

UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

PATRONS MULTI-ÉCHELLES DE COMPOSITION ET DE RICHESSE
SPÉCIFIQUE DES COMMUNAUTÉS DE LICHENS LE LONG D'UN
GRADIENT CLIMATIQUE EN FORÊT BORÉALE MIXTE

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RÉSUMÉ

Les connaissances sur les relations entre les communautés écologiques et le climat sont importantes pour anticiper les impacts que les changements climatiques auront sur elles. Toutefois, les processus opérant à différentes échelles qui interagissent entre elles compliquent notre compréhension. Les lichens étant étroitement liés aux conditions d'eau et de température de leur environnement, les gradients macro-climatiques peuvent participer à façonner leurs communautés. L'objectif général de notre étude était d'évaluer l'effet d'un gradient climatique sur les communautés de macrolichens. Spécifiquement, nous cherchions à 1) identifier les déterminants de la composition en espèces à l'échelle du site et à l'échelle du substrat le long du gradient climatique, et 2) établir si la richesse spécifique à l'échelle du site et à l'échelle du substrat est déterminée par le gradient climatique. Pour ce faire, nous avons effectué des inventaires de macrolichens sur quatre types de substrats (épinettes, bouleaux, chicots et roches) le long du gradient climatique généré par le lac Supérieur. Nous avons inventorié 54 sites situés à différentes distances de la rive dans les forêts boréales mixtes de la côte nord du lac. Nos résultats ont démontré que la composition à l'échelle du site et à l'échelle du substrat était avant tout déterminée par la latitude. En sus, l'échelle du site était surtout déterminée par la distance du lac Supérieur, tandis que l'échelle du substrat était surtout déterminée par la structure forestière, notamment par le diamètre à hauteur de poitrine (DHP) maximal du site et par le pourcentage de couvert forestier. La distance du lac Supérieur n'avait pas d'impact direct ou indirect sur la richesse spécifique, et ce à aucune des deux échelles. Cependant, les effets des facteurs locaux et des variables liées aux substrats étaient moindres près du lac. Nos résultats soulignent l'importance de considérer l'échelle spatiale dans l'analyse de la composition en espèces de lichens, puisque les gradients climatiques régionaux avaient plus d'influence sur l'échelle du site alors que les facteurs locaux avaient plus d'influence sur l'échelle du substrat. L'absence de tendance dans la richesse spécifique suggère un remplacement des espèces le long du gradient climatique, lequel pourrait potentiellement être lié aux traits fonctionnels des espèces. Ainsi, les changements attendus dans les conditions climatiques de la forêt boréale ne mèneraient pas nécessairement à une diminution de la richesse spécifique locale dans les peuplements mixtes, mais l'aire de répartition des espèces hygrophytes pourrait se voir rétrécie. Les peuplements avec des gros arbres et avec un important couvert forestier pourraient être visés pour la conservation de ces espèces.

CHAPITRE I

INTRODUCTION GÉNÉRALE

1.1 Mise en contexte et problématique

Une connaissance approfondie des patrons de distribution des lichens en forêt boréale et de leur réponse aux conditions environnementales est primordiale pour assurer la conservation de leur biodiversité. En effet, les manques d'informations sur la distribution géographique des espèces (lacunes wallacéennes) et sur la réponse des espèces aux conditions abiotiques (lacunes hutchinsoniennes) ont été identifiés comme étant des cibles prioritaires pour combler les déficits dans les données actuelles sur la biodiversité (Hortal et al., 2015). Ces connaissances sont cruciales pour éviter la disparition d'espèces que pourraient occasionner les changements profonds que subit actuellement la biosphère (IPBES, 2019). Les lichens sont menacés par les mêmes phénomènes que l'ensemble de la biodiversité : la perte d'habitats et le recul du couvert des vieilles forêts contribuent au déclin de leurs populations (Goward, 1994; Scheidegger & Werth, 2009; Selva, 1994), les changements climatiques risquent d'apporter d'importantes modifications à leur distribution (Ellis et al., 2007) et la pollution a des effets négatifs sur plusieurs espèces (Giordani et al., 2002; Hawksworth & Rose, 1970; van Herk et al., 2003). Or, les lichens jouent un rôle important dans les écosystèmes. Ils participent aux cycles de l'eau et de l'azote, abritent une grande diversité de microfaune et s'insèrent dans divers réseaux trophiques (Ellis, 2012). Ils sont aussi des indicateurs utiles pour évaluer la qualité de l'air (Abas, 2021; Augusto

et al., 2013; Conti & Cecchetti, 2001; Frati & Brunialti, 2023) ainsi que la résilience et la continuité des écosystèmes forestiers (Arsenault & Goward, 2016; Dymytrova et al., 2018; McMullin & Wiersma, 2019; Wiersma & McMullin, 2022).

À cheval entre le Canada et les États-Unis, les Grands Lacs Laurentiens forment un réseau de lacs d'eau douce d'une superficie de 244 100 km² issu de la fonte de l'inlandsis Laurentidien à la fin de la glaciation wisconsinienne. Ils exercent une forte influence sur le climat régional. En effet, sur un gradient climatique de 80 km de rayon, ils modèrent les températures, en plus d'induire une diminution des précipitations et du déficit de pression de vapeur durant l'été (Bates et al., 1993; Changnon & Jones, 1972; Notaro et al., 2013; Scott & Huff, 1997). En raison de ses grandes dimensions, le lac Supérieur est celui qui entraîne les modifications climatiques les plus importantes (Scott & Huff, 1997). Le climat qu'il induit permet l'établissement de communautés de lichens typiquement océaniques sur la zone côtière de sa rive nord (Brodo et al., 2001).

Les lichens sont des organismes poïkilohydriques, c'est-à-dire que, n'ayant pas de mécanisme de régulation de leur teneur en eau, celle-ci varie passivement avec l'environnement. Leur présence et leur abondance sont donc grandement influencées par les précipitations, la rosée et l'humidité relative de l'air (Gauslaa, 2014). Les communautés de lichens dépendent ainsi des gradients macro-climatiques régionaux (Giordani & Incerti, 2008; McCune et al., 1997; Werth et al., 2005), mais aussi de facteurs liés aux micro-habitats, tels que la présence de bryophytes (Colesie et al., 2012; Ellis, 2020), la proximité de cours d'eau (Ellis, 2020; Lidén & Hilmo, 2005) et la structure forestière (Arsenault & Goward, 2016; Marini et al., 2011; Merinero et al., 2014; Mežaka et al., 2012). Bien que certaines études se soient intéressées aux

interactions entre le macroclimat, les micro-habitats et la distribution des lichens (e. g. Lidén & Hilmo, 2005; Merinero et al., 2014; Rutherford & Rebertus, 2022), les données manquent en ce qui concerne la forêt boréale. La présente étude a pour objectif de déterminer comment l'interaction entre le gradient climatique généré par le lac Supérieur et les substrats influence les communautés de lichens.

1.2 État des connaissances

1.2.1 Caractéristiques et classification des lichens

Les lichens sont des organismes qui résultent de symbioses complexes. Dans sa forme la plus simplifiée, l'association comprend un partenaire fongique, le mycobionte, et au moins un partenaire photosynthétique, le photobionte. Le photobionte fournit le mycobionte en glucides issus de la photosynthèse, alors que le mycobionte offre au photobionte une structure le protégeant de la dessiccation et de l'herbivorie. Des recherches aussi ont démontré la présence d'abondantes communautés bactériennes (Bates et al., 2012) et de levures basidiomycètes (Mark et al., 2020; Spribille et al., 2016) au sein des thalles. L'importance des microorganismes dans l'association reste à déterminer, mais il a été suggéré que les lichens pourraient être considérés comme des écosystèmes formés des partenaires fongiques et photosynthétiques et d'un nombre indéterminé d'organismes microscopiques (Hawksworth & Grube, 2020).

Les associations de lichens ne portent pas de nom scientifique : les partenaires sont nommés et classifiés individuellement. On réfère donc aux lichens par le nom scientifique de leur mycobionte primaire, un Ascomycète pour la grande majorité, qui

peut toutefois être associé à différentes espèces de photobiontes. Le photobionte peut être une algue verte, une cyanobactérie ou parfois les deux. On appelle *chlorolichens* les lichens dont le photobionte primaire est une algue verte, *cyanolichens* ceux dont le photobionte primaire est une cyanobactérie et *céphalolichens* ceux dont le photobionte primaire est une algue verte et dont le photobionte secondaire est une cyanobactérie, laquelle forme des amas sur la surface du thalle appelés céphalodies (Gauslaa et al., 2012; Lange & Wagenitz, 2003).

Les lichens peuvent être divisés en trois grands groupes selon la morphologie de leur thalle : les lichens crustacés, qui forment une croûte adhérant étroitement au substrat et dépourvue de cortex inférieur; les lichens foliacés, dont le thalle est plat, partiellement attaché au substrat et ayant des cortex inférieur et supérieur distincts; et les lichens fruticuleux, qui ont le thalle saillant et minimalement attaché à la surface du substrat, et dont les lobes sont plats ou cylindriques, sans claire distinction entre les cortex inférieur et supérieur. Les lichens foliacés et fruticuleux sont parfois regroupés sous le nom de *macrolichens*, en opposition aux lichens crustacés, les *microlichens*, une classification principalement basée sur des raisons pratiques. En effet, les lichens crustacés requièrent un plus grand effort d'identification, des analyses de chromatographie sur couche mince des composés chimiques secondaires s'imposant pour bon nombre d'espèces. Ainsi, bien que les microlichens contribuent de façon importante à la diversité (Dietrich & Scheidegger, 1996; Ellis & Coppins, 2006; Honegger, 2008), plusieurs recherches se concentrent sur les macrolichens (e.g. Arsenault & Goward, 2016; Coyle & Hurlbert, 2016; Geiser & Neitlich, 2007; McCune et al., 1997; Werth et al., 2005), d'autant plus qu'ils ont été reconnus comme étant de bons indicateurs de la diversité globale de lichens (Bergamini et al., 2005, 2007).

1.2.2 Facteurs d'habitat des lichens

1.2.2.1 Disponibilité en eau

Les lichens sont étroitement liés aux conditions hydriques de leur environnement. Étant poïkilohydriques, ils n'ont pas de mécanismes de régulation de leur teneur en eau et sont ainsi hydratés et actifs lorsque l'eau est disponible et desséchés et dormants lorsqu'elle ne l'est pas. Cette tolérance à la dessiccation a contribué à leur succès écologique dans une grande variété de milieux (Kappen & Valladares, 1999). Bien sûr, le niveau de stress hydrique que les espèces tolèrent est spécifique aux conditions d'humidité auxquelles elles sont adaptées dans leur habitat naturel (Bewley, 1979; Green et al., 2011). Green et coll. (1991) ont même démontré que *Pseudocyphellaria dissimilis*, une espèce de cyanolichen foliacé ombrophile, est sensible à la dessiccation. Les lichens atteignent une photosynthèse nette maximale lorsque leur teneur en eau est optimale, ce qui semble être lorsque les cellules algales et fongiques sont complètement turgescentes (Green et al., 2008). Cette teneur optimale en eau varie largement entre les espèces (Lange et al., 1993) et est considérablement plus élevée chez les cyanolichens (Green et al., 2008). Au-delà de la teneur optimale en eau, l'hydratation excessive peut accroître la résistance du thalle à la diffusion du CO₂ et ainsi inhiber la photosynthèse, un phénomène nommé dépression de suprasaturation (Lange et al., 1993, 2001; Lange & Tenhunen, 1981).

Les lichens peuvent utiliser une variété de sources d'hydratation pour activer leur métabolisme. Toutes les espèces absorbent l'eau de pluie et de la rosée (i.e. condensation de vapeur d'eau) et les chlorolichens et les céphalolichens ont également la capacité d'utiliser l'humidité de l'air, laquelle est inaccessible à la plupart des plantes

vasculaires (Gauslaa, 2014). Le mécanisme par lequel un lichen absorbe l'eau de l'humidité de l'air est essentiellement le processus inversé de l'évaporation: lorsque son potentiel hydrique est inférieur à celui de son environnement, l'eau se déplace vers le thalle jusqu'à l'atteinte d'un équilibre (Palmqvist et al., 2008). Un tel gradient se crée généralement à des températures inférieures à 20°C ou à une humidité relative d'au moins 75% (Palmqvist et al., 2008). Les cyanolichens, quant à eux, nécessitent de l'eau liquide pour initier la photosynthèse (Lange et al., 1986), car ils requièrent une teneur en eau plus élevée pour atteindre une photosynthèse nette positive, laquelle ne peut être atteinte avec l'humidité de l'air seulement (Green et al., 2011). En effet, l'hydratation par l'humidité de l'air chez les chlorolichens et les céphalolichens est nettement plus lente que celle par l'eau liquide et ne permet pas d'atteindre la photosynthèse nette maximale (Jonsson Čabrajčić et al., 2010; Scheidegger et al., 1995). En revanche, l'hydratation par l'eau liquide peut réactiver la photosynthèse en quelques minutes (Lange et al., 1986), mais peut mener à la dépression de suprasaturation, laquelle ne survient pas avec l'humidité de l'air (Gauslaa, 2014). L'étendue du compromis entre l'hydratation par l'humidité de l'air et l'hydratation par l'eau liquide varie entre les espèces et entre les habitats.

Comme la disponibilité en eau influence la performance des espèces, les conditions hydriques façonnent les communautés de lichens. Les gradients macro-climatiques de précipitations et d'humidité influencent la présence de lichens (Ellis, 2020; Jesberger & Sheard, 1973), l'abondance des nombreuses espèces (Giordani & Incerti, 2008; Lidén & Hilmo, 2005; Merinero et al., 2014), la composition des communautés (Jovan & McCune, 2004; Werth et al., 2005) et leur richesse spécifique (Marini et al., 2011). Ces gradients sont souvent associés à des gradients de température, laquelle joue un rôle dans l'efficacité de la photosynthèse des espèces (Green et al., 2008). Des études ont démontré que la température contribue elle-aussi à déterminer la composition des

communautés de lichens (Giordani & Incerti, 2008; Jovan & McCune, 2004; McCune et al., 1997; Werth et al., 2005). Les gradients macro-climatiques interagissent avec des facteurs à plus petites échelles et modifient les exigences des espèces quant à la qualité de leur habitat (Lõhmus et al., 2023; Scheidegger & Werth, 2009). Par exemple, en climat humide, les espèces de la communauté *Lobarion* colonisent un vaste étendu d'habitats, incluant les peuplements jeunes et fragmentés, alors qu'en climat plus sec, elles sont confinées aux peuplements plus vieux et plus continus (Ellis & Coppins, 2007; Peterson & McCune, 2001). De la même manière, en climat continental, les vieilles forêts constituent des refuges pour des espèces hygrophytes, ce qui serait dû en partie aux conditions microclimatiques qu'elles créent (Arsenault & Goward, 2016).

À une plus petite échelle, des facteurs locaux peuvent influencer les conditions hydriques. Les cours d'eau, par exemple, ont une influence sur l'humidité relative de leur environnement (Anderson et al., 2007; Danehy & Kirpes, 2000). Dans un macroclimat plus sec, le microclimat qu'ils génèrent favorise la présence et l'abondance de lichens (Ellis, 2020; Lidén & Hilmo, 2005). La présence de bryophytes peut également avoir un impact sur la présence et la croissance de certaines espèces de lichens (Colesie et al., 2012; Ellis, 2020). Les thalles associés aux bryophytes se dessèchent plus lentement, probablement grâce à la capacité de rétention d'eau de ces derniers qui permet le maintien d'un microclimat humide (Colesie et al., 2012). Ainsi, en environnement xérique, 70% des thalles du cyanolichen *Peltigera rufescens* observés étaient associés à des mousses (Colesie et al., 2012). Cependant, en climat très humide, le couvert et le nombre d'espèces de bryophytes épiphytes surpassent ceux des lichens (Glime & Hong, 2002), suggérant une compétition pour l'occupation des substrats. Cette compétition pourrait aussi avoir lieu à de plus petites échelles, car les micro-habitats les plus humides sont également dominés par les mousses (Boudreault et al., 2008b).

1.2.2.2 Substrats

Un substrat peut être défini comme étant une surface propice à l'établissement et à la croissance de lichens, ce qui inclut entre autres l'écorce, le bois mort et les surfaces rocheuses. La plupart des lichens sont limitées à certains substrats, bien que cette spécificité soit variable entre les espèces (Brodo et al., 2001). La disponibilité en substrats dans un peuplement est influencée par la structure forestière. Les peuplements plus vieux et moins aménagés offrent une plus grande variété de substrats et abritent plus d'espèces de lichens (Boudreault, et al., 2008b; Lesica et al., 1991; Spribille et al., 2008).

Chez les communautés épiphytes, l'espèce de l'arbre hôte est un déterminant majeur de la composition et de la richesse spécifique (Arsenault & Goward, 2016; Jesberger & Sheard, 1973; Kuusinen, 1996; McDonald et al., 2017; Mežaka et al., 2012). À l'échelle du peuplement, une plus grande diversité d'arbres peut faire augmenter la richesse de lichens (Uliczka & Angelstam, 1999). Des observations ont démontré que les feuillus ont une plus grande contribution à la biodiversité que les conifères (McDonald et al., 2017; Uliczka & Angelstam, 1999; Wigle et al., 2021), ce qui peut en partie être expliqué par la plus grande acidité de ces derniers (Hauck, 2011). Bien que le pH de l'écorce ne soit pas indépendant de l'espèce (Barkman, 1958; Jesberger & Sheard, 1973), il est reconnu comme étant un important déterminant de la composition (Kuusinen, 1996; Mežaka et al., 2012; Wigle et al., 2021). Paul et coll. (2009) ont suggéré que l'exclusion des espèces alcalinophiles sur l'écorce acide pourrait être due à une absorption excessive de Fe^{2+} qui entrainerait des symptômes de toxicité. Le pH de l'écorce serait également corrélé négativement à l'âge de l'arbre, du moins chez les peupliers (*Populus*) (Barkman, 1958; Boudreault et al., 2008b).

L'âge de l'arbre est un autre facteur important de la richesse spécifique qu'il supporte (Lie et al., 2009; Nascimbene et al., 2009; Uliczka & Angelstam, 1999), bien qu'il soit difficile de le séparer de la taille de l'arbre. Cependant, certains facteurs de sites peuvent influencer l'interaction âge-taille, et une étude de Lie et coll. (2009) dans des forêts où l'âge et la taille des arbres n'étaient pas corrélés a démontré que les deux variables affectent indépendamment et positivement la diversité de lichens. Plusieurs hypothèses ont été avancées pour expliquer la relation entre l'âge et la taille de l'arbre et la diversité de lichens : les vieux arbres pourraient permettre un plus grand temps de colonisation, les gros arbres pourraient offrir une plus grande surface de colonisation, ou la relation pourrait être due à une question de méthodes, où l'échantillonnage d'une plus grande surface mènerait à l'observation de plus d'espèces (Lie et al., 2009; Nascimbene et al., 2009). Une autre explication pourrait être que les propriétés physiques de l'écorce changent avec l'âge (Uliczka & Angelstam, 1999). Par exemple, la rugosité de l'écorce peut être associée à l'âge de l'arbre (Boudreault et al., 2008b), en plus d'être associée à l'espèce (Barkman, 1958). Les crevasses des écorces plus rugueuses retiennent l'eau et offre un micro-habitat propice à la colonisation (Barkman, 1958; Brodo, 1973), ce qui peut expliquer que la rugosité constitue un déterminant de la composition des communautés (Boudreault et al., 2008b; Merinero et al., 2014). En bref, il est important de prendre en compte que les facteurs d'habitats des lichens épiphytes sont fortement interreliés, ce qui peut rendre difficile la dissociation des différents effets.

La présence de bois mort dans un peuplement est un important facteur de la diversité des communautés de lichens (Lesica et al., 1991). Spribille et coll. (2016) ont observé que 10% des espèces recensées, principalement des lichens crustacés, se retrouvaient obligatoirement sur le bois mort dans les régions étudiées. Le bois mort diffère des arbres vivants par son pH souvent moins acides (Hauck, 2011), sa plus grande rétention d'eau (Barkman, 1958) et sa surface moins cortiquée. On inclut dans le bois mort les

chicots, les souches et le bois mort au sol. Bien qu'ils soient moins humides, les chicots ont tendance à supporter une plus grande diversité de lichens (Dittrich et al., 2014; Humphrey et al., 2002), ce qui pourrait en partie être dû à une plus grande exposition à lumière. Le niveau de décomposition du bois a aussi une importance sur la composition et la diversité des communautés. Le bois mort faiblement décomposé supporte plus d'espèces épiphytes, alors que le bois mort plus décomposé supporte plus d'espèces terricoles (Arsenault & Goward, 2016). La diversité semble atteindre un sommet à des classes de décomposition intermédiaires, ce qui pourrait être lié à une plus grande hétérogénéité de micro-habitats (Humphrey et al., 2002).

Les lichens font partie des rares organismes qui colonisent les surfaces rocheuses. Bien que la plupart des espèces soient adaptées à croître exclusivement sur les roches, et souvent sur un type spécifique (Brodo et al., 2001), certaines sont retrouvées sur les roches ainsi que sur l'écorce (Werth et al., 2005). La présence de roches dans les forêts peut donc servir de refuges après une perturbation (Werth et al., 2005), en plus de favoriser la diversité (Humphrey et al., 2002). La composition chimique des roches influence la composition des communautés qu'elles abritent. La teneur en carbonate de calcium est un important déterminant des communautés saxicoles : les espèces retrouvées sur les roches calcaires diffèrent de celles retrouvées sur les roches siliceuses (Brodo et al., 2001). Le pH pourrait également avoir un impact sur la composition en espèces, mais il est corrélé à plusieurs autres facteurs, comme l'âge et la composition minérale, ce qui rend difficile la dissociation des effets (Brodo, 1973). Les communautés saxicoles sont aussi dépendantes de la disponibilité en eau sur la surface rocheuse, laquelle peut être influencée par la capacité de rétention de la roche (Brodo et al., 2001) et par sa pente (John & Dale, 1990). Dû en partie aux variations de la disponibilité en eau, mais aussi aux variations de température et d'exposition au soleil,

l'élévation et l'orientation peuvent déterminer la distribution des espèces sur une surface rocheuse (John, 1990; John & Dale, 1990).

1.2.2.3 Lumière

La lumière est un important facteur d'habitat pour les lichens. Il est cependant important de souligner que la disponibilité en lumière est étroitement liée la disponibilité en eau, puisque la radiation solaire affecte la température et la perte d'eau des thalles (Barkman, 1958; Gauslaa, 2014). Ainsi, une lumière indirecte favorise la photosynthèse et stimule la croissance, mais une exposition directe peut induire un dessiccation rapide et être défavorable aux lichens (Gauslaa, 2014). La disponibilité en lumière influence les communautés à l'échelle du peuplement ainsi qu'à l'échelle des substrats. Les peuplements plus denses ont un couvert plus fermé, ce qui peut limiter la diversité (Dymytrova et al., 2014; Humphrey et al., 2002; Uliczka & Angelstam, 1999) et l'abondance (Nascimbene et al., 2009) des communautés de lichens. À l'inverse, une étude a démontré que les bordures de forêt exposées vers le sud supportaient une plus faible diversité de lichens que l'intérieur des forêts, ce qui pourrait être dû à une radiation solaire intensive (Kivistö & Kuusinen, 2000). Les conditions semblent donc optimales à une exposition moyenne. La composition en espèces varie elle-aussi avec la disponibilité en lumière. Les communautés retrouvées dans les zones les plus exposées des forêts diffèrent de celle des zones ombragées, et Hauck et coll. (2007) ont trouvé que les premières étaient dominées par des espèces produisant des substances de protection solaire plus efficaces, comme la mélanine, l'acide usnique, la pariétine et les dérivés d'acide pulvinique. Enfin, un gradient vertical peut être observé dans les communautés de lichens épiphytes d'un même substrat. En effet, la diversité et l'abondance de lichens sont souvent plus importantes

sur les branches de la canopée, qui sont plus exposées au soleil, que sur les bases de troncs, plus ombragées (Hauck, 2011).

1.2.2.4 Pressions anthropiques

L'activité humaine change l'environnement des lichens et exerce des pressions sur les communautés. La perte d'habitats due à l'exploitation forestière est particulièrement répandue et est considérée comme une menace majeure pour la biodiversité de lichens (Scheidegger & Werth, 2009). Les coupes réduisent la complexité de la structure forestière, diminuant ainsi la disponibilité et la diversité des substrats (Ellis, 2012; Lesica et al., 1991; Spribille et al., 2008). Elles induisent une perte directe d'habitat pour les lichens épiphytes, en plus d'affecter les communautés à proximité occupant les substrats restants. En effet, ces dernières deviennent exposées à une plus grande radiation solaire et à des températures plus élevées, ce qui peut mener à une réduction de la diversité (Gignac & Dale, 2005). La pollution atmosphérique émise par les activités humaines peut également avoir des effets néfastes sur la diversité de lichens (Giordani et al., 2002). Bien que dans certains cas la richesse spécifique des communautés n'est pas affectée par les contaminants, la composition en espèces est influencée (Ellis & Coppins, 2010). Les principaux polluants qui ont un effet connu sur les lichens sont le SO₂ et l'azote (NH_x, NO_x) (Giordani et al., 2002; Hawksworth & Rose, 1970; van Herk et al., 2003). Toutefois, dans les forêts boréales d'Amérique du Nord, la contamination au SO₂ est essentiellement historique et les émissions d'azote sont restreintes aux zones agricoles et aux environs des villes densément peuplées (Hauck, 2011). Les lichens peuvent également accumuler les métaux lourds (Aznar et al., 2008) et potentiellement développer des symptômes de toxicité.

1.3 Objectifs de l'étude et hypothèses de travail

1.3.1 Objectifs de l'étude

L'objectif général de l'étude est d'évaluer l'effet du gradient climatique généré par le lac Supérieur sur les communautés de macrolichens épiphytes, épixyliques et saxicoles des forêts mixtes de la côte nord du lac Supérieur. Pour ce faire, nous avons défini deux objectifs spécifiques :

- 1) Identifier les principaux déterminants de la composition en espèces de macrolichens le long du gradient climatique généré par le lac Supérieur et comparer leurs effets à l'échelle du site et à l'échelle du substrat.
- 2) Établir si la richesse spécifique des communautés de macrolichens est déterminée par le gradient climatique généré par le lac Supérieur à l'échelle du site et à l'échelle du substrat.

1.3.2 Hypothèses de travail

Nous posons l'hypothèse générale que les conditions climatiques filtrent les espèces retrouvées dans les communautés (Vellend, 2016) et que la disponibilité en eau de l'environnement influence les communautés de lichens. Nous nous attendons à ce que la distance du lac Supérieur soit le principal déterminant de la composition des communautés à l'échelle du site, mais que la composition à l'échelle du substrat sera plutôt affectée par des facteurs locaux. Similairement, nous nous attendons à ce que la

distance du lac Supérieur détermine la richesse spécifique à l'échelle du site, mais qu'elle ait peu d'impact à l'échelle du substrat.

CHAPITRE II

MULTI-SCALE PATTERNS OF LICHEN COMPOSITION AND SPECIES RICHNESS ALONG A CLIMATIC GRADIENT IN MIXED-WOOD BOREAL FORESTS

2.1 Abstract

Understanding communities' relationships with climate is important to anticipate the impacts of climate change, but processes that operate at many interacting scales challenge our comprehension. Lichens are closely linked to their habitat water and temperature conditions, thus macroclimatic gradients and substrates can play an important role in shaping their communities. Our general objective was to assess the effect of a climatic gradient on macrolichen communities. Specifically, we aimed to 1) identify species composition drivers at site and substrate scales along a climatic gradient, and 2) determine whether species richness measured at the site and substrate scales is driven by the climatic gradient. To do so, we conducted macrolichens surveys along Lake Superior's climatic gradient. We surveyed living spruce and birch trees, snags, and rocks on 54 sites located at different distances from the north shore of Lake Superior in mixed-wood boreal forests. Site-scale and substrate-scale composition were both primarily driven by latitude. Additionally, the site scale was also driven by the distance from Lake Superior, meanwhile the substrate scale was mostly driven by forest structure for spruce trees, deciduous trees, and snags, notably by site maximum DBH and by canopy cover. Rock substrate-scale composition was only driven by latitude and longitude. Distance from Lake Superior did not have direct nor indirect impacts on species richness at any scale. However, local and substrate factors' effects

were less important for richness near the lake. Our results highlight the importance of scale when studying lichen species composition, as large-scale gradients had more influence on the site scale and local factors had more influence at the substrate scale. The absence of trend in species richness suggests species replacement along the climatic gradient, which could potentially be linked to species traits. Therefore, the expected changes in climate in the boreal forest would not necessarily lead to decreases in local species richness in the mixed-wood stands, but the range of the hygrophytic species could shrink. Stands with large trees and important canopy cover could be targeted for their conservation.

2.2 Introduction

Understanding species response to abiotic conditions is of primary interest for biodiversity studies (Hortal et al., 2015) and species relationships with climate are important to anticipate the effect that climate change will have on them. The consequences of the changing climate include shifts in species distribution (Lenoir & Svenning, 2015), leading to the rearrangement of community structure. Those shifts are linked with resource availability, which is impacted by environmental conditions and shapes communities (Vellend, 2016). However, communities can be influenced by different processes that operate at many interacting scales, which challenges our comprehension of patterns (Levin, 1992; Peters et al., 2007). Multi-scale approaches are necessary to understand the relative importance of the different spatial scales on biodiversity. As forest lichens occur on substrates which are themselves nested in forest stands, they provide an ideal model to study the multi-scale effects of environmental conditions (Ellis, 2012).

As lichens are closely linked to the water and temperature conditions of their environment (Gauslaa, 2014; Green et al., 2008), macroclimatic gradients play an important role in shaping their communities. Precipitation and humidity gradients drive lichen species occurrence (Ellis, 2020; Jesberger & Sheard, 1973) and abundance (Giordani & Incerti, 2008; Lidén & Hilmo, 2005; Merinero et al., 2014), and influence community composition (Jovan & McCune, 2004; Werth et al., 2005) and species richness (Marini et al., 2011). Temperature gradients also influence lichen communities by driving species composition (Giordani & Incerti, 2008; Jovan & McCune, 2004; McCune et al., 1997; Werth et al., 2005). In forested areas, these macroclimatic gradients can modify species' habitat quality requirements by allowing a faster colonisation of a wider range of habitats in the more humid areas (Arsenault & Goward, 2016; Ellis & Coppins, 2007; Goward, 1994, 1995; Peterson & McCune, 2001).

At a smaller spatial scale, substrate factors also influence lichen communities. Epiphytic communities are driven by host tree species (Arsenault & Goward, 2016; Jesberger & Sheard, 1973; Kuusinen, 1996; McDonald et al., 2017; Mežaka et al., 2012; Wigle et al., 2021), host tree bark pH (Kuusinen, 1996; Mežaka et al., 2012; Wigle et al., 2021), and host tree size (Lie et al., 2009; McDonald et al., 2017; Nascimbene et al., 2009). On deadwood substrates, communities are also influenced by the level of decay (Arsenault & Goward, 2016; Humphrey et al., 2002). When variables from different scales are considered, substrate factors tend to have a larger effect on substrate-scale communities and populations (Ellis & Coppins, 2006; Merinero et al., 2014; Mežaka et al., 2012). Conversely, site-scale communities and populations tend to respond more to regional gradients (Coyle & Hurlbert, 2016; Ellis & Coppins, 2006; Merinero et al., 2014; Werth et al., 2005).

A few studies focused on the effect of climatic gradients on lichens in the Scandinavian (Lidén & Hilmo, 2005; Werth et al., 2005) and Canadian (Jesberger & Sheard, 1973) boreal forest. However, considering that boreal forests represent 1/3 of the planet's forested area (Brandt et al., 2013), more studies are needed in this biome to perfect our understanding of lichens' response to climate and to anticipate eventual impacts of climate change. In Canada, Lake Superior generates a climatic gradient extending into the forests on its north shore, providing an ideal setting for the study of the effect of macroclimate on lichens. Our general objective was to assess the effect of the climatic gradient on the communities of macrolichens (i.e. foliose and fruticose lichens) of the mixed-wood forests of the north shore of Lake Superior. It was based on the general hypothesis that resource availability drives ecological communities, and that therefore water availability influences lichen communities. Our first specific objective was to identify the main drivers of macrolichen composition at the site scale and at the substrate scale along the Lake Superior climatic gradient. We expected that the distance from the lake would be the primary driver of site-scale composition, but that substrate-scale composition would be more influenced by local factors. Our second specific objective was to determine whether macrolichen species richness measured at the site and substrate scales is driven by Lake Superior climatic gradient. We expected that the distance from the lake would have strong effect on site-scale richness, but weak effect on substrate-scale richness.

2.3 Methods

2.3.1 Study area

Lake Superior is the largest of the five Laurentian Great Lakes, with its surface area reaching 82, 103 km². The Laurentian Great Lakes are a freshwater network that was created from the melting of the Laurentide Ice Sheet at the end of the Wisconsin glaciation. Lake Superior extends from 84°28'W to 92°06'W and from 46°25'N to 48°59'N. Its southern shore is located in the United States (Wisconsin and Michigan), while its northern shore is located in both United States (Minnesota) and Canada (Ontario).

The Great Lakes shape the regional climate. Along an 80 km climatic gradient perpendicular to their shores, they moderate temperatures and lower summer precipitation and summer vapour pressure deficit (Bates et al., 1993; Changnon & Jones, 1972; Notaro et al., 2013; Scott & Huff, 1997). Lake Superior has the strongest effect among the Great Lakes. In summer, the maximum lake effect is responsible for a 6°C decrease in the maximum temperature, a 20% decrease in precipitation and an 8% decrease in water pressure deficit. From fall to spring, the maximum lake effect induces an 8°C rise in the minimum temperature and a 105% increase in precipitation (Scott & Huff, 1997).

Our study area is on the North Shore of Lake Superior, and it extends up to 100 km from the coast, between Nipigon and Batchawana Bay. It is in the Ontario Shield ecozone and falls mostly in the boreal forest region but also partly in the Great Lakes

– St. Lawrence forest region (Crins et al., 2009). It crosses four ecoregions, which are defined as areas nested within an ecozone that are defined by a characteristic range and pattern in climatic variables (Crins et al., 2009). Throughout the study area, mixed forests cover 23.5 to 33.2% of the area, coniferous forests 12.1 to 28.1% and deciduous forests 7.2 to 22.2%, while water represents 6.7 to 17.1% of the landcover (Crins et al., 2009). Mean annual temperature ranges between -1.7 and 6.2 °C and annual precipitation varies from 645 to 1148 mm, with 204 to 304 mm during summer (Mackey et al., 1996b, 1996a) (See Appendix A for details).

2.3.2 Site selection

Eight 100 km transects were positioned perpendicularly to the northern coast of Lake Superior (Figure 2.1). Each of these transects included ten potential sampling sites located at 0, 1, 2.5, 5, 10, 20, 35, 55, 75 and 100 km respectively from the coast. Potential site density was higher at the coastal end of the gradient, as changes in communities are expected to be stronger in this area. Transect positions were selected so that the sampling sites were located in mixed forests containing spruce (*Picea* spp.) and birch (*Betula* spp.) trees, in forests more than 80 years old, and in accessible locations (<1 km from a road or trail or access by boat). Transect positioning was completed with ArcMap (ESRI, 2020), using geospatial data from the second edition from the *Forest Resources Inventory* (Ontario Ministry of Natural Resources and Forestry, 2020a), the *Ontario Road Network Road Net Element* (Ontario Ministry of Natural Resources and Forestry, 2019b) and the *MNRF Road Segments* (Ontario Ministry of Natural Resources and Forestry, 2020b). Many potential sites were dismissed because the field reality did not reflect the selection criteria. Limited road access in conservation areas was a major obstacle for site selection. Following these

restrictions, only 54 of the potential sites were selected. Sampling took place between May 2021 and June 2022.

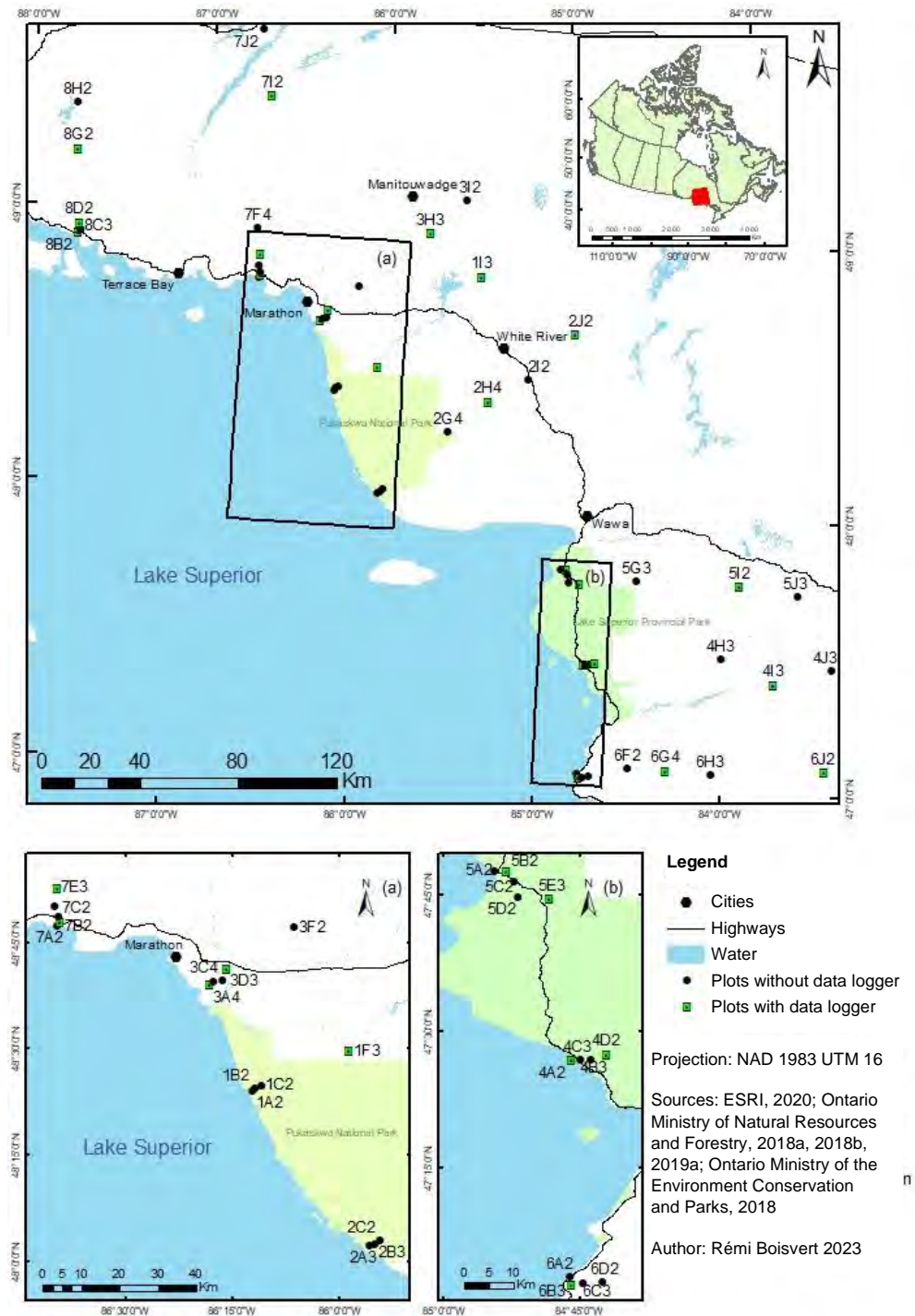


Figure 2.1 Map of the study area including the plots sampled. The black dots represent the sites without data loggers and the green squares represent the sites where a data logger was installed from September 19, 2021, to September 10, 2022.

2.3.3 Macrolichen survey

In each sampling site, a macrolichen survey was conducted on four types of substrates: live spruce (*Picea mariana* (Miller) Britton, Sterns & Poggenburgh or *Picea glauca* (Moench) Voss) and birch (*Betula papyrifera* Marshall or *Betula alleghaniensis* Britton) trees, snags (any species), and rock surfaces. Spruce and birch tree substrates included bark at the base of the tree (0-40 cm height), bark of the trunk of the tree (40-200 cm height), and branches (up to 200 cm height) of living trees with a height over 1.30 m and a diameter at breast height (DBH) of 7 cm or larger although the majority were over 10 cm in DBH. Snag substrates included bark and wood at the base of the snag (0-40 cm height, bark of the trunk (40-200 cm height), exposed wood of the trunk (40-200 cm height), and branches (up to 200 cm height) of dead trees of any species with a height over 1.30 m and a DBH of 7 cm or larger. Rock surfaces included any boulders that had an exposed area greater than 1 m². For each of these substrate types, the five biggest units located in a 12 m radius from the center point of the site were selected for macrolichen surveys. If there were less than five units within the 12 m radius, the closest units outside of this distance were selected. All observed species were collected for further identification in the laboratory. Identifications were mainly based on the keys of Brodo (2016), but also those of Hinds & Hinds (2007) and Ahti et al. (2013). Identifications were made using a stereoscope, spot tests (with a 10% aqueous solution of potassium hydroxide, bleach, and a 1g/100mL Steiner solution of para-phenylenediamine) and long-wave UV tests. Thin layer chromatography (TLC) was conducted at the Canadian Museum of Nature on species that could not be identified with the previously mentioned techniques.

2.3.4 Site and substrate characterisation

Along with the macrolichen surveys, forest structure of sampling sites was characterised by several measurements. Canopy cover was estimated from the center point of each site with a spherical crown densiometer (Forestry Suppliers, Convex Model A). Basal area was calculated for each tree species present using a 2 factor wedge prism. Total basal area was also recorded. DBH was measured for each tree included in the basal area measurement. Using these values, site mean and maximum DBH were extracted. Ratio of deciduous trees was also calculated from the trees included in the basal area. For the three largest trees of each site, a tree core was collected, sanded, and dated. From those samples, site minimum age was determined. Three 2 cm² spruce and birch bark samples were collected from randomly selected trees in a 12 m radius from the center point. Bark samples were dried, then soaked in 30 mL of distilled water for 2 hours and water pH was measured after 5, 30, 60 and 120 minutes. Site mean bark pH for each genus was calculated from the final pH measures. Data loggers (HOBO Pro V2 Temp/RH) were installed at a height of 40 cm from the ground at the center point of 22 sites. These sites were randomly selected so that there were three data loggers per transect (distributed in three distance groups from the coast: 0-5 km, 10-35 km, and 55-100 km), except for transects 1 and 2 where data from the weather stations of Environment Canada and Pukaskwa National Park were used in the 0-5 km distance group (Figure 2.1). Data loggers were installed from September 19, 2021, to September 10, 2022, and recorded temperature and relative humidity once every hour. From this data, mean values for spring, summer and fall were extracted for both temperature and relative humidity and for each distance group. The longest period of temperature over the 90th percentile was averaged for each distance group, along with the longest period of relative humidity under the 10th percentile. Maximum temperature and year first and last days of temperature over the 90th percentile were also averaged for each distance group.

Substrate factors were also characterised. Substrate DBH and substrate species were recorded for spruce trees, birch trees, and snags. If species could not be identified with certainty in the field, substrate genus was recorded instead. Species was not recorded for highly decayed snags that did not allow reliable identification in the field. Snags' level of decay was visually estimated using a five-point scale based on Hunter (1990, as cited by Humphrey et al., 2002). Rock substrate height, width and length were measured. A size index was given to each rock substrate by multiplying the two largest measurements.

2.3.6 Statistical analysis

All statistical analyses were conducted in R 4.1.1 (R Core Team, 2021). In order to address the first objective, lichen species composition, using presence-absence data, was analyzed at the site scale and at the substrate scale. Only specimens identified to the species level were included in the analyses, except for the *Melanohalea* group (this includes *Melanohalea halei*, *Melanohalea septentrionalis*, and *Melanohalea olivacea*), for which there was no species level identifications due to low confidence in species determination. Composition was analyzed with principal coordinates analyses (PCoA) using the *wcmdscale* function from *vegan* package (Oksanen et al., 2020). At the site scale, a PCoA was conducted on all sites, followed by two separate post-hoc PCoAs for the sites of the southeast zone (transects 4, 5, 6) and for the ones of the northwest zone (transects 1, 2, 3, 7 and 8). At the substrate scale, PCoAs were performed separately for the four different types of substrates. All PCoAs were based on dissimilarity matrices using Jaccard distance which were created with the *vegdist* function from *vegan* package (Oksanen et al., 2020). Significant ($p \leq 0.05$) environmental variables were added to the ordinations and their effect on species

composition was verified with permutation tests of 999 iterations using the `envfit` function from *vegan* package (Oksanen et al., 2020). Indicator species associated with the distance from the lake were identified using the `multipatt` function from *indicspecies* package (De Cáceres & Legendre, 2009). The analysis was conducted at the site scale with distance as grouping factor, in which sites were grouped based on distance from the shore : near (0 – 5 km), intermediate (10 – 35 km), or far (55 – 100 km). Only significant ($p \leq 0.05$) indicators were considered.

In order to meet the second objective, species richness analyses were conducted at the site scale and at the substrate scale. Only sites inside the 80 km climate gradient (0-75 km) were included in the analyses. All fixed-effect variable values were standardised with the R built-in `scale` function (R Core Team, 2021). Linear regressions with the `lm` function of the R stats package (R Core Team, 2021) were used to assess the direct effect of the distance from the lake on site species richness. To extract the variation that was not explained by forest structure, a first series of multivariate regressions with site species richness as response variable and canopy cover, deciduous tree ratio, total basal area, maximum DBH, and minimum age as fixed-effect variables were used. Residuals from these models were used as response variables for a second series of multivariate regressions with latitude and distance from the lake as fixed-effect variables, including the interaction between the two. Similar analyses were used at the substrate scale, but with generalized linear mixed models (GLMMs) with the `glmmTMB` function in the *glmmTMB* package (Brooks et al., 2017). Substrate types were analysed separately, and site was included as a random-effect variable. As richness was following a Poisson distribution, Poisson family models were used for the first series of regressions. Since the residuals from these regressions were following a normal distribution, gaussian family models were used for the second series of regressions. Overdispersion was verified for the first series of regressions and, when

detected, a correction for negative binomial distribution was added. Significance of all explanatory variables was set at a p-value threshold of 0.05.

Several post-hoc analyses were conducted in the aim to explain the pattern observed in the data. Post-hoc GLMMs were performed to compare the importance of site factors and substrate factors on species richness at different distance groups from the coast. Sites were divided in function of their distance from the lake (near, 0-5 km; intermediate, 10-35 km; far, 55 100 km) and analyses were made with the `glmmTMB` function on spruce, birch, snag, and rock substrate-scale data separately, with Poisson family models. Canopy cover, deciduous tree ratio, total basal area, maximum DBH, minimum age, altitude, and substrate factors (substrate DBH for spruce, birch, and snags; decay level for snags; size index for rocks) were standardised with the R built-in `scale` function and included as fixed-effect variables. Species richness was included as the response variable and site was included as a random-effect variable. Overdispersion was verified for the first series of regressions and, when detected, a correction for negative binomial distribution was added. Significance of all explanatory variables was set at a p-value threshold of 0.05.

Post-hoc breakpoint and covariance-based structural equation modelling (SEM) analyses were performed to assess the indirect effect of distance from the lake on site and substrate species richness. Breakpoint analyses were conducted first to identify potential breakpoints in species richness response to distance from the lake. Site-scale richness and substrate-scale richness for each type of substrate were analysed with the segmented function from the *segmented* package (Muggeo, 2008). Breakpoint analyses were performed on linear models using `lm` function from R (R Core Team, 2021) with distance from Lake Superior as the explanatory variable and richness as the response

variable. Total site richness was used for the site scale model and mean site richness for a given substrate was used for the substrate scale models. Two to three starting values were specified following a visual inspection of the pattern. Based on the identified breakpoints, site-scale and substrate-scale datasets were divided in subsets to conduct covariance-based SEM. Subsets with less than 10 observations were merged with another group. The model structure showed in Figure 2.2 was tested on each subset with the *sem* function from the *lavaan* package (Rosseel, 2012) on standardised data. A bootstrap with 10 000 iterations was integrated to each model. Model results were considered only if the model structure was not rejected (Bollen-Stine bootstrap $p > 0.05$).

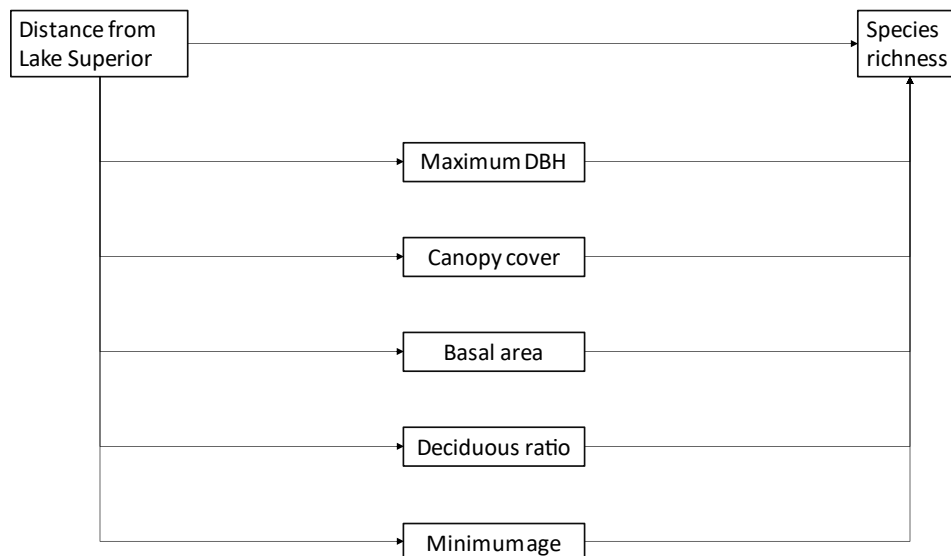


Figure 2.2 Model structure tested with the SEM analyses.

2.4 Results

2.4.1 Climatic data

The climatic data extracted from our data loggers and from Pukaskwa National Park weather stations showed some of the expected gradient patterns in climate, especially in temperatures (Appendix B). Maximum temperature was highest far from Lake Superior and lowest near Lake Superior. Mean summer temperature showed a similar pattern, although the differences between distance groups were less important. Mean fall temperature showed an opposite pattern, with the highest values being found near Lake Superior and the lowest being found far from it. Periods of consecutive temperatures in the highest 10th percentile were longer near Lake Superior and shorter far from it. No clear gradient pattern was found in relative humidity, although mean relative humidity in spring and summer were considerably higher near Lake Superior than at intermediate distances. For most variables, the standard-error was higher for the intermediate distance group.

2.4.2 Community composition

Hypothesis 1.1: Site-scale composition is primarily driven by Lake Superior climatic gradient.

The site-scale PCoA results showed that community composition was driven by two principal factors: latitude, which was correlated with axis 1 ($R^2=0.54$, $p=0.001$), and distance from Lake Superior, which was correlated with axis 2 ($R^2=0.37$, $p=0.001$) (Figure 2.3a, Table 2.1). Axis 1 was markedly better at explaining the variation in

composition (22.41%) than was axis 2 (7.13%). This translates in a clear distinction between two geographic zones within our study area. The southeast zone includes transects 4, 5, and 6 and is found mostly on the right part of the ordination graph, and the northwest zone includes transects 1, 2, 3, 7 and 8 and is found mostly on the left part of the ordination graph (Figure 2.3a). Altitude was positively correlated with distance from Lake Superior, and forest structure variables were negatively correlated with latitude, suggesting that sites with large trees, important deciduous ratio and high canopy cover tended to be more common in the south of the study area. (Figure 2.3a). Species such as *Melanelixia fuliginosa* (Fr. ex Duby) O. Blanco, A. Crespo, Divakar, Essl. D. Hawksw. & Lumbsch, *Parmotrema crinitum* (Ach.) Choisy, and *Punctelia rudecta* (Ach.) Krog were more likely to be found in the southeast zone, at lower latitudes, while *Bryoria* spp., *Parmeliopsis* spp., *Usnea* spp., and *Vulpicida pinastri* (Scop.) J.-E. Mattsson & M. J. Lai tended to be more frequent in the northwest zone, at higher latitudes (Figure 2.3b). Sites closer to the lake were associated with species such as *Umbilicaria muhlenbergii* (Ach.) Tuck., *Hypotrachyna revoluta* (Flörke) Hale, *Cladonia chlorophaea* group, *Flavoparmelia caperata* Nyl. and *Pseudevernia consocians* (Vain.) Hale & Culb., while sites further from the lake were associated with species such as *Ramalina thrausta* (Ach.) Nyl., *Phaeophyscia pusilloides* (Zahlbr.) Essl., *Physcia aipolia* (Ehrh. ex Humb.) Fűrnr, and *Heterodermia galactophylla* (Tuck.) Culb. (Figure 2.3b).

Nine species were identified as significant indicators of distance from Lake Superior with the indicator species analysis (Table 2.2). *Pseudevernia consocians* (Vain.) Hale & Culb. and *Punctelia caseana* Lendemmer & Hodk. were indicators of sites at near and intermediate distances from the lake (0-35 km). *Tuckermanopsis sepincola* (Ehrh.) Hale, *Cladonia botrytes* (K. Hagen) Willd. and *Cladonia carneola* (Fr.) Fr. were indicators of sites at intermediate distances from the lake (10-35 km). *Tuckermanopsis*

orbata (Nyl.) M.J. Lai, *Tuckermanopsis americana* (Spreng.) Hale and *Bryoria fuscescens* (Gyelnik) Brodo & D. Hawksw. were indicators of sites at intermediate and far distances from the lake (10-100 km). *Ramalina thrausta* (Ach.) Nyl. was indicator of sites far from the lake (55-100 km). No species were indicators of distances closest to the lake (0-5 km).

To verify if the same variables were driving composition inside the southeast and northwest zones, two separate post-hoc PCoAs were conducted. The results show that distance from Lake Superior is the only significant variable present in both ordinations. In the southeast zone PCoA, axis 1 (24.33%) explained a larger proportion of the variation in the composition than axis 2 (9.87%) (Figure 2.4a). All variables that were significantly correlated with the axes in the permutation test were primarily associated with axis 1 (Figure 2.4a, Table 2.1). Distance from the lake and deciduous tree ratio had the strongest correlations with the axes (respectively $R^2=0.38$, $p=0.008$ and $R^2=0.38$, $p=0.016$) (Table 2.1). In the northwest zone PCoA, axis 1 and axis 2 similarly explained the variation in composition (respectively 15.15% and 12.14%) (Figure 2.4b). The permutation test showed that altitude, which was primarily associated with axis 1, and distance from Lake Superior, which was primarily correlated with axis 2, were the variables with the strongest correlations with the ordination axes (respectively $R^2=0.41$, $p=0.001$ and $R^2=0.39$, $p=0.003$) (Figure 2.4b, Table 2.1).

Hypothesis 1.2: Substrate-scale composition is primarily driven by local factors.

Substrate-scale PCoAs showed that latitude is the main driver of composition for all substrates (Figure 2.5). Comparatively to site-scale PCoAs, substrate scale PCoAs showed that distance from Lake Superior had less effect on composition than most forest structure variables. This pattern was observed on all substrates except for rocks,

on which neither distance from lake nor forest structure variables had effect on composition. In the spruce PCoA, axis 1 explained 10.65% of the variation in the composition and axis 2, 6.58% (Figure 2.5a). The permutation test showed that, latitude aside ($R^2=0.41$, $p=0.001$), the main variables correlated with the axes were longitude ($R^2=0.28$, $p=0.001$) and canopy cover ($R^2=0.20$, $p=0.001$), which were primarily associated with axis 1, together with maximum DBH ($R^2=0.27$, $p=0.001$) and deciduous tree ratio ($R^2=0.20$, $p=0.001$), which were primarily associated with axis 2 (Figure 2.5a, Table 2.1). All four variables were negatively correlated with latitude. In the birch PCoA, axis 1 was explained 10.25% of the variation and axis 2, 6.24% (Figure 2.4b). The permutation test showed that, other than latitude ($R^2=0.42$, $p=0.001$), the main variables correlated with the axes were longitude ($R^2=0.28$, $p=0.001$) and maximum DBH ($R^2=0.23$, $p=0.001$) (Table 2.1). They were primarily associated with axes 1 and 2, respectively, and were both negatively correlated with latitude (Figure 2.5b). In the snag PCoA, axis 1 accounted for 9.22% of the variation and axis 2, 5.1% (Figure 2.4c) The permutation test showed that, apart from latitude ($R^2=0.35$, $p=0.001$), longitude ($R^2=0.23$, $p=0.001$) was the main variable correlated with the axes, and it was correlated with all forest structure variables, which were partly associated with axis 2 and negatively correlated with latitude (Figure 2.4c, Table 2.1). In the rock PCoA, axis 1 and axis 2 explained respectively 16.63 and 10.95% of the variation in the composition (Figure 2.4d). The permutation test showed that only latitude ($R^2=0.10$, $p=0.014$) and longitude ($R^2=0.08$, $p=0.025$) were significantly correlated with the axes (Table 2.1). Both were associated with axis 2 (Figure 2.4d).

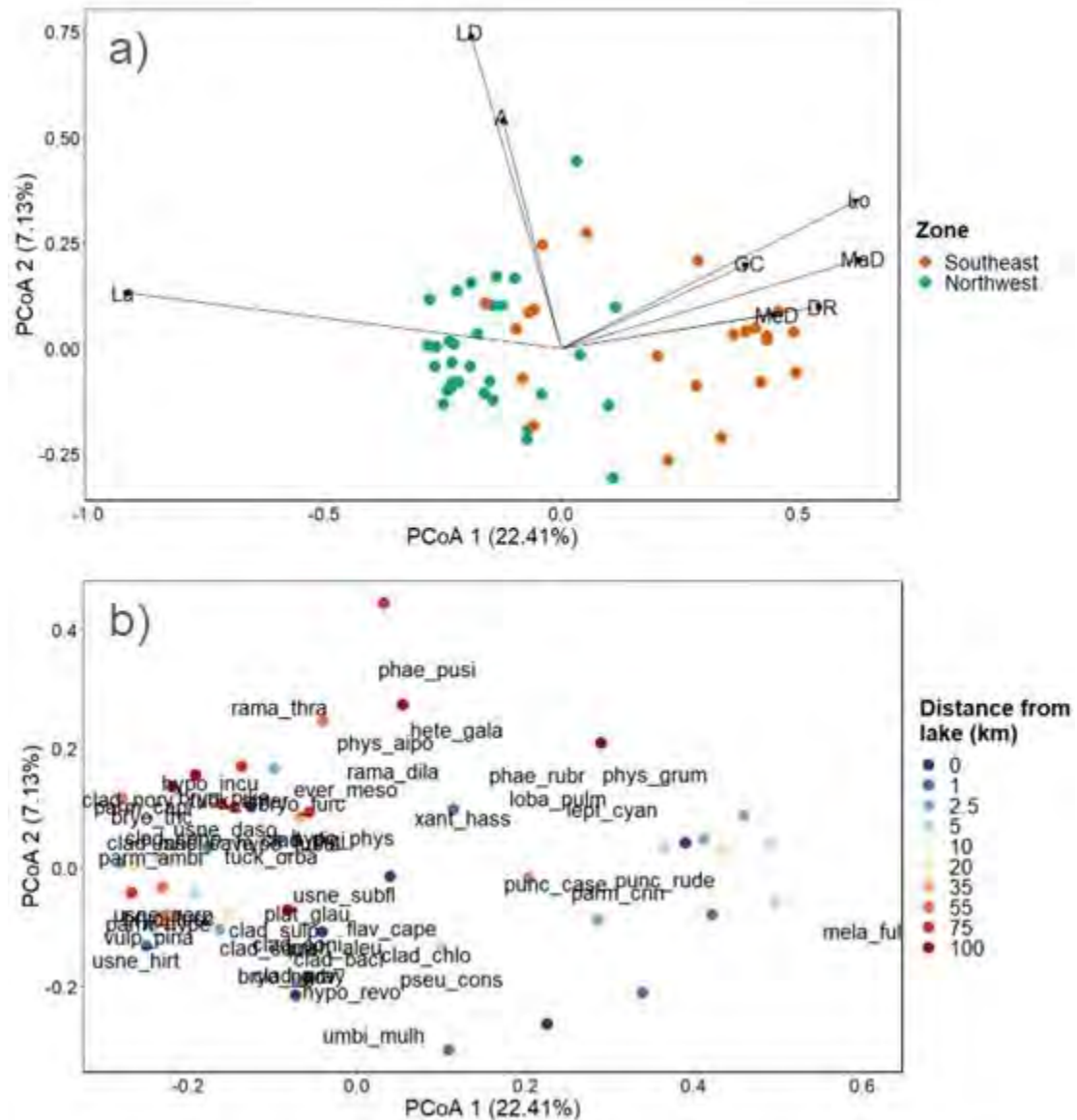


Figure 2.3 Site-scale principal coordinates analyses (PCoA) ordinations for all sites ($n=54$). Sites are represented by dots, with color indicating the geographic zone in a), and the distance from Lake Superior in b). Significant environmental variables tested with permutation tests are included in a), and significant species composition is included in b). Eigenvalue of each axis is shown in parenthesis. Species are shown by their species code (See Appendix E for species codes). A=Altitude; CC=Canopy cover; DR=Deciduous tree ratio; LD=Lake distance; La=Latitude; Lo=Longitude; MaD=Maximum DBH; MeD=Mean DBH.

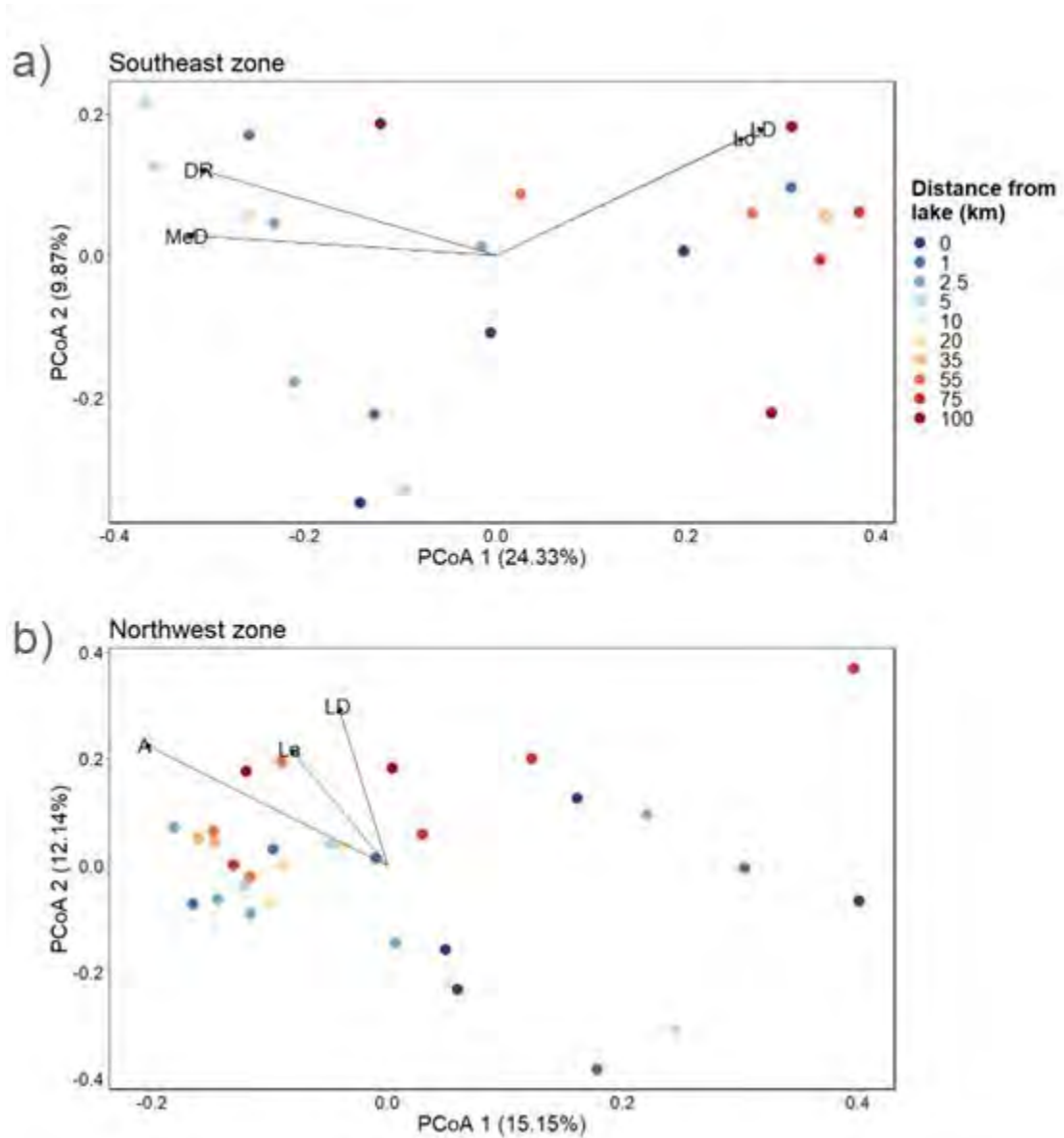


Figure 2.4 Site-scale principal coordinates analyses (PCoA) ordinations for a) east zone sites (transects 1, 2, 3 7 and 8; n=22), and b) north zone sites (transect 4,5 and 6; n=32). Sites are represented by dots, with color indicating the distance from Lake Superior. Significant environmental variables tested with permutation tests are included. Eigenvalue of each axis is shown in parenthesis. A=Altitude; DR=Deciduous tree ratio; LD=Lake distance; La=Latitude; Lo=Longitude, MeD=Mean DBH.

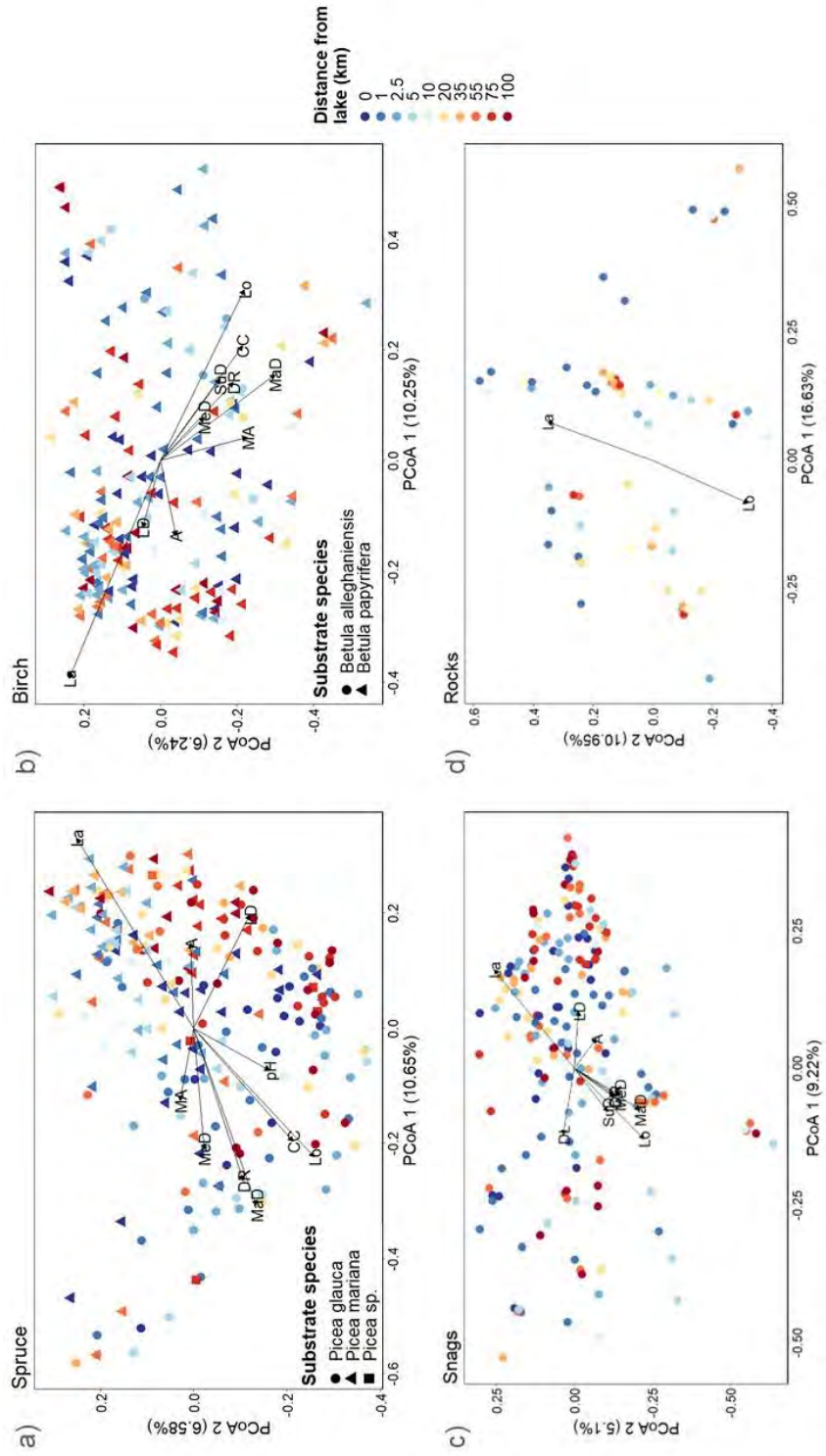


Figure 2.5 Substrate-scale principal coordinates analyses (PCoA) ordinations for a) spruce (n=245), b) birch (n=230), c) snags (n=221), and d) rocks (n=88). Sites are represented by dots, triangles and squares, with color indicating the distance from Lake Superior and shape indicating the substrate species in a) and b). Significant environmental variables tested with permutational tests are included. Eigenvalue of each axis is shown in parenthesis. A=Altitude; CC=Canopy cover; DL=Decay level; DR=Deciduous tree ratio; LD=Lake distance; La=Latitude; Lo=Longitude; MeD=Maximum DBH; MA=Mean DBH; MeD=Mean DBH; MA= Minimum age; pH=Mean spruce bark pH; SuD=Substrate DBH

Table 2.1 Results of the permutation tests of 999 iterations on the environmental variables for each PCoA. Only significant ($p \leq 0.05$) variables are included. Distance from Lake Superior, canopy cover, maximum DBH, mean DBH, deciduous ratio, altitude, latitude, longitude, minimum age, and mean spruce bark pH were recorded at the site scale. Substrate species, substrate DBH, and substrate decay level were recorded at the substrate scale.

Environmental variables	R ²	P-value	Environmental variables	R ²	P-value
Site-scale PCoAs			Birches (n=230)		
All sites (n=54)			Distance from Lake Superior	0.03	0.038
Distance from Lake Superior	0.37	0.001	Canopy cover	0.18	0.001
Canopy cover	0.12	0.033	Maximum DBH	0.23	0.001
Maximum DBH	0.28	0.001	Mean DBH	0.04	0.026
Mean DBH	0.13	0.021	Deciduous ratio	0.11	0.004
Deciduous ratio	0.19	0.006	Altitude	0.04	0.017
Altitude	0.20	0.006	Latitude	0.42	0.001
Latitude	0.54	0.001	Longitude	0.28	0.001
Longitude	0.32	0.001	Minimum age	0.11	0.001
East zone (n=22)			Substrate DBH	0.09	0.001
Distance from Lake Superior	0.38	0.008	Substrate species	0.02	0.022
Mean DBH	0.36	0.012	Snags (n=221)		
Deciduous ratio	0.38	0.016	Distance from Lake Superior	0.04	0.020
Longitude	0.32	0.021	Canopy cover	0.07	0.002
North zone (n=32)			Maximum DBH	0.18	0.001
Distance from Lake Superior	0.39	0.003	Mean DBH	0.09	0.001
Altitude	0.41	0.001	Deciduous ratio	0.07	0.001
Latitude	0.24	0.021	Altitude	0.03	0.041
Substrate-scale PCoAs			Latitude	0.35	0.001
Spruces (n=245)			Longitude	0.23	0.001
Distance from Lake Superior	0.13	0.001	Substrate DBH	0.06	0.002
Canopy cover	0.20	0.001	Substrate decay level	0.06	0.003
Maximum DBH	0.27	0.001	Rocks (n=88)		
Mean DBH	0.11	0.001	Latitude	0.10	0.011
Deciduous ratio	0.20	0.001	Longitude	0.08	0.026
Altitude	0.05	0.002			
Latitude	0.41	0.001			
Longitude	0.28	0.001			
Minimum age	0.04	0.012			
Mean spruce bark pH	0.08	0.001			
Substrate species	0.17	0.001			

Table 2.2 Indicator species associated with distance from Lake Superior. Component A indicates the specificity of the species. Component B indicates the fidelity of the species. Association statistics are shown in the *stat* column.

Indicator species	A	B	stat	p-value
Intermediate distances (10-35 km)				
<i>Tuckermanopsis sepincola</i> (Ehrh.) Hale	1.000	0.333	0.577	0.005
<i>Cladonia botrytes</i> (K. Hagen) Willd.	0.842	0.333	0.530	0.015
<i>Cladonia carneola</i> (Fr.) Fr.	1.000	0.222	0.471	0.035
Far distances (55-100 km)				
<i>Ramalina thrausta</i> (Ach.) Nyl.	0.675	0.375	0.503	0.050
Near and intermediate distances (0-35 km)				
<i>Pseudevernia consocians</i> (Vain.) Hale & Culb.	0.946	0.553	0.723	0.005
<i>Punctelia caseana</i> Lendemer & Hodk.	1.000	0.395	0.628	0.010
Intermediate and far distances (10-100 km)				
<i>Tuckermanopsis orbata</i> (Nyl.) M.J. Lai	0.803	0.800	0.801	0.010
<i>Tuckermanopsis americana</i> (Spreng.) Hale	0.806	0.760	0.783	0.005
<i>Bryoria fuscescens</i> (Gyelnik) Brodo & D. Hawksw.	0.877	0.600	0.725	0.005

2.4.3 Species richness

Hypotheses 2.1 and 2.2: Species richness is 2.1) strongly driven by Lake Superior climatic gradient at the site, and 2.2) weakly driven by Lake Superior climatic gradient at the substrate scale.

Similar richness patterns were found at the site scale and at the substrate scale, on every substrate (Figure 2.6, Figure 2.7). Although sites directly by the shore had generally slightly less species, distance from Lake Superior tended to be negatively correlated with richness up to 20 km. Species richness increased at 35 km from the coast. From 35 to 75 km, it showed a negative correlation with distance from the lake but stayed

relatively high. However, both site-scale linear regression and substrate-scale GLMMs showed that, once the effects of canopy cover, deciduous tree ratio, total basal area, maximum DBH, and minimum age were removed, species richness was not significantly influenced by the distance from Lake Superior at any scale (Table 2.3, Table 2.4). A significant positive effect of latitude was found at the site scale and on rocks at the substrate scale. The interaction between the effect of the distance from Lake Superior and the effect of the latitude was not significant at any scale.

Post-hoc GLMMs were performed to compare the importance of site and substrate factors on richness at near (0-5 km), intermediate (10-35 km), and far (55-100 km) distances from Lake Superior. Rocks were removed from the analyses since the number of substrates sampled was insufficient to conduct the GLMMs without convergence problems. On spruce and birch substrates, more site and substrate factors had significant effects on richness at intermediate and far distances than at near distance (Appendix H). Also, on both substrates, the pseudo- R^2 was more important at intermediate distances than at near distances. On snags, no pattern was found in the number of site and substrate factors that had significant effects, but the pseudo- R^2 was more important at intermediate distances than at near distances (Appendix H).

Post-hoc breakpoint and SEM analyses were conducted to verify if the distance from Lake Superior could explain the patterns observed in the data through its effect on forest structure. Breakpoint analyses identified two breakpoints for the site-scale model (7.8 and 34.9 km), two breakpoints for the spruce substrate-scale model (7.7 and 35.0 km), three breakpoints for the birch substrate-scale model (2.2, 7.7 and 40.5 km), two breakpoints for the snag substrate-scale model (5.3 and 35 km) and no breakpoint for the rock substrate-scale model. For the SEM analyses, sites between 10 and 75 km were

grouped together to have sufficient observations to perform all analyses. Our model structure was rejected for the following subsets: 0-5 km site-scale richness, 0-5 km spruce substrate-scale richness, and 0-5 km snags substrate-scale richness. In all the non-rejected models, distance from Lake Superior did not have a significant indirect effect on species richness (Appendix I).

Table 2.3 Results of the site-scale linear multivariate regression with the distance from Lake Superior and latitude as explanatory variables and with, as response the variable, the residuals of a linear regression with species richness as response variable and canopy cover, deciduous trees ratio, total basal area, maximum DBH, and minimum age as explanatory variables. Significant effects are shown in bold.

Variables	Estimates	t value	p-value
Distance	1.701 ± 1.389	1.225	0.228
Latitude	3.440 ± 1.096	3.139	0.003
Distance:Latitude	-1.035 ± 1.335	-0.775	0.443

Table 2.4 Results of the substrate-scale generalized linear mixed models with the distance from Lake Superior and latitude as explanatory variables and with, as the response the variable, the residuals of generalized linear mixed models with species richness as response variable and canopy cover, deciduous trees ratio, total basal area, maximum DBH, and minimum age as fixed-effect variables, and site as random-effect variable. Significant effects are shown in bold.

Variables	Estimates	z value	p-value
Spruces			
Distance	0.166 ± 0.267	0.622	0.534
Latitude	0.204 ± 0.212	0.962	0.336
Distance:Latitude	-0.090 ± 0.256	-0.353	0.724
Birches			
Distance	-0.004 ± 0.228	-0.019	0.985
Latitude	0.155 ± 0.188	0.824	0.410
Distance:Latitude	-0.002 ± 0.218	-0.007	0.994
Snags			
Distance	-0.019 ± 0.275	-0.071	0.944
Latitude	0.333 ± 0.218	1.526	0.127
Distance:Latitude	-0.056 ± 0.266	-0.209	0.834
Rocks			
Distance	-0.068 ± 0.190	-0.359	0.720
Latitude	0.300 ± 0.142	2.107	0.035
Distance:Latitude	-0.141 ± 0.203	-0.691	0.490

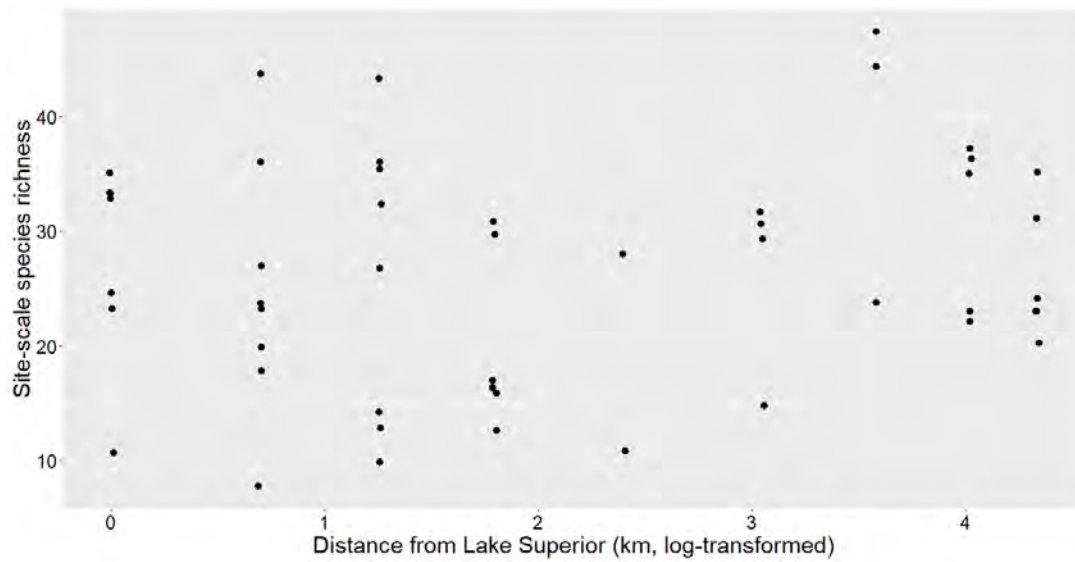


Figure 2.6 Site-scale species richness as a function of site distance from Lake Superior. Distance is log-transformed to facilitate visualisation. Only sites from 0 to 75 km from the lake are included.

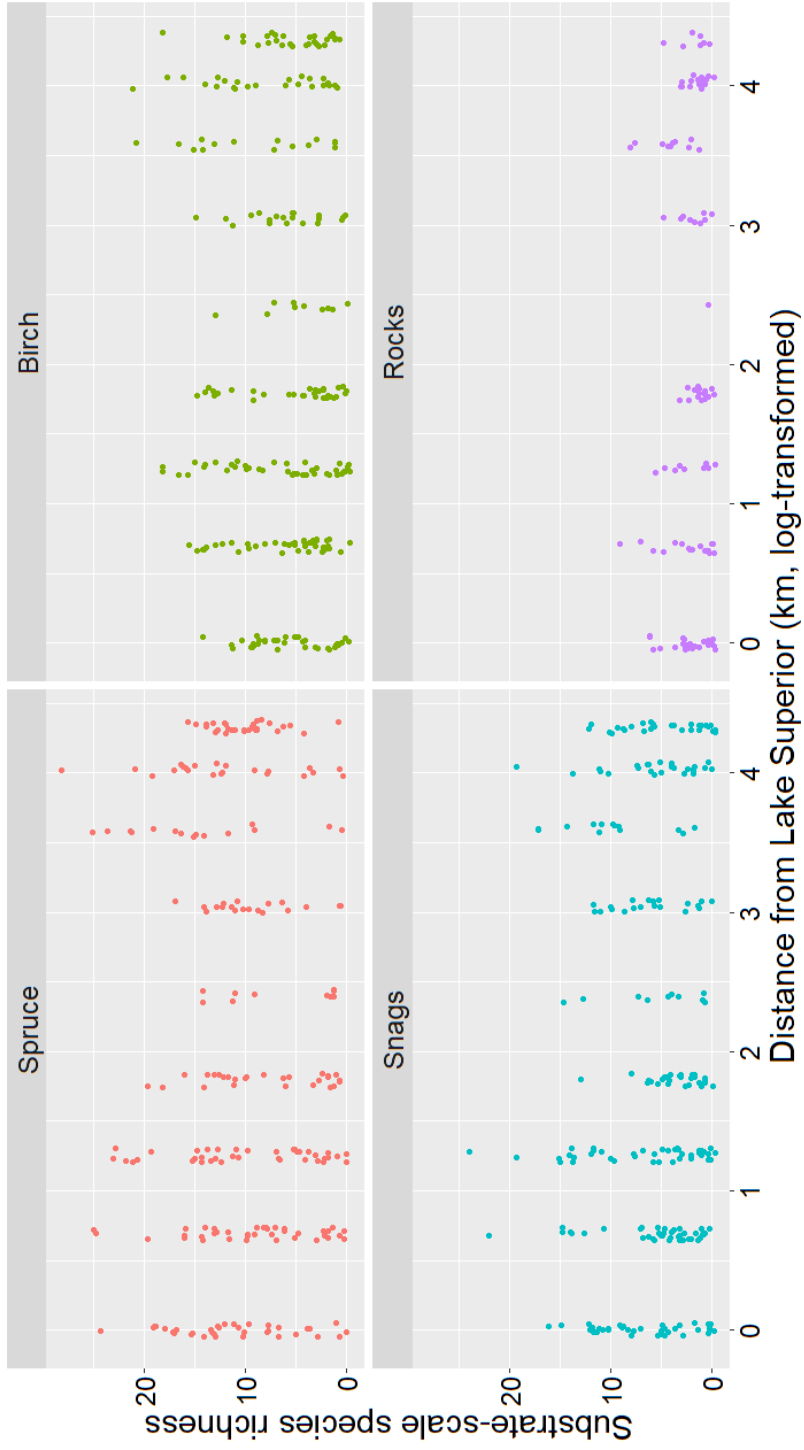


Figure 2.7 Substrate-scale species richness of spruce, birch, snag, and rock substrate as a function of site distance from Lake Superior. Only sites from 0 to 75 km from the lake are included.

2.5 Discussion

2.5.1 Community composition

Our results demonstrate that the relative importance of drivers of lichen composition varies across scales. When considering the whole study area, the latitudinal gradient was the main driver of the composition for both site and substrate scales. The latitudinal gradient could be explained by a shift in the regional species pool within our study area. This shift could be due to several factors. First, the large latitude range of our study area (~300 km) could allow us to capture the dispersal limit of individual species. Second, our study area stands in a transition zone between the forest regions of the Great Lake – St. Lawrence and the boreal forest (Crins et al., 2009), which could be associated with distinct lichen communities. Finally, there is a large-scale latitudinal temperature gradient within our study area (Mackey et al., 1996b, 1996a; See Appendix A) that could contribute to filtering species composition. The idea of a shift in the regional species pool is supported by the available species distribution. Several species associated with the southeast zone are in the northern limit of their range (e.g., *Melanelixia fuliginosa* (Fr. ex Duby) O. Blanco, A. Crespo, Divakar, Essl. D. Hawksw. & Lumbsch, *Parmotrema crinitum* (Ach.) Choisy), while many species associated with the northwest zone are in the southern limit of their range (e.g., *Bryoria fuscescens* (Gyelnik) Brodo & D. Hawksw., *Bryoria nadvornikiana* (Gyelnik) Brodo & D. Hawksw., *Bryoria pikei* Brodo & D. Hawksw., *Parmeliopsis hyperopta* (Ach.) Arnold, *Parmeliopsis ambigua* (Hoffm.) Nyl., and *Usnea dasopoga* (Ach.) Nyl.) (Brodo et al., 2001).

At similar latitudes, Lake Superior climatic gradient was the only consistent environmental filter for the site-scale composition. This is consistent with our hypothesis and with other studies that found that regional factors had stronger effects than local factors on local communities (Coyle & Hurlbert, 2016; Werth et al., 2005). Species that were found to be indicators of Lake Superior proximity could be species that require high air humidity. This is supported by the available distribution data which shows that they are primarily associated with coastal zones (Brodo et al., 2001; Lendemer & Hodkinson, 2010), although their presence has also been reported inland (T. Spribille, personal communication, June 3, 2023). In our study area, they had high specificity for sites at 35 km or less from the lake, which suggests that the optimal climatic conditions generated by the lake extend to at least 35 km from the coast. *Ramalina thrausta* (Ach.) Nyl. was an indicator of sites at 55 km and more from the coast. This is surprising as this species is normally associated with high humidity forests (Brodo et al., 2001). Its association with further distances from the lake in our study area could be due to its large surface to biomass ratio. Indeed, thin alectorioid lichens have highly efficient humidity uptake (Gauslaa, 2014), which could allow *Ramalina thrausta* (Ach.) Nyl. to thrive in low humidity environment. However, it is not clear that this is what drives the species distribution in our study area, as no other alectorioid species were found to be indicator of high distances from Lake Superior.

Although spruce, birch and snag substrate-scale communities were significantly influenced by the Lake Superior climatic gradient, the effect was relatively small compared to the influence of forest structure variables, suggesting that local factors are more important for small-scale composition. Site maximum DBH was a major driver for all three substrates, and it was correlated with canopy cover, which was another important driver of composition on spruce and birch. Tree size and canopy cover can be associated with site productivity, and these three variables were found to drive

substrate-scale epiphytic composition in *Populus tremuloides* stands (Boudreault, Coxson, et al., 2008). It is hard to isolate the effect of each of those variables, but this productivity gradient can have two potential effects on substrate micro-habitat conditions. First, more productive sites could generate better water conditions on substrates, on the one hand because high canopy cover prevents the evaporation caused by solar radiation, and on the other hand because larger trees have a rougher bark (Hazell et al., 1998), which allows better water retention (Barkman, 1958; Brodo, 1973). Second, substrate light conditions are dependant on canopy cover and they are known to drive species composition, as species tolerance to irradiation depends on the photoprotective substances they produce (Hauck et al., 2007). Rock substrate composition was only influenced by latitude and longitude, which suggests that dispersal limitation is the main constraint of saxicolous species.

Surprisingly, contrary to our hypothesis, substrate factors did not have strong effects on substrate-scale species composition compared to other factors, with the exception of host tree species that had a relatively strong effect on spruce communities. The importance of spruce species could be due to their bark characteristics, as bark roughness has been found to be a driver of composition (Boudreault et al., 2008b; Merinero et al., 2014). As black spruce trees have rougher bark than white spruce trees, they may be better at retaining water, therefore providing better microhabitat conditions for species that have higher water requirements. However, spruce species are clearly related to latitude in our study and we cannot reject that the effect is due to the latitudinal gradient. Site factors overpassed the effect of host tree size for all spruce, birch and snag substrates. This could be due to the limited range of tree size in our study, as forests of similar ages were selected and only the larger trees were sampled. Other factors that were not considered in our study can influence species composition, such as bark roughness (Boudreault et al., 2008b; Merinero et al., 2014), bark chemistry

(Boudreault et al., 2008b), solar radiation on substrate (Giordani et al., 2014), and site's topography. As these factors would probably have higher impact on substrate-scale communities, this might be the reason why the variations explained by the substrate-scale ordinations were considerably smaller than those explained by the site-scale ordinations.

2.5.2 Species richness

In contrast to species composition, species richness was not impacted by distance from Lake Superior, directly or indirectly. This was true for both site-scale and substrate-scale species richness, which goes against our hypotheses that the distance from the lake would have strong effect on the site scale and weak effect the substrate scale. This absence of trend could be due to species replacement along the gradient, which could possibly be driven by species functional traits. Indeed, it was previously found that species richness response to climate was photobiont-dependent (Marini et al., 2011). In our study, a different response to the distance from lake among functional groups could be due to a shift in the water source along the gradient. As the continental end of the gradient has a higher maximal temperature, lichens in this area are more likely to get hydrated from dew (Gauslaa, 2014), while lichens in the coastal end of the gradient are more likely to get hydrated from air humidity. Interestingly, species richness of the site scale and of the substrate scale for spruce trees, birch trees, and snags peaked at 35 km, which was confirmed by the breakpoint analyses. This could be the result of an overlap between the coastal-adapted species and the continental-adapted species, which would support the mid-domain effect theory on environmental gradients (Letten et al., 2013). However, sampling in this part of the gradient was insufficient to confirm this hypothesis.

The slightly lower richness found on sites directly by the shore could be explained by an edge effect. It was found that certain species' abundance and occurrence are responding to the edge effect in forest remnants created by logging (Barry et al., 2015; Boudreault et al., 2008a; Esseen & Renhorn, 1998; Hilmo & Holien, 2002; Rheault et al., 2003). This could be due in part to weather events, as high lichen mortality seems to be associated with storms and as strong wind causes physical damages on lichen thalli (Esseen, 1985; Esseen & Renhorn, 1998). Storms could also potentially induce a higher tree mortality near the shore which could affect lichen communities as it was suggested by Rheault et al. (2003) for logging-created edges. In addition, high speed winds are associated with lower air humidity (Ravi & D'Odorico, 2005) and reduce dew formation (Xiao et al., 2013). They could therefore locally counteract the effect of the lake on water availability. Strong winds and the stochastic events that they cause could also explain the large variance in species richness that was observed between 0 and 5 km from the coast, especially at the site scale. The high water availability in this part of the gradient could allow the establishment of a large number of species, but the frequent disturbances could lower species richness locally. This potentially larger importance of stochastic events is also supported by the absence of significative effects of any of distance from lake, local factors, or substrate factors on sites from 0 to 5 km the shore.

2.6 Conclusion

Our study highlights the importance of spatial scale when studying lichen species composition. It shows that the relative importance of lichen composition drivers varies across scales. Although the latitudinal gradient had the most effect within the study area, our results suggest that site-scale composition tends to be more influenced by

large-scale climatic gradients while substrate-scale composition tend to be more influenced by local forest structure factors, notably site maximum DBH and canopy cover. Species richness was not driven by the climatic gradient in our study, suggesting a species replacement along the gradient. This replacement could be linked to functional traits and to a shift in the water source along the gradient, with the continental part being more likely to provide lichens with liquid water through dew, and the coastal part being more likely to provide water through air humidity. Further analyses considering functional traits, as growth form, photobiont type or water holding capacity, would be interesting to verify this hypothesis. A higher sampling effort in the middle part of the gradient, especially around 35 km from the coast, would also be useful to test the mid-domain effect theory on environmental gradients, although access by road to this part of the gradient is often limited. Overall, our results suggest that the warmer temperatures and higher drought occurrence expected in the boreal forest (Price et al., 2013; Sheffield & Wood, 2008; Wotton et al., 2010) would not necessarily lead to decreases in local species richness in the mixed-wood stands, but the range of the species associated with high humidity conditions could shrink. As forest structure seems to impact substrate-scale water availability, stands with large trees and important canopy cover could be targeted for the conservation of hygrophytic species.

CHAPITRE III

CONCLUSION GÉNÉRALE

Notre étude souligne l'importance de considérer l'échelle spatiale lors de l'analyse de la composition en espèces des communautés de lichens. En effet, nos résultats ont démontré que l'importance relative des déterminants de la composition varie en fonction de l'échelle. Sur l'ensemble de l'aire d'étude, le gradient latitudinal est le facteur ayant l'effet le plus fort sur les deux échelles, ce qui est probablement dû à une transition du pool d'espèces du sud vers le nord. À l'échelle du site, en considérant des latitudes similaires, la distance par rapport au lac Supérieur est le principal déterminant de la composition, suggérant que les gradients climatiques régionaux déterminent la disponibilité en eau à cette échelle. À l'échelle du substrat, les variables de structure forestière ont un effet relatif sur la composition plus un portant que la distance par rapport au lac, suggérant que les facteurs locaux ont plus d'impact sur la disponibilité en eau à cette échelle.

Dans notre étude, la richesse spécifique n'était pas déterminée par le gradient climatique, ni de façon directe, ni de façon indirecte. Ce résultat suggère qu'on observe un remplacement des espèces le long du gradient, lequel pourrait potentiellement être lié à un remplacement de la source d'hydratation des lichens et aux traits fonctionnels des espèces. En effet, les lichens de la partie continentale du gradient sont plus susceptibles d'être hydratés par l'eau liquide générée par la rosée, tandis que les lichens de la partie côtière du gradient sont plus susceptibles d'être hydratés par l'humidité de l'air. De futures analyses pourraient permettre de vérifier cette hypothèse en comparant

la réponse de divers groupes fonctionnels au gradient climatique. De plus, un effort d'échantillonnage accru dans le milieu du gradient, particulièrement autour de 35 km, pourrait être intéressant pour vérifier si les espèces adaptées à la côte et celles adaptées au climat continental se chevauchent à cet endroit, induisant un pic de richesse comme on semble l'observer dans nos résultats. Notre étude a aussi démontré que les facteurs de site et de substrat avaient moins d'effets sur la richesse spécifique près du lac qu'à des distances intermédiaires ou éloignées. Nous posons l'hypothèse que les conditions hydriques que génère le lac sur de petites distances permettraient l'établissement d'un grand nombre d'espèces, mais que les événements stochastiques reliés aux grands vents pourraient faire varier la richesse localement.

Notre étude contribue à combler les lacunes dans les données sur la biodiversité, notamment les lacunes wallacéennes, en générant des données sur la distribution des espèces d'un groupe d'organismes relativement peu étudié, et les lacunes hutchinsoniennes, en approfondissant les connaissances sur la réponse des lichens aux conditions climatiques. Nos résultats permettent également de mieux anticiper les effets qu'auront les changements climatiques sur les communautés de lichens. Nous avançons que les températures plus élevées et la plus grande fréquence des sécheresses qui sont attendues dans la forêt boréale (Price et al., 2013; Sheffield & Wood, 2008; Wotton et al., 2010) ne mèneraient pas nécessairement à une diminution locale de la richesse spécifique dans les peuplements mixtes. Cependant, l'aire de répartition des espèces associées à des conditions hydriques élevées pourrait se voir rétrécie. Comme la structure forestière semble influencer la disponibilité en eau à l'échelle du substrat, les peuplements avec des gros arbres et ayant une couverture forestière importante pourraient être visés pour la conservation des espèces hygrophytes.

ANNEXE A

Land cover and climate data of the four ecoregions found in the study area. Ecoregions are ordered following their geographic position in the study area, from northwest to southeast. Land cover data are extracted from Crins et al. (2009) and the climate data are extracted from Mackey et al. (1996b, 1996a). Only area proportions for mixed forests, coniferous forests, deciduous forests, and water bodies are shown in the land cover column. Location of the ecoregions can be found in Crins et al. (2009), along with supplementary information.

Ecoregion	Land cover	Mean annual temperature	Mean annual precipitations	Mean summer precipitations
Lake Nipigon (northwest)	23.5% mixed forests 23.0% coniferous forests 17.1% water bodies 9.0% deciduous forests	-1.7 to 2.1 °C	645 to 879 mm	231 to 298 mm
Lake Abitibi	29.5% mixed forests 28.1% coniferous forests 7.2% deciduous forests 7.2% water bodies	-0.5 to 2.5 °C	652 to 1029 mm	220 to 291 mm
Lake Temagami	33.2% mixed forests 19.9% coniferous forests 17.1% deciduous forests 10.9% water bodies	0.8 to 4.3 °C	725 to 1148 mm	217 to 291 mm
Georgian Bay (southeast)	32.0% mixed forests 22.2% deciduous forests 12.1% coniferous forests 11.0% water bodies	2.8 to 6.2 °C	771 to 1134 mm	204 to 304 mm

ANNEXE B

Climatic data based on hourly records from September 19, 2021, to September 10, 2022. Recording sites near Lake Superior include 3A3, 3D3, 4A2, 4D2, 5B2, 7B2, 8B2, 8D2 and Bonamie weather station (Pukaskwa National Park); recording sites at intermediate distances from Lake Superior include 1F3, 6G4, 5E3, 7E3, 8G2 and Lurch weather station (Pukaskwa National Park); recording sites far from Lake Superior include 1I3, 2H4, 2J2, 3H3, 4I3, 5I2, 6J2, 7I2.

	Near (0-5 km) (n=9)	Intermediate (10-35 km) (n=6)	Far (55-100 km) (n=8)
Maximum temperature (°C)	26.99 ± 1.82	29.80 ± 4.90	30.06 ± 1.03
Mean spring temperature (°C)	5.04 ± 0.77	5.59 ± 1.00	5.39 ± 0.21
Mean summer temperature (°C)	14.57 ± 0.88	14.69 ± 2.49	15.26 ± 0.21
Mean fall temperature (°C)	2.84 ± 1.22	1.87 ± 0.78	0.96 ± 0.33
Length of longest 90 th percentile temperature period (hrs)	52.00 ± 8.23	37.00 ± 17.89	36.63 ± 1.19
Year first day of ≥ 90 th percentile temperature (number of days from January 1 st)	127.22 ± 3.35	128.83 ± 2.23	128.5 ± 1.41
Year last day of ≥ 90 th percentile temperature (number of days from January 1 st)	288.22 ± 3.11	287.83 ± 4.58	289.75 ± 4.17
Mean spring relative humidity (%)	80.81 ± 4.75	71.02 ± 9.20	83.50 ± 7.47
Mean summer relative humidity (%)	88.21 ± 3.11	82.83 ± 9.87	89.96 ± 5.15
Mean fall relative humidity (%)	90.52 ± 4.21	92.07 ± 3.36	89.66 ± 10.50
Length of longest ≤ 10 th percentile relative humidity period (h)	45.56 ± 15.93	44.67 ± 31.47	47.00 ± 22.24

ANNEXE C

Environmental variables of the individual sites. Mean and maximum DBH and deciduous ratio were calculated from the trees included in the basal area count. Canopy cover was estimated using a densiometer from the site center point.

Site	Lake distance (km)	Altitude (m)	Mean DBH (cm)	Max DBH (cm)	Basal area	Canopy cover (%)	Deciduous ratio (%)	Min age	Mean spruce bark pH	Mean birch bark pH
East zone										
4A2	0	177.9	18.5 ± 6.5	34.5	24	59.4	25.0	139	4.6 ± 0.4	5.5 ± 0.5
4B3	1.0	210.1	26.2 ± 15.1	54.5	30	75.5	40.0	146	5.0 ± 0.4	5.6 ± 0.3
4C3	2.5	289.9	33.0 ± 17.8	70.0	24	85.9	91.7	94	5.4 ± 0.5	5.4 ± 0.6
4D2	5.0	277.0	23.6 ± 11.0	37.5	22	73.4	54.5	81	5.1 ± 0.0	5.5 ± 0.2
4H3	55.0	422.7	29.1 ± 14.8	55.0	26	75.5	30.8	132	5.0 ± 0.2	5.8 ± 0.9
4I3	75.0	434.3	27.1 ± 20.0	80.0	32	72.4	31.3	89	4.9 ± 0.1	5.7 ± 0.3
4J3	100.0	493.4	21.4 ± 12.4	53.5	30	80.2	66.7	62	5.1 ± 0.3	5.4 ± 0.1
5A2	0	211.8	24.1 ± 10.7	43.5	30	55.7	13.3	105	4.9 ± 0.1	5.3 ± 0.4
5B2	1.0	249.9	17.7 ± 9.0	36.5	34	72.9	11.8	87	5.5 ± 0.8	5.2 ± 0.4
5C2	2.5	332.5	15.9 ± 10.4	48.0	36	66.7	83.3	123	5.0 ± 0.3	5.1 ± 0.2
5D2	5.0	403.9	21.2 ± 15.5	53.0	36	76.6	61.1	109	5.1 ± 0.3	5.5 ± 0.3
5E3	10.0	359.7	25.2 ± 15.0	69.5	34	71.9	29.4	136	4.6 ± 0.0	5.3 ± 0.2
5G3	35.0	385.8	13.5 ± 6.1	22.0	24	83.3	25.0	135	4.7 ± 0.3	5.3 ± 0.1
5I2	75.0	491.1	17.7 ± 7.1	27.0	14	71.9	14.3	101	4.9 ± 0.4	5.2 ± 0.1
5J3	100.0	452.1	15.7 ± 4.8	23.5	24	78.6	25.0	40	NA	5.3 ± 0.3
6A2	0	190.9	20.3 ± 7.8	34.0	30	61.5	26.7	128	5.4 ± 0.4	5.4 ± 0.2
6B3	1.0	209.5	22.6 ± 9.4	43.0	34	71.4	76.5	114	5.0 ± 0.25	5.3 ± 0.1
6C3	2.5	265.6	34.6 ± 17.5	72.5	18	85.4	66.7	106	4.7 ± 0.4	5.2 ± 0.3
6D2	5.0	279.0	27.7 ± 12.4	50.5	20	82.3	50.0	86	5.2 ± 0.1	5.6 ± 0.2
6F2	20.0	450.2	27.1 ± 12.9	51.0	44	79.2	45.5	131	5.2 ± 0.1	5.2 ± 0.2
6H3	55.0	448.4	29.3 ± 9.6	42.5	16	79.7	87.5	75	5.4 ± 0.2	5.5 ± 0.2
6I2	100.0	440.6	16.6 ± 5.0	23.5	22	63.5	9.1	25	5.3 ± 0.2	5.5 ± 0.7
North zone										
1A2	0	186.9	20.1 ± 9.0	30.0	16	88.5	12.5	NA	4.9 ± 0.1	5.5 ± 0.3
1B2	1.0	274.6	18.3 ± 7.6	29.0	16	74.0	50.0	NA	4.9 ± 0.1	5.6 ± 0.15
1C2	2.5	242.2	23.4 ± 7.2	35.5	36	82.8	33.3	NA	5.5 ± 0.1	6.5 ± 0.5
1F3	20.0	406.1	20.4 ± 9.2	42.0	34	82.8	64.7	NA	NA	NA
1I3	75.0	347.9	24.7 ± 6.7	33.5	34	66.1	41.2	166	4.6 ± 0.5	5.1 ± 0.5
2A3	0	195.1	25.4 ± 8.8	39.0	24	94.8	41.7	112	6.7 ± 0.1	6.7 ± 0.2
2B3	1.0	255.7	12.1 ± 3.4	16.5	22	92.7	0	113	6.7 ± 0.2	7.0 ± 0.1
2C2	2.5	332.6	17.7 ± 10.9	37.0	20	96.9	20.0	166	6.9 ± 0.1	6.7 ± 0.1
2G4	35.0	457.3	25.3 ± 6.0	35.5	32	66.7	25.0	91	5.1 ± 0.2	5.0 ± 0.4
2H4	55.0	489.3	22.9 ± 4.5	30.0	36	53.1	5.6	67	4.3 ± 0.4	5.6 ± 0.1
2I2	75.0	442.9	26.3 ± 13.9	45.5	18	62.0	44.4	117	4.9 ± 0.6	5.2 ± 0.2
2J2	100.0	444.8	24.5 ± 12.1	48.5	24	73.4	33.3	144	4.3 ± 0.1	5.5 ± 0.1
3A4	0	187.6	22.4 ± 7.5	34.0	28	60.9	28.6	88	4.9 ± 0.2	5.4 ± 0.2
3B3	1.0	266.7	21.6 ± 9.0	40.0	38	68.8	52.6	86	5.0 ± 0.2	5.5 ± 0.3
3C4	2.5	194.7	18.2 ± 5.1	27.5	42	66.1	38.1	92	4.3 ± 0.4	5.7 ± 0.3
3D3	5.0	251.7	18.2 ± 5.8	35.5	48	64.1	20.8	110	5.0 ± 0.2	5.0 ± 0.4
3F2	20.0	321.3	21.3 ± 6.2	35.0	32	59.9	43.8	109	4.9 ± 0.3	5.3 ± 0.4
3H3	55.0	337.4	16.5 ± 6.5	33.0	26	63.0	38.5	118	4.5 ± 0.3	5.1 ± 0.3
3I2	75.0	320.4	23.5 ± 10.2	53.0	46	66.1	21.7	65	5.1 ± 0.3	5.3 ± 0.1
7A2	0	201.8	19.5 ± 5.5	32.5	42	56.8	33.3	62	4.8 ± 0.2	5.5 ± 0.4
7B2	1.0	308.0	23.7 ± 11.6	35.0	38	76.0	42.1	119	5.0 ± 0.1	5.6 ± 0.3
7C2	2.5	382.1	20.6 ± 5.0	30.0	22	55.7	27.3	84	4.9 ± 0.2	5.2 ± 0.1
7D2	5.0	328.8	27.7 ± 9.0	44.0	30	70.3	40.0	115	4.9 ± 0.3	5.6 ± 0.3

7E3	10.0	347.1	16.7 ± 8.1	39.5	46	62.0	26.1	119	4.7 ± 0.3	5.3 ± 0.2
7F4	20.0	325.0	17.3 ± 6.9	32.5	34	71.9	47.1	137	5.5 ± 0.3	4.8 ± 0.1
7I2	75.0	371.4	18.2 ± 7.7	34.0	24	62.5	58.3	83	5.4 ± 0.1	5.3 ± 0.60
7J2	100.0	355.0	21.9 ± 5.4	31.5	34	62.5	23.5	63	5.0 ± 0.7	5.2 ± 0.4
8B2	1.0	215.1	28.5 ± 7.5	39.0	24	70.3	25.0	68	5.5 ± 0.5	4.8 ± 0.2
8C3	2.5	344.6	22.8 ± 3.0	27.0	22	50.0	0.0	94	5.4 ± 0.7	4.7 ± 0.2
8D2	5.0	273.7	21.98 ± 9.6	39.0	42	57.3	33.3	50	4.9 ± 0.2	5.4 ± 0.3
8G2	35.0	438.0	22.1 ± 6.5	30.0	20	62.0	40.0	98	4.4 ± 0.4	5.3 ± 0.2
8H2	55.0	440.1	20.0 ± 8.8	36.0	30	76.0	46.7	84	5.0 ± 0.2	5.7 ± 1.2

ANNEXE D

Number of replicates and species (for *Picea*, *Betula*, and snags) per site for each substrate type. A maximum of five replicates per substrate type was sampled in each site. Species that could not be identified with certainty in the field are either identified by their genus, or are shown as NA.

Site	Species and number of the <i>Picea</i> substrates sampled	Species and number of the <i>Betula</i> substrates sampled	Species and number of the snag substrates sampled	Number of rock substrates sampled
East zone				
4A2	<i>Picea mariana</i> (5)	<i>Betula papyrifera</i> (5)	<i>Abies balsamea</i> (3), <i>Betula papyrifera</i> (2)	5
4B3	<i>Picea glauca</i> (3)	<i>Betula papyrifera</i> (5)	<i>Abies balsamea</i> (5)	1
4C3	<i>Picea glauca</i> (5)	<i>Betula alleghaniensis</i> (2), <i>Betula papyrifera</i> (3)	<i>Abies balsamea</i> (2), <i>Betula papyrifera</i> (1), NA (2)	1
4D2	<i>Picea glauca</i> (5)	<i>Betula alleghaniensis</i> (5)	<i>Abies balsamea</i> (1), <i>Betula papyrifera</i> (1), <i>Picea glauca</i> (2), NA (1)	5
4H3	<i>Picea mariana</i> (5)	<i>Betula papyrifera</i> (5)	<i>Abies balsamea</i> (2), <i>Betula papyrifera</i> (2), <i>Picea</i> sp. (1)	5
4I3	<i>Picea</i> sp. (5)	<i>Betula papyrifera</i> (5)	<i>Betula papyrifera</i> (4), <i>Picea</i> sp. (1)	5
4J3	<i>Picea glauca</i> (4)	<i>Betula papyrifera</i> (5)	<i>Abies balsamea</i> (1), <i>Betula papyrifera</i> (2), <i>Populus tremuloides</i> (2)	No rocks sampled
5A2	<i>Picea mariana</i> (5)	<i>Betula papyrifera</i> (5)	<i>Abies balsamea</i> (2), <i>Betula papyrifera</i> (1), <i>Picea mariana</i> (1), <i>Sorbus</i> sp. (1)	5
5B2	<i>Picea mariana</i> (5)	<i>Betula papyrifera</i> (5)	<i>Abies balsamea</i> (2), <i>Betula papyrifera</i> (2), <i>Picea mariana</i> (1)	No rocks sampled
5C2	<i>Picea glauca</i> (5)	<i>Betula alleghaniensis</i> (2), <i>Betula papyrifera</i> (3)	<i>Abies balsamea</i> (3), <i>Betula papyrifera</i> (2)	2

Site	Species and number of the <i>Picea</i> substrates sampled	Species and number of the <i>Betula</i> substrates sampled	Species and number of the snag substrates sampled	Number of rock substrates sampled
5D2	<i>Picea glauca</i> (5)	<i>Betula alleghaniensis</i> (3), <i>Betula papyrifera</i> (2)	<i>Abies balsamea</i> (2), <i>Betula papyrifera</i> (3)	5
5E3	<i>Picea glauca</i> (5)	<i>Betula alleghaniensis</i> (1), <i>Betula papyrifera</i> (4)	<i>Acer</i> sp. (1), <i>Picea glauca</i> (2), <i>Thuja occidentalis</i> (2)	No rocks sampled
5G3	<i>Picea glauca</i> (5)	<i>Betula papyrifera</i> (5)	<i>Betula papyrifera</i> (2), NA (1)	5
5I2	<i>Picea mariana</i> (5)	<i>Betula papyrifera</i> (5)	<i>Abies balsamea</i> (2), <i>Betula papyrifera</i> (1), <i>Populus tremuloides</i> (2)	No rocks sampled
5J3	<i>Picea glauca</i> (5)	<i>Betula papyrifera</i> (5)	<i>Abies balsamea</i> (1), <i>Betula papyrifera</i> (1), <i>Picea</i> sp. (2)	5
6A2	<i>Picea glauca</i> (5)	<i>Betula papyrifera</i> (5)	<i>Abies balsamea</i> (2), <i>Betula papyrifera</i> (3)	5
6B3	<i>Picea glauca</i> (5)	<i>Betula papyrifera</i> (5)	<i>Abies balsamea</i> (1), <i>Acer pensylvanicum</i> (1), <i>Betula papyrifera</i> (3),	No rocks sampled
6C3	<i>Picea glauca</i> (5)	<i>Betula papyrifera</i> (5)	<i>Abies balsamea</i> (1), <i>Betula papyrifera</i> (4)	2
6D2	<i>Picea glauca</i> (3)	<i>Betula papyrifera</i> (5)	<i>Abies balsamea</i> (2), <i>Acer rubrum</i> (1), <i>Acer</i> sp. (1), <i>Betula papyrifera</i> (1)	1
6F2	<i>Picea glauca</i> (5)	<i>Betula alleghaniensis</i> (5)	<i>Abies balsamea</i> (2), <i>Acer saccharum</i> (1), <i>Betula papyrifera</i> (1), NA (1)	5
6H3	<i>Picea glauca</i> (2)	<i>Betula papyrifera</i> (2), <i>Betula alleghaniensis</i> (3)	<i>Abies balsamea</i> (1), <i>Acer</i> sp. (3), <i>Betula papyrifera</i> (1)	5
6J2	<i>Picea glauca</i> (2), <i>Picea mariana</i> (3)	<i>Betula papyrifera</i> (5)	<i>Abies balsamea</i> (1), <i>Pinus banksiana</i> (2), NA (2)	2
North zone				
1A2	<i>Picea glauca</i> (5)	<i>Betula papyrifera</i> (5)	<i>Betula papyrifera</i> (2), <i>Picea glauca</i> (3)	5
1B2	<i>Picea glauca</i> (1), <i>Picea mariana</i> (4)	<i>Betula papyrifera</i> (5)	<i>Betula papyrifera</i> (1), <i>Pinus banksiana</i> (4)	4

Site	Species and number of the <i>Picea</i> substrates sampled	Species and number of the <i>Betula</i> substrates sampled	Species and number of the snag substrates sampled	Number of rock substrates sampled
1C2	<i>Picea glauca</i> (5)	<i>Betula papyrifera</i> (5)	<i>Abies balsamea</i> (1), <i>Betula papyrifera</i> (1), <i>Picea glauca</i> (2), NA (1)	No rocks sampled
1F3	<i>Picea glauca</i> (2), <i>Picea mariana</i> (1), <i>Picea</i> sp. (2)	<i>Betula papyrifera</i> (5)	<i>Abies balsamea</i> (1), <i>Betula papyrifera</i> (2), <i>Picea glauca</i> (1), NA (1)	No rocks sampled
1I3	<i>Picea mariana</i> (5)	<i>Betula papyrifera</i> (5)	<i>Betula papyrifera</i> (2), <i>Picea mariana</i> (1), NA (2)	No rocks sampled
2A3	<i>Picea glauca</i> (5)	<i>Betula papyrifera</i> (5)	<i>Abies balsamea</i> (3), <i>Betula papyrifera</i> (1), <i>Picea glauca</i> (1)	No rocks sampled
2B3	<i>Picea glauca</i> (5)	<i>Betula papyrifera</i> (5)	<i>Betula papyrifera</i> (2), <i>Populus tremuloides</i> (1), NA (1)	4
2C2	<i>Picea glauca</i> (5)	<i>Betula papyrifera</i> (5)	<i>Abies balsamea</i> (2), <i>Betula papyrifera</i> (2), <i>Thuja occidentalis</i> (1)	3
2G4	<i>Picea mariana</i> (5)	<i>Betula papyrifera</i> (5)	<i>Picea</i> sp. (1), <i>Pinus banksiana</i> (4)	3
2H4	<i>Picea mariana</i> (5)	<i>Betula papyrifera</i> (5)	<i>Betula papyrifera</i> (2), <i>Picea mariana</i> (1), <i>Populus tremuloides</i> (2)	3
2I2	<i>Picea glauca</i> (5)	<i>Betula papyrifera</i> (5)	<i>Betula papyrifera</i> (2), <i>Populus tremuloides</i> (2), NA (1)	2
2J2	<i>Picea glauca</i> (5)	<i>Betula papyrifera</i> (5)	<i>Betula papyrifera</i> (2), NA (2)	5
3A4	<i>Picea mariana</i> (5)	<i>Betula papyrifera</i> (5)	<i>Abies balsamea</i> (3), <i>Betula papyrifera</i> (1), NA (1)	No rocks sampled
3B3	<i>Picea glauca</i> (5)	<i>Betula papyrifera</i> (5)	<i>Abies balsamea</i> (2), <i>Betula papyrifera</i> (2), <i>Sorbus</i> sp. (1)	2
3C4	<i>Picea mariana</i> (5)	<i>Betula papyrifera</i> (5)	<i>Abies balsamea</i> (2), <i>Picea mariana</i> (2),	No rocks sampled

Site	Species and number of the <i>Picea</i> substrates sampled	Species and number of the <i>Betula</i> substrates sampled	Species and number of the snag substrates sampled	Number of rock substrates sampled
			<i>Populus tremuloides</i> (1)	
3D3	<i>Picea glauca</i> (1), <i>Picea mariana</i> (4)	<i>Betula papyrifera</i> (5)	<i>Abies balsamea</i> (3), <i>Picea mariana</i> (2)	No rocks sampled
3F2	<i>Picea mariana</i> (5)	<i>Betula papyrifera</i> (5)	<i>Betula papyrifera</i> (4), <i>Picea mariana</i> (1)	No rocks sampled
3H3	<i>Picea glauca</i> (1), <i>Picea mariana</i> (3), <i>Picea</i> sp. (1)	<i>Betula papyrifera</i> (5)	<i>Betula papyrifera</i> (1), NA (4)	3
3I2	<i>Picea glauca</i> (5)	<i>Betula papyrifera</i> (5)	<i>Abies balsamea</i> (2), <i>Betula papyrifera</i> (1), <i>Thuja occidentalis</i> (2)	No rocks sampled
7A2	<i>Picea mariana</i> (5)	<i>Betula papyrifera</i> (5)	<i>Betula papyrifera</i> (3), <i>Picea mariana</i> (2)	5
7B2	<i>Picea mariana</i> (5)	<i>Betula papyrifera</i> (5)	<i>Abies balsamea</i> (3), <i>Betula papyrifera</i> (2)	4
7C2	<i>Picea mariana</i> (5)	<i>Betula papyrifera</i> (5)	<i>Betula papyrifera</i> (3), <i>Picea mariana</i> (2)	1
7D2	<i>Picea mariana</i> (5)	<i>Betula papyrifera</i> (5)	<i>Abies balsamea</i> (2), <i>Betula papyrifera</i> (3)	4
7E3	<i>Picea mariana</i> (5)	<i>Betula papyrifera</i> (5)	<i>Betula papyrifera</i> (3), <i>Picea mariana</i> (2)	1
7F4	<i>Picea glauca</i> (5)	<i>Betula papyrifera</i> (5)	<i>Abies balsamea</i> (1), <i>Betula papyrifera</i> (4)	4
7I2	<i>Picea glauca</i> (5)	<i>Betula papyrifera</i> (5)	<i>Abies balsamea</i> (1), <i>Betula papyrifera</i> (1), <i>Pinus banksiana</i> (2), <i>Populus</i> <i>tremuloides</i> (1)	No rocks sampled
7J2	<i>Picea mariana</i> (5)	<i>Betula papyrifera</i> (5)	<i>Abies balsamea</i> (2), <i>Picea mariana</i> (3)	No rocks sampled
8B2	<i>Picea glauca</i> (5)	<i>Betula papyrifera</i> (5)	<i>Betula papyrifera</i> (4), <i>Sorbus</i> sp. (1)	1
8C3	<i>Picea mariana</i> (5)	<i>Betula papyrifera</i> (5)	<i>Betula papyrifera</i> (2), <i>Picea mariana</i> (3)	No rocks sampled
8D2	<i>Picea mariana</i> (5)	<i>Betula papyrifera</i> (5)	<i>Betula papyrifera</i> (3)	No rocks sampled
8G2	<i>Picea mariana</i> (4), <i>Picea</i> sp. (1)	<i>Betula papyrifera</i> (5)	<i>Betula papyrifera</i> (4), <i>Picea mariana</i> (1)	3

Site	Species and number of the <i>Picea</i> substrates sampled	Species and number of the <i>Betula</i> substrates sampled	Species and number of the snag substrates sampled	Number of rock substrates sampled
8H2	<i>Picea glauca</i> (5)	<i>Betula papyrifera</i> (5)	<i>Abies balsamea</i> (1), <i>Betula papyrifera</i> (4)	1

ANNEXE E

Names and authorities and codes of the species found.

Species	Code
<i>Anaptychia palmulata</i> (Michaux) Vain.	anap_palm
<i>Bryoria americana</i> (Motyka) Holien	bryo_amer
<i>Bryoria furcellata</i> (Fr.) Brodo & D. Hawksw.	bryo_furc
<i>Bryoria fuscescens</i> (Gyelnik) Brodo & D. Hawksw.	bryo_fusc
<i>Bryoria nadvornikiana</i> (Gyelnik) Brodo & D. Hawksw.	bryo_nadv
<i>Bryoria pikei</i> Brodo & D. Hawksw.	bryo_pike
<i>Bryoria trichodes</i> (Michaux) Brodo & D. Hawksw.	bryo_tric
<i>Cetrelia olivetorum</i> (Nyl.) Culb. & C. Culb.	cetr_oliv
<i>Cladonia arbuscula subsp. mitis</i> (Sandst.) Ruoss	clad_arbu_mitis
<i>Cladonia bacilliformis</i> (Nyl.) Sarnth.	clad_baci
<i>Cladonia botrytes</i> (K. Hagen) Willd.	clad_botr
<i>Cladonia caespiticia</i> (Pers.) Flörke	clad_caes
<i>Cladonia carneola</i> (Fr.) Fr.	clad_carn
<i>Cladonia cenotea</i> (Ach.) Schaer.	clad_ceno
<i>Cladonia chlorophaea</i> (group)	clad_chlo
<i>Cladonia coccifera</i> (L.) Willd.	clad_cocc
<i>Cladonia coniocraea</i> (Flörke)	clad_coni
<i>Cladonia cornuta subsp. cornuta</i>	clad_corn_corn
<i>Cladonia crispata</i> (Ach.) Flotow	clad_cris
<i>Cladonia decorticata</i> (Flörke) Sprengel	clad_deco
<i>Cladonia deformis</i> (L.) Hoffm.	Clad_defo
<i>Cladonia digitata</i> (L.) Hoffm.	clad_digi
<i>Cladonia fimbriata</i> (L.) Fr.	clad_fimb
<i>Cladonia floerkeana</i> (Fr.) Flörke	clad_floe
<i>Cladonia glauca</i> Flörke	clad_glau
<i>Cladonia grayi</i> G. Merr. ex Sandst.	clad_gray
<i>Cladonia incrassata</i> Flörke	clad_incr
<i>Cladonia macilenta</i> Hoffm.	clad_maci
<i>Cladonia magyarica</i> Vain.	clad_magy
<i>Cladonia norvegica</i> Tønsberg & Holien	clad_norv
<i>Cladonia ochrochlora</i> Flörke	clad_ochr

Species	Code
<i>Cladonia peziziformis</i> (With.) J. R. Laundon	clad_pezi
<i>Cladonia phyllophora</i> Ehrh. ex Hoffm.	clad_phyl
<i>Cladonia pleurota</i> (Flörke) Schaer.	clad_pleu
<i>Cladonia pyxidata</i> (L.) Hoffm.	clad_pyxi
<i>Cladonia ramulosa</i> (With.) J.R. Laundon	clad_ramu
<i>Cladonia rangiferina</i> (L.) F.H. Wigg.	clad_rang
<i>Cladonia rei</i> Schaer.	clad_rei
<i>Cladonia scabriuscula</i> (Delise) Nyl.	clad_scab
<i>Cladonia squamosa</i> Hoffm.	clad_squa
<i>Cladonia stygia</i> (Fr.) Ruoss	clad_styg
<i>Cladonia subulata</i> (L.) Weber ex F. H. Wigg.	clad_subu
<i>Cladonia sulphurina</i> (Michaux) Fr.	clad_sulp
<i>Cladonia turgida</i> Hoffm.	clad_turd
<i>Dolichousnea longissima</i> (Ach.) Articus	doli_long
<i>Evernia mesomorpha</i> Nyl.	ever_meso
<i>Flavoparmelia caperata</i> Nyl.	flav_cape
<i>Flavopunctelia flaventior</i> (Stirton) Hale	flav_flav
<i>Flavopunctelia soledica</i> (Nyl.) Hale	flav_sore
<i>Heterodermia galactophylla</i> (Tuck.) Culb.	hete_gala
<i>Heterodermia obscurata</i> (Nyl.) Trevisan	hete_obsc
<i>Heterodermia speciosa</i> (Wulfen) Trevisan	hete_spec
<i>Hypocenomyce scalaris</i> (Ach. ex Lilj.) M. Choisy	hypo_scal
<i>Hypogymnia incurvoides</i> Rass.	hypo_incu
<i>Hypogymnia physodes</i> (L.) Nyl.	hypo_phys
<i>Hypogymnia tubulosa</i> (Schaer.) Hav.	hypo_tubu
<i>Hypotrachyna revoluta</i> (Flörke) Hale	hypo_revo
<i>Imshaugia aleurites</i> (Ach.) S. F. Meyer	imsh_aleu
<i>Imshaugia placorodia</i> (Ach.) S. F. Meyer	imsh_plac
<i>Leptogium cyanescens</i> (Rabenh.) Körb.	lept_cyan
<i>Lobaria pulmonaria</i> (L.) Hoffm.	loba_pulm
<i>Melanelia hepatizon</i> (Ach.) Thell	mela_hepa
<i>Melanelixia fuliginosa</i> (Fr. ex Duby) O. Blanco, A. Crespo, Divakar, Essl. D. Hawksw. & Lumbsch	mela_fuli
<i>Melanelixia subaurifera</i> (Nyl.) O. Blanco, A. Crespo, Divakar, Essl. D. Hawksw. & Lumbsch	mela_suba
<i>Melanohalea exasperatula</i> (De Not.) O. Blanco, A. Crespo, Divakar, Essl. D. Hawksw. & Lumbsch	mela_exas
<i>Menegazzia terebrata</i> (Hoffm.) A. Massal.	mene_tere

Species	Code
<i>Nephroma bellum</i> (Sprengel) Tuck.	neph_bell
<i>Nephroma parile</i> (Ach.) Ach.	neph_bell
<i>Nephroma resupinatum</i> (L.) Ach.	neph_resu
<i>Parmelia saxatilis</i> (L.) Ach.	parm_saxa
<i>Parmelia squarrosa</i> Hale	parm_squa
<i>Parmelia sulcata</i> Taylor	parm_sulc
<i>Parmeliopsis ambigua</i> (Hoffm.) Nyl.	parm_ambi
<i>Parmeliopsis capitata</i> R.C. Harris	parm_capi
<i>Parmeliopsis hyperopta</i> (Ach.) Arnold	parm_hype
<i>Parmotrema arnoldii</i> (Du Rietx) Hale	parm_arno
<i>Parmotrema crinitum</i> (Ach.) Choisy	parm_crin
<i>Peltigera aphthosa</i> (L.) Willd.	pelt_apht
<i>Peltigera canina</i> (L.) Willd.	pelt_cani
<i>Peltigera elisabethae</i> Gyelnik	pelt_elis
<i>Peltigera neopolydactyla</i> (Gyelnik) Gyelnik	pelt_neop
<i>Peltigera polydactylon</i> (necker) Hoffm.	pelt_poly
<i>Peltigera praetextata</i> (Flörke ex Schommerf.) Zopf	pelt_prae
<i>Phaeophyscia hispidula</i> (Ach.) Essl.	phae_hisp
<i>Phaeophyscia pusilloides</i> (Zahlbr.) Essl.	phae_pusi
<i>Phaeophyscia rubropulchra</i> (Degel.) Essl.	phae_rubr
<i>Physcia adscendens</i> (Fr.) H. Olivier	phys_adsc
<i>Physcia aipolia</i> (Ehrh. ex Humb.) Fürnr	phys_aipo
<i>Physcia stellaris</i> (L.) Nyl.	phys_stel
<i>Physcia tenella</i> (Scop.) DC.	phys_tene
<i>Physconia detersa</i> (Nyl.) Poelt	phys_dete
<i>Physconia grumosa</i> Kashiw. & Poelt	phys_grum
<i>Physconia leucoleiptes</i> (Tuck.) Essl.	phys_leuc
<i>Physconia perisidiosa</i> (Erichsen) Moberg	phys_peri
<i>Platismatia glauca</i> (L.) Culb. & C. Culb.	plat_glau
<i>Platismatia tuckermanii</i> W.L. Culb. & C. F. Culb.	plati_tuck
<i>Polyblastidium japonicum</i> (M. Satô) Kalb	poly_japo
<i>Pseudevernia consocians</i> (Vain.) Hale & Culb.	pseu_cons
<i>Punctelia caseana</i> Lendemmer & Hodk.	punc_case
<i>Punctelia rudecta</i> (Ach.) Krog	punc_rude
<i>Pyxine sorediata</i> (Ach.) Mont.	pyxi_sore
<i>Ramalina americana</i> Hale	rama_amer
<i>Ramalina dilacerata</i> (Hoffm.) Hoffm.	rama_dila
<i>Ramalina farinacea</i> (L.) Ach.	rama_fari

Species	Code
<i>Ramalina intermedia</i> (Delise ex Nyl.) Nyl.	rama_inte
<i>Ramalina roesleri</i> (Hochst. ex Schaer.) Hue	rama_roes
<i>Ramalina thrausta</i> (Ach.) Nyl.	rama_thra
<i>Ricasolia quercizans</i> (Michx.) Stizenb.	rica_quer
<i>Tuckermanopsis americana</i> (Spreng.) Hale	tuck_amer
<i>Tuckermanopsis ciliaris</i> (Ach.) Gyeln.	tuck_cili
<i>Tuckermanopsis orbata</i> (Nyl.) M.J. Lai	tuck_orb
<i>Tuckermanopsis sepincola</i> (Ehrh.) Hale	tuck_sepi
<i>Umbilicaria mammulata</i> (Ach.) Tuck.	umbi_mamm
<i>Umbilicaria muhlenbergii</i> (Ach.) Tuck.	umbi_muhl
<i>Usnea cavernosa</i> Tuck.	usne_cave
<i>Usnea dasopoga</i> (Ach.) Nyl.	usne_daso
<i>Usnea glabrescens</i> (nyl. ex Vain.) Vain.	usne_glab
<i>Usnea hirta</i> (L.) Weber ex F.H. Wigg.	usne_hir
<i>Usnea perplexans</i> Stirt.	usne_perp
<i>Usnea subfloridana</i> Stirton	usne_subf
<i>Usnocetraria oakesiana</i> (Tuck.) M.J. Lai & J.C. Wei	usno_oake
<i>Vulpicida pinastri</i> (Scop.) J.-E. Mattsson & M. J. Lai	vulp_pina
<i>Xanthomendoza hasseana</i> (Räsänen) Søchting, Kärnefelt & S.Y. Kondr.	xant_hass

Species	Site																					
	4A2	4B3	4C3	4D2	4H3	4I3	4J3	5A2	5B2	5C2	5D2	5E3	5G3	5I2	5J3	6A2	6B3	6C3	6D2	6F2	6H3	6J2
<i>Flavopunctelia soledica</i>	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Heterodermia galactophylla</i>	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Heterodermia obscurata</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Heterodermia</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Heterodermia speciosa</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hypocenomyce scalaris</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hypogymnia incurvoides</i>	6	1	0	1	4	0	2	0	1	0	0	0	3	5	3	0	0	0	0	0	1	1
<i>Hypogymnia physodes</i>	9	1	1	1	1	3	5	1	2	0	0	0	2	3	2	2	0	1	0	0	0	2
<i>Hypogymnia</i> sp.	5	0	0	0	3	1	0	1	4	1	0	1	0	5	0	0	0	0	1	0	1	0
<i>Hypogymnia tubulosa</i>	1	0	0	1	1	2	0	1	0	0	0	0	2	6	1	1	0	1	0	0	0	5
<i>Imshaugia aleurites</i>	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
<i>Leptogium cyanescens</i>	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Lobaria pulmonaria</i>	0	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	2	0
<i>Melanelia</i> group	3	0	0	1	2	0	4	0	0	1	2	1	0	1	0	0	0	2	1	2	0	1
<i>Melanelixia fuliginosa</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	2	0	0	0
<i>Melanelixia subaurifera</i>	5	0	0	0	1	0	1	0	0	1	2	1	0	3	0	0	0	0	2	4	1	1
<i>Melanohalea exasperatula</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Melanohalea</i> group	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Menegazzia terebrata</i>	0	1	0	0	0	0	0	0	1	0	0	0	0	2	2	0	0	0	0	0	0	0
<i>Parmelia saxatilis</i>	1	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Parmelia</i> sp.	3	0	0	0	4	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	1	0
<i>Parmelia squarrosa</i>	6	5	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0

Species	Site																						
	4A2	4B3	4C3	4D2	4H3	4I3	4I3	4J3	5A2	5B2	5C2	5D2	5E3	5G3	5I2	5J3	6A2	6B3	6C3	6D2	6F2	6H3	6J2
<i>Parmelia sulcata</i>	13	4	1	2	4	5	5	5	3	1	5	1	1	4	14	7	2	0	3	2	2	2	5
<i>Parmeliopsis ambigua</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Parmeliopsis capitata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	0	0	0	0
<i>Parmeliopsis hyperota</i>	0	0	0	0	2	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	1
<i>Parmeliopsis</i> sp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Parmotrema crinitum</i>	0	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Peltigera elisabethae</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Peltigera polydactylon</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Peltigera</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Phaeophyscia hispidula</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Phaeophyscia pusilloides</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Phaeophyscia rubropulchra</i>	0	0	0	0	0	0	0	3	0	0	0	2	0	0	0	0	0	2	0	2	3	0	0
<i>Physcia aipolia</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Physcia</i> sp.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Physconia deterosa</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Physconia grumosa</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
<i>Physconia perisidiosa</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Physconia</i> sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Platismasia glauca</i>	1	0	0	0	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	0
<i>Platismatia</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Platismatia tuckermanii</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Polyblastidium japonicum</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pseudevernia consocians</i>	4	1	0	1	0	0	0	0	3	0	0	0	1	0	0	0	2	0	0	1	1	0	0

Species	Site																						
	4A2	4B3	4C3	4D2	4H3	4I3	4I3	4J3	5A2	5B2	5C2	5D2	5E3	5G3	5I2	5J3	6A2	6B3	6C3	6D2	6E2	6H3	6J2
<i>Punctelia caseana</i>	8	1	0	1	0	0	0	0	1	0	1	2	0	0	0	0	1	0	2	0	0	0	0
<i>Punctelia rudecta</i>	5	6	1	5	0	0	1	1	1	0	0	3	2	0	0	0	4	1	2	3	5	3	0
<i>Punctelia</i> sp.	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Pyxine soreidiata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Ramalina dilacerata</i>	0	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ramalina farinacea</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ramalina thrausta</i>	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ricasolia quercizans</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tuckermanopsis americana</i>	1	0	0	0	1	3	0	0	2	0	0	0	0	1	5	3	0	0	0	0	0	0	3
<i>Tuckermanopsis orbata</i>	0	0	0	0	3	3	0	0	1	0	0	0	0	2	2	3	0	0	0	0	0	0	5
<i>Tuckermanopsis sepincola</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Tuckermanopsis</i> sp.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Umbilicaria mulhenbergii</i>	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Unknown species	2	0	1	3	0	0	0	2	0	0	0	0	0	3	0	0	1	0	1	1	2	0	2
<i>Usnea cavernosa</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Usnea dasopoga</i>	6	0	0	0	2	0	3	0	4	0	0	0	0	0	9	0	0	0	0	0	0	0	1
<i>Usnea hirta</i>	7	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Usnea perplexans</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Usnea</i> sp.	2	0	0	1	1	3	0	1	6	0	0	0	0	0	3	0	1	0	0	0	1	0	2
<i>Usnea subfloridana</i>	11	0	0	1	1	1	0	0	0	0	0	0	0	3	3	4	1	0	0	0	0	1	0
<i>Usnocetraria oakesiana</i>	11	0	8	2	13	2	4	0	3	4	3	4	4	2	0	0	0	4	5	4	1	3	1
<i>Vulpicida pinastri</i>	2	0	0	0	1	0	0	1	3	0	0	0	0	3	4	0	0	1	0	0	0	0	1
<i>Xanthomendoza hasseana</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Species	Site
<i>Xanthoria</i> group	4A2 0
	4B3 0
	4C3 0
	4D2 0
	4H3 0
	4I3 0
	4J3 1
	5A2 0
	5B2 0
	5C2 0
	5D2 0
	5E3 0
	5G3 0
	5I2 0
	5J3 0
	6A2 0
	6B3 0
	6C3 0
	6D2 0
	6F2 0
	6H3 0
	6J2 0

ANNEXE G

Species found in the north zone. Numbers represent the total of individual substrates that species were found on in a site.

Species	Site																																
	1A2	1B2	1C2	1I3	2A3	2B3	2C2	2G4	2H4	2I2	2J2	3A4	3B3	3C4	3D3	3E2	3H3	3I2	7A2	7B2	7C2	7D2	7E3	7F4	7I2	7J2	8B2	8C3	8D2	8G2	8H2		
<i>Bryoria americana</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Bryoria furcellata</i>	0	11	0	3	5	1	0	4	11	8	4	5	1	0	3	0	2	9	0	2	1	8	3	1	3	0	7	2	9	7	9	5	
<i>Bryoria fuscescens</i>	0	4	0	4	1	0	0	7	5	2	0	0	1	0	1	0	1	3	2	0	0	3	0	2	0	10	0	3	6	8	7		
<i>Bryoria nadvornikiana</i>	0	6	0	2	1	2	0	3	4	0	2	2	0	8	0	4	3	0	7	2	6	5	5	3	0	9	2	9	7	9	7		
<i>Bryoria pikei</i>	0	2	0	0	0	0	2	4	3	4	1	0	0	0	0	4	0	1	2	1	1	3	1	1	0	5	1	4	3	4	1		
<i>Bryoria</i> sp.	1	6	1	5	1	0	1	2	3	2	4	1	0	0	0	6	3	2	2	1	1	1	1	4	1	1	6	0	5	4	5	6	
<i>Bryoria trichodes</i>	0	5	0	2	1	1	0	1	2	3	2	0	0	6	0	7	1	1	1	6	5	6	7	3	0	1	2	10	3	7	2		
<i>Cladonia arbuscula</i> subsp. <i>mitis</i>	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	
<i>Cladonia bacilliformis</i>	0	2	1	1	2	0	1	2	3	0	0	0	0	2	0	0	2	1	0	1	0	2	1	0	0	0	0	3	0	4	1		
<i>Cladonia botrytes</i>	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0		
<i>Cladonia caespiticia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0		
<i>Cladonia carneola</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0		
<i>Cladonia cenotea</i>	3	7	1	4	6	9	2	8	5	6	0	1	0	4	10	0	1	7	4	2	7	9	6	3	4	0	4	2	9	3	6	2	
<i>Cladonia chlorophaea</i>	9	9	2	1	1	4	8	4	4	4	7	2	6	10	3	7	3	9	3	9	4	9	7	2	6	0	9	8	7	5	13	5	

Species	Site																															
	1A2	1B2	1C2	1F3	1I3	2A3	2B3	2C2	2G4	2H4	2I2	2J2	3A4	3B3	3C4	3D3	3F2	3H3	3I2	7A2	7B2	7C2	7D2	7E3	7F4	7I2	7J2	8B2	8C3	8D2	8G2	8H2
<i>Cladonia</i> sp.	4	4	10	5	6	4	9	4	10	5	8	8	6	8	6	12	7	3	8	3	10	3	5	9	8	10	11	6	7	6	3	11
<i>Cladonia</i> sp. 2	0	2	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	2	3
<i>Cladonia squamosa</i>	5	10	0	3	0	1	0	5	9	2	0	0	1	1	1	0	2	0	0	1	0	3	5	2	0	0	0	0	0	4	4	0
<i>Cladonia stygia</i>	0	1	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cladonia stygia-rangiferina</i> group	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
<i>Cladonia subulata</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cladonia sulphurina</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	1	0
<i>Cladonia turgida</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Dolichousnea longissima</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	5	0	0	0	0	0	0	0
<i>Evernia mesomorpha</i>	11	9	5	9	7	3	4	6	14	13	9	7	6	2	10	2	11	7	13	15	6	13	7	7	9	10	13	6	11	10	11	10
<i>Flavoparmelia caperata</i>	8	1	0	0	0	4	4	3	0	0	0	1	3	0	0	0	0	0	1	6	0	1	0	0	0	0	0	0	0	1	1	0
<i>Flavoparmelia</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Flavopunctelia soredica</i>	4	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Heterodermia galactophylla</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Heterodermia obscurata</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Heterodermia</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Heterodermia speciosa</i>	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Hypocnemysce scalaris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
<i>Hypogymnia incurvoides</i>	6	9	8	5	2	3	3	12	12	11	2	5	0	4	8	1	6	3	7	4	3	8	5	6	5	3	1	8	11	9	9	4

Species	Site																															
	1A2	1B2	1C2	1F3	1I3	2A3	2B3	2C2	2G4	2H4	2I2	2J2	3A4	3B3	3C4	3D3	3F2	3H3	3I2	7A2	7B2	7C2	7D2	7E3	7F4	7I2	7J2	8B2	8C3	8D2	8G2	8H2
<i>Hypogymnia physodes</i>	17	14	6	10	13	10	4	8	12	10	8	6	10	5	11	4	11	10	10	16	11	15	13	10	9	7	14	8	12	10	14	8
<i>Hypogymnia</i> sp.	5	6	1	3	0	1	1	1	1	4	3	6	0	0	0	0	2	2	2	3	0	1	1	5	0	4	4	4	6	3	5	5
<i>Hypogymnia tubulosa</i>	0	3	2	1	1	0	2	0	4	6	0	3	0	0	1	0	0	0	3	3	0	2	2	1	1	4	6	0	1	3	1	2
<i>Hypotrachyna revoluta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Imshaugia aleurites</i>	0	6	0	1	4	2	0	4	10	7	0	0	3	2	6	0	3	7	3	0	4	15	2	6	2	0	3	0	6	0	8	1
<i>Imshaugia placorodia</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lobaria pulmonaria</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Melanelia</i> group	3	1	1	3	1	0	1	0	2	0	1	1	0	0	0	0	0	3	1	4	0	1	1	0	1	3	0	3	1	0	1	0
<i>Melanelia hepaticon</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Melanelixia subaurifera</i>	9	4	3	1	0	3	2	4	2	1	1	0	4	0	1	0	1	0	4	7	0	1	3	0	5	1	0	7	1	1	1	0
<i>Melanohalea exasperatula</i>	3	2	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	3	2	0	0	0	0	0	1	0	0	0	0	0	1
<i>Melanohalea</i> group	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1
<i>Menegazzia</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Menegazzia terebrata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0
<i>Nephroma bellum</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Nephroma parile</i>	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Nephroma resupinatum</i>	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Parmelia saxatilis</i>	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
<i>Parmelia</i> sp.	3	4	1	4	0	3	2	0	2	0	1	4	0	0	1	0	2	3	6	2	3	2	1	0	1	1	0	3	2	2	1	4
<i>Parmelia squarrosa</i>	1	0	2	0	0	9	3	4	0	0	0	0	4	0	2	1	1	0	0	9	9	6	8	4	0	0	0	4	1	3	0	2

ANNEXE H

Results of the substrate-scale generalized linear mixed models on distance groups with species richness as response variable and standardised canopy cover, deciduous trees ratio, total basal area, maximum DBH, minimum age, altitude, and substrate factors as fixed-effect variables, and site as random-effect variable. Significant effects are shown in bold.

Explanatory variables	Near distances			Intermediate distances			Far distances		
	Estimates	z-value	p-value	Estimates	z-value	p-value	Estimates	z-value	p-value
Spruce	$R^2m=0.47$			$R^2m=0.89$			$R^2m=0.38$		
Maximum DBH	-0.22 ± 0.15	-1.50	0.133	-0.71 ± 0.14	-5.24	<0.001	-0.16 ± 0.07	-2.25	0.024
Canopy cover	-0.06 ± 0.09	-0.63	0.527	-0.59 ± 0.19	-3.07	0.002	-0.24 ± 0.12	-2.02	0.043
Deciduous ratio	-0.26 ± 0.12	-2.20	0.028	0.10 ± 0.09	0.64	0.521	0.03 ± 0.11	0.29	0.769
Basal area	-0.04 ± 0.10	-0.36	0.722	0.13 ± 0.09	4.45	0.148	0.23 ± 0.11	2.16	0.031
Minimum age	-0.13 ± 0.11	-1.11	0.266	0.07 ± 0.29	0.22	0.824	0.08 ± 0.06	1.27	0.204
Altitude	-0.04 ± 0.13	-0.29	0.776	0.43 ± 0.20	2.18	0.029	0.14 ± 0.15	0.93	0.354
Substrate DBH	0.03 ± 0.05	0.68	0.497	-0.03 ± 0.07	-0.37	0.692	-0.02 ± 0.06	-0.37	0.715
Birch	$R^2m=0.18$			$R^2m=0.66$			$R^2m=0.45$		
Maximum DBH	-0.17 ± 0.20	-0.86	0.392	0.09 ± 0.14	0.63	0.528	-0.36 ± 0.13	-2.54	0.011
Canopy cover	-0.03 ± 0.13	-0.24	0.807	0.13 ± 0.29	0.45	0.652	-0.22 ± 0.22	-1.01	0.314
Deciduous ratio	-0.12 ± 0.17	-0.69	0.489	0.33 ± 0.22	1.51	0.131	0.00 ± 0.16	0.00	1.000
Basal area	-0.01 ± 0.15	-0.06	0.949	0.15 ± 0.11	1.42	0.155	0.35 ± 0.17	2.06	0.039
Minimum age	-0.13 ± 0.15	-0.86	0.389	-1.18 ± 0.39	-2.99	0.003	0.20 ± 0.11	1.83	0.067
Altitude	0.28 ± 0.18	1.56	0.119	-0.11 ± 0.30	-0.37	0.710	-0.04 ± 0.26	-0.15	0.881
Substrate DBH	0.06 ± 0.05	1.15	0.249	-0.24 ± 0.19	-1.27	0.205	0.30 ± 0.12	2.57	0.010
Snags	$R^2m=0.34$			$R^2m=0.68$			$R^2m=0.25$		
Maximum DBH	-0.29 ± 0.16	-1.85	0.064	-0.35 ± 0.13	-2.69	0.007	-0.12 ± 0.08	-1.50	0.134
Canopy cover	-0.12 ± 0.09	-1.28	0.200	-0.51 ± 0.30	-1.70	0.089	-0.02 ± 0.13	-0.15	0.884
Deciduous ratio	-0.15 ± 0.13	-1.16	0.247	-0.03 ± 0.22	-0.14	0.891	-0.03 ± 0.09	-0.38	0.703
Basal area	0.00 ± 0.11	-0.03	0.974	0.15 ± 0.11	1.29	0.198	0.14 ± 0.10	1.41	0.159

ANNEXE I

Results of the covariance-based SEM.

Subset	Response variable	Explanatory variable	Estimates	z-value	p-value
Sites 0-5 km	<i>Model structure rejected</i>				
Sites 10-75 km	Canopy cover	Lake distance	-0.11 ± 0.3	-0.49	0.63
	Maximum DBH	Lake distance	0.06 ± 0.46	0.13	0.90
	Basal area	Lake distance	0.61 ± 0.39	-1.58	0.11
	Deciduous ratio	Lake distance	0.02 ± 0.24	0.10	0.92
	Minimum age	Lake distance	-0.45 ± 0.29	-1.55	0.12
	Species richness	Lake distance	0.09 ± 4.77	0.02	0.99
	Species richness	Canopy cover	-3.39 ± 3.60	-0.94	0.35
	Species richness	Maximum DBH	-4.31 ± 2.62	-1.64	0.10
	Species richness	Basal area	1.09 ± 2.87	0.38	0.71
	Species richness	Deciduous ratio	-0.75 ± 3.96	-0.19	0.85
	Species richness	Minimum age	-2.79 ± 3.47	-0.81	0.42
	Spruce 0-5 km	<i>Model structure rejected</i>			
Spruce 10-75 km	Canopy cover	Lake distance	-0.08 ± 0.17	-0.49	0.62
	Maximum DBH	Lake distance	0.05 ± 0.36	0.13	0.90
	Basal area	Lake distance	-0.46 ± 0.29	-1.57	0.12
	Deciduous ratio	Lake distance	0.02 ± 0.19	0.10	0.92
	Minimum age	Lake distance	0.41 ± 0.26	-1.54	0.12
	Species richness	Lake distance	-0.14 ± 1.59	-0.09	0.93
	Species richness	Canopy cover	-2.37 ± 1.63	-1.46	0.15
	Species richness	Maximum DBH	-2.25 ± 1.24	-1.81	0.07
	Species richness	Basal area	-0.15 ± 1.27	-0.12	0.91
	Species richness	Deciduous ratio	-0.87 ± 1.57	-0.55	0.58
	Species richness	Minimum age	-1.45 ± 1.33	-1.09	0.28
	Birch 0-1 km	Canopy cover	Lake distance	25.58 ± 15.96	1.60
Maximum DBH		Lake distance	3.20 ± 8.72	0.37	0.71
Basal area		Lake distance	5.34 ± 10.18	0.52	0.60
Deciduous ratio		Lake distance	9.28 ± 12.81	0.73	0.47
Minimum age		Lake distance	-0.97 ± 13.62	-0.07	0.94
Species richness		Lake distance	-17.29 ± 348.62	-0.05	0.96
Species richness		Canopy cover	0.74 ± 7.14	0.10	0.92
Species richness		Maximum DBH	0.45 ± 9.96	0.05	0.96
Species richness		Basal area	0.36 ± 4.15	0.09	0.93
Species richness		Deciduous ratio	0.23 ± 3.36	0.07	0.95
Species richness		Minimum age	-1.17 ± 2.72	-0.43	0.67
Birch 2.5-5 km		Canopy cover	Lake distance	-1.86 ± 6.58	-0.28
	Maximum DBH	Lake distance	-1.10 ± 6.76	-0.16	0.87
	Basal area	Lake distance	8.13 ± 6.25	1.30	0.19
	Deciduous ratio	Lake distance	-1.73 ± 6.14	-0.28	0.78
	Minimum age	Lake distance	-6.73 ± 5.40	-1.25	0.21
	Species richness	Lake distance	-19.11 ± 75.58	-0.25	0.80

Subset	Response variable	Explanatory variable	Estimates	z-value	p-value	
Birch 10-75 km	Species richness	Canopy cover	-0.81 ± 4.85	-0.17	0.87	
	Species richness	Maximum DBH	-0.51 ± 3.67	-0.14	0.89	
	Species richness	Basal area	-0.77 ± 3.40	-0.23	0.82	
	Species richness	Deciduous ratio	-2.03 ± 2.79	-0.73	0.47	
	Species richness	Minimum age	-0.54 ± 6.26	-0.09	0.93	
	Canopy cover	Lake distance	-0.08 ± 0.17	-0.50	0.62	
	Maximum DBH	Lake distance	0.05 ± 0.36	0.13	0.90	
	Basal area	Lake distance	-0.46 ± 0.29	-1.57	0.12	
	Deciduous ratio	Lake distance	0.02 ± 0.19	0.10	0.92	
	Minimum age	Lake distance	-0.41 ± 0.26	-1.55	0.12	
	Species richness	Lake distance	-0.09 ± 1.49	-0.06	0.95	
	Species richness	Canopy cover	-2.38 ± 1.78	-0.06	0.95	
	Species richness	Maximum DBH	-1.46 ± 1.10	-1.33	0.19	
	Species richness	Basal area	0.53 ± 1.15	0.46	0.64	
	Species richness	Deciduous ratio	-0.65 ± 1.82	-0.36	0.72	
Species richness	Minimum age	-0.87 ± 1.40	-0.62	0.53		
Snags 0-5 km	<i>Model structure rejected</i>					
Snags 10-75 km	Canopy cover	Lake distance	-0.08 ± 0.17	-0.49	0.62	
	Maximum DBH	Lake distance	0.05 ± 0.36	0.13	0.90	
	Basal area	Lake distance	-0.46 ± 0.29	-1.59	0.11	
	Deciduous ratio	Lake distance	0.02 ± 0.19	0.10	0.92	
	Minimum age	Lake distance	-0.41 ± 0.26	-1.55	0.12	
	Species richness	Lake distance	-0.87 ± 1.08	-0.81	0.42	
	Species richness	Canopy cover	-1.34 ± 1.16	-1.15	0.25	
	Species richness	Maximum DBH	-1.21 ± 0.72	-1.69	0.09	
	Species richness	Basal area	0.78 ± 0.85	0.91	0.36	
	Species richness	Deciduous ratio	-0.06 ± 1.18	-0.05	0.93	
	Species richness	Minimum age	-1.33 ± 1.03	-1.29	0.20	
	Rocks 0-75 km	Canopy cover	Lake distance	-0.12 ± 0.17	-0.72	0.47
		Maximum DBH	Lake distance	0.11 ± 0.25	0.42	0.67
		Basal area	Lake distance	-0.15 ± 0.15	-0.95	0.34
		Deciduous ratio	Lake distance	-0.03 ± 0.20	-0.15	0.88
Minimum age		Lake distance	-0.14 ± 0.18	-0.78	0.44	
Species richness		Lake distance	0.08 ± 0.31	0.26	0.80	
Species richness		Canopy cover	-0.43 ± 0.31	-1.20	0.23	
Species richness		Maximum DBH	-0.41 ± 0.29	-1.40	0.16	
Species richness		Basal area	-0.55 ± 0.32	-1.70	0.09	
Species richness		Deciduous ratio	-0.06 ± 0.33	1.30	0.19	
Species richness		Minimum age	-0.06 ± 0.27	-0.20	0.44	

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