a latitudinal or an elevational gradient, as it was observed in Germany (Bässler et al. 2016). We believe that the apparent increase in functional diversity towards northern latitudes is mainly due to the loss of dominance of certain traits along the gradient, rather than to diversification of functional traits. Indeed, the dominance of branched fruticose lichens in the lichen woodlands (Payette and Delwaide 2018) likely decreased the functional diversity south of the treeline.

1.6.2. Implications for ecosystems

As our results suggest that competition with vascular plants is one of the most important drivers of lichen communities, important changes are to be expected with ongoing climate change. Indeed, vascular plant abundance increases rapidly in northern ecosystems (Lang et al. 2012, McManus et al. 2012, Ropars and Boudreau 2012, Moffat et al. 2016, Alatalo et al.

2017) in response to warmer temperatures and longer growing seasons. Considering future climate change scenarios, some models predict that shrub cover may increase upwards by 50 to 70% in northern ecosystems (Pearson et al. 2013, Lemay et al. 2018). Our findings corroborate the results of previous studies by supporting a decline in lichen cover and species richness associated with arctic greening (Cornelissen et al. 2001, Elmendorf et al. 2012, Lang et al. 2012, Moffat et al. 2016) and suggest that an important restructuration of lichen communities is probably underway.

Replacement of lichens by vascular plants could have major impacts on climate regulation. The transition from a light-colored lichen cover to a darker cover of shrubs or other vascular plants would decrease the Earth's surface albedo and increase the absorption of solar radiation, which would induce positive feedback on atmospheric warming (Bernier et al. 2011, Pearson et al. 2013). Such a phenomenon was observed along a latitudinal gradient in Alaska, where a decline of lichen cover and an increase in canopy complexity resulted in a significant reduction of land surface albedo (Beringer et al. 2005). Warmer soil temperatures resulting from greater absorption of solar radiation may promote shrub expansion and lead to feedbacks likely to amplify high latitude warming (Chapin et al. 2005, Myers-Smith et al. 2011).

Contrasting with the reduced lichen cover and species richness in vegetation types dominated by vascular plants, we found no effect of vegetation type on functional diversity. Functional diversity was only reduced locally under shrub cover and did not translate into lower functional diversity in shrublands, probably because of the presence of open patches in between shrubs. With further climate warming, expected shifts in vegetation types and shrub expansion may thereby not alter lichen functional diversity at the global scale. Thus, the lichens' contribution to ecosystem functioning may be resilient to further changes in northern vegetation, even if a decline in species richness may be associated with shrub expansion.

1.7. Conclusion

By surveying lichen communities across a ~ 640-km latitudinal gradient in Nunavik, we identified competition with vascular plants and regional climate as the main determinants of lichen communities in Nunavik. Our results revealed that the diversity of vegetation types and available substrates promoted greater species richness at the regional and local scales, respectively. The observed lichen cover decline with latitude could be induced by regional edaphic characteristics or past disturbances, which were not quantified in this study. With further climate warming promoting an increase in the abundance of vascular plants in the Arctic and considering the negative impact of vascular plants on lichens, our results suggest that lichen communities are undergoing a major restructuring. However, we found little influence of vascular plants on functional diversity, suggesting that the loss of species richness may not translate into a loss of ecosystem functions.

1.8. Acknowledgment

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2. Shrub canopy induces a decline in lichen abundance and diversity in Nunavik (Québec, Canada)

2.1. Résumé

L’augmentation généralisée de l'abondance des espèces arbustives en milieu nordique engendre une diminution de l’abondance des lichens, qui sont impliqués dans plusieurs rôles écologiques. À l’aide de relevés en milieu ouvert, à la marge et sous la canopée de 65 arbustes, nous avons évalué l’impact de l’avancée des arbustes sur les lichens. Nous avons observé une diminution de l’abondance, de la richesse spécifique et de l’équitabilité des communautés lichéniques sous couvert arbustif. Les arbustes simplifient également la communauté lichénique en retenant les espèces tolérantes à un plus grand éventail de conditions. La réduction de la richesse spécifique et de l’équitabilité est plus grande au centre qu’à la marge de l’arbuste, ce qui laisse présager que l'effet de la présence des arbustes sur la diversité augmente avec le temps. Nos résultats suggèrent donc qu’une restructuration des communautés lichéniques est en cours et est appelée à s’accentuer avec l’avancée des espèces arbustives.

2.2. Abstract

Lichens are an important component of biodiversity in northern ecosystems and are involved in diverse ecological processes. They contribute to nutrient availability through nitrogen fixation, are a substantial part of caribou winter diet and influence global climate by increasing land surface albedo. Over the last decades, increased primary productivity in northern ecosystems, mainly associated with the expansion of shrub species, has led to a decline of lichen-dominated areas. We evaluated the impacts of shrubs on lichens by comparing lichen communities in the open environment and underneath dwarf birch (*Betula glandulosa*) canopy in Nunavik, Canada. Our results showed a decrease in abundance, richness and evenness, and a shift in community composition between open areas and understory. These changes were mainly induced by the presence of a shrub canopy rather than by its characteristics, as shrub height and canopy closure had little effect. Richness and evenness dropped from shrub edge to shrub center, suggesting that that the intensity of the decline was positively correlated to the time spent under the shrub canopy. Important changes in lichen communities are therefore expected to occur with further shrub expansion and may have substantial unfavorable implications for global climate and ecosystem functioning.

2.3. Introduction

Lichen-dominated areas are restricted to high latitude regions and cover ca. 8% of Earth's land surface (Nash 2008). Lichens are a major component of these regions' biodiversity, as their species richness is often greater than that of vascular plants (Longton 1988). Lichens also play critical roles in arctic and subarctic ecosystem functioning. They contribute to nutrient availability by absorbing nutrients directly from the air and precipitation (Asplund and Wardle 2017). Nearly 10% of lichen species engage in symbiotic association with nitrogen-fixing bacteria, playing a role in the nitrogen budget by leaking ammonium into the ecosystem (Darnajoux et al. 2014, Zhang et al. 2016). By weathering mineral substrate, lichens release nutrients from superficial rocks and contribute to pedogenesis, which favors the establishment of vascular plants and induce primary succession (Chen et al. 2000). Lichens are also important for caribou as they constitute as much as 50% of their winter diet (Heggberget et al. 2002, Ophof et al. 2013). Moreover, areas dominated by pale-colored lichen have a high land surface albedo (Beringer et al. 2005, Bernier et al. 2011), thereby reflecting a substantial portion of solar radiation, which has implications for global climate regulation.

A decrease of lichen abundance triggered by climate warming has been reported by long-term experimental studies. Conversely, there is an increase in the biomass of vascular species, suggesting that climate warming has an indirect effect on lichens via increased competition (Cornelissen et al. 2001, Elmendorf et al. 2012, Lang et al. 2012, Edwards and Henry 2016, Moffat et al. 2016). In both North America and Europe, experimental warming studies have also reported a decline of lichen species richness and evenness (Lang et al. 2012, Alatalo et al. 2017). Decline in lichen species richness was observed over a long-term monitoring study (45-60 years) in Northern Europe, in regions experimenting an increase of the abundance of evergreen shrubs (Maliniemi et al. 2018). A negative relationship was found between shrub abundance and lichen species richness, suggesting that competition for light eradicates lichen species from understory vegetation (Pajunen et al. 2011). Indeed, lichen growth and survival depend on photosynthesis products provided by their photobiont, either a green alga, a cyanobacterium or both, to the fungus, and thus rely on light availability.

Since the early 1980s, satellite imagery analyses have shown a major increase in Normalized Difference Vegetation Index (NDVI), which indicates a generalized increase in primary productivity at the circumpolar scale; in Siberia (Forbes et al. 2010), Nunavik (McManus et al. 2012), Yukon (Fraser et al. 2014) and Canada and Alaska (Ju and Masek 2016). Aerial photography analyses and field surveys have linked this greening to the expansion of shrub species (Ropars and Boudreau 2012, Tremblay et al. 2012, Fraser et al. 2014, Moffat et al. 2016). Shrubs gain in abundance as they benefit from warmer temperatures, a longer growth-season and increased precipitation (Myers-Smith et al. 2011, Elmendorf et al. 2012). Concurrently, aerial photography has revealed an important decline of lichen-dominated areas at high latitudes (Tremblay et al. 2012, Fraser et al. 2014, Moffat et al. 2016). In North America, Nunavik (northern Québec, Canada) has experienced one of the highest increases in NVDI since 1984 (Ju and Masek 2016). For example, near Umiujaq, Provencher-Nolet et al. (2014) observed a decrease of 42.8 ha of lichen-dominated areas, of which 97% was replaced by shrub-dominated vegetation.

Considering the prime ecological importance of lichens and their overall decline induced by shrub expansion in northern ecosystems, the aim of this study is to assess the impact of the shrub canopy on lichen communities in Nunavik over a latitudinal gradient. We compare abundance, species richness, evenness and composition of lichen communities under shrub canopy and in open areas. We also evaluated the effect of shrub height, canopy closure and time spent under shrub canopy by surveying lichens at the shrub center and at the shrub edge. We hypothesize that lichen abundance and diversity will be negatively affected by the shrub canopy and that this effect will increase over time. We also expect that changes in community composition will be detected between shrub understory and open areas.

2.4. Methods

2.4.1. Study sites

In August 2018, we visited three regions along a latitudinal gradient in Nunavik (Québec, Canada, Figure 2.1); from South to North: Clearwater Lake (56°20'N - 74°27'W), Boniface River (57°45'N - 76°10'W), and Payne Lake (59°55'N - 74°63'W). Clearwater Lake is located 125 km east of Hudson Bay and about 190 km south of treeline, in the discontinuous permafrost zone. Mean annual temperature is -3.0 °C and mean annual precipitation amounts to ca. 550 mm (Centre d'études nordiques, 2019). Boniface River is located 35 km east of Hudson Bay and 10 km south of treeline, in the discontinuous permafrost zone. Mean annual temperature is -4.0°C and mean annual precipitation averages ca. 500 mm (Centre d'études nordiques, 2019). Vegetation at Clearwater Lake and Boniface river is mainly lichen woodland, shrubland and subarctic heath. Lichen woodland refers to forests with a tree cover ranging from 10 to 40% (usually dominated by black spruce *Picea mariana* Miller in Nunavik) and with a lichen cover > 40%. Shrublands are characterized by an erect (0.3 – 2 m high) deciduous shrub cover >70% often dominated by dwarf birch *Betula glandulosa* Michx in Nunavik. Subarctic heaths are characterized by a deciduous shrub cover < 30% and are usually dominated by lichens, mosses and ericaceous species. The northernmost region, Payne Lake, is located about 180 km east of Hudson Bay and about 200 km north of treeline, in the continuous permafrost zone, on the Ungava Peninsula plateau. The area is characterized by an arctic climate; with a mean annual temperature of -7.5°C (precipitation data not available, Centre d'études nordiques, 2019). Vegetation in this area is devoid of trees and is dominated by lichens, mosses and herbaceous plants with an erect or prostrate shrub cover < 30% in the tundra or ranging between 30 and 70% in the shrub tundra.

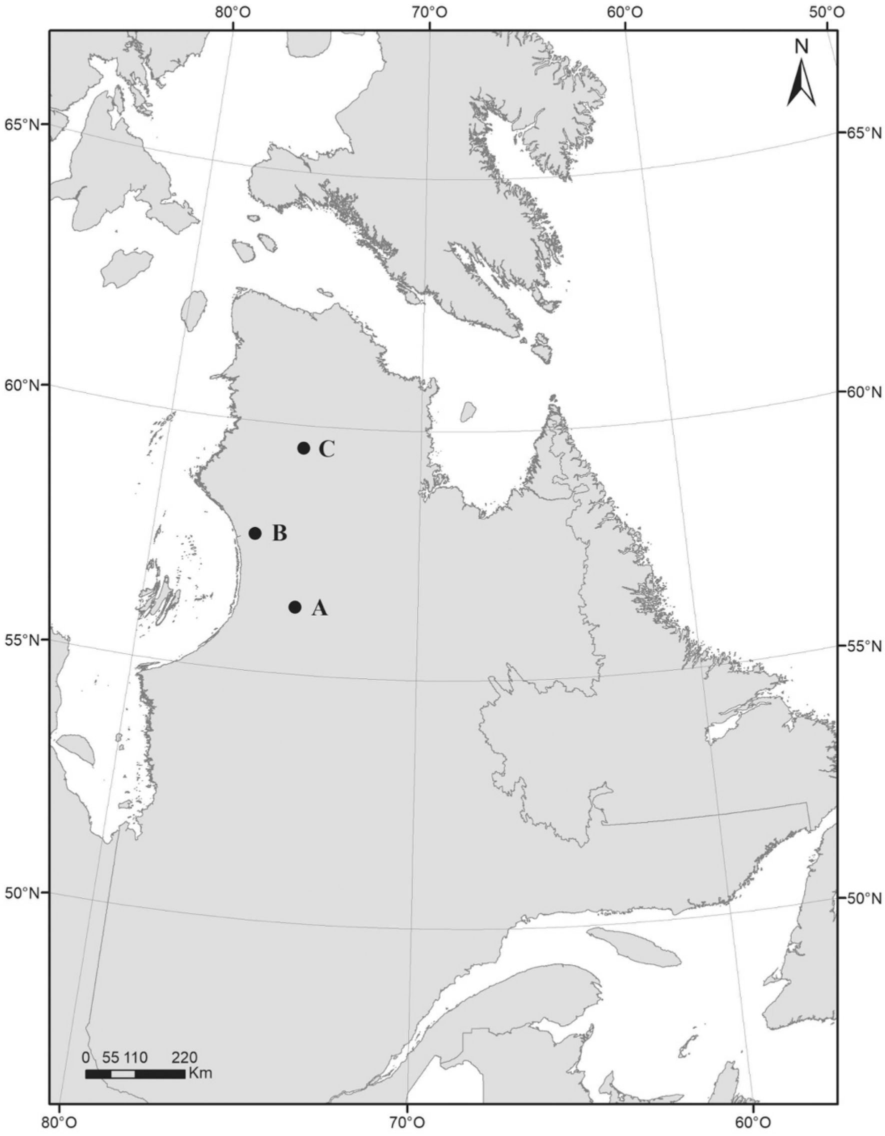

Figure 2.1. Location of the three regions sampled in August 2018: A) Clearwater Lake, B) Boniface River and C) Payne Lake in Nunavik, Québec, Canada.

For each of the study regions, the dominant vegetation types were identified according to their land surface cover, based on the Quebec Northern Vegetation Map produced by the Ministère des Forêts, de la Faune et des Parcs (MFFP 2018) of the Government of Québec. For each of the selected vegetation types, three sites were randomly selected in a radius of five kilometers around the research stations using ArcGIS (version 10.5). While three sites per vegetation type (lichen woodland, shrubland and subarctic heath) were sampled at the

Clearwater Lake station, only one site per vegetation type was sampled at the Boniface River station (due to logistical problems encountered because of wild animals). At the Payne Lake station, we sampled three sites each in tundra and shrub tundra, which were the two dominant vegetation types. Overall, a total of 18 sites were studied along the gradient.

2.4.2. Data collection

For each site, we selected five individuals of *B. glandulosa*, the species mainly associated with shrub expansion in Nunavik (Ropars and Boudreau 2012, Tremblay et al. 2012, Ropars et al. 2015b). Sampled individuals were isolated from other shrubs and trees, had a diameter > 2 m and a canopy closure as homogeneous as possible. Sampled individuals were located at least 10 meters apart from each other. As an uneven shrub edge would have resulted in heterogenous light availability at the ground level, we selected the more homogeneous shrub edge to determine the survey's orientation. Lichens were identified on three 40 cm long linear surveys: in the central portion of the shrub, at the shrub's inner edge and in the open area, all of which were separated by 40 cm (Figure 2.2). Using a measuring tape placed on the ground, we first positioned the shrub edge survey at the shrub margin. To do so, we placed the tape at the shrub margin and deployed it towards the center of the shrub. Once this survey was set-up, the tape was deployed towards both the shrub center and the open area to determine the location of the two other surveys (shrub center and open area). Because sampled shrubs were > 2 m in diameter, the shrub center survey was always located in the central portion of the shrub (and not at the opposite margin, past the center). Average height of shrub individuals was measured, and canopy closure was visually evaluated using four classes; 0-25% closure, 25-50%, 50-75% and 75-100%. We also recorded survey orientation, taking the azimuth from the shrub center to the open area survey using a compass.

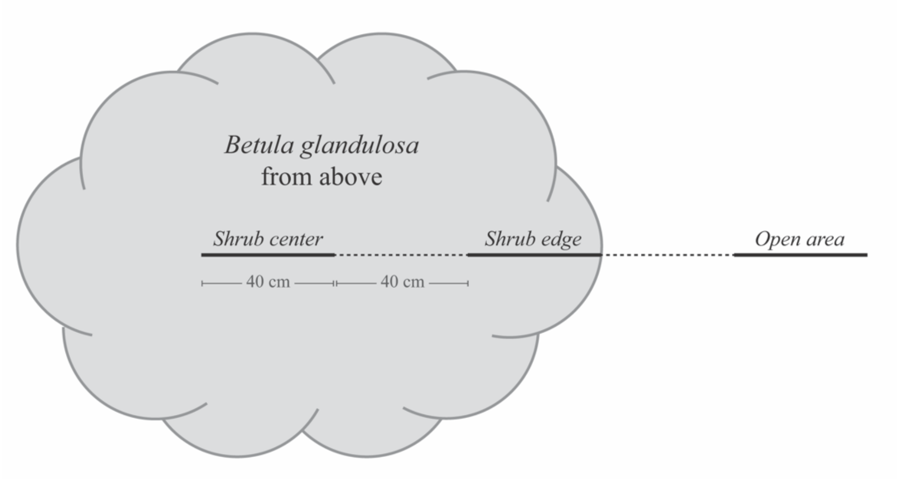

Figure 2.2. Position of the three linear surveys conducted near and underneath each of the 75 *Betula glandulosa* individuals sampled in Nunavik, Québec, Canada. Sampling was carried-out on 40 cm-long linear surveys and separated from the other surveys by 40 cm. The end of the inner edge survey was aligned with the shrub edge so that is was completely under the shrub canopy.

For each of the surveys, macrolichens (fruticose, foliose and squamulose lichens) were identified to the species level using the floras of Thomson (1984), Hinds and Hinds (2007) and Brodo et al. (2016). Species nomenclature followed Brodo et al. (2016). Species cover was measured as the number of centimeters it covered in a one-centimeter-wide area along the measuring tape and recorded to the nearest centimeter. Species for which cover was < 1 cm were assigned a cover of 0.5 cm. *Cladonia arbuscula* Wallr. and *Cladonia mitis* Sandst. were both identified as *C. mitis*, since PD (phenylethylenediamine) spot test, necessary to distinguish both species, was not performed during fieldwork. *Cladonia sulphurina* Michx. and *Cladonia deformis* Hoffm. were also recorded together as *C. sulphurina*, since distinction between these two species is mainly based on the presence of squamatic acid revealed by UV light, which was not used during fieldwork. *Cladonia borealis* Stenroos and *Cladonia coccifera* Willd. were both identified as *C. borealis* because they are morphologically very similar. For the same reason, *Cladonia stygia* Ruoss and *Cladonia rangiferina* Wigg. were pooled. *Stereocaulon* species were only identified to the genus. Other specimens that could not be identified directly in the field were collected for further identification at the Herbier Louis-Marie (Laval University, Qc, Canada), where a dissecting microscope was used, and chemical spot tests were conducted. The cover of *Cladonia* species primary thallus was measured but all specimens were recorded as *Cladonia* spp. and were therefore not included in richness and diversity analyses. Crustose lichen cover was also evaluated but species were not identified.

2.4.3. Statistical analyses

Mixed models were used to evaluate the impact of shrub canopy on abundance, species richness and evenness of lichen communities, using Region, Site and Shrub ID as nested random effects. Response variables were: 1) percentage lichen cover on the ground as a measure of abundance, 2) species richness and 3) Shannon Index as a measure of evenness. As multiple parameters constituted potential explanatory variables (vegetation type, shrub height, canopy closure and survey position), model selection using the Akaike Information Criterion (AICc) was implemented to identify which model or set of models best fitted the response variables. Candidate models were chosen a priori (Table 2.1) and all included the survey position (three levels: shrub center, shrub edge and open area) in order to evaluate the impact of shrub canopy on lichen cover, richness and diversity. The performance of models was assessed with AICc weights. Because model selection could not identify a unique model explaining the observed data (AICc weights < 0.90), model averaging was used to evaluate the effect of the parameters survey position, canopy closure, shrub height and vegetation type on the response variables (Burnham and Anderson 2002, Mazerolle 2006). We calculated a model-averaged coefficient, i.e. a weighted mean coefficient for every parameter considering all models included in the model selection. Confidence intervals (CI, 95%) based on model-averaged coefficient and unconditional variances were computed with the R package AICcmodavg (Mazerolle 2015). We concluded to an effect of a parameter on the response variable whenever the 95% IC of its model-averaged coefficient did not include 0. Linear models were used for lichen cover and evenness as data were normally distributed. Generalized linear models were used for species richness, using a Poisson distribution. Mixed models were conducted on 65 out of the 75 individual shrubs (195 of the 225 total surveys), as measurement of canopy closure was missing for 10 shrub individuals. Marginal coefficients of determination (R^2) were also implemented to better describe the tested models using the package MuMIn (Bartoń 2019).

Table 2.1. AICc model selection table for the three response variables (lichen cover, species richness and evenness) on a latitudinal gradient in Nunavik, Québec, Canada. Second column presents parameters included in the different models. Nested random effects Station/Site/ShrubID were included in each model. Marginal coefficients of determination (R^2) are shown to describe the tested models.

Models	Parameters	K	AICc	Delta_AICc	ModelLik	AICcWt	R^2
Cover							
Shrub characteristics	Position + Shrub Height + Canopy closure	9	-222.9	0	1	0.81	0.54
Survey position	Position	7	-219.99	2.91	0.23	0.19	0.49
Vegetation type	Position + Vegetation type	12	-212.17	10.73	0	0.00	0.55
Null	1	5	-55.3	167.6	0	0.00	0
Richness							
Survey position	Position	6	804.49	0	1	0.82	0.49
Shrub characteristics	Position + Shrub Height + Canopy closure	8	807.93	3.44	0.18	0.15	0.49
Vegetation type	Position + Vegetation type	11	810.61	6.12	0.05	0.04	0.50
Null	1	4	977.77	173.28	0	0.00	0
Evenness							
Shrub characteristics	Position + Shrub Height + Canopy closure	9	247.39	0	1	0.71	0.46
Survey position	Position	7	249.33	1.94	0.38	0.27	0.43
Vegetation type	Position + Vegetation type	12	253.85	6.46	0.04	0.03	0.46
Null	1	5	360.29	112.9	0	0.00	0

In order to compare lichen communities between survey positions, non-metric multidimensional scaling (nMDS) was performed on an adjusted Bray-Curtis dissimilarity matrix based on species abundance using the package vegan (Oksanen et al. 2018). A “dummy” species was added to the species matrix to compute an adjusted Bray-Curtis index as the original Bray-Curtis index produced non-defined values when comparing surveys without any species (Clarke et al. 2006). Bray-Curtis indices grouped by survey position were tested for homogeneity of dispersion using the PERMDISP function of PRIMER (version 6.0, Anderson et al. 2008). PRIMER’s PERMANOVA and pairwise PERMANOVA were then performed to detect differences between positions of the centroids of Bray-Curtis index values grouped by survey positions. Region, Site and Shrub ID were used as nested random effects to restrict permutations. P-values obtained through pairwise PERMANOVA were corrected for multiple testing using Bonferroni correction. In order to evaluate ecological preferences of species for survey positions, Pearson’s Phi coefficient of correlation was calculated (equation 1; Chytrý et al. 2002) using the package indicspecies and a presence/absence community matrix (De Cáceres 2013)

$$r_{\phi} = \frac{\mathrm{N} \times n_p - n \times N_p}{\sqrt{(N \times n - n^2) \times (N \times N_p - {N_p}^2)}} \quad (1)$$

where N is the total number of sites, Np the number of sites for the particular vegetation unit, n the total number of sites in which the species of interest has been reported and np the number of sites for the particular vegetation unit in which the species has been recorded. All analyses were performed in R 3.5.2 and PRIMER 6.0.

2.5. Results

2.5.1. Community data

Overall, 34 macrolichen species were identified in the 225 surveys conducted in the three study regions (Table 2.2). Thirty-one of these species were found in open areas, 27 at the shrub edge and 19 at the center of shrub individuals.

2.5.2. Abundance, species richness and evenness

Model selection for lichen cover indicated that two models (*Shrub characteristics* and *Survey position*) accounted for 100% of the AICc weight, with weights of 0.81 and 0.19, respectively (Table 2.1). However, model-averaged coefficients and 95% CI found no effect of *shrub height* and *canopy closure* on lichen cover (Table 2.3). Model averaging revealed that *survey position* was the only parameter having an effect on lichen cover as the model-averaged CI for this coefficient excluded 0 (Table 2.3). Model-averaged lichen cover (± unconditional SE) was lower for shrub center (19.7 ± 3.9 %) compared to shrub edge (26.6 ± 3.9 %) and open area (54.1 ± 3.9 %; Figure 2.3a). Lichen cover did not differ between shrub edge and shrub center as the 95% IC on their model-averaged coefficients overlap. The *vegetation type* parameter did not induce differences in lichen cover since the model including this parameter had an AICc weight of 0.0.

The two most plausible models explaining lichen species richness, *Survey position* and *Shrub characteristics*, accounted for 97% of the total AICc weight, with respective weights of 0.82 and 0.15 (Table 2.1). Model averaging indicated that the only parameter affecting species richness was *survey position* (Table 2.3). Model-averaged species richness differed between all survey positions; 7.62 ± 0.40 species in open area, 4.26 ± 0.28 at shrub edge and 2.56 ± 0.21 at shrub center (Figure 2.3b). The *vegetation type* parameter did not influence species richness.

Model selection for evenness found that two models accounted for 98% of the AICc weight. Models *Shrub characteristics* and *Survey position*, which accounted for 0.71 and 0.27 of the AICc weight, respectively, performed similarly (ΔAICc = 1.94, Table 2.1). Model averaging found that shrub characteristics were not significant predictors of evenness. Once more, the only parameter influencing lichen evenness was *survey position* (Table 2.3). Model-averaged evenness differed between all survey positions and was 1.58 ± 0.06 in open area, 1.08 ± 0.06 at shrub edge and 0.63 ± 0.06 at shrub center (Figure 2.3c). The *vegetation type* parameter had no influence on community evenness.

2.5.3. Community composition

Ordination mapping of dissimilarities among the communities grouped by survey position suggested differences in lichen community composition between shrub understory (i.e. shrub center and shrub edge) and open area (Figure 2.4). Pairwise PERMANOVA pointed out significant differences in community composition between shrub center and open area ($p < 0.01$) and between shrub edge and open area ($p < 0.01$). No difference was found between shrub center and shrub edge. Since PERMDISP analysis showed similar multivariate dispersions for all three survey positions, differences observed with the PERMANOVA likely result from real changes in species composition. Phi coefficient of correlation indicated that 16 species were positively associated with open area and two with both shrub edge and open area (Table 2.4). No species was found to be associated with shrub center, while the remaining 16 species were not associated with any survey position.

Table 2.2. Lichen species and total cover (cm) in open area, shrub edge and shrub center linear surveys (40 cm) recorded around and underneath 75 *Betula glandulosa* individuals at Clearwater Lake, Boniface River and Payne Lake in Nunavik, Québec, Canada. *Cladonia* sp. refers to primary thallus of *Cladonia* species that could not be identified to the species level.

Species	Open area	Shrub edge	Shrub center
Alectoria ochroleuca	49.5	13	22
Bryocaulon divergens	39	7.5	1.5
Bryoria nitidula	4	1	—
Cetraria islandica	10.5	13.5	4
Cetraria nigricans	34.5	—	—
Cetrariella delisei	1	—	—
Cladonia amaurocrea	35.5	13.5	—
Cladonia bellidiflora	2.5	1	—
Cladonia borealis	17.5	3	—
Cladonia cenotea	—	0.5	—
Cladonia chlorophea	2.5	—	—
Cladonia cornuta	10	7	3.5
Cladonia crispata	24.5	9.5	1.5
Cladonia fimbriata	7	1	—
Cladonia gracilis	9.5	13.5	8
Cladonia macilenta	1	—	—
Cladonia macrophylla	13.5	3	—
Cladonia mitis	207.5	47	8.5
Cladonia ochrochlora	0.5	—	0.5
Cladonia phyllophora	2	0.5	—
Cladonia pleurota	29	14	3.5
Cladonia pyxidata	0.5	1	1
Cladonia rangiferina	164.5	160	161
Cladonia sp.	37	8	—
Cladonia squamosa	19.5	7.5	—
Cladonia stellaris	323.5	253.5	202
Cladonia sulphurina	7.5	1	0.5
Cladonia uncialis	66.5	20	21
Cladonia verticilata	0.5	—	—
crustose on soil	96.5	4	—
crustose on wood	1	—	—
crustose on rock	3	3	—
epiphyte	0.5	6	9
Flavocetraria cucullata	26.5	22.5	48.5
Flavocetraria nivalis	198.5	79	37
Peltigera malacea	—	6	1
Peltigera scabrosa	—	—	9
Sphaerophorus globosus	7.5	0.5	—
Stereocaulon sp.	112	29	6.5

Table 2.3. Model-averaged coefficients for survey position (shrub edge and shrub center), shrub canopy closure and shrub height for response variables (lichen cover, species richness and evenness) on a latitudinal gradient in Nunavik, Québec, Canada. Reference level is survey position *open area*. Models *Shrubs characteristics* and *Survey position* were used to estimate coefficients, based on AICc results.

Parameter	Model averaged coefficient	Unconditional SE	Lower CI	Upper CI
Cover				
PositionEdge	-0.275	0.020	-0.314	-0.235
PositionCenter	-0.344	0.020	-0.384	-0.304
Canopy closure	-0.065	0.040	-0.143	0.013
Shrub height	0.00	0.001	-0.002	0.001
Richness				
PositionEdge	-0.606	0.073	-0.748	-0.463
PositionCenter	-1.146	0.088	-1.319	-0.974
Canopy closure	-0.009	0.035	-0.079	0.060
Shrub height	-0.007	0.035	-0.076	0.061
Evenness				
PositionEdge	-0.514	0.072	-0.655	-0.373
PositionCenter	-1.005	0.072	-1.146	-0.864
Canopy closure	-0.028	0.064	-0.153	0.097
Shrub height	-0.002	0.003	-0.007	0.002

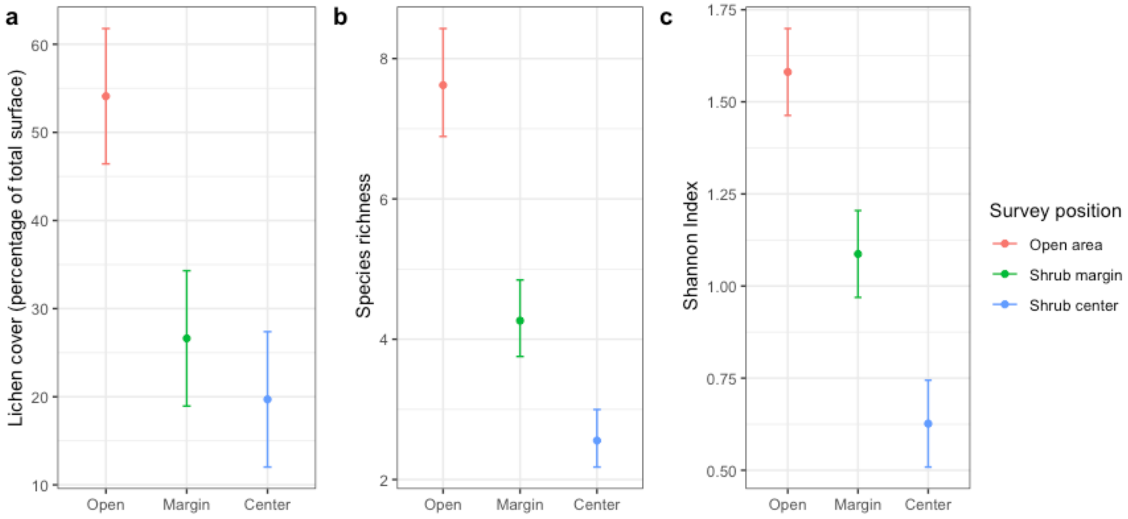

Figure 2.3. Model-averaged a) lichen cover (as percentage of the ground total surface), b) species richness and c) evenness (Shannon index) for the different survey positions. Means and 95% CI were computed by model averaging based on model selection. Sixty-five of the 75 *Betula glandulosa* individuals sampled in Nunavik, Québec, Canada were considered for this analysis.

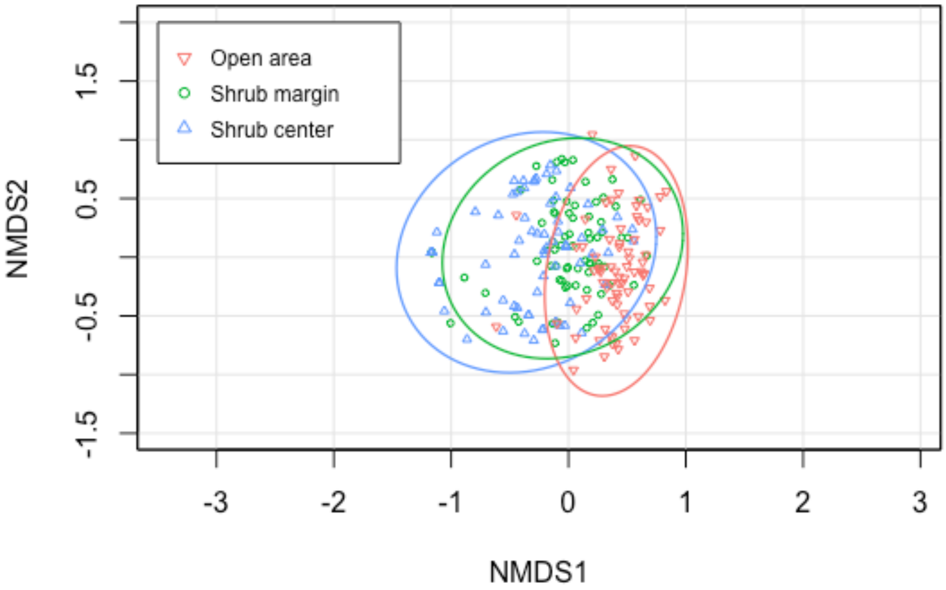

Figure 2.4. Ordination plot showing the first two of the three axes of a non-metric multidimensional scaling (NMDS) based on dissimilarity matrices computed with adjusted Bray-Curtis index on the 225 surveys conducted near and underneath 75 *Betula glandulosa* individuals in Nunavik, Québec, Canada. Stress is of 0.157.

Table 2.4. Pearson's Phi coefficient of correlation of lichen species with survey positions near and underneath 75 *Betula glandulosa* individuals at Clearwater Lake, Boniface River and Payne Lake in Nunavik, Québec, Canada. P-values were computed through 999 permutations. *Preference* column indicates that the species is significantly and positively associated with this survey position.

Species	**Shrub center**	**Shrub edge**	**Open area**	**Center + Edge**	**Center + Open**	**Edge + Open**	**p**	**Preference**
Cladonia amaurocrea	0.449	-0.136	-0.314	0.314	0.136	-0.449	0.001	Open area
Flavocetraria nivalis[3]	0.447	-0.006	-0.441	0.441	0.006	-0.447	0.001	Open area
Cetraria nigricans[3]	0.404	-0.202	-0.202	0.202	0.202	-0.404	0.001	Open area
Cladonia mitis[1]	0.376	-0.014	-0.363	0.363	0.014	-0.376	0.001	Open area
Bryocaulon divergens[3]	0.374	-0.146	-0.228	0.228	0.146	-0.374	0.001	Open area
Cladonia pleurota[3]	0.348	-0.085	-0.263	0.263	0.085	-0.348	0.001	Open area
Alectoria ochroleuca	0.338	-0.135	-0.203	0.203	0.135	-0.338	0.001	Open area
Cladonia crispata[3]	0.305	-0.108	-0.197	0.197	0.108	-0.305	0.001	Open area
Cladonia squamosa	0.305	-0.049	-0.256	0.256	0.049	-0.305	0.001	Open area
Cladonia borealis[1]	0.265	-0.076	-0.189	0.189	0.076	-0.265	0.001	Open area
Cladonia macrophylla	0.241	-0.096	-0.144	0.144	0.096	-0.241	0.004	Open area
Sphaerophorus	0.241	-0.096	-0.144	0.144	0.096	-0.241	0.002	Open area
Cladonia rangiferina[1]	0.237	-0.068	-0.169	0.169	0.068	-0.237	0.001	Open area
Cladonia fimbriata[2]	0.233	-0.073	-0.160	0.160	0.073	-0.233	0.002	Open area
Cladonia sulphurina[1]	0.210	-0.084	-0.126	0.126	0.084	-0.210	0.007	Open area
Stereocaulon sp.	0.174	0.025	-0.199	0.199	-0.025	-0.174	0.015	Edge + Open area
Cladonia chlorophea[2]	0.190	-0.095	-0.095	0.095	0.095	-0.190	0.034	Open area
Cladonia uncialis	0.170	0.008	-0.178	0.178	-0.008	-0.170	0.022	Edge + Open area
Cladonia stellaris	0.014	0.137	-0.151	0.151	-0.137	-0.014	0.087	
Cetraria islandica	0.140	-0.010	-0.130	0.130	0.010	-0.140	0.123	
Cladonia cornuta	0.092	0.031	-0.122	0.122	-0.031	-0.092	0.255	
Cladonia bellidiflora	0.117	0.00	-0.117	0.117	0.00	-0.117	0.378	
Bryoria nitidula	0.085	0.021	-0.107	0.107	-0.021	-0.085	0.382	
Cetrariella delisei	0.094	-0.047	-0.047	0.047	0.047	-0.094	1	
Cladonia cenotea	-0.047	0.094	-0.047	0.047	-0.094	0.047	1	
Cladonia macilenta	0.094	-0.047	-0.047	0.047	0.047	-0.094	1	
Cladonia verticilata	0.094	-0.047	-0.047	0.047	0.047	-0.094	1	
Peltigera scabrosa	-0.047	-0.047	0.094	-0.094	0.047	0.047	1	
Cladonia gracilis	0.080	0.00	-0.08	0.080	0.00	-0.080	0.578	
Flavocetraria cucullata	0.056	-0.070	0.014	-0.014	0.070	-0.056	0.609	
Cladonia ochrochlora	0.033	-0.067	0.033	-0.033	0.067	-0.033	1	
Cladonia phyllophora	0.033	0.033	-0.067	0.067	-0.033	-0.033	1	
Peltigera malacea	-0.067	0.033	0.033	-0.033	-0.033	0.067	1	
Cladonia pyxidata	0.00	0.00	0.00	0.00	0.00	0.00	1	

1. Species recorded as having a habitat restricted to full sun (Brodo et al. 2001).
2. Species recorded as having a habitat restricted to full sun or partial shade (Brodo et al. 2001).
3. Species recorded as having a habitat restricted to open areas (Brodo et al. 2001, Ahti et al. 2013)

2.6. Discussion

2.6.1. Overall impact of shrubs

The results confirm our hypothesis and demonstrate a clear impact of shrub canopy on lichen communities. Our results corroborate previous studies, which recorded a negative impact of shrubs on lichen abundance (Chapin et al. 1995, Cornelissen et al. 2001, Elmendorf et al. 2012, Fraser et al. 2014, Provencher-Nolet et al. 2014) and diversity (Pajunen et al. 2011, Lang et al. 2012, Alatalo et al. 2017). Model averaging indicated that *survey position* was the only parameter affecting lichen cover and diversity; all other parameters (*vegetation type*, *shrub height* and *canopy closure*) having no significant effect. Consequently, our results suggest that shrubs have detrimental impacts on lichens, regardless of the surrounding vegetation and with only little effect of their height and canopy closure.

As previously suggested, competition for light is likely to be the main driver of lichen decline with shrub cover increase (Chapin et al. 1995, Cornelissen et al. 2001, Joly et al. 2009, Pajunen et al. 2011, Lang et al. 2012). Because of their slow growth rate, lichens are poor competitors and may suffer from shade caused by both the shrub vertical structure and litter accumulation. Shrubs may also lead to greater soil nutrient availability, by increasing the amount of organic matter and warming soils during winter (Sturm et al. 2000b), which may affect lichens that perform better in nutrient-poor habitats where they experience less competition.

Additionally, shrub branches and canopy act as snow traps, increasing overall snow cover (Sturm et al. 2000b, Paradis et al. 2016), with a negative impact on lichen survival (Wahren et al. 2005, Bidussi et al. 2016). Bidussi et al. (2016) showed growth reduction, chlorophyll degradation and higher decomposition rate for some lichen species under increased snow depths. In our study, two of the species identified as having a low snow-tolerance (*Flavocetraria nivalis* and *Alectoria ochroleuca*) were found to be positively associated with open areas.

Interestingly, we observed significant differences in lichen cover, richness and evenness even though our methodology restricted us to surveying lichen communities in open environments with discontinuous shrub cover. We believe that differences in lichen communities would have been exacerbated if we had compared sites with contrasting vegetation cover (open tundra vs dense continuous shrub cover). This hypothesis is supported by our observations of sparse lichen cover and decaying fruticose lichens underneath dense shrub canopies at Clearwater Lake. Therefore, as shrub expansion continues, the shift from prostrated vegetation to dense shrub stands may induce greater changes in lichen communities than that observed herein.

2.6.2. Temporal component of changes

The effect of an increasing shrub canopy on lichens over time may also be estimated herein since time spent under shrub canopy was greater for the lichens encountered near the shrub center than at the shrub edge. Our results indicate a rather rapid decline of lichen cover under shrub canopy, which was about 50% lower at shrub edge than in open area. However, lichen cover decline appears to slow down after the initial phase of decline, as lichen cover did not differ between shrub edge and shrub center. In comparison, a review of experimental warming studies reported a negative effect of a growing vascular plant cover on lichen abundance that was constant over time (Elmendorf et al. 2012), which was not captured herein. However, species richness and evenness seem to decrease with time spent under shrub canopy, as both dropped significantly from shrub edge to shrub center. Considering that community composition did not differ between these two positions, certain species seem to remain present in both shrub edge and shrub center surveys, even if species richness and evenness decline from the shrub edge to the shrub center, suggesting that a stochastic simplification of community composition occurs underneath the shrub canopy.

According to the ecological preferences of the species, 16 species were significantly associated with open area and thus, seemed to be rapidly eliminated from the understory community, probably because of their low tolerance to low-light environments or increased snow cover. Most of these species are known to be mostly associated with full sun habitats or with open areas (Brodo et al. 2001, Ahti et al. 2013 see Table 2.4 for details). In comparison, species associated with both shrub edge and open area may be more tolerant to shade or to other environmental variables and persist under shrub canopy following shrub lateral expansion. The remaining species, showing no significant associations with survey positions, are likely to have a wider habitat range, being as present in the understory as in the open environment. No lichen species showed an ecological preference for the shrub center, a result similar to that of Pajunen et al. (2011). Therefore, our results suggest that shrubs are mainly deleterious to northern lichens as no species showed a positive association with shrubs and that positive effects, if present, are limited.

2.6.3. Implications for ecosystems

As lichens are an important component of northern biodiversity, loss in lichen diversity would reduce overall ecosystem diversity, which may in turn impact ecosystem integrity. Less diverse ecosystems being more vulnerable to a changing environment (Chapin III et al. 2000), a decline in northern biodiversity may threaten the resilience of these ecosystems, which are experiencing strong pressure with global change. Because lichens provide ecosystem services, their disappearance could have significant deleterious effects on ecosystem dynamics. For example, a decline in nitrogen-fixing species, recently observed through long-term monitoring of lichen communities, may deplete nitrogen availability in northern ecosystems (Maliniemi et al. 2018), where poor soils limit primary productivity.

A generalized decline in lichen cover may also have a major impact on regional and global climate. Indeed, the transition from a light-colored lichen ground cover to a darker shrub cover would decrease earth's surface albedo and increase the absorption of solar radiation, therefore inducing positive feedback on atmospheric warming (Bernier et al. 2011, Pearson et al. 2013). For example, a decrease in albedo observed along a latitudinal gradient in Alaska was mainly driven by a decrease in reflective surfaces (i.e. lichens) and an increase in canopy complexity (Beringer et al. 2005). Greater absorption of solar radiation by ground cover may alter soil temperatures and amplify shrub expansion, which would lead to multiple feedbacks associated with shrub expansion that are likely to amplify high-latitude warming in the coming years (Chapin et al. 2005, Myers-Smith et al. 2011).

2.7. Conclusion

We observed a clear negative impact of shrub canopy on both lichen abundance and diversity. Being greater at the shrub center than at the shrub edge, the impact of shrub canopy on lichen diversity appears to increase over time. The negative impact of shrubs was consistent across the different vegetation types studied and with little influence of shrub height and degree of canopy closure. As suggested by other studies, competition for light is likely to be the main driver of the observed decline in lichen abundance and diversity. Lichens may gradually be excluded from shrub understory owing to their low shade-tolerance. As land cover change models based on climate change scenarios predict an increase of woody vegetation abundance that could reach as much as 50% in northern ecosystems by 2050 (Pearson et al. 2013), severe changes in lichen communities are to be expected. Lichen abundance is likely to decline greatly and will impact other species that rely on this resource such as caribou, as well as affect land surface albedo, which is important in climate regulation. Loss in lichen diversity may also decrease the overall diversity of northern ecosystems and disturb their functioning.

2.8. Disclosure statement

No potential conflict of interest was reported by the authors

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Conclusion

Les objectifs du présent mémoire étaient d'identifier les patrons et déterminants de l'abondance et de la diversité des lichens au Nunavik et d'évaluer l'influence des arbustes sur les lichens. Considérant le phénomène d'arbustation en cours dans les écosystèmes nordiques et la restructuration des communautés végétales qui s'en suit, ce mémoire visait ainsi à améliorer notre compréhension de l'impact des changements climatiques sur les lichens. Malgré leurs multiples rôles écologiques dans les écosystèmes nordiques, les lichens demeurent relativement peu étudiés et sont généralement considérés comme un unique groupe fonctionnel plutôt qu'en termes d'espèces. Nos résultats contribuent à combler ce manque de connaissances en documentant l'influence des facteurs abiotiques et biotiques sur les communautés lichéniques. Les différentes approches que nous avons utilisées soulignent l'importance de la végétation vasculaire dans la détermination de l'abondance, de la diversité et de la composition des communautés lichéniques. Ce faisant, nos résultats corroborent les résultats d'études de réchauffement expérimental (Lang et al. 2012, Alatalo et al. 2017) et de photographies aériennes (Fraser et al. 2014, Provencher-Nolet et al. 2014) en mettent en évidence la vulnérabilité des lichens face à la compétition accrue avec les plantes vasculaires promue par les changements climatiques.

Patrons et déterminants de l'abondance et de la diversité des lichens

En raison de leur métabolisme poïkilohydrique et de leur croissance lente, les lichens sont particulièrement sensibles aux variations des conditions environnementales et apparaissent vulnérables dans le présent contexte de changements climatiques. En vue de mieux comprendre l'influence des facteurs environnementaux sur l'abondance et la diversité des lichens au Nunavik, nous avons caractérisé les communautés lichéniques dans les types de végétation dominants le long d'un gradient latitudinal s'étendant de la toundra forestière à la toundra rase. Bien que de plus en plus d'études s'intéressent aux facteurs environnementaux influençant les lichens, leur nombre demeure limité (Giordani et al. 2014, Matos et al. 2015, Nelson et al. 2015a, 2015b). Notre étude s'inscrit donc dans cet effort et identifie les facteurs abiotiques et biotiques impliqués dans la détermination des patrons d'abondance, de diversité et de composition des communautés à différentes échelles spatiales au Nunavik.

Nos résultats révèlent que le type de formation végétale et la latitude sont les facteurs environnementaux les plus influents dans la détermination des patrons d'abondance et de diversité des lichens. La différenciation de la composition des communautés lichéniques selon les domaines bioclimatiques du Québec appuie également l'importance de la végétation et de la latitude. Ainsi, les interactions compétitives, qui varient selon les formations végétales, et les conditions climatiques régionales apparaissent comme étant les mécanismes déterminants des communautés lichéniques au Nunavik.

Le long du gradient latitudinal, la richesse spécifique régionale est favorisée par la diversité des types de végétation présents dans une région, alors que la richesse spécifique locale est favorisée par la diversité des substrats de croissance disponibles. La richesse spécifique des lichens augmente donc en fonction de la diversité des niches disponibles (Holt 2007, Nelson 2013), tant à l'échelle du gradient latitudinal qu'à l'échelle locale. Le couvert lichénique diminue avec la latitude, ce qui contraste avec les résultats d'études réalisées dans l'Arctique canadien (Vonlanthen et al. 2008, Epstein et al. 2008) et pourrait s'expliquer par les caractéristiques édaphiques locales et les perturbations passées. Pour sa part, la diversité fonctionnelle des communautés lichéniques augmente avec la latitude, ce qui semble résulter d'une perte de la dominance de certains traits plutôt que d'une réelle diversification.

Aux deux échelles spatiales considérées, les interactions compétitives avec la végétation vasculaire ont un impact négatif sur les lichens. À l'échelle du gradient latitudinal, le couvert lichénique et la richesse spécifique sont plus faibles dans les types de végétation dominés par les plantes vasculaires, la diversité fonctionnelle n'est toutefois pas affectée. À l'échelle locale, le couvert arbustif et graminoïde diminue l'abondance, la richesse spécifique et la diversité fonctionnelle des lichens sous-jacents. Ces résultats soulignent la faible compétitivité des espèces lichéniques vis-à-vis des plantes vasculaires de même que leur vulnérabilité dans le présent contexte de changements climatiques. L'augmentation de l'abondance des plantes vasculaires pourrait ainsi engendrer une diminution de l'abondance et de la diversité des lichens. Cette diminution pourrait toutefois ne pas se transposer en perte de fonctions écosystémiques à l'échelle du territoire.

Influence de la canopée arbustive sur les communautés lichéniques

Dans les dernières décennies, plusieurs études ont démontré un effet indirect des changements climatiques sur les lichens par l'entremise des espèces arbustives (Cornelissen et al. 2001, Alatalo et al. 2017). En effet, le recul des zones dominées par les lichens à l'échelle circumpolaire (Ropars and Boudreau 2012, Tremblay et al. 2012, Provencher-Nolet et al. 2014, Moffat et al. 2016) de même que la diminution de l'abondance et de la diversité des lichens dans les expériences de réchauffement (Chapin et al. 1995, Elmendorf et al. 2012, Zamin et al. 2014, Alatalo et al. 2017) semblent résulter d'une compétition accrue avec les plantes vasculaires. Le premier chapitre de ce mémoire met également en lumière l'importance de la végétation en tant que déterminant principal des patrons d'abondance et de diversité des lichens au Nunavik et l'impact négatif des plantes vasculaires à différentes échelles spatiales. Dans ce deuxième chapitre, en vue de mieux comprendre les changements induits par la présence d'une canopée arbustive sur les communautés lichéniques à l'échelle locale, nous avons évalué le couvert des espèces lichéniques présentes en milieu ouvert, à la marge et au centre d'arbustes. Cette approche permet l'inclusion d'une dimension temporelle à l'étude des changements qui s'opèrent sous la canopée arbustive.

Nos résultats démontrent une réduction de plus de 50% du couvert lichénique entre le milieu ouvert et la marge des arbustes et soulignent la rapidité du changement qui se produit en réponse au développement d'une canopée arbustive. Une diminution de la richesse spécifique et de l'équitabilité est également observée entre le milieu ouvert et le milieu arbustif, diminution qui s'accentue entre la marge de l'arbuste et son centre. L'effet négatif de la présence des arbustes sur la diversité des lichens semble donc augmenter avec le temps. Par ailleurs, la composition des communautés lichéniques diffère entre le milieu ouvert et le milieu sous arbuste. Alors que plusieurs espèces de lichens se retrouvent exclusivement en milieu ouvert, les espèces présentes sous la canopée sont également retrouvées en milieu ouvert. La canopée arbustive semble donc engendrer une simplification de la communauté lichénique en excluant les espèces nécessitant un milieu ouvert et en préservant celles pouvant tolérer un plus grand éventail de conditions.

L'effet négatif des arbustes sur les lichens semble principalement résulter d'une compétition accrue pour la lumière, dont la disponibilité au sol diminue en raison de la présence de la canopée arbustive et de la production de litière. L'exclusion d'espèces sensibles à une accumulation accrue de neige (Bidussi et al. 2016) suggère cependant que l'effet négatif des arbustes s'effectue également via une modification des conditions nivales (Sturm et al. 2000b, Paradis et al. 2016). Toutefois, l'effet relatif des différents mécanismes sous-tendant l'exclusion de certaines espèces lichéniques sous la canopée arbustive devrait être évalué de manière plus exhaustive, de manière à mieux expliquer la dynamique des communautés lichéniques sous arbustes.

Synthèse des acquis

En combinant diverses méthodologies et en travaillant à différentes échelles spatiales, nos résultats soulignent l'impact de la végétation vasculaire sur les lichens du Nunavik. En profilant la composition des communautés lichéniques de même que les patrons d'abondance et de diversité des lichens le long d'un gradient latitudinal, le type de formation végétale s'est révélé être le facteur le plus influent à l'échelle du gradient. En augmentant la force des interactions compétitives et en modifiant les conditions du milieu, la présence des plantes vasculaires réduit le couvert et la diversité des lichens à l'échelle locale. L'effet des arbustes sur la diversité lichénique semble également s'accroître avec le temps. De plus, la présence des arbustes modifie la composition des communautés lichénique en excluant les espèces les moins tolérantes à un changement des conditions.

Dans les prochaines décennies, les changements climatiques sont susceptibles d'induire un décalage des grandes formations végétales vers le Nord (Arctic Climate Impact Assessment 2004). De plus, certains modèles prédisent une augmentation de la présence des arbustes de 50 à 70% dans les écosystèmes nordiques (Pearson et al. 2013, Lemay et al. 2018). Considérant l'influence prépondérante de la végétation sur les lichens relevée dans ce mémoire, nos résultats suggèrent qu'une restructuration majeure des communautés lichéniques accompagnera ces changements. L'augmentation généralisée de la présence des plantes vasculaires pourrait ainsi engendrer une diminution de l'abondance des lichens de même qu'un déclin grandissant de la diversité lichénique. Malgré cette potentielle perte de diversité, la stabilité de la diversité fonctionnelle observée dans les différents types de végétation laisse supposer que la contribution des lichens aux fonctions écosystémiques pourrait s'avérer résistante aux changements de végétation à venir.

Limites de l'étude et perspectives de recherche

Bien que nous ayons identifié des patrons d'abondance et de diversité latitudinaux, nous n'avons pas été en mesure de déterminer l'importance des facteurs climatiques sur les communautés lichéniques. En effet, les fortes corrélations entre les variables climatiques et la latitude ont empêché la détection statistique de relations directes entre le climat et les communautés lichéniques et ne nous ont permis que d'utiliser la latitude comme un proxy pour le climat. L'évaluation de l'effet spécifique des variables climatiques sur les communautés lichéniques au Nunavik devrait toutefois être abordée dans de prochaines études afin d'améliorer nos capacités à prédire l'évolution de la végétation dans les années à venir. Un dispositif créé à cet effet dans des sites similaires se différenciant principalement par des variables climatiques isolées pourrait permettre de quantifier l'impact relatif des différents facteurs climatiques sur les communautés lichéniques.

L'utilisation des traits fonctionnels a partiellement permis de pallier à ce problème en révélant certains patrons non identifiables avec une simple analyse taxonomique, notamment l'influence côtière sur la composition des communautés dans la région de Baie Déception. Une importante variabilité intraspécifique des traits fonctionnels chez les lichens a toutefois été révélée dans des études récentes (Asplund and Wardle 2014, Roos et al. 2019) et suggère que les traits fonctionnels devraient être mesurés directement sur les spécimens plutôt que suite à l'identification de l'espèce comme il a été le cas dans le présent mémoire. De plus, bien que les traits fonctionnels utilisés dans ce mémoire aient été théoriquement identifiés comme de bons indicateurs de la réponse des lichens aux conditions environnementales (Giordani et al. 2014, Matos et al. 2015, Nelson et al. 2015b, Bässler et al. 2016, Prieto et al. 2017, Rubio-Salcedo et al. 2017), d'autres traits auraient pu être considérés. Des expérimentations demeurent nécessaires en vue de sélectionner les traits les plus performants parmi ceux proposés (Cornelissen et al. 2007) et afin d'homogénéiser l'utilisation des traits fonctionnels pour les lichens.

Finalement, les récentes révisions moléculaires des groupes taxonomiques lichéniques révèlent la présence de nombreuses espèces cryptiques (Crespo and Pérez-Ortega 2009). Cette nouvelle taxonomie basée sur des critères moléculaires plutôt que morphologiques questionne la pertinence de l'utilisation de la richesse spécifique pour définir la biodiversité, et souligne sa faible robustesse et l'absence potentielle de distinctions significatives entre les espèces. Ainsi, l'utilisation de la diversité fonctionnelle comme indicateur de la biodiversité pourrait être plus adéquate (McGill et al. 2006, Cadotte et al. 2011), encore faut-il que celle-ci soit basée sur des traits fonctionnels représentatifs de l'effet des conditions environnementales sur les organismes et de la contribution de ces derniers aux fonctions écosystémiques.

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Annexe 1: Tableaux supplémentaires

Table S1. Sampled dominant vegetation types and their description in sampling regions according to the 2018 Québec Northern Vegetation Map produced by the *Ministère des Forêts, de la Faune et des Parcs* of the Government of Québec. The last column presents the revised nomenclature we used for analysis.

Regions	**Dominant vegetation types (MFFP)**	**Description**	**Revised nomenclature**
Clearwater Lake, Boniface River	Lichen woodland	Forests with a tree cover ranging from 10 to 40% (usually dominated by black spruce *Picea mariana* Miller) and with a lichen cover > 40%	Woodland
	Shrubland	Erect (0.3 – 2 m high) deciduous shrub cover > 70% often dominated by *Betula glandulosa* Michx	Shrubland
	Subarctic Heath	Deciduous erect shrub cover < 30%, usually dominated by lichens, mosses and ericaceous species	Open
Le Roy Lake, Payne Lake	Tundra	Dominated by lichens, mosses and herbaceous, with < 30% of erect or prostrate shrubs	Open
Le Roy Lake Payne Lake, Deception Bay	Shrub tundra	Deciduous shrub cover (*Betula glandulosa,* erect or prostrate) > 30 % and dominated by lichens, mosses and ericaceous species	Shrubland
Chukotat River	Prostrate tundra	Dominated by prostrate shrubs < 20 cm and where bare substratum cover up to 50%	Herbaceous
Chukotat River, Deception Bay	Herbaceous tundra (6)	Dominated by prostrate shrubs species (< 20 cm) and where herbaceous cover > 10%	Herbaceous

Table S2. Traits and respective functional groups description based on the literature (Brodo et al. 2001, Nash 2008, Nelson et al. 2015b)

Functional traits	**Functional group**	**Description**
Main type of photobiont	Green alga	Main photobiont is a green alga
	Cyanobacteria	Main photobiont is a cyanobacterium
	Tripartite	Main photobiont is a green alga, but cyanobacteria are also present in specialized structures (cephalodia)
Thallus growth form	Fruticose	Erect or pendant thallus, without clearly distinguishable upper and lower surface
	branched	Highly branched and shrubby-like (including "reindeer-lichens", i.e. branched *Cladonia*)
	cladoniiform	Unbranched or little branched stalk (including most *Cladonia* and *Stereocaulon*)
	filamentous	Hair-like filaments (including *Alectoria* and *Bryoria*)
	Foliose	Flattened thallus with easily distinguishable upper and lower surfaces
	3D	Erect foliose growth form (including *Cetraria* and related genera)
	broad	Partly attached to the substrate, lobes > 2 mm wide
	appressed	Partly attached to the substrate, usually with narrow lobes < 2 mm wide
	Squamulose	Thallus composed of small scales
	Crustose	Thallus firmly attached to the substrate, forming a crust
Asexual propagules	Isidia	Corticated outgrowth of the surface, usually cylindrical or granular, containing both fungus and photobiont (vegetative reproduction structure)
	Soredia	Powdery or granular balls of hyphae, containing photobiont (vegetative reproduction structure)
	Lobules	Minute lobes having the same basic anatomy as the main thallus (vegetative reproduction structure)

Table S3. Abundance of lichen species in terms of percentage of the total lichen surveyed per region among 6 regions distributed along a latitudinal gradient in Nunavik, Canada. Forty-two (42) sites were sampled in 6 regions along a latitudinal gradient: Clearwater Lake (CL, 56°20'N), Boniface River (BR, 57°45'N), Le Roy Lake (LR, 58°29'N) Payne Lake (PL, 59°32'N), Chukotat River (CR, 61°18'N) and Deception Bay (DB, 62°05'N).

Species	**CL**	**BR**	**LL**	**PL**	**CR**	**DB**
Alectoria ochroleuca	0.75	0.93	5.14	4.46	0.00	2.51
Allantoparmelia almquistii	0.00	0.13	1.51	1.40	0.00	0.00
Allantoparmelia alpicola	0.00	0.13	1.68	1.34	0.28	0.11
Arctocetraria andrejevii	0.00	0.00	0.00	0.00	1.14	0.00
Arctoparmelia centrifuga	1.13	0.50	3.77	1.32	1.04	1.17
Arctoparmelia incurva	0.00	0.00	0.00	0.00	0.00	0.05
Asahinea scolanderi	0.00	0.00	0.14	0.00	0.00	0.00
Brodoa oroarctica	0.00	0.00	0.00	0.05	0.00	0.00
Bryocaulon divergens	0.04	0.71	5.41	6.81	0.00	0.91
Bryoria nitidula	0.23	0.31	0.30	0.17	0.00	0.00
Bryoria sp.	0.00	0.00	0.01	0.01	0.00	0.00
Cetraria aculeata	0.13	0.31	0.03	0.00	0.00	0.11
Cetraria ericetorum	0.00	0.02	0.08	0.00	0.00	0.00
Cetraria islandica	0.51	0.61	0.66	1.80	4.32	1.44
Cetraria laevigata	0.00	0.00	0.03	0.00	0.00	0.00
Cetraria nigricans	1.66	0.82	0.65	0.33	0.00	0.00
Cetrariella delisei	0.07	0.27	0.00	0.00	2.90	0.00
Cladonia amaurocrea	2.38	1.26	0.45	0.70	3.89	1.12
Cladonia bellidiflora	0.33	0.86	0.50	0.45	0.00	0.00
Cladonia borealis	0.83	0.49	0.73	0.40	1.61	0.59
Cladonia carneola	0.00	0.01	0.19	0.00	0.00	0.00
Cladonia cenotea	0.01	0.02	0.03	0.00	0.05	0.00
Cladonia chlorophaea	0.22	0.07	0.49	0.09	0.09	0.96
Cladonia coniocrea	0.02	0.00	0.00	0.00	0.00	0.00
Cladonia cornuta	0.78	0.54	0.80	0.57	0.00	0.59
Cladonia crispata	1.83	1.55	0.07	0.07	0.76	0.00
Cladonia cyanipes	0.04	0.02	0.12	0.04	0.05	0.05
Cladonia fimbriata	0.14	0.06	0.18	0.26	0.00	0.11
Cladonia gracilis	2.03	1.57	1.34	0.90	3.61	2.03
Cladonia macilenta	0.02	0.01	0.00	0.05	0.00	0.00
Cladonia macrophylla	0.02	0.34	0.98	0.20	0.24	0.11
Cladonia mitis	14.56	11.37	8.44	3.40	3.89	3.31
Cladonia ochrochlora	0.02	0.00	0.00	0.00	0.14	0.21
Cladonia phyllophora	0.26	0.04	0.00	0.00	0.00	0.53

Species	**CL**	**BR**	**LL**	**PL**	**CR**	**DB**
Cladonia pleurota	1.10	1.04	0.96	2.04	0.09	0.00
Cladonia pocillum	0.00	0.00	0.00	0.00	0.19	0.00
Cladonia pyxidata	0.07	0.20	0.07	0.08	1.42	0.69
Cladonia rangiferina	7.02	15.79	18.29	18.82	5.89	4.91
Cladonia scabriuscula	0.00	0.02	0.00	0.00	0.00	0.00
Cladonia sp.	2.49	0.65	2.58	1.16	10.78	0.48
Cladonia squamosa	1.05	0.69	0.46	0.50	0.38	0.00
Cladonia stellaris	33.57	33.28	6.38	8.17	0.00	0.00
Cladonia stricta/trassii	0.00	0.02	0.00	0.00	2.09	0.00
Cladonia sulphurina	0.55	0.46	1.03	0.61	0.00	0.00
Cladonia uncialis	3.29	1.72	0.00	0.16	0.00	0.00
Cladonia verticilata	0.02	0.03	0.01	0.00	0.00	0.00
Unidentified crustose species	8.39	6.74	18.76	23.04	38.98	10.41
Dactylina arctica	0.00	0.00	0.00	0.15	1.19	0.16
Dactylina ramulosa	0.00	0.00	0.00	0.00	0.09	0.00
Unidentified epiphytic species	0.46	0.96	0.00	0.75	0.00	0.00
Flavocetraria cucullata	0.21	0.12	3.73	5.62	1.28	7.79
Flavocetraria nivalis	5.68	3.65	7.45	6.55	1.00	3.15
Gowardia nigricans	0.13	0.02	0.03	0.05	0.00	0.48
Lobaria linita	0.00	0.00	0.00	0.00	0.00	0.11
Melanelia hepatizon	0.05	0.50	0.34	0.45	0.00	0.00
Melanelia stygia	0.19	0.46	0.19	0.38	0.00	0.00
Montanelia disjuncta	0.00	0.00	0.00	0.00	0.00	0.53
Montanelia panniformis	0.11	0.00	0.14	0.03	0.00	0.00
Nephroma arcticum	0.07	1.27	0.00	0.00	0.00	0.00
Nephroma expallidum	0.00	0.00	0.00	0.00	0.00	0.85
Parmelia omphalodes	0.06	0.27	0.31	0.93	0.00	1.17
Parmelia saxatilis	0.03	0.06	2.47	1.53	0.00	0.91
Parmelia skultii	0.00	0.00	0.03	0.00	0.00	0.00
Parmelia squarrosa	0.00	0.00	0.03	0.05	0.00	0.11
Parmelia sulcata	0.00	0.00	0.00	0.21	0.00	0.00
Parmeliopsis ambigua	0.00	0.00	0.00	0.01	0.00	0.00
Parmeliopsis hyperopta	0.03	0.02	0.01	0.01	0.00	0.00
Peltigera aphtosa	0.60	0.66	0.00	0.00	1.95	18.69
Peltigera canina	0.00	0.13	0.00	0.00	0.28	2.46
Peltigera collina	0.00	0.02	0.00	0.00	0.00	0.00
Peltigera didactyla	0.00	0.00	0.00	0.00	0.00	0.91
Peltigera extenuata	0.00	0.00	0.00	0.00	0.05	0.32
Peltigera malacea	0.13	0.00	0.00	0.05	0.00	2.14

Species	**CL**	**BR**	**LL**	**PL**	**CR**	**DB**
Peltigera neopolydactyla	0.00	0.08	0.00	0.00	0.00	0.00
Peltigera polydactylon	0.14	0.02	0.00	0.15	1.66	0.11
Peltigera rufescens	0.00	0.00	0.00	0.00	0.05	1.07
Peltigera scabrosa	0.62	1.10	0.22	0.00	1.09	9.29
Peltigera sp.	0.00	0.00	0.00	0.00	0.24	0.43
Phaeophysia sciastra	0.01	0.00	0.00	0.00	0.00	0.00
Pilophorus robustus	0.00	0.00	0.00	0.00	0.09	0.00
Platismatia glauca	0.00	0.00	0.31	0.21	0.00	0.00
Protopannaria pezizoides	0.00	0.00	0.00	0.00	0.33	0.00
Pseudephebe minuscula	0.00	0.00	0.00	0.15	0.00	0.85
Pseudephebe pubescens	0.00	0.00	0.00	0.05	0.00	0.00
Psoroma hypnorum	0.00	0.00	0.00	0.00	0.00	0.21
Solorina bispora	0.00	0.00	0.00	0.00	0.00	0.43
Solorina crocea	0.00	0.00	0.00	0.00	0.85	0.00
Sphaerophorus fragilis	0.00	0.02	0.27	0.34	0.00	0.00
Sphaerophorus globosus	0.08	0.30	0.68	0.30	2.42	1.01
Stereocaulon sp.	5.48	6.07	0.00	0.01	2.66	7.21
Thamnolia sp.	0.00	0.00	0.00	0.00	0.43	7.21
Tuckermanopsis sepincola	0.01	0.02	0.03	0.00	0.00	0.00
Umbilicaria deusta	0.00	0.00	0.00	0.00	0.19	0.00
Umbilicaria hyperborea	0.06	0.21	0.58	0.37	0.09	0.00
Umbilicaria muehlenbergi	0.03	0.00	0.00	0.00	0.00	0.00
Umbilicaria polyphylla	0.03	0.09	0.00	0.03	0.00	0.00
Umbilicaria proboscidea	0.20	0.20	0.68	1.80	0.00	0.00
Umbilicaria sp.	0.00	0.14	0.03	0.32	0.00	0.00
Umbilicaria torrefacta	0.00	0.05	0.11	0.00	0.00	0.00
Vulpicida pinastri	0.00	0.00	0.00	0.03	0.00	0.00

Table S4. Pearson's point biserial coefficient of correlation (rpb) of lichen's functional traits with regions and associated dominant vegetation types on a latitudinal gradient in Nunavik, Québec. Only traits with significant associations are presented ($p < 0.05$). From south to north, regions sampled were Clearwater Lake (CL), Boniface River (BR), Le Roy Lake (LR) Payne Lake (PL), Chukotat River (CR) and Deception Bay (DB).

	Traits	**Associated region (r_{pb} | p-value)**	**Associated vegetation type (r_{pb} | p-value)**
Photobiont	Cyanolichen	DB (0.704 | 0,001)	
	Tripartite	DB (0.637 | 0.002)	
Propagules	Isidias	LR + PR (0.584 | 0.008)	
Growth form	Crustose	LR + PR (0.494 | 0.02)	Open (0.643 | 0.001)
	Foliose - 3D	CR (0.508 | 0.014)	Herbaceous (0.595 | 0.002)
	Foliose - appressed	LR + PR (0.686 | 0.001)	Shrubland + Open (0.536 | 0.007)
	Foliose - broad	DB (0.73 | 0.001)	Herbaceous (0.420 | 0.046)
	Fruticose - branched	CL + BR (0.767 | 0.001)	Woodland + Shrubland + Open (0.654 | 0.001)
	Fruticose - Cladoniiform	CR + DB (0.561 | 0.006)	Woodland + Herbaceous (0.567 | 0.004)
	Fruticose - Filamentous	LR + PR (0.734 | 0.001)	Open (0.482 | 0.016)

Table S5. Bonferroni-adjusted p-values of the pairwise PERMANOVA analyses performed on species compositions (grey background) and on functional composition (white background) of macrolichens communities surveyed in six regions along a latitudinal gradient in Nunavik (Québec Canada). From south to north, regions sampled were Clearwater Lake (CL), Boniface River (BR), Le Roy Lake (LL) Payne Lake (PL), Chukotat River (CR) and Deception Bay (DB). Non-significant values are presented in bold.

	BR	LL	PL	CR	DB
CL	**1.00**	0.015	0.015	0.015	0.015
BR	**1.00**	0.015	0.030	0.015	0.045
LL	0.015	0.015	**1.00**	0.015	0.060
PL	0.030	0.030	**1.00**	0.030	0.060
CR	0.015	0.030	0.060	0.075	0.045
DB	0.015	0.015	0.015	0.045	**0.195**

Tableau S6. Types de végétation tels que définis par la cartographie de la végétation en milieu nordique du MFFP (2018).

Code	Désignation	Description
AAB	Arbustaie arctique basse (0,3 à 1 m)	Plus de 70 % d'arbustes* en milieu arctique (toundra). Les arbustes bas (0,3 à 1 m) font plus de 50 % du couvert arbustif.
AAH	Arbustaie arctique haute (> 1 m)	Plus de 70 % d'arbustes* en milieu arctique (toundra). Les arbustes hauts (> 1 m) font plus de 50 % du couvert arbustif. Toujours en bordure de cours d'eau.
AAM	Arbustaie arctique basse et mares de thermokarst	Plus de 70 % d'arbustes* en milieu arctique (toundra) et mares de thermokarst nombreuses
AB	Arbustaie basse (0,3 à 2 m)	Plus de 70 % d'arbustes* en milieu boréal ou subarctique. Les arbustes bas (0,3 à 2 m) font plus de 50 % du couvert arbustif.
ABM	Arbustaie et mares de thermokarst	Plus de 70 % d'arbustes* et mares de thermokarst nombreuses, en milieu boréal ou subarctique
AH	Arbustaie haute (> 2 m)	Plus de 70 % d'arbustes* en milieu boréal ou subarctique. Les arbustes hauts (> 2 m) font plus de 50 % du couvert arbustif. Toujours en bordure de cours d'eau.
LLA	Lande à lichens et arbustes	Entre 30 et 70 % d'arbustes* parmi une végétation de lichens, d'éricacées, de mousses et de conifères. Correspond généralement à un stade de développement après feu vers une forêt ouverte.
LSA	Lande subarctique avec arbustes	Lande subarctique ayant entre 30 et 70 % d'arbustes*.
TAO	Toundra avec arbustes et ostioles	Toundra ayant entre 30 et 70 % d'arbustes dressés* et des ostioles en grand nombre (entre 10 et 50 % de couverture). Les plantes vasculaires sont plus abondantes que dans la classe TDA. En terrain plat ou peu incliné.
TDA	Toundra ayant entre 30 et 70 % d'arbustes dressés*	Toundra ayant entre 30 et 70 % d'arbustes dressés*
LL	Lande à lichens	Plus de 30 % de lichens et moins de 30 % d'arbustes*. Correspond à une lande boisée (< 10 % d'arbres) ou à un stade de développement après feu vers une forêt ouverte à lichens.
LS	Lande subarctique	Agencement de végétation de toundra (c.-à-d. sans arbres et composée d'un mélange de lichens, d'éricacées, d'arbustes, d'herbacées et de mousses) et de petits peuplements forestiers ou de landes boisées. Moins de 10 % d'arbres et moins de 30 % d'arbustes*. Généralement dominé par les lichens.
LSC	Lande subarctique de combe à neige	Lande subarctique en position topographique de forte accumulation de neige où la composition végétale se distingue des sites adjacents à cause d'un retard dans la saison de croissance.
LSM	Lande subarctique et mares de thermokarst	Lande subarctique ayant de nombreuses mares de thermokarst. Les arbustes* sont généralement assez abondants. Associée aux dépôts marins.
TD	Toundra à arbustes dressés	Végétation composée d'un mélange d'arbustes dressés*, d'arbustes prostrés ou rampants, d'herbacées, de lichens et de mousses. Moins de 30 % d'arbustes dressés*.
TDC	Toundra de combe à neige	Toundra en position topographique de forte accumulation de neige où la composition végétale se distingue des sites adjacents à cause d'un retard dans la saison de croissance.
TDM	Toundra à arbustes dressés avec mares de thermokarst	Toundra ayant de nombreuses mares de thermokarst et les arbustes dressés* sont généralement assez abondants. Associé aux dépôts marins.

Code	Désignation	Description
TDO	Toundra à arbustes dressés avec ostioles	Toundra ayant moins de 30 % d'arbustes dressés* et des ostioles en grand nombre (entre 10 et 50 % de couverture). Les plantes vasculaires sont plus abondantes que dans la classe TD. En terrain plat ou peu incliné.
LLR	Lande à lichens avec > 10 % de substrat rocheux	Entre 10 et 50 % de roc, fragments rocheux et sol minéral à nu, parmi une végétation de lichens, d'éricacées, d'arbustes, de mousses et de conifères.
LSR	Lande subarctique avec 10-50 % de substrat rocheux	Lande subarctique ayant moins de 30 % d'arbustes* et entre 10 et 50 % de roc, fragments rocheux ou sol minéral à nu.
RLS	Lande subarctique dominée par le substrat rocheux	Entre 50 et 80 % de roc, fragments rocheux ou sol minéral à nu, avec une végétation éparse de lichens, d'éricacées, d'arbustes, de mousses et de conifères arborescents.
RTD	Toundra à arbustes dressés dominée par le substrat rocheux	Toundra ayant entre 50 et 90 % de roc, fragments rocheux et sol minéral à nu.
RTP	Toundra à arbustes prostrés dominée par le substrat rocheux	Toundra à arbustes prostrés ayant entre 50 et 80 % de roc, fragments rocheux et sol minéral à nu.
TDR	Toundra à arbustes dressés avec 10- 50 % de substrat rocheux	Toundra ayant moins de 30 % d'arbustes dressés et entre 10 et 50 % de roc, fragments rocheux et sol minéral à nu.
TH	Toundra herbacée avec arbustes prostrés	Toundra à arbustes prostrés ayant plus de 10 % d'herbacées. Associé aux versants avec ruissellement nival.
TP	Toundra à arbustes prostrés	Toundra sans arbustes dressés. La végétation dépasse difficilement 20 cm de haut et le substrat minéral affleure régulièrement (jusqu'à 50 % de roc, fragments rocheux et sol minéral à nu).
TPO	Toundra à arbustes prostrés avec ostioles	Toundra à arbustes prostrés ayant des ostioles (ou autres formes périglaciaires apparentées) en grand nombre (entre 10 et 50 % de couverture). Les plantes vasculaires sont plus abondantes que dans la classe TP. En terrain plat ou peu incliné.
Rcm	Forêt de résineux avec sous-bois de lichens et mousse	Forêt de résineux avec entre 40 et 60 % de lichens sur la superficie totale de lichens, mousses et éricacées, densité de résineux entre 10% et 60%
Rc	Forêt de résineux avec sous-bois de lichens	Forêt de résineux avec plus de 60 % de couverture de lichens sur la superficie totale de lichens, mousses et éricacées, densité de résineux entre 10% et 60%
F	Forêt de feuillus	Forêt de feuillus, avec une densité de feuillus entre 10 et 80%
M	Forêt mélangée	Forêt contenant des feuillus et des résineux, avec une densité de feuillus entre 10 et 80%
Ra	Forêt de résineux avec sous-bois arbustif	Forêt de résineux avec plus de 50 % de saule, bouleau glanduleux ou aulne, densité de résineux entre 10% et 60%
Rm	Forêt de résineux avec sous-bois de mousses et éricacées	Forêt de résineux avec moins de 40 % de couverture de lichens sur la superficie totale de lichens, mousses et éricacées, densité de résineux >10%
EAU	Eau	Lac, cours d'eau, site inondé
MR	Marais et marécage d'eau douce	Herbaçaie ou arbustaie submergée lors des hautes eaux printanières.*
MS	Marais d'eau salé	Herbaçaie sous influence tidale d'eau salée ou saumâtre.*

Code	Désignation	Description
TMR	Tourbière minérotrophe riveraine	Tourbière bordant un cours d'eau ou un plan d'eau et inondée lors de la crue printanière.
TMS	Tourbière minérotrophe structurée	Alternance de lanières herbacées et de mares allongées et linéaires.
TMU	Tourbière minérotrophe uniforme	Végétation homogène (platières) composée principalement de plantes herbacées.
TOM	Tourbière ombrotrophe à mares	Présence de grandes mares. Tourbière généralement de grande superficie.
TOP	Tourbière à palses	Tourbière dont les palses et les mares sont nombreuses.
TOR	Tourbière ombrotrophe ridée	Alternance de lanières arbustives et de dépressions herbacées.
TOS	Tourbière ombrotrophe structurée	Alternance de lanières arbustives et de mares allongées et arquées.
TOU	Tourbière ombrotrophe uniforme	Végétation homogène (platières et plateaux) dominée par des herbaçaies ou des arbustaies. En milieu boréal et subarctique.
TAR	Tourbière arctique ou toundra humide	Tourbière située en toundra ou toundra sur sol minéral montrant de grandes zones de ruissellement superficiel. Les tourbières sont minérotrophes et l'accumulation de tourbe est réduite due aux conditions arctiques. Plus de 50 % de couverture par les sites humides.
TAA	Tourbière arctique avec 30-70 % d'arbustes dressés	Tourbière arctique ayant de 30 à 70 % d'arbustes dressés (> 30 cm; bouleau glanduleux, aulnes, saules).
AR	Affleurements et fragments rocheux	Roc à nu ou fragments rocheux, incluant de vastes champs de blocs sur collines dans l'extrême nord. Moins de 20 % de végétation.
CB	Champs de blocs	Plus de 50 % de couverture par des champs de blocs. Dans des sites propices au délavage du matériel dans les plaines et dépressions topographiques. Moins de 20 % de végétation.
NE	Neige	Neige accumulée dans des dépressions topographiques aux latitudes et altitudes les plus élevées. Observé en juillet ou août.
SD	Surface dénudée	Sable, plages et autres surfaces sans végétation. Moins de 20 % de végétation.
BR	Brûlis total	75 % des arbres morts
IH	Infrastructure humaine	Habitations, rues, routes, barrage, poste hydroélectrique, etc.
ILE	Île de moins de 8 ha	Île présente dans la BNDT** et inférieure à l'aire minimale de cartographie.
LTE	Ligne de transport d'énergie	

* Réfère aux arbustes érigés (> 30 cm de haut) feuillus, ce qui comprend le bouleau glanduleux, les saules et les aulnes, et exclus les éricacées.

**Base nationale de données topographiques de Ressources naturelles Canada

Annexe 2: Figures supplémentaires

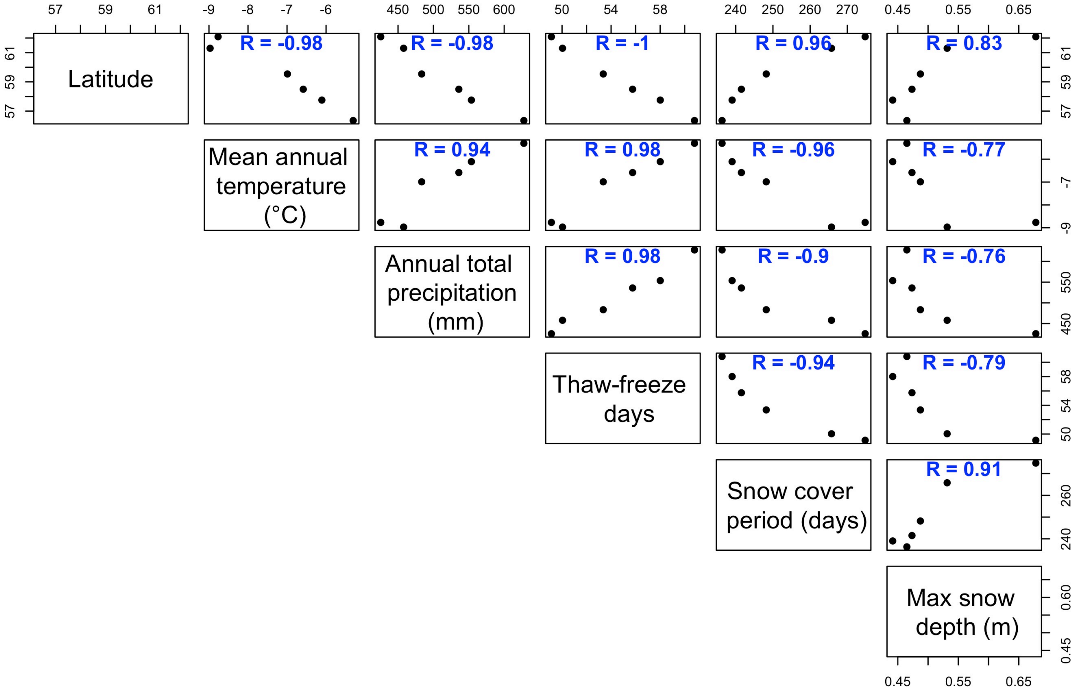
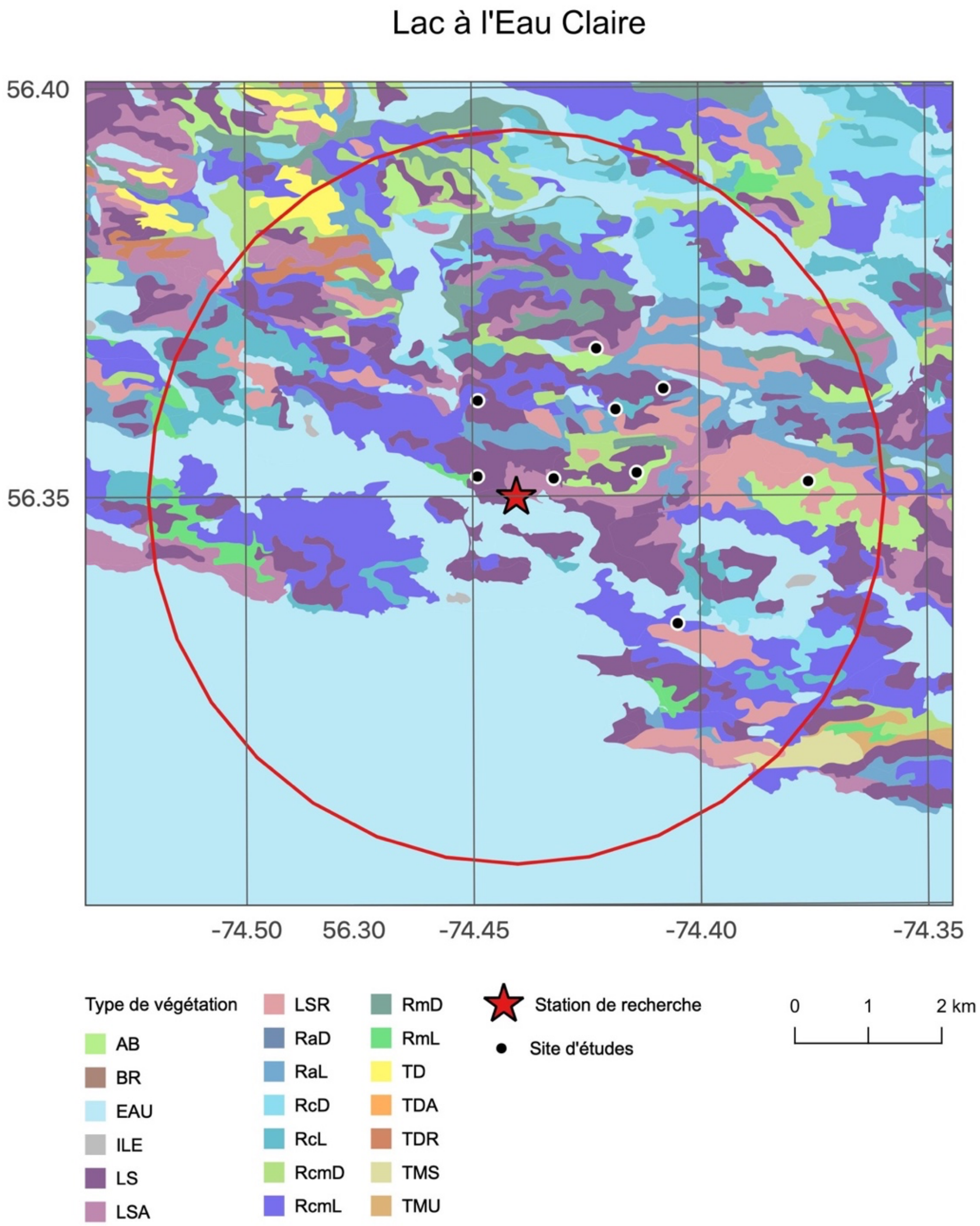


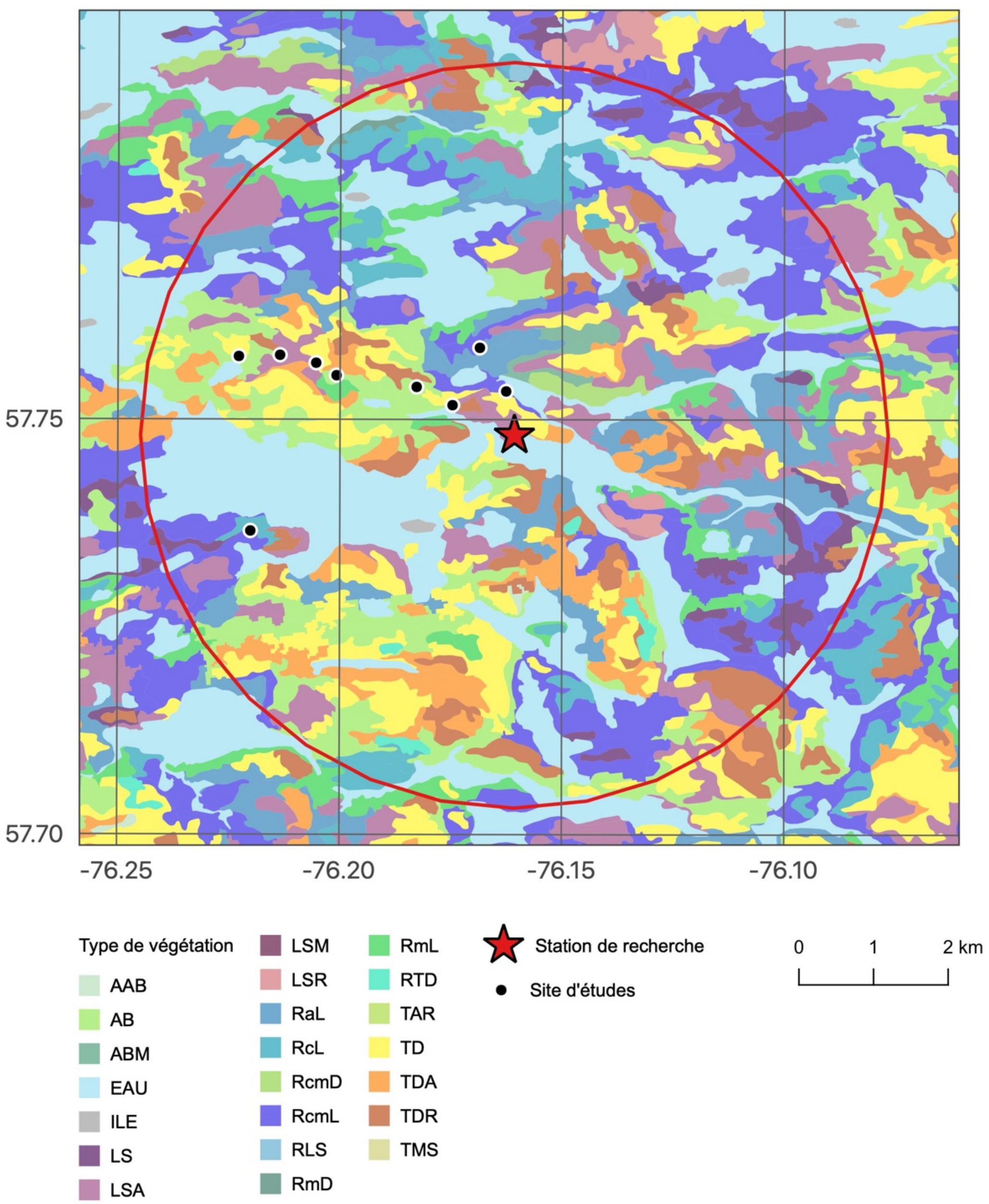
Figure S1. Correlation between climate variables and latitude. Pearson coefficient of correlation (r) is indicated in *blue* on each of the plots.



Ministère des Forêts, de la Faune et des Parcs,2018. Cartographie écologique de la végétation du nord québécois. Gouvernement du Québec.

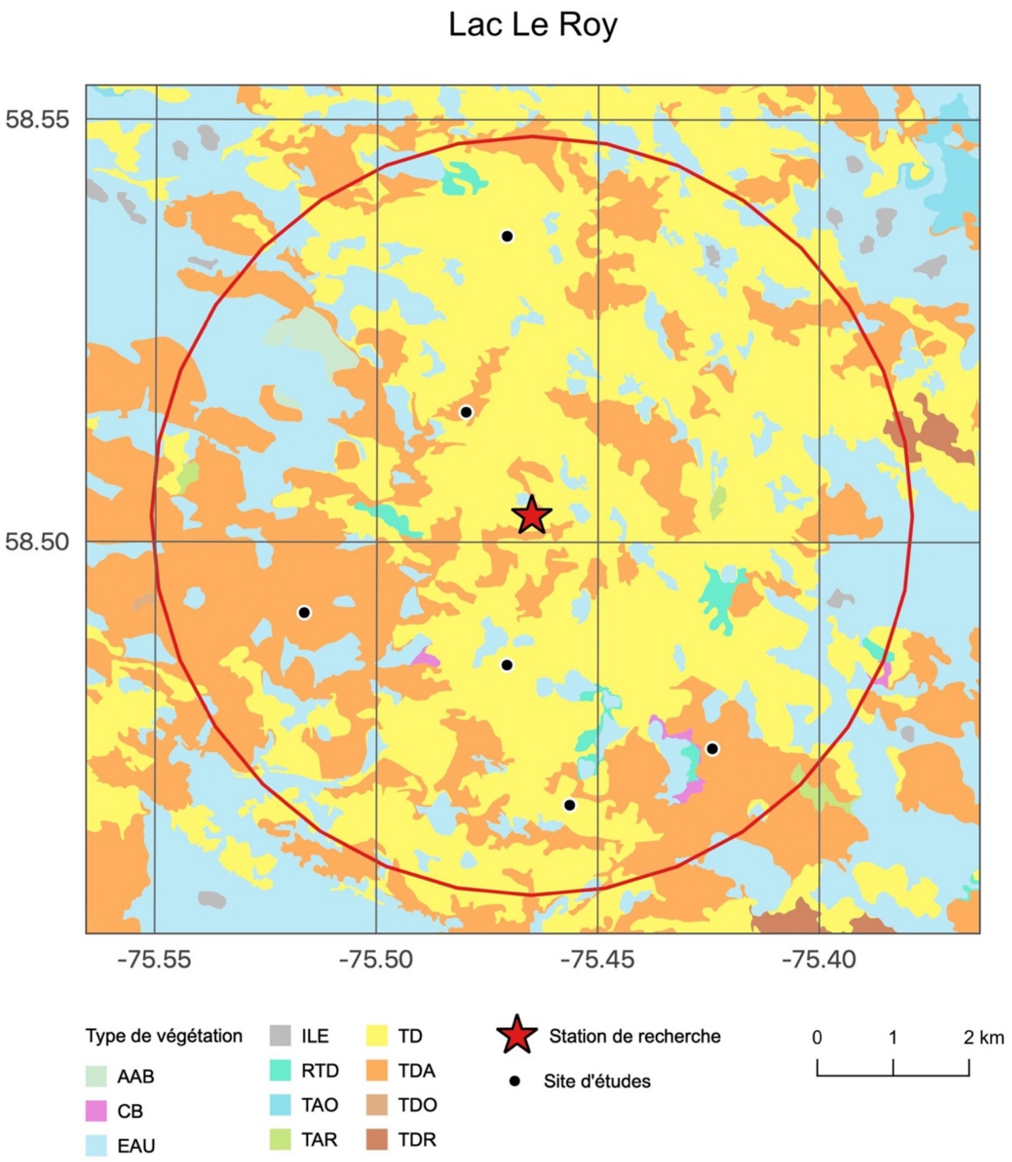
Figure S2. Types de végétation (MFFP 2018) et sites d'échantillonnage dans un rayon de cinq kilomètres autour de la station de recherche du Lac à L'Eau Claire. Le tableau S6 présente la signification des codes utilisés pour définir les types de végétation.

Rivière Boniface



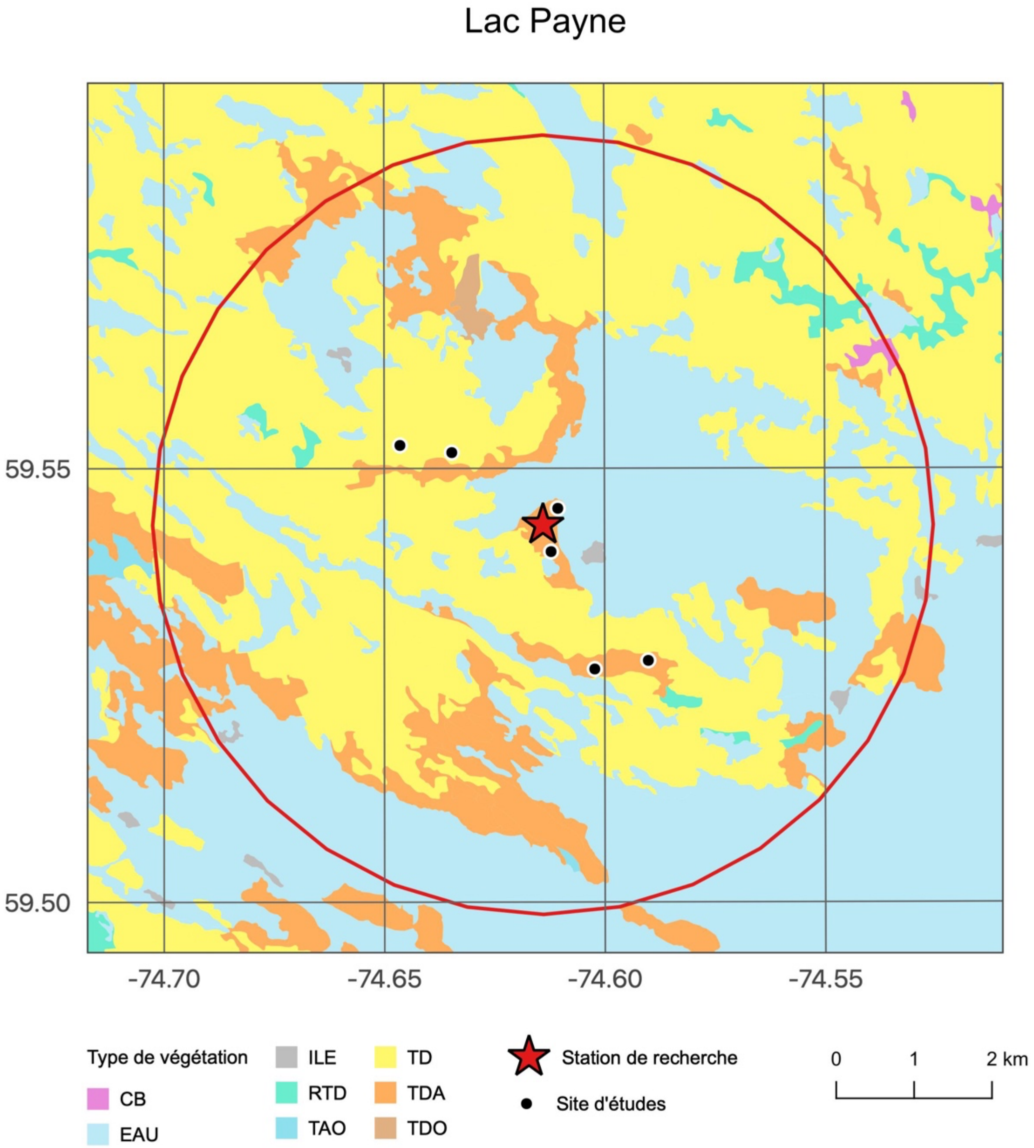
Ministère des Forêts, de la Faune et des Parcs,2018. Cartographie écologique de la végétation du nord québécois. Gouvernement du Québec.

Figure S3. Types de végétation (MFFP 2018) et sites d'échantillonnage dans un rayon de cinq kilomètres autour de la station de recherche de la rivière Boniface. Le tableau S6 présente la signification des codes utilisés pour définir les types de végétation.



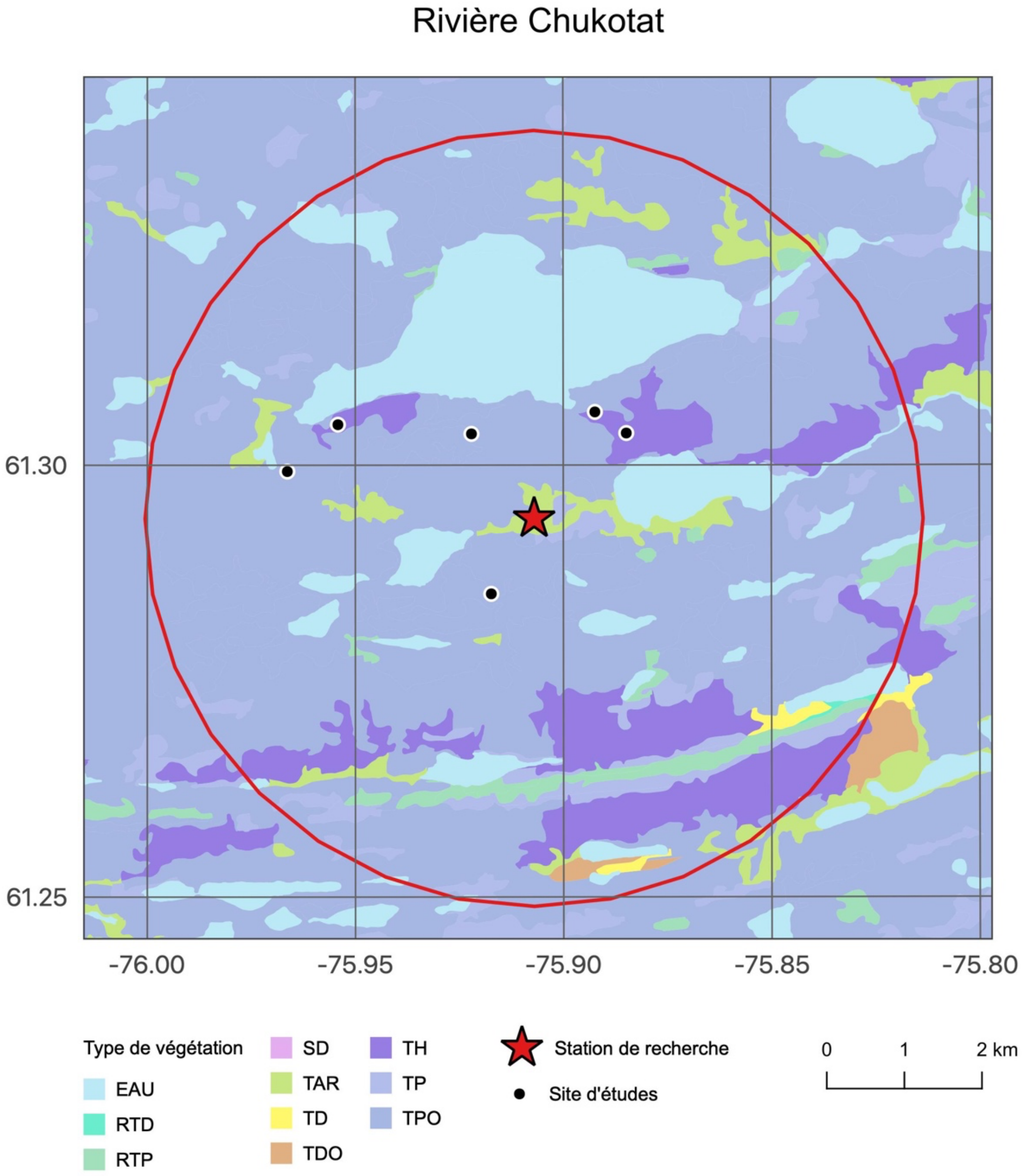
Ministère des Forêts, de la Faune et des Parcs,2018. Cartographie écologique de la végétation du nord québécois. Gouvernement du Québec.

Figure S4. Types de végétation (MFFP 2018) et sites d'échantillonnage dans un rayon de cinq kilomètres autour de la station de recherche du Lac Le Roy. Le tableau S6 présente la signification des codes utilisés pour définir les types de végétation.



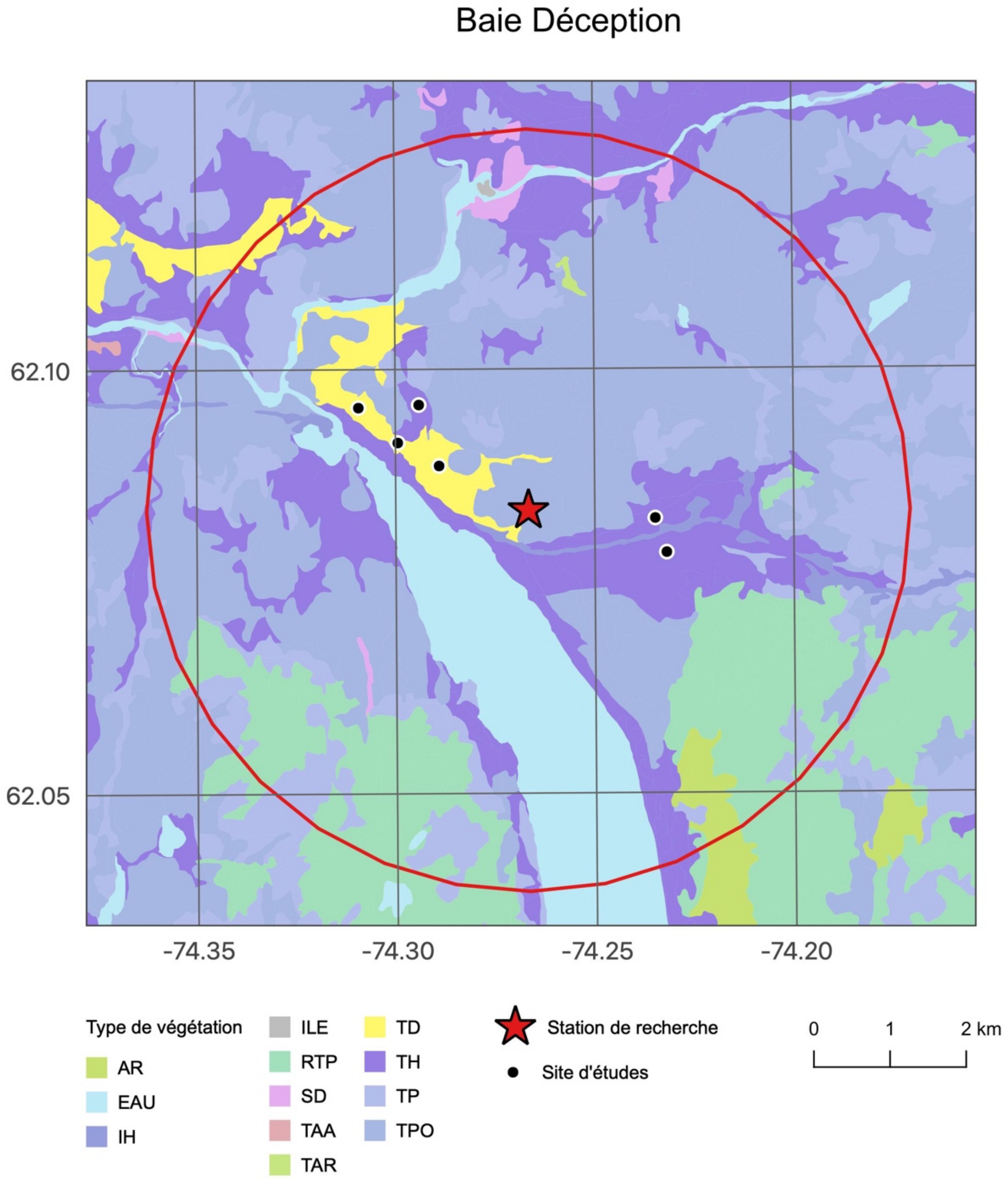
Ministère des Forêts, de la Faune et des Parcs,2018. Cartographie écologique de la végétation du nord québécois. Gouvernement du Québec.

Figure S5. Types de végétation (MFFP 2018) et sites d'échantillonnage dans un rayon de cinq kilomètres autour de la station de recherche du Lac Payne. Le tableau S6 présente la signification des codes utilisés pour définir les types de végétation.



Ministère des Forêts, de la Faune et des Parcs,2018. Cartographie écologique de la végétation du nord québécois. Gouvernement du Québec.

Figure S6. Types de végétation (MFFP 2018) et sites d’échantillonnage dans un rayon de cinq kilomètres autour de la station de recherche de la rivière Chukotat. Le tableau S6 présente la signification des codes utilisés pour définir les types de végétation.



Ministère des Forêts, de la Faune et des Parcs,2018. Cartographie écologique de la végétation du nord québécois. Gouvernement du Québec.

Figure S7. Types de végétation (MFFP 2018) et sites d'échantillonnage dans un rayon de cinq kilomètres autour de la station de recherche de Baie Déception. Le tableau S6 présente la signification des codes utilisés pour définir les types de végétation.