UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

FACTEURS ENVIRONNEMENTAUX INFLUENÇANT LA BIODIVERSITÉ DES LICHENS À DIFFÉRENTES ÉCHELLES DANS LE NORD-OUEST DU QUÉBEC

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INFLUENTIAL ENVIRONMENTAL FACTORS OF LICHEN DIVERSITY ON MULTIPLE SCALES IN NORTHWESTERN QUEBEC

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FORWARD

This thesis is presented in article form, with multiple authors. The lead author, Tana Route, was principally responsible for study design, data collection, data analysis, interpretation of results, and writing this thesis. Nicole Fenton contributed to the development of the study design and analysis. Decisions on plot locations were made jointly with Marc-Frédéric Indorf, and he later contributed some of his data. Mirelle Martel aided in the identification of lichen specimens.

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RÉSUMÉ

Le nord-ouest du Québec compte actuellement une population humaine relativement petite, peu d'impacts humains et moins d'études sur la diversité des lichens. Cependant, d'autres développements dans les secteurs minier, hydroélectrique et touristique sont prévus à l'avenir. Cela pose plusieurs problèmes: 1) comme nous avons peu d'informations sur les espèces de lichens présentes et les habitats qui sont importants pour elles, il est difficile pour les gestionnaires de ressources d'atténuer la diversité et la perte d'habitat pendant le développement du projet; et 2) il peut être difficile d'atténuer les impacts sur les habitats sans une bonne compréhension des facteurs environnementaux, comme l'humidité, qui influencent la diversité des lichens. Par conséquent, ce projet vise à étudier la biodiversité des lichens et les facteurs environnementaux qui affectent cette biodiversité dans trois habitats différents selon les définitions de Leboeuf et al (2012) - tourbières uniformes ombrotrophes, tourbières uniformes ombrotrophes à épinettes noires, et tourbières uniformes minérotrophes - qui couvrent une grande partie du nord-ouest du Québec. Pour ce faire, nous considérons la diversité des lichens à trois échelles différentes, définies ici comme: alpha, changements dans la diversité des lichens entre les microhabitats; beta, changements dans la diversité des lichens entre les trois types de tourbières; et gamma, différences dans la diversité des lichens entre les trois secteurs de la région d'étude.

Pour atteindre cet objectif, trois secteurs d'étude placés de manière relativement équidistante le long d'un gradient nord-sud et est-ouest de 600 km à travers la région d'Eeyou Istchee ont été sélectionnés. Ces secteurs étaient centrés sur trois mines - Casa Berardi, Whabouchi et Renard - bien que nous ayons évité les tourbières qui ont probablement eu des impacts de l'exploitation minière, car ce n'était pas le but de notre étude. Trois réplicatsde tourbières uniformes ombrotrophes, tourbières uniformes ombrotrophes à épinettes noires, et tourbières uniformes minérotrophes choisies sur chaque site. Dans chaque réplicat, deux transects de 20 mètres ont été mis en place, l'un allant du nord au sud à partir d'un point central et l'autre allant d'un point de bordure sélectionné au hasard vers le point central. Des spécimens de lichen ont été collectés et une mesure d'abondance de lichen évaluéedans des microhabitats à moins d'un mètre de chaque côté de la ligne de transect. Un capteur d'humidité relative de l'air et de température a été placé au centre de chaque ligne de transect, où une lecture de l'ouverture du couvert a également été prise. Pour réduire la probabilité de disparition de la diversité des espèces, un protocole d'échantillonnage de l'habitat floristique (FHS) d'une heure a été suivi. Dans la méthode FHS, les microhabitats et les zones non couvertes par les transects ont été ciblés et recherchés pour les espèces non encore collectées. Tous les échantillons de lichens ont été identifiés pour les espèces en laboratoire, en utilisant des tests chimiques ponctuels si nécessaire. Les échantillons particulièrement difficiles ou importants seront confirmés par Thin Layer Chromatography (TLC). Des modèles linéaires mixtes et de régression linéaire sur la richesse et l'abondance des espèces ont été utilisés à l’aide du logiciel R.

Soixante-seize espèces de lichens ont été documentées dans cette étude, et les arbres et les gaules étaient les microhabitats les plus riches en lichens. À l'échelle alpha, la tourbe et les chicots, bien qu'ils soient moins diversifiés individuellement pour les lichens, étaient associés à de vastes et uniques bassins d'espèces de lichens. À l'échelle beta, les tourbières uniformes minérotrophes étaient moins diversifiés en lichens que les tourbières uniformes ombrotrophes ou les tourbières uniformes ombrotrophes à épinette noires. Étant donné que la tourbe et les chicots ont été trouvés moins fréquemment dans les tourbières uniformes minérotrophes, on fait l'hypothèse que la plus faible diversité dans les tourbières uniformes minérotrophes est due en grande partie à la faible disponibilité de ces deux microhabitats. La disponibilité des microhabitats était également la clé de la diversité significativement plus élevée des lichens au site le plus au nord. Dans ce cas, ce sont les roches, largement absentes de tous les autres sites, qui sont de la plus grande importance. La diversité des lichens à l'échelle gamma a également augmenté du sud vers le nord, plusieurs espèces ne se trouvant que dans le site le plus au nord, une tendance qui se reflète dans l'augmentation de l'humidité relative de l'air et des températures globales plus basses. On fais l'hypothèse que ces tendances dans la diversité des lichens gamma et les facteurs environnementaux sont liés, bien que la façon exacte dont la température influence ou interagit avec d'autres facteurs environnementaux ne soit pas claire. Ces résultats aideront les gestionnaires de ressources à atténuer la perte de biodiversité des espèces de lichens en informant les décisions qui concernent directement les habitats des tourbières qui sont plus importants pour la conservation des lichens.

ABSTRACT

Northwestern Quebec currently has a relatively small human population, few human impacts, and fewer studies on lichen diversity. However, further development in mining, hydroelectric, and tourism is planned for the future. This poses several problems: 1) as we have little information about what lichen species are present and which habitats are important to them, it is difficult for resource managers to mitigate diversity and habitat loss during project development; and 2) it may be difficult to mitigate impacts to habitats without a good understanding of environmental factors, like humidity, that influence lichen diversity. Therefore, this project seeks to study lichen diversity and certain environmental factors that affect that diversity in three different habitats following Leboeuf et al (2012)'s definitions – Uniform Bogs, Spruce Bogs, and Uniform Fens – that cover a large part of the northwestern Quebec region. To do this, we consider lichen diversity on three different scales, here defined as: alpha, changes in lichen diversity between microhabitats; beta, changes in lichen diversity between peatland types; and gamma, differences in lichen diversity between sectors of the study region.

To meet this aim, three study sectors placed relatively equidistantly along a 600 km transect in the Eeyou Istchee Region were selected. The transect covered both north-south and east-west gradients. The sectors were centered around three mines – Casa Berardi, Whabouchi, and Renard – though we avoided peatlands that likely had impacts from mining, as this was not the aim of our study. Three replicates each of Uniform Bogs, Spruce Bogs, and Uniform Fens were chosen at each site. In each replicate, two 20 meter transects were set up, one running north-south from a central point and the other running from a randomly selected edge point towards the central point. Lichen specimens and a lichen abundance measure were collected on microhabitats within one meter of either side of the transect line. A sensor for relative air humidity and temperature was placed at the center of each transect line, where a canopy opening reading was also taken. To reduce the likelihood of missing species diversity, a one-hour Floristic Habitat Sampling (FHS) protocol was followed. In the FHS method, microhabitats and areas not covered by the transects were targeted and searched for species not yet collected. All lichen samples were identified to species in the laboratory, using chemical spot tests as necessary. Particularly difficult or important specimens will be confirmed with Thin Layer Chromatography (TLC). Mixed linear models and linear regressions on species richness and abundance were run in R software.

Seventy-six lichen species were documented in this study, and trees and saplings were the most lichen rich microhabitats. On the alpha scale, peat and snags, while less lichen diverse individually, were associated with large and unique pools of lichen species. On a beta scale, Unique Fens were less lichen diverse than Uniform Bogs or Spruce Bogs. Since both peat and snags were found less frequently in Uniform Fens, we hypothesize that the lower diversity in Uniform Fens is due in large part to the low availability of these two microhabitats. Microhabitat availability was also key to the significantly higher lichen diversity at the northernmost site. In this case it was rocks, largely absent at all other sites, that were of the greatest importance. Gamma scale lichen diversity also increased from the south to the north with several species only found in the most northern site, a pattern reflected in increasing relative air humidity and lower overall temperatures. We hypothesize that these trends in gamma lichen diversity and environmental factors are linked, though exactly how temperature influences or interacts with other environmental factors is unclear. These results will aid resource managers to mitigate biodiversity loss of lichen species by informing decisions as to which peatland habitats are of higher importance for lichen conservation.

CHAPTER I

GENERAL INTRODUCTION

1.0 Context

It is important to understand the biodiversity of peatland lichens in Northern Quebec to make management decisions. At this time, we have no extensive floristic study for the area, especially for lichens. Yet, although currently relatively undeveloped, the region of northwestern Quebec is under planning for further development from mining and other activities (Société du Plan Nord, 2014). Therefore, informed management decisions and conservation efforts are necessary to prevent lichen biodiversity loss, yet impossible to make without better knowledge of the region's lichen flora. Within northwestern Quebec, peatlands make up a large part of the territory, and lichens may contribute between 25-46% of their primary productivity (Pearson, 1969). This makes it important to understand lichen diversity specifically within peatlands for this region of Quebec. In order to make good management decisions or to carry out potential future restorations, it is also necessary to have an understanding of some of the environmental factors, such as microhabitat availability, light availability, relative air humidity, temperature, and minimum stand age which may affect peatland lichen diversity. Without better understanding an essential factor such as humidity for species diversity and community assemblage in wetlands, management decisions may not be effective.

1.1 Background to the Lichens

Lichens are a complex symbiotic relationship. In its most basic form, this consists of a fungi (mycobiont) and an algae or cyanobacteria (photobiont). Once lichenized, the mycobiont provides a structure that protects the photobiont from desiccation, and most herbivory through the production of chemical compounds. The photobiont provides energy for the mycobiont generated from photosynthesis. This allows the partners to survive in habitats that would otherwise be inhospitable to them. Lichens that have both algae and cyanobacteria photobionts, the latter in specialized structures called cephalodia, are called tripartite lichens. When one mycobiont can form a symbiosis with either algae or cyanobacteria, the different morphotypes are known as photosymbiodemes. Within the range of one lichen species, the mycobiont may associate with different photobionts from separate clades (O'Brien, Miadlikowska, & Lutzoni, 2013; Yahr, Vilgalys, & DePriest, 2006). Likely, this is because algae and cyanobacteria from different clades are more successful in different parts of a region and are either preferentially chosen by the mycobiont or are simply the most available for lichenization (Yahr et al., 2006). Mycobionts may also lichenize 'non-compatible' algae as a means to survive until compatible algae are found. Most mycobionts come from the Ascomycetes, but research shows that a secondary fungal partner from the Basidiomycetes is imbedded in the peripheral cortex of many lichens (Spribrille et al., 2016). However, after a more recent study failed to find these Basidiomycetes in the majority of their lichen samples, lichenologists are still trying to understand when, where, in what abundance, and under what circumstances these tertiary fungal partners appear (Lendemer et al, 2019). Additionally, bacteria are known to live on and in lichens, and have been proposed as important symbiotic partners (Grube & Berg, 2009). Together, these many disparate parts create the whole organism of the lichen, sometimes referred to as the holobiont, which can function as its own miniature ecosystem (Hawksworth & Grube, 2020).

The form of the lichen holobiont comes in three basic growth forms: fruticose lichens, which grow erect or pendant and have no discernable lower or upper surface; foliose lichens, which are flattened and have a recognizable upper and lower surface; and crustose lichens, which form crusts over a substrate and the lower surface of which has no cortex (a cuticle or skin-like structure) but rather comes into direct contact with the substrate. Fruticose and foliose lichens are also often grouped together under the term macrolichens. This differentiates them from the crustose, or microlichens, whose identifying structures are generally not visible with the naked eye. As they usually lack easily recognizable features and require more microscopy work, they are more difficult to identify to species. For this reason, many studies that are limited by time or funding focus only on macrolichens.

1.2 Lichens on Alpha, Beta, and Gamma Scales

The scale at which lichen diversity is measured matters. For example, Humphrey et al. (2002), found 42% of lichen species only once in their plots, a phenomenon termed "local rarity", but which they attributed to the insufficient size of their plots to "capture a representative sample". In other words, this "local rarity" would disappear if the lichen diversity were sampled on a larger scale. Additionally, particular factors may affect lichen diversity differently at smaller versus larger scales. An example of an environmental factor that affects lichen diversity on different scales is humidity. With humidity, a pattern emerges in which moister and more humid regions and habitats have greater lichen diversity (Coyle & Hurlbert, 2016). However, when comparing different microhabitats within a given habitat, lichens in the moister and more humid microhabitats are more likely to be outcompeted by bryophytes (Boudreault et al., 2008).

The above-mentioned example does not use 'scale' in the sense of a numeric distance, however. Distance in terms of meters or other similar measurement systems does not always make as much ecological sense as the environmental difference between microhabitats, habitats, and regions. It is therefore easier to explore patterns of lichen diversity by using the concepts of alpha, beta, and gamma scales. Some papers will describe alpha scale as differences on what might be termed a single microhabitat – for example, changes in lichen diversity between the canopy, trunk, and base of a single tree. Beta scale is then the changes in lichen diversity between different microhabitats within the same habitat. This study however will define alpha scale as changes between microhabitats within a habitat. Beta scale then refers to changes between different habitats, and gamma scale as changes across the study region. ‘Changes’ more specifically means increases or decreases in lichen species richness, environmental factors, or the interaction of the two.

1.3 Lichens in Peatlands

In one bog, Pearson (1969) estimated that lichens contributed between 25-46% of the primary productivity. This suggests that lichens are of very high importance to peatland systems, yet the literature still reveals large gaps in our knowledge of peatland lichens, especially in Eastern Canada. The first of those gaps important to this study is the basic understanding of lichen diversity within peatlands and among different types of peatlands. The second is a better comprehension of the environmental factors that affect lichen diversity in peatlands.

However, in order to understand lichens in peatlands, we must first start by understanding what a peatland is, and why they are important. In Canada, a peatland is a habitat with at least 40 centimeters of peat, peat being organic material decomposing in an anoxic environment (NWWG 1997). Peatlands are important because they store large amounts of carbon, between 41.5 and 489 Pg depending on the source consulted (Vasander & Kettunen, 2006). Additionally, peatlands make up 13% of Canada’s land cover, making them an important habitat on a national scale (Warner and Asada, 2006). Peatlands can also be split into many different categories. As fens and bogs had the highest overall percentage of total peatland studied in the three sectors, they are the most important categories for this study. The difference between the two is that fens receive groundwater as their main water source, while bogs’ main water source is from rain.

Returning to lichens, the literature shows that bogs are more lichen diverse than fens across Canada (Warner and Asada, 2006). On closer inspection, however, of the five papers cited in Warner and Asada (2006) for the mid-Boreal region (to which the Eeyou Istchee belongs) only one is from Quebec – the others are all from Alberta and its environs (Beilman, 2001; Chee and Vitt, 1989; Karlin and Bliss, 1984; Vitt and Chee, 1990; Garneau, 2001). Additionally, lichens are either not considered or included peripherally to other objectives, and there are some difficulties interpreting the lichen data. Several write about the treatment of lichen nomenclature in their methodology, but then don't report any lichen species, yet never state if this was because they never found any lichens or for another reason (Beilman, 2001; Chee and Vitt, 1989; Karlin and Bliss, 1984; Vitt and Chee, 1990). Garneau (2001) reports several species of lichens that are preferential to bogs, but there is no information on how this determination was made. Additionally, none of these papers addressed epiphytic lichens. I was only able to find two papers on epiphytic lichens in peatlands, only one of which was in North America (Pearson, 1969). 20 epiphytic macrolichen species were recorded from a single bog in Minnesota studied by Pearson (1969), while the average number of mainly terricolous lichens found in peatlands across Canada according to Warner and Asada (2006) was about 10. Meanwhile, a study in peatland 'swamps' of Sweden that considered terricolous, epiphytic, and epixylic lichens found a species richness of 44 (Ohlson et al, 1997). Given these numbers, a large proportion of lichen diversity is being missed if we do not consider epiphytic lichens. Thus, what emerges is a much more piece-meal picture of our understanding of lichens in peatlands. While it may be possible to say that bogs are more lichen diverse on a national scale, narrowed down to specific regions the data becomes less clear. As none of the studies I examined used by Warner and Asada (2006) in Canada included epiphytic lichens, it is also possible that patterns could change with the inclusion of this important group.

As fens are generally known to be more plant diverse than bogs due to fens' greater nutrient availability, this begs the question – why is it potentially the other way around for lichens? Unfortunately, the only paper to compare lichen diversity in fens versus bogs did not include any data on why this might be (Warner and Asada, 2006). Lichen diversity on an alpha scale within peatlands was linked to humidity variability and light availability in Pearson, (1969). However, as alpha scale effects may not have the same result on a beta or gamma scale, nothing conclusive can be stated from this current literature.

1.4 Lichens and Hydration Sources

Like all other organisms, lichens need water in order to survive. Unlike other organisms, their high area to biomass ratio helps them to utilize hydration sources that would ordinarily be inaccessible (Gauslaa, 2014). In addition to rain, lichens are able to obtain hydration from humidity, fog, and dew. These different hydration sources take on different levels of importance for different lichen morphologies and habitats, however. Cyanolichens need liquid water in the form of rain or dew, while those with green algae as a photobiont are more likely to be able to utilize humid air (Gauslaa, 2014). While foliose lichens appear to almost exclusively use rain as a hydration source, fruticose and alectorioid lichens can use dew and humid air to a far greater extent (Gauslaa, 2014). While humidity seems to be more important to lichens in shaded canopies, rain becomes more important at the top of the canopy and dew in forest gaps (Gauslaa, 2014). On the landscape, rain can be of greater importance on hilltops, while humidity gains in importance in ravines or northern slopes; dew gains precedence as a hydration source in the toe of the slope or on open land (Gauslaa, 2014). There is some interaction between the different sources of hydration of course. Humid air occurs after rain, and dew is more likely to form when the relative air humidity is high.

Being able to utilize a greater range of hydration sources may be evolutionarily advantageous to lichens, but there are tradeoffs between rain, humidity, and dew. Lichens experience a phenomenon called suprasaturation depression, often shortened to suprasaturation. This means that when the lichen thallus reaches an internal water content above a certain amount – what exactly that amount is differs with the species – there will be a decrease in photosynthetic activation due to increased diffusion resistances (Lange, 1980). The subsequent loss of photosynthetic activity can be detrimental to the lichen. While suprasaturation is common after rain, it is less common with dew and rare with humidity (Gauslaa, 2014). Despite the fact that it does not come with the drawback of suprasaturation, however, only 3-23% of "realized [photosynthtic] activity" occurred when lichens were hydrated from humid air alone (Cabraijic et al, 2010). This may be due to the fact that it takes considerably longer to become hydrated under humid air conditions. High water contents also were never documented under hydration from humid air alone, which might not have been enough for photosynthetic activity even though suprasaturation did not occur (Cabrajic et al, 2010). The study by Cabrajic et al (2010) did not test the tradeoff with suprasaturation, however. Additionally, in habitats or areas where high humidity is consistent and lasts for a prolonged period of time, humid air could still be a significant source of hydration. Cabrajic et al (2010) also hypothesized that humid air is important in extending the hydration period after a rain.

Humidity must confer some ecological benefit to lichens, however, because higher humidity has been correlated with higher lichen diversity on beta and gamma scales. Several studies have suggested that moister, more humid habitats tend to have higher lichen species diversity (Heylen, Hermy, and Schrevens, 2005; Humphrey et al, 2002). On the gamma scale, humid regions also have higher lichen diversity (Jovan and McCune, 2004). Things become different on the alpha scale, however. In high humidity conditions, bryophytes will outcompete lichens (Boudreault et al., 2008). Even when more humid niches were not taken up by bryophytes, Pearson (1969) found that lichens often preferred less humid and more variable (in terms of humidity levels) niches. His hypothesis was that the photobiont or mycobiont outgrows the other partner in conditions of constant high humidity. This suggests that there is an optimum level of humidity for lichens. The majority of the above studies, however, measured humidity by means of a qualitative observation. While this is a time-effective method that allows more data points in more places to be taken, it is only a ‘snapshot in time’. For example, after a rain a habitat or microhabitat is more likely to be recorded as humid, even if it is less humid on average. This makes further studies that use quantitative methods to record relative air humidity important to confirm these trends. Additionally, only one of these studies specifically included a peatland, where high humidity occurs more often and is likely of greater importance to the lichens growing in these environments.

1.5 Microhabitat Availability

In this study we will refer to the substrates that lichens grow on as microhabitats. This is based on the assumption that lichens are influenced not only by the surface that they are directly growing on in terms of such things as nutrient availability and chemical makeup, but by the conditions that that surface creates. For example, lichens growing on the base of a tree will generally have a moister and more shaded microhabitat than lichens growing on open rock.

Lichens are very specific to the microhabitats they grow on. In one study 38% of the dominant species were preferential to a single type of microhabitat (Peck et al, 2004). These microhabitats include a wide variety of substrates, such as rocks, logs, litter, soil, snags, and trees. It perhaps makes intuitive sense, then, that the more microhabitats that are available to lichens in a particular area or habitat, the higher the lichen diversity will be. This has in fact been shown to be true (Peck et al, 2004; Gignac, 2005). The existence of even one rare or uncommon microhabitat, such as a rock pile or a tree tip-up, significantly increased species richness in observed plots (Peck et al, 2004;

McCune and Lesica, 1992). It is likely for this reason that larger plots, which are more likely to contain a greater diversity of microhabitats, capture greater species richness (McCune and Lesica, 1992). Other researchers have utilized Floristic Habitat Sampling (FHS), a method that specifically targets microhabitats within an area rather than relying on plots, to study bryophytes (Newmaster, et al 2005). However, it has also been successfully applied to lichens (McMullin & Wiersma, 2017). High microhabitat availability does not always equal higher lichen species richness, however. In the study by Peck et al., (2004), the relationship between microhabitat availability and species richness was not significant for every site they investigated. Other environmental factors such as humidity, temperature, and disturbance likely have an effect or interaction with microhabitat availability.

1.6 Lichens and Individual Tree and Stand Ages

The age of a forest stand or an individual tree is an important alpha or beta scale feature that depends on history such as fire, blowdown, logging, and other disturbances. Late successional or ‘old-growth’ forests have been shown to have high lichen diversity, possibly because of high alpha-level microhabitat heterogeneity (Humphrey et al., 2002; Nascimbene et al., 2009; Gignac & Dale, 2005). This may also be due to the longer length of time available for lichen establishment and colonization, but also other features of old forests such as low light levels and increased humidity (Dymytrova et al., 2014; Arsenault & Goward, 2016). Even one old tree in a stand could significantly increase the overall diversity (Dymytrova et al., 2014). However, an absolute increase in lichen diversity with age of tree or stand is not always true (Arsenault & Goward, 2016; Heylen et al., 2005). Particularly interesting for this study, no strong correlation between age and diversity was seen in Canadian Clay Belt forests, which the authors believed could be caused by paludification (Boudreault et al., 2002). Additionally, Heylen et al. (2005) found that young forests had a high diversity of lichens. This would suggest a bi-modal curve, in which both young and old forests might have high diversity, with stands in the middle age ranges being less diverse. Such bimodal peaks can also be seen in the reported total number of lichen species by age class in Humphrey et al. (2002). Thus, stands of different ages would likely increase overall beta diversity. However, Svoboda, Peksa, & Veselá (2010) did not find a strong correlation between stand age and lichen diversity in central Europe; the reason for this may have been high heterogeneity in some of their other measured environmental factors, such as climate and pollution, which may have interacted with or somehow obscured stand age influence. As they surveyed across a region, it may be that at the gamma scale the effects of age do not have as significant an influence.

1.7 Lichens on Deadwood

Deadwood includes both snags and logs. Snags are dead trees that are still standing upright, here including stumps as well as completely intact dead trees. Logs are dead trees that have fallen and have one side in contact with the soil or peat. According to the literature, snags are more lichen diverse than logs (Humphrey et al, 2002; Santaniello et al, 2017). However, not all snags are the same. When classified into 5 increasing stages of decay, Humphrey et al (2002) found that the three most decayed stages hosted the highest lichen species richness. The increase in lichen species richness occurs after the bark has fallen off the wood, a finding that is also confirmed by other studies (Humphrey et al, 2002; Runnel et al, 2013). The finding that wood that is more decayed and therefore softer would seem to be at odds with Santaniello et al, (2017), who found that harder wood tended to have higher lichen species richness. This could be because Santaniello et al (2017) were working with a specific type of snag (kelo trees) in a specific habitat. It was also found that lichen species richness increased with estimated time since death of the deadwood (Santaniello et al, 2017; Runnel et al, 2013).

1.8 Disturbance

Disturbances that can affect lichen diversity include logging, industrial development, air pollution, and fire. As the majority of the Eeyou Istchee Bay James Region lies north of Quebec's commercial timberline, logging is not a major issue to lichen diversity in this region (Ministère des Ressources naturelles du Québec, 2013). The main concern to lichen diversity is from development - such as of housing, industry, and roads – and the reduction or elimination of habitats. While the Eeyou Istchee Region is currently little developed, plans to increase mining of such products as gold, lithium, and diamonds as well as hydro-electric dams and tourism in the region are being prepared (Société du Plan Nord, 2014).

Given the lack of development in the Eeyou Istchee, air pollution is currently of lesser concern, as it is in the often-remote northern reaches of the boreal forest in general (Hauck, 2011). However, increased development will bring with it increased air pollution. As the effect of air pollution on lichen diversity is a major topic in lichenology, it is worth further discussion. Historically, SO_2 has been of the highest concern to lichen diversity, causing significant loss of species richness (Hauck, 2011). Today, knowledge of the ill-effects of SO_2 has led to the pronounced reduction of this pollutant and the recovery of overall species richness in some areas (Hultengren, Gralén, & Pleijel, 2004). However, an analysis of lichen diversity response to air pollution that took into consideration not only SO_2, but also nitrogen deposition, ammonia, nitrogen oxides, and ozone, showed that overall air pollution still has an impact on lichen species composition (Ellis & Coppins, 2010).

Fire is a natural disturbance, but one that can still have an impact on lichen richness. Unfortunately, studies on the relationship between fire and lichen diversity are very few (Hauck, 2011). Bartels & Chen (2015) found that it took epiphytic lichens at least 7 years to establish after fire, after which diversity increased up to about 146 years after fire, but then declined again post-146 years. They attributed this to the loss of pioneer and early successional species, suggesting that some level of natural disturbance is necessary to maintain diversity on the landscape (Bartels & Chen, 2015). For terricolous lichens, re-establishment time may be even longer – nearing 50 years, as shown in a study in northern Québec (Auclair, 1985). However, Zouaoui et al (2014) found that time since fire did not have a significant impact on overall lichen diversity – though it was one of the most important factors in lichen species composition. Both studies raise questions about our understanding of lichen dispersal and the importance of 'fire-skip' forests (Bartels & Chen, 2015; Zouaoui et al, 2014).

1.9 Objectives

1) To characterize the lichen diversity of dominant peatland types in northwestern Quebec on alpha, beta, and gamma scales.
2) To understand the effects on lichen diversity of environmental factors such as microhabitat availability, light availability, minimum stand age, relative air humidity, and temperature on alpha, beta, and gamma scales.

1.10 Hypothesis

Differences in microhabitat availability, canopy openness, the minimum average age of trees in the stand (hereafter minimum stand age), and relative air humidity will be expected to create different lichen species richness and composition between peatland types; these alpha and beta-level diversity variables will also interact with regional differences in these environmental factors to further separate lichen species richness and composition on a gamma scale.

CHAPTER II

INFLUENTIAL ENVIRONMENTAL FACTORS OF LICHEN DIVERSITY ON MULTIPLE SCALES IN NORTHWESTERN QUEBEC

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2.1 Résumé and Abstract

Résumé

La richesse et la composition des espèces de lichens n'ont pas été étudiées auparavant, à la connaissance des auteurs, dans les tourbières du nord-ouest du Québec. Sans cette connaissance, les décisions de gestion et de conservation concernant les lichens dans cette région sont difficiles à prendre. Nous avons donc choisi trois secteurs d'étude dans le nord-ouest du Québec pour étudier trois types de tourbières différents: les tourbières uniformes, tourbières uniformes ombrotrophes à épinettes noires et les tourbières uniformes minérotrophes. Dans chaque secteur d'étude, trois répétitions de chaque type de tourbière ont été sélectionnées et des données recueillies sur deux transects ainsi que par échantillonnage par habitat floristic, *Floristic Habitat Sampling*. Les données recueillies étaient les suivantes: espèces de lichens, humidité relative de l'air, température, disponibilité des microhabitats, ouverture du couvert et âge minimum du peuplement. L'analyse des données révèle que les tourbières uniformes et tourbières uniformes ombrotrophes à épinettes noires sont plus riches en espèces de lichens que les tourbières uniformes minérotrophes. Cela est probablement dû à l'abondance des microhabitats de chicots et de tourbe dans ces deux premiers. La richesse spécifique des lichens augmente avec la latitude – moins d'espèces dans le secteur d'étude le plus méridional et plus d'espèces au nord – un résultat que nous avons observé en corrélation avec une augmentation des températures et de l'humidité relative de l'air.

La composition des espèces de lichens est largement similaire entre les types de tourbières et les secteurs d'étude, bien que quelques modèles mineurs soient apparus. Le genre *Peltigera* n'a été trouvé que dans les tourbières épinettes, et est observé seulement quatre fois (ou dans 15% des replicats). Le secteur le plus au nord semble avoir le plus grand nombre d'espèces de lichens total et partage davantage de similarités avec le secteur d'étude central que le secteur le plus au sud. Sur la base de ces résultats, les tourbières uniformes et tourbières uniformes ombrotrophes à épinettes noires ayant une plus grande disponibilité de microhabitats en chicots et en tourbe sont d'une grande importance pour la conservation de lichens. Cependant, les tourbières uniformes minérotrophes doivent être recherchés pour les espèces rares qui peuvent ne pas être trouvées dans d'autres types de tourbières. À l'échelle régionale, une humidité relative de l'air plus élevée semble être nécessaire pour la richesse en lichens, qui pourrait servir à informer les réflexions futures sur la façon dont le changement climatique peut avoir un impact sur la diversité de la région ou du gradient (dans ce cas, un transect de 600 km).

Mots clés : Lichen, Diversité, Richesse, Composition, Tourbières

Abstract

Lichen species richness and composition has not previously been studied in peatlands of northwestern Québec, to the knowledge of the authors. Without this information on lichen species richness and composition, management and conservation decisions concerning lichens in this region are difficult to make. We therefore chose three study sectors across the northwestern Québec region in which to study three different peatland types – Uniform Bogs, Spruce Bogs, and Uniform Fens. In each study sector, three replicates of each peatland type were selected and data collected on two transects as well as by Floristic Habitat Sampling. Data collected were: lichen species, relative air humidity, temperature, microhabitat availability, canopy openness, and minimum stand age. The analysis of the data reveal that Uniform Bogs and Spruce Bogs are more lichen species rich than Uniform Fens. This is likely due to the greater availability of snags and peat as microhabitats in the former two. Lichen species richness also increased from the southernmost study sector to the northernmost, which we linked to increasing relative air humidity and temperatures. Lichen species composition was largely similar between the peatland types and the study sectors, although a few minor patterns did appear. First, the genus *Peltigera* was found only in Spruce Bogs, though it was only found a total of four times (in 15% of plots). The northernmost sector also appeared to have the highest number of total lichen species, and to overlap more with the central study sector than the southernmost study sector. Based on these results, Uniform Bogs and Spruce Bogs with greater availabilities of snags and peat microhabitats are of greater importance for lichen conservation. However, Uniform Fens should be searched for rare species that may not be found in other peatland types. On the regional scale, higher relative air humidity appears to be important to lichen richness, which can be taken into account in future considerations on how climate change may impact the diversity of the region or gradient (in this case a 600 km transect).

Keywords: Lichen, Diversity, Richness, Composition, Peatland

2.2 Introduction

Although peatlands are recognized as a globally important ecosystem type and are threatened by increasing development and climate change, their lichen flora is not well understood. Peatlands are considered to be an important ecosystem globally because of the vast amounts of carbon that they store, estimated to be between 41.5 and 489 Pg (Vasander & Kettunen, 2006). Storage in peatlands keeps this large amount of carbon out of the atmosphere where it would become a greenhouse gas and contribute to climate change. Lichens, a symbiotic relationship between a fungus and an algae or cyanobacteria, have been estimated to contribute between 25-46% of the primary productivity of a bog (Pearson, 1969). This makes them potentially a vital part of the peatland ecosystem, yet there is much to be understood about even basic lichen ecology in peatlands. For example, lichen diversity in peatlands, between different peatland types, or in peatlands across a region is little understood. Lichen species composition can be fairly specific to regions and habitats, and there is little data on this in Northwestern Quebec besides Zornican's (1980) unpublished data. Still less understood are the environmental factors that may cause any differences in diversity and species composition between peatland types or peatlands located across a region. These differences in lichen diversity can be studied on threes scales: alpha – differences between microhabitats, such as trees and snags; beta – differences between habitats, here our three peatland types; and gamma – differences across a region.

What we do know is that on the beta scale, bogs (ombrotrophic) tend to be more lichen diverse than fens (minerotrophic) in Canada (Warner and Asada, 2006). However, Warner and Asada's (2006) review of the literature reveals that for the mid-Boreal region only one study is from the Eastern boreal, so comparisons on the gamma scale in northwestern Quebec cannot be made (Garneau, 2001). Further, although they describe methodologies that include lichens, some of the studies considered in Warner and Asada's (2006) review did not report lichen presence or absence and did not give a reason for this omission (Beilman, 2001; Chee and Vitt, 1989; Karlin and Bliss, 1984; Vitt and Chee, 1990; Garneau, 2001). Moreover, on the alpha scale, epiphytic lichens were not considered in the studies reviewed by Warner and Asada (2006) for the mid-Boreal. Yet in two other studies that did consider epiphytic lichens in peatlands, researchers found 2-4 times the number of species (Pearson, 1969; Ohlson et al, 1997). Thus, we are potentially missing an important part of peatland diversity if we do not consider epiphytic lichens. Unfortunately, neither of these papers on epiphytic lichens compared bogs versus fens. So, it may seem that when we consider all the available data across Canada, patterns in lichen diversity between peatlands are fairly clear (Warner & Asada, 2006). However, when we look more closely at alpha diversity, such as differences between terricolous and epiphytic microhabitats, and the available data on beta scale differences between fens and bogs, the patterns in lichen diversity are less clear. Additionally, having so few studies that report lichen species in peatlands, especially in Canada, means that we don't have a good idea of what these trends mean for species composition.

The papers reviewed by Warner and Asada (2006) also do not address why one type of peatland might be more lichen diverse than another (Beilman, 2001; Chee and Vitt, 1989; Karlin and Bliss, 1984; Vitt and Chee, 1990; Garneau, 2001). Here we have to examine studies outside of peatlands on lichen diversity in order to make some suppositions. One such supposition is about humidity, a potentially important source of hydration for lichens (Gauslaa, 2014). As wetlands – among which peatlands are counted – have been found to be more humid than other habitats, it is possible that relative air humidity is an important environmental factor affecting lichen diversity in different peatland types and across the northwestern Quebec region (Bai et al, 2013). On gamma scales, elevated humidity has been shown to be correlated with increased lichen diversity (Jovan and McCune, 2004). On beta scales some studies have suggested that lichen diversity was higher in habitats that had higher humidity levels, but these remain open questions (Humphrey et al, 2002; Dymytrova et al, 2014). On the alpha scale, mosses may out-compete lichens at elevated humidity levels (Boudreault et al., 2008).

Lichen species can be very specific to the microhabitat that they grow on. It therefore makes sense that microhabitat availability – the amount and variety of microhabitats available to be colonized – could have an impact on lichen diversity in peatlands. Greater microhabitat availability has been shown to increase lichen diversity on a beta scale (Peck et al, 2004). Even a single rare microhabitat can increase beta lichen diversity (Peck et al, 2004). However, a higher diversity of microhabitats does not always result in greater lichen diversity, which suggests that other environmental factors may either interact with microhabitat availability or have a greater influence on lichen diversity (Peck et al, 2004). Since lichen species can be so specific to microhabitats, it is also possible that greater availability of certain microhabitats in one type of peatland or part of a region could have an effect on species composition.

Many studies, mainly comparing forests on a beta scale, have found an influence of tree and stand age on lichen diversity and species composition. In many of these studies, older forests have higher lichen diversity (Humphrey et al., 2002; Nascimbene et al., 2009; Gignac & Dale, 2005). The older the stand the more time for lichens to establish and grow, which may be the main reason for this trend (Dymytrova et al., 2014). This was the reason suggested for a significant impact of stand age on lichen species composition in one study (Jüriado et al, 2009). Other reasons for increased lichen diversity may be that many old stands are characterized by low light and higher humidity, as well as more structural diversity which likely mean more microhabitats for lichens (Arsenault & Goward, 2016; Bergeron and Fenton, 2012). However, some studies have not shown a relation between old forests and increased lichen diversity (Arsenault & Goward, 2016; Boudreault et al., 2002). Another study also did not find that stand age significantly affected lichen species composition (Mezaka, Brumelis, and Piterans, 2012). It therefore cannot be taken for granted that older stands will have higher lichen diversity or markedly different lichen species composition, or that other environmental factors may not play an equal or greater role in lichen diversity, especially for habitats such as peatlands, which are very different from forests.

Disturbance can be natural, such as wildfires, or human-made in the form of pollution, land development, and other impacts. Both wildfire and land development have the obvious impact on lichen diversity on alpha and beta scales of removing microhabitats and habitats. Peatlands are also not considered in most studies on fire effects. Pollution, mainly from SO_2, has also historically caused decreases in lichen diversity on all scales (Hauck, 2011). With changes in regulations and sources of pollutants, however, impacts from SO_2 have declined while other pollutants such as NO_x have increased (Hauck, 2011). While the new pollution regime does not depauperate lichen populations as before, it has still been shown to cause changes in lichen species composition across gamma scales (Ellis & Coppins, 2010). Many parts of the boreal forest, however, are currently fairly remote and the lichen diversity is little impacted by human disturbance (Hauck, 2011; Werth et al, 2005). This gives researchers in the boreal forest the opportunity to study lichen diversity, composition, and the role of other environmental factors on these before human impacts become more pronounced. By doing so, we may also be able to mitigate the impacts from human disturbance as development increases in such areas as northwestern Quebec.

This study, then, has several questions to answer: 1) Are there differences in epiphytic and terricolous lichen diversity and species composition between different peatland types on a beta scale in northwestern Quebec? 2) Are there differences in lichen diversity and species composition in peatlands on a gamma scale in northwestern Quebec? 3) If there are differences in lichen diversity, can these differences be linked to the environmental factors: relative air humidity, temperature, the average minimum age of trees in the stand (hereafter minimum stand age), disturbance, and canopy openness?

2.3 Methodology

2.3.1 Study Area

The Eeyou Istchee James Bay region of northwestern Québec, Canada is located between 49° and 55° N, and 70° and 79° W. The region is in the Boreal zone with an average annual temperature between 1.0°C and -2.5°C (Grondin & Saucier, 2009). It is dominated by coniferous forests, becoming open conifer-lichen forests in the northern part (Ministère Environnement et Lutte contre les changements climatiques). It falls within the mid-Boreal wetland region according to Warner & Asada (2006), where peatlands have been forming since around 9,000 years B.P. Peatlands are relatively frequent, but more so in the southern part of the Eeyou Istchee James Bay region than in the northern (Grondin & Saucier, 2009). The region is sparsely populated by Cree communities, many of whom continue to provide for themselves off their ancestral territories. It is also little developed, though mining of lithium, gold, and diamonds as well as damming for hydroelectricity are both present (Société du Plan Nord, 2014).

2.3.2 Field methods

Three roughly equidistant sectors were studied along a 600 km north-south and east-west gradient during June, July, and August of 2017. The most southern study sector was Casa Berardi (49°12’07’’ N, 79°17’35’’ W), the central sector was Whabouchi (51°40’47’’ N, 75°51’13’’ W), and the most northern sector was Renard (52°49’01’’ N, 72°12’07’’ W) (see Appendix A for further information). In Canada, peatlands are defined as having at least 40 cm of peat - organic material decomposing in an anoxic environment (NWWG 1997). At these sectors, three dominant peatland types (see Appendix A for exact percentages) as defined by Lebeuf et al (2012) were selected for study:

> Uniform Fen (UF)– relatively flat and homogenous, though the vegetation can be diverse. Open water is rare.

Uniform Bog (UB) – relatively flat in terrain, dominated by one to all of the following: herbaceous vegetation, Ericaceous vegetation, or lichens.

Black Spruce (*Picea mariana*) Bog (SB) – relatively dense cover of black spruce (*Picea mariana*) that develops on organic soil. At least 10% of the spruce must be taller than 4 m for it to be considered a black spruce bog; under that it is classified as a Uniform Bog.

Leboeuf et al (2012) does not include water source in their definitions of peatlands, as they were focused on aerial and remote sensing mapping and ground truthed only a small area. However, it is assumed that the primary water source for Uniform Fens is ground water, while that of Uniform Bogs and Spruce Bogs is rainfall.

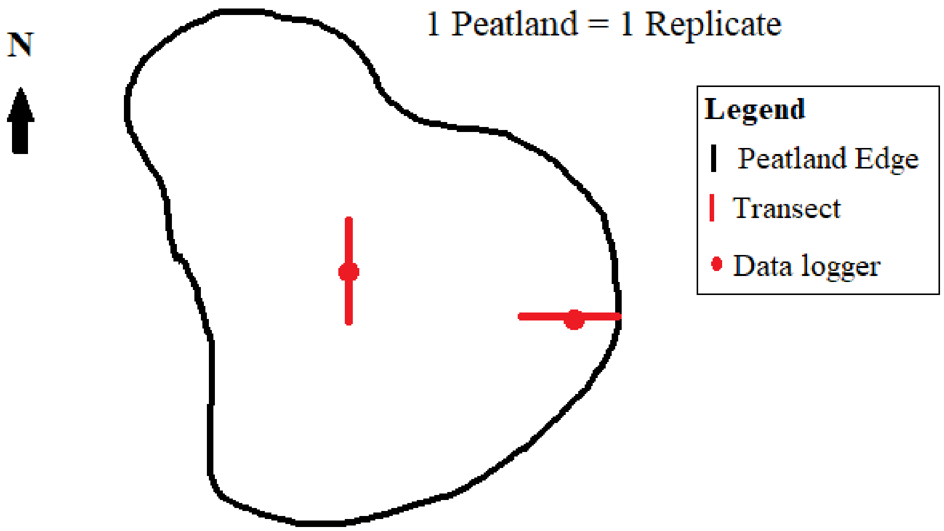

Figure 2.1. Diagram showing location of 20 m transects and data loggers within a replicate.

Three replicates – each replicate being an entire peatland – of each peatland type were sampled in each sector for lichen species richness and abundance, relative air humidity and temperature differences, and disturbance presence. This resulted in a total of 9 replicates per sector and 27 replicates total for the project. In each replicate two 20 meter transects were set up, one at a central point of the peatland and the other running from the peatland edge towards the center. The peatland edge was determined by marked change in vegetation and peat depth. Peat depth was measured using a metal and fiberglass rod designed to go through peat but not the substrate of soil or rock underneath the peat; when the rod struck substrate, a mark was made on the rod at the top of the peat, and the length of the rod from this point to the end of the rod that had hit substrate was then measured.

On each transect, the first ten occurrences for each of eleven pre-determined microhabitats were sampled for lichens: seedlings, dead seedlings, saplings, trees, tree bases, snags, coarse woody debris (CWD), peat, bare peat, moss, and rock (Table 4.1). In this study the substrates that lichens grow on are termed microhabitats. This is based on the assumption that lichens are influenced not only by the surface that they are directly growing on in terms of such things as nutrient availability and chemical makeup, but by the conditions that that surface creates. For example, lichens growing on the base of a tree will generally have a moister and more shaded microhabitat than lichens growing on open rock. The division between seedlings, saplings, and trees was made to broadly split trees into age groups since it was not possible to core every tree for a more accurate age. These divisions were based on U.S. Forest Service designations ("Forest Inventory", 2016). If peat or bare peat microhabitats were larger than a meter in width, then the exact measurement of this width was recorded. During sampling, representative specimens of all macro- and microlichen species were collected, including extra specimens for genera with especially cryptic species (i.e. *Bryoria*). Epiphytic lichens from trees, saplings, and snags were collected up to ~ 2 meters from the ground. Tree and sapling species were also recorded, but were almost exclusively *Picea mariana* with a few *Larix laricina.* To increase the capture of lichen diversity, Floristic Habitat Sampling (FHS) was used in addition to the transects. In this method, microhabitats and lichen species not encountered on the transects were targeted and collected during one hour throughout the entire peatland (Newmaster et al, 2005).

A data logger which recorded relative air humidity and air temperature was placed several centimeters above the peat at the center of each transect (N=2 per peatland). Data loggers remained in the field for one year. A densiometer reading of the percentage of open canopy was also taken at the center of the transect. Any disturbance within 300 meters – or up to 5 km in the case of mines - that potentially changed the habitat and growing conditions for lichens was noted. This included direct impacts such as snowmobile trails in the peatland, and indirect impacts such as nearby roads that could generate dust. A tree core was taken just above the root collar from at least three saplings or trees in each replicate, unless less than three saplings/trees were encountered on the transect lines.

2.3.3 Laboratory

Lichen nomenclature followed Brodo (2016). Lichen species were identified using a compound microscope and chemical spot tests. Where determination of species was particularly difficult, they were treated as groups. All species of *Usnea* were treated as a group due to the tiny size of the majority of thalli encountered. Crustose lichens except the *Mycoblastus sanginuarious/sanginarioides* genus and *Icmadophila ericetorum*, which could be easily recognized, were treated as one large group. *Cladonia chlorophaea, Cladonia cryptochlorophaea,* and *Cladonia merochlorophaea* were also lumped into a *Cladonia chlorophaea* group due to initial Thin Layer Chromatography (TLC) results that suggested these species were difficult to distinguish between using spot tests. Additional Thin Layer Chromatography (TLC) analysis to confirm particularly difficult or interesting species is currently in-progress.

Lastly, tree cores were sanded and individual rings counted and recorded. The oldest reliable core was then used to date the minimum age of the stand, as due to decay data were not reliable enough to estimate exact stand ages.

2.3.4 Statistical Analyses

Species richness was used to make inferences about lichen diversity, as previously done by Boch et al (2019). A linear mixed model was used to test for significant differences in lichen species richness per microhabitat among sectors, peatland types, and microhabitats. Replicates and transects were used as random effects, while sector, type, disturbance, and percent canopy cover were used as fixed effects. Total lichen richness data was square-root transformed to meet the assumption of normality. Then a linear regression was used to test for differences in total species richness between the sectors and peatland types. Aikaike Information Criterion (AIC) was used to choose the most parsimonious model for species richness among microhabitats by finding the model with the lowest AIC score. AICc was similarly used to choose the most parsimonious model for species richness among peatlands and sectors by finding the model with the lowest AICc score. (See Appendix C for the models and their AIC/AICc values.)

ANOVAs were used to test for differences in microhabitat availability and canopy openness among the sectors and peatland types. G-tests were used to evaluate significant differences in frequency of temperature and humidity events. Data from twelve data loggers for Casa Berardi and Whabouchi were useable for these temperature and humidity tests. However, data from only three data loggers was useable for Renard. For this reason, no statistical tests were run on the humidity and temperature data at Renard versus Casa Berardi or Whabouchi. Those results that could be obtained at Renard are reported where they are relevant for projecting trends, but are considered as suggestive only. ‘High’ relative air humidity was considered as anything above 75%, as this is the lowest percentage at which lichens have been shown to activate, although this may be an optimistically low threshold (Nash III et al, 1990).

The other thresholds for ‘low humidity’, ‘high temperature’, and ‘low temperature’ were established by dividing the data into deciles and choosing the lowest and highest decile for each category respectively. This is a modified version of the method used in Fenton and Frego (2005). The average number of occurrences of peat, snag, tree, and sapling microhabitats in each peatland were calculated.

Venn Diagrams were used to compare overlaps in lichen species composition between peatland types and sectors.

Normality was visually confirmed for all tests. Linear mixed models from the nlme package, ANOVAs with TukeyHSD post-hoc tests, and G-tests were run in R (R Core Team, 2018, version 3.5.1) software.

Table 2.1. Microhabitat Definitions

Microhabitat	Definition
Seedling	Greater than 20 cm in height and less than 2.4 cm DBH (“Forest Inventory”, 2016)
Dead Seedling	Same as above, but dead
Sapling	2.5-7.5 DBH (“Forest Inventory”, 2016)
Tree	7.6 cm DBH and greater (“Forest Inventory”, 2016)
Tree Base	The bark at the base of a tree or sapling where in meets the peat
Snag	Dead Tree or Sapling
Coarse Woody Debris (CWD)	Dead tree or branch, lying with one side touching the peat
Peat	Decomposed organic material formed in an anoxic environment, supporting vascular or non-vascular plants
Bare Peat	Peat without vascular or non-vascular plants
Moss	Surface of mosses
Rock	Exposed rock surfaces

2.4 Results

2.4.1 Species Richness

In total, 76 separate species or subspecies of lichen were identified (Appendix B). For microhabitats as collectively, 52 species were found on trees and 41 on saplings, 60 on snags, and 45 on peat microhabitats. Twenty-five species were found on rock microhabitats, but rocks only occurred a total of 6 times throughout the entire study, and 5 of these occurrences were at Renard. Not all lichen species were solely associated with one microhabitat. Richness per individual occurrence of these microhabitats showed a different pattern from the number of species found collectively on these microhabitats, however. Individually, trees and saplings were significantly the most diverse microhabitats and not significantly different from each other (Figure 4.2). Snags and peat, despite being associated with large pools of species collectively, were individually significantly less diverse (Figure 4.2). As rocks were found so few times and the richness per rock microhabitat varied greatly, unfortunately more information would be necessary to understand individual richness in this microhabitat (Figure 4.2).

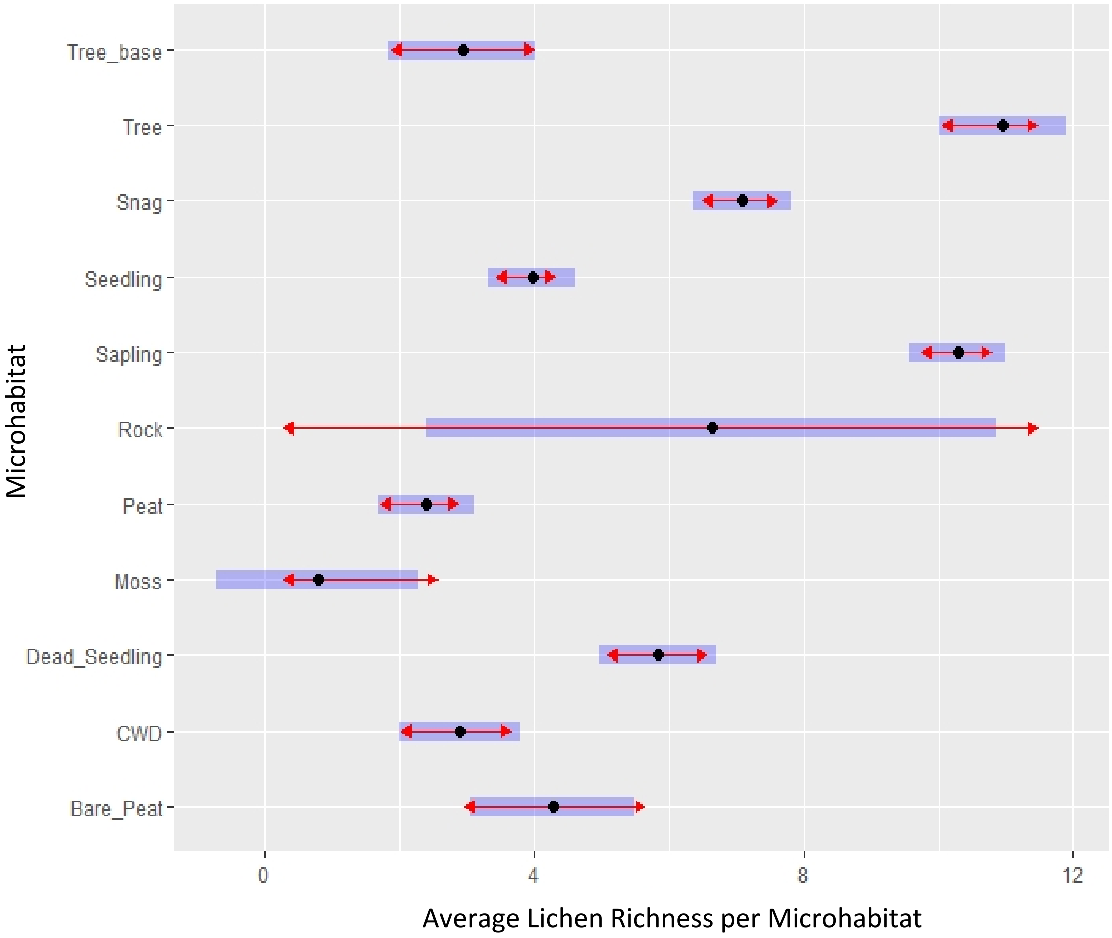

Figure 2.2. Average Lichen Richness per Microhabitat in Northwestern Quebec. Blue boxes indicate confidence intervals; where red arrows do not overlap, there is a significant difference.

Total lichen richness was significantly higher in Spruce Bogs and Uniform Bogs than in Uniform Fens by an average of ~10 species (Figure 4.3). Among the sectors, Renard was significantly more diverse than Casa Berardi (*p* = 0.0014378) and Whabouchi (*p* = 0.0148359). While Casa Berardi and Whabouchi were not significantly different from each other in richness, the average number of species found at Whabouchi was higher than at Casa Berardi, the three sectors thus forming a trend of increasing lichen diversity from south to north (Figure 4.4). Excluding rocks as a microhabitat, which almost exclusively occurred at Renard, eliminates the significant difference between Renard and the other sites (Figure 4.5). However, the increase in species richness from south to north is still visible (Figure 4.5).

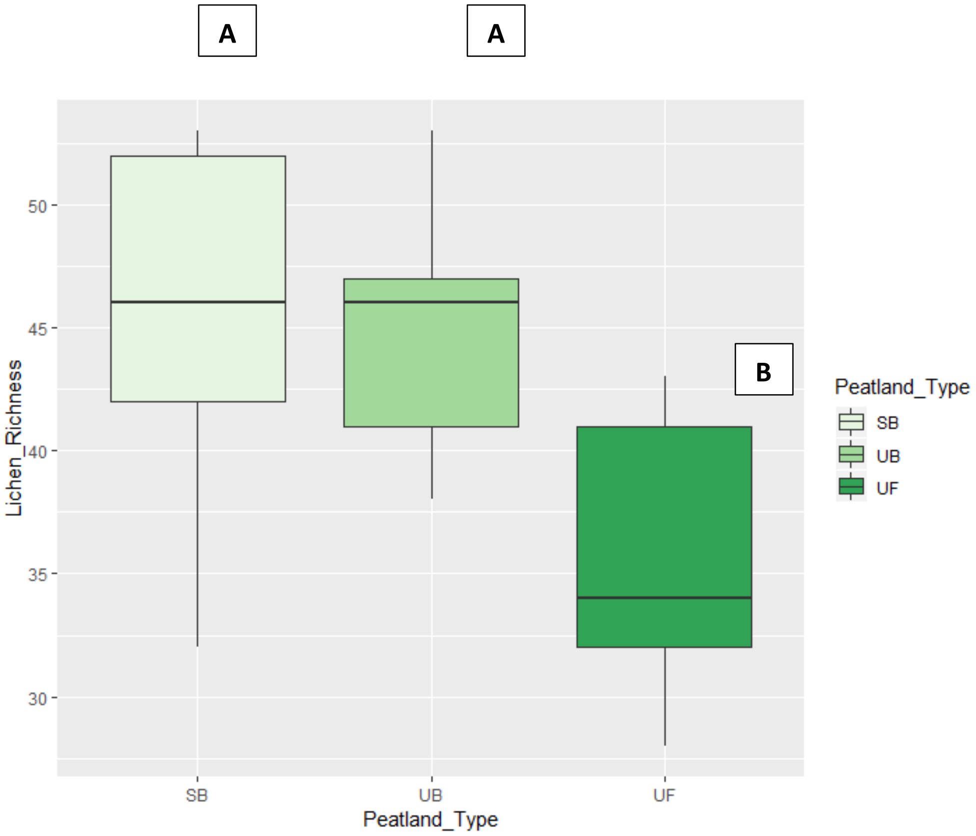

Figure 2.3. Total Lichen Richness in Three Peatland Types in Northwestern Quebec. SB = Spruce Bog, UB = Uniform Bog, UF = Uniform Fen. Boxplots are Tukey style (whiskers are the largest or smallest observation less than or greater than (or sometimes equal to) the respective hinges +/- 1.5*IQR).

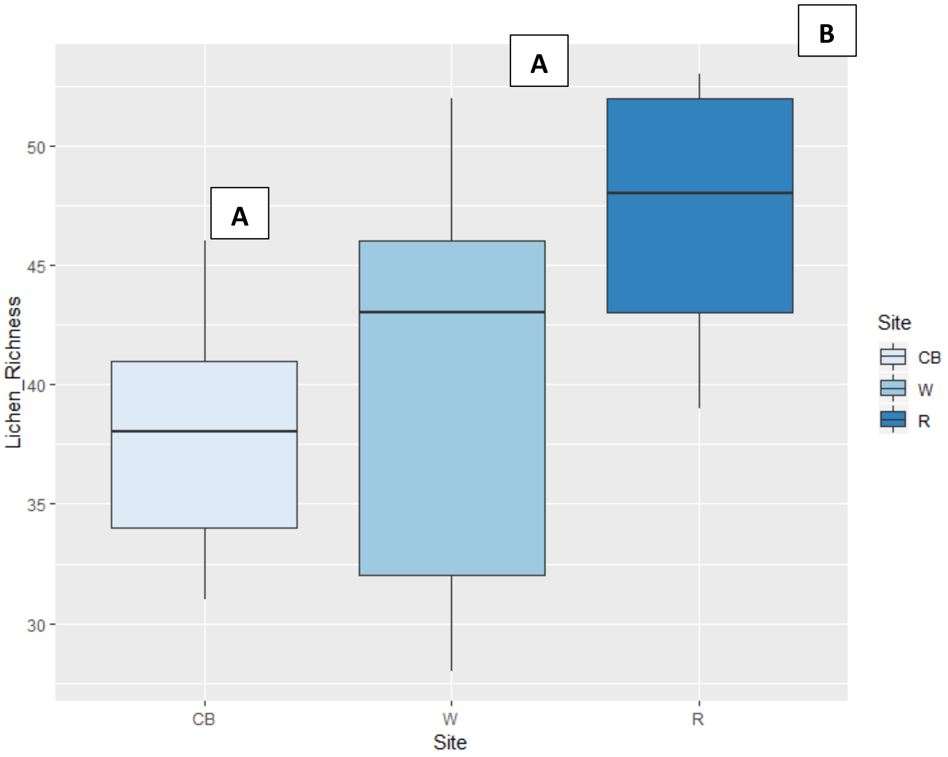

Figure 2.4. Total Lichen Richness in Three Sectors in Northwestern Quebec. CB = Casa Berardi, W = Whabouchi, R = Renard. Boxplots are Tukey style (whiskers are the largest or smallest observation less than or greater than (or sometimes equal to) the respective hinges +/- 1.5*IQR).

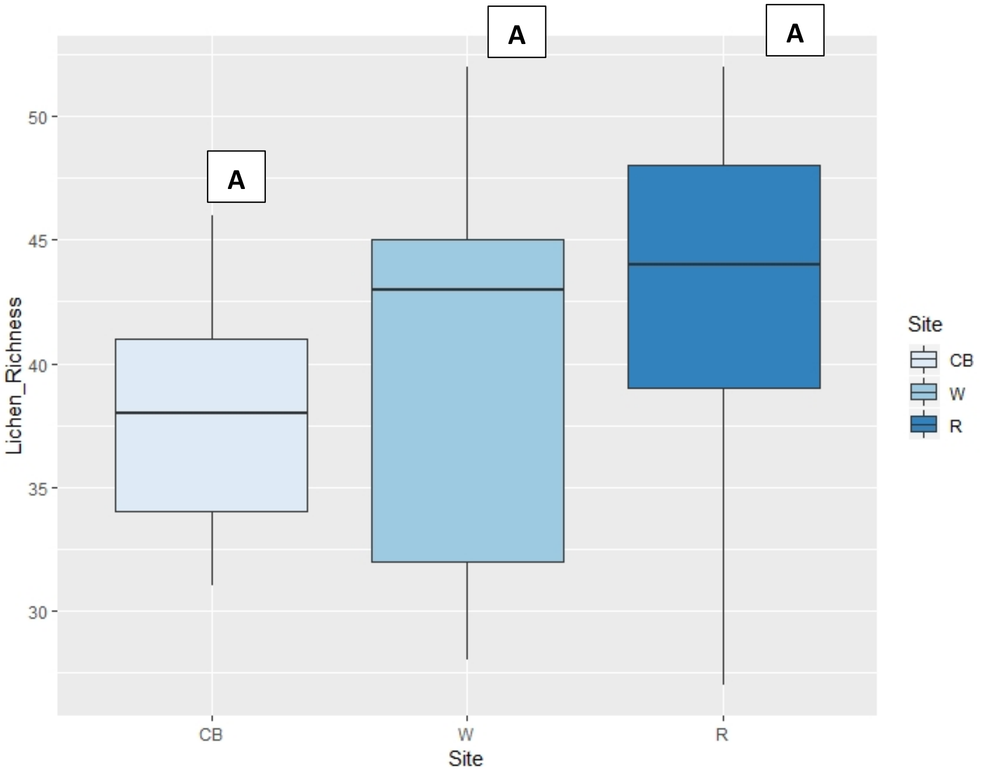

Figure 2.5. Total Lichen Richness in Three Sectors in Northwestern Quebec, Excluding Rock Microhabitats. CB = Casa Berardi, W = Whabouchi, R = Renard. Boxplots are Tukey style (whiskers are the largest or smallest observation less than or greater than (or sometimes equal to) the respective hinges +/- 1.5*IQR).

2.4.2 Species Composition

The three peatland types were remarkably similar in species composition (Figure 4.6). The majority of the species identified were present at all three different peatland types. Of the species found only in one or two peatland types, the majority were recorded only once throughout the entire study (Appendix B). Spruce Bogs and Uniform Fens may appear from Figure 4.4 to have a surprisingly large overlap in species composition, but three of the six species listed were found only on rock microhabitats. However, three species from the cyanobacterial genus *Peltigera* (four specimens recorded total), were all found in Spruce Bogs. The other cyanobacterial lichen found, *Stereocaulon*, showed no such preference and was found in all of the peatland types.

While all three sectors were also fairly similar in species composition, there appears to be slightly more overlap between Whabouchi and Renard (Figure 4.7). Here again the majority of species found at only one or two sectors were found only once throughout the entire study. Four species, however, were found more frequently: *Cladonia cornuta ssp cornuta* 24 times, *Cladonia uncialis* 20 times, and *Cetraria ericetorum ssp ericetorum* 24 times, and *Cetraria islandica ssp crispiformis* 33 times (Appendix B). All four of these species occurred at both Whabouchi and Renard. Of the species found only at Renard, just three of the twelve are attributable exclusively to rock microhabitats.

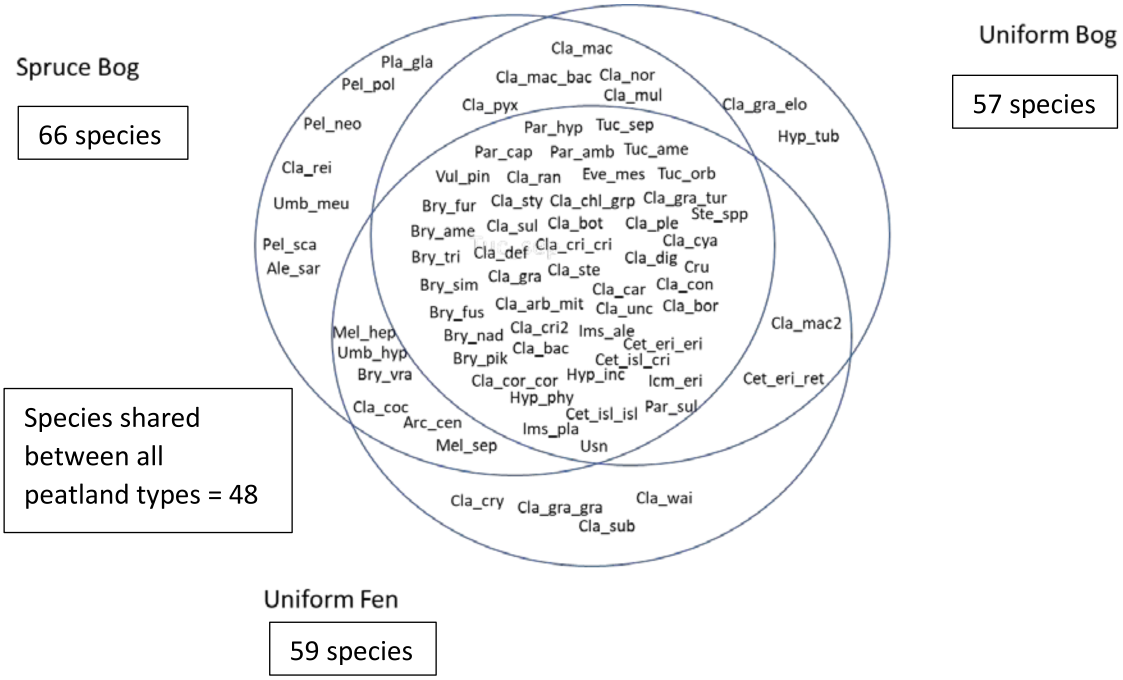

Figure 2.6. Venn Diagram of Lichen Species Composition in the Three Peatland Types in Northwestern Quebec. Each abbreviation represents a species or subspecies of lichen. Full names can be found in Appendix B.

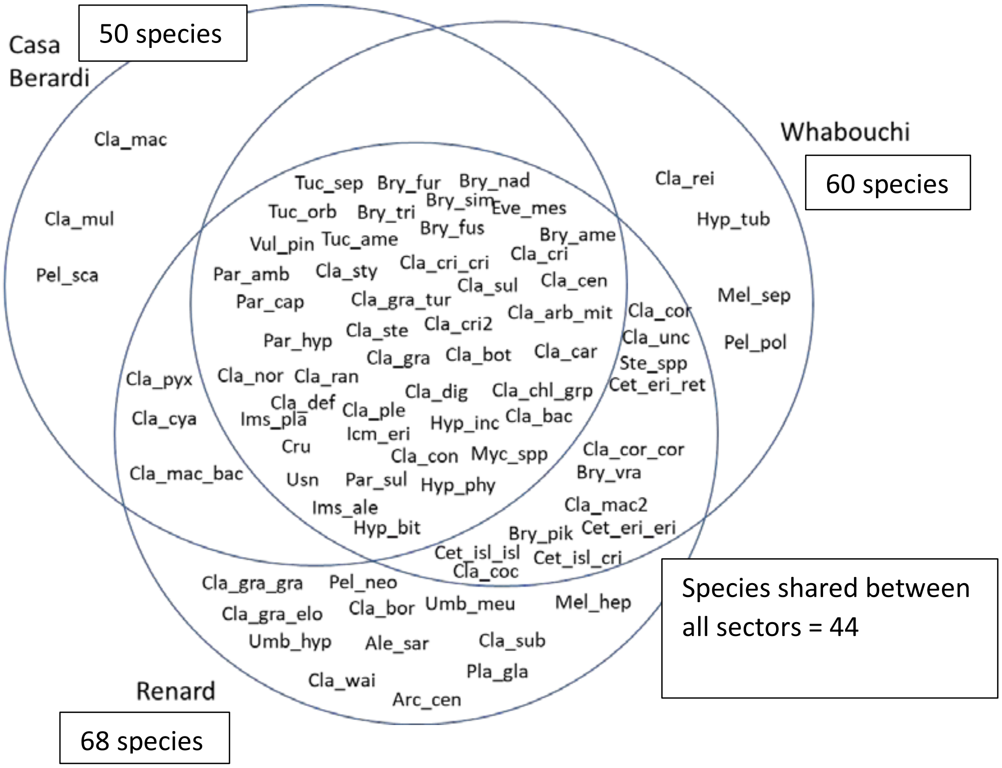

Figure 2.7. Venn Diagram of Lichen Species Composition in the Three Sectors in Northwestern Quebec. Each abbreviation represents a species or subspecies of lichen. Full names can be found in Appendix B.

2.4.3 Microhabitat Availability

The availability of microhabitats is the frequency with which the microhabitats were encountered on the transect lines (Table 4.2 shows the availability of the microhabitats that were noted as important in terms of total richness or association with large pools of species above). Snags and peat were encountered significantly more often in Spruce Bogs and Uniform Bogs than in Uniform Fens. This is the same trend as previously seen with higher diversity in Spruce Bogs and Uniform Bogs versus Uniform Fens. Additionally, peat microhabitats greater than one meter in width occurred only once in Uniform Fens, whereas they occurred 10 times in Spruce Bogs and 8 in Uniform Bogs.

For saplings, a significant increase in the availability is seen from Uniform Fens to Uniform Bogs to Spruce Bogs.

Table 2.2. Occurrence of Microhabitats at Three Peatland Types in Northwestern Quebec

	Average number of occurrences[a]		
Microhabitat	Spruce bog	Uniform bog	Uniform fen
Peat	13.6	13.6	4.4
Snag	9.5	10	4.5
Tree	6.5	1.89	0.56
Sapling	15.3	7.33	2.3

a = Average number of occurrences: the average number of times the microhabitat occurred in each peatland type

2.4.4 Temperature, Humidity, Canopy Openness, and Minimum Stand Age

From the viewpoint of trying to explain trends in species richness, no clear patterns in humidity or temperature were seen between the peatland types. For the sectors, relative air humidity over 75% is significantly more frequent at Whabouchi than at Casa Berardi ($p < 0.05$), while low relative air humidity (below 50.14%) is more frequent at Casa Berardi than at Whabouchi ($p < 0.05$) (Table 4.3). The frequency of high temperatures (greater than 25.96 °C) is also more frequent at Casa Berardi than at Whabouchi ($p < 0.05$) (Table 4.3). All of these trends, when expressed as percentages of overall time, continue at Renard (Table 4.3). Low temperatures (less than 2.69 °C) are significantly less frequent at Whabouchi than at Casa Berardi ($p < 0.05$), but expressed as a percentage of overall time and with the addition of Renard, it would seem that all three sectors are actually relatively similar (Table 4.3).

Table 2.3. Percentage of Time at Different Humidity and Temperature Levels at Three Sectors in Northwestern Quebec

	Sector		
	CB	W	R
% rh over 75	69%	77%	79%
Frequency*	6901	7695	-
% low rh	10%	7%	4%
Frequency*	1035	707	-
% low temp	11%	9%	12%
Frequency*	1088	905	-
% high temp	13%*	7%*	4%
Frequency*	1305	695	-

* significant difference between Casa Berardi and Whabouchi; Renard was excluded from these analyses

Frequencies are the number of times data loggers recorded readings in each category

Percentages represent the percentage of overall readings were in each category

Inundations, where the water level rose far enough to submerge the data loggers, were also inadvertently recorded. These results show that inundations occurred significantly more frequently in Uniform Fens than in Uniform Bogs ($p < 0.05$), and not at all for Spruce Bogs.

Neither canopy openness nor minimum stand age showed clear patterns that could be linked to lichen richness or species composition among the three sectors or three peatland types (see appendix D for further information).

2.5 Discussion

2.5.1 Beta and Alpha Diversity

We found that fens are less lichen diverse than bogs in northwestern Quebec, which confirms the pattern found in other parts of Canada by Warner and Asada (2006). The inclusion of epiphytic lichens in our study did not change this trend, but instead reinforced it. However, even the least diverse of our peatlands, at 28, was nearly three times more diverse than the numbers reported for other Canadian peatlands (Warner and Asada, 2006). This is probably largely due to the inclusion of trees, saplings, snags, and rocks as microhabitats, and because of our focus on lichen diversity rather than their peripheral inclusion as part of a study with different aims. This finding of such an exponentially larger number of species underlines the need for further study of lichens in peatlands across Canada. This will aid managers and researchers to better understand lichen diversity and contribution to this important habitat type.

Our data suggests that the lower lichen diversity in Uniform Fens is due to microhabitat availability. While any given peat or snag microhabitat is not as diverse as a tree or sapling microhabitat, they are associated with large and unique pools of lichen species. Due to the fact that each individual peat and snag microhabitat is less diverse, these microhabitats must occur more often in a peatland in order to capture more of the unique diversity associated with them. Yet both snag and peat microhabitats occurred only about half as often in Uniform Fens as in Uniform Bogs or Spruce Bogs. In addition, the peat microhabitats in Uniform Fens were far less likely to reach a size larger than one meter in width in Uniform Bogs or Spruce Bogs. For trees and saplings, the microhabitats identified as important due to their high lichen richness per occurrence, again there are far fewer occurrences of these microhabitats in Uniform Fens than in Uniform Bogs or Spruce Bogs.

But why do Uniform Fens have fewer peat, snag, tree, and sapling microhabitats compared to Uniform Bogs and Spruce Bogs? We suggest it could be due to inundation with water. We found that the sensors on the humidity and temperature loggers were sometimes immersed in water, despite being placed several centimeters above the top of the peat. This occurred significantly more often in Uniform Fens than in Uniform Bogs, and never happened in Spruce Bogs. Most likely this is connected to the greater dependence of Uniform Fens on groundwater sources rather than rainfall. Such an immersion would make peat a difficult place for lichen to establish and maintain a population. It might also kill seedlings before they could become saplings, trees, or snags, thus reducing the number of microhabitats. Another possibility is that nutrient availability plays a role. Studies have found that some secondary lichen substances aid lichens in the uptake of micro-nutrients, which likely helps them to grow successfully in nutrient-poor and acidic habitats (Hauck et al, 2009a; Hauck et al, 2009b). This would suggest that lichens are more successful in Uniform Bogs and Spruce Bogs, which are generally known to be nutrient-poor and more acidic, than in Uniform Fens where they may be out-competed by other plants that cannot tolerate these conditions as well. However, data on nutrient availability and pH in the peatlands we studied do not support this hypothesis, though further analysis remains to be done (Indorf, 2019, unpublished data).

The species composition of the three peatland types was very similar. This suggests that the environmental conditions in all three peatland types met the needs of the same general pool of lichen species when they could find the necessary microhabitat to grow on. This underlines the importance of microhabitat availability to the overall peatland lichen richness. The only potential exception to this is the cyanobacterial lichen genus *Peltigera*, found on peat only in the Spruce Bogs. The environmental factors that we measured do not seem to explain why this is the case. It may be that an environmental factor, such as dew, that we did not measure was of higher importance to *Peltigera*. Alternatively, it may be a matter of scale. One of the environmental factors that we measured on the peatland scale, such as light availability, may have been significantly different in the particular microhabitats where the *Peltigera* were collected. However, with only three species and a total of four specimens collected, both the occurrence of *Peltigera* only in Spruce Bogs and the reasons why need to be confirmed.

2.5.2 Gamma Diversity

Rock habitats appear to be the most important environmental factor for Renard's significantly higher lichen diversity. If we eliminate rock microhabitats from the analysis, the significant difference disappears. It is unclear why there were more rocks at Renard in particular. It is possible it is a random fluke of glaciation. However, the increase in lichen diversity from the south to the north, albeit less pronounced, does not disappear when rock microhabitats are removed. It is likely that if a further northern site was sampled significances would appear. This raises the possibility that there is a reason for this increase in lichen diversity.

These data suggest that the increase in lichen diversity from south to north could be linked to relative air humidity and temperature. As shown by increasing events of relative air humidity over 75% and decreasing events of relative air humidity under 50.14%, relative air humidity increased from the south to the north along with lichen diversity. Humidity is known to be an important source of hydration for lichens, and other regional studies have found similar patterns of increased lichen diversity correlating with increased humidity (Gauslaa, 2014; Jovan & McCune, 2004). Thus, it is highly probable that increasing relative air humidity and increasing lichen diversity are linked in this study as well.

The lichen diversity/temperature interaction is less clear. While the frequency of temperatures below 2.69°C was more or less similar across the transect, the frequency of temperatures above 25.96°C decreased, i.e. the sectors were overall cooler the further north along the transect. Several regional studies have found that lichen diversity increases in areas with warmer temperatures versus cooler temperatures (Jovan and McCune, 2004; Marini, Nascimbene, and Nimis, 2011). However, increasing the scale to the national level in the US, Coyle and Hurlbert (2004) found that lichen diversity did increase in areas with lower average temperatures. The reason why is unclear, however. A study on arctic lichens in warming climate scenarios found that at increasing temperatures lichens were overshadowed or out-competed by vascular plants (Cornelissen et al, 2001). However, our study concerned lichens in peatlands where competition from vascular plants is minimal and unlikely to have a considerable effect. It is possible that if less competition with vascular plants has allowed higher lichen diversity in the uplands, it would allow these species to disperse into the peatlands. It is also possible that there is an interaction between temperature and humidity, as suggested by Werth et al (2005), although in their study they were suggesting a trade-off between demands for high humidity in oceanic climates versus demands for warmer temperatures in the continental interior. This is very different from the present situation being discussed, which would suggest a potential interaction between high humidity and lower average temperatures. It is possible that there is an interaction with another environmental factor not measured, or that the trend in temperature is purely incidental and has less effect on lichen diversity than does humidity.

Whabouchi and Renard have more overlap in species composition with each other than with Casa Berardi. Not only do they share more species, but several of the species that they share occur with relative frequency. This is not true for the three species that Casa Berardi and Renard share, which all occurred much less often. This reflects the pattern of increasing lichen richness moving north.

2.5.3 Stand Age and Disturbance

Stand age did not have an influence on lichen species richness in this study. This is consistent with another study on lichen diversity in the region (Boudreault et al., 2002). This suggests that other environmental factors, most likely microhabitat availability and humidity, have a stronger influence on lichen diversity in peatlands. However, further studies that include younger stands could reveal different patterns.

Disturbance also did not influence lichen richness in this study. This is not unusual for a study in the boreal forest, which gives managers in northwestern Quebec an opportunity to protect lichen diversity before human disturbances increase (Hauck, 2011). As wildfire damage was extensive in at least one of the sectors, the lack of impact on lichen species richness could suggest that peatlands can act as refuges from fire for lichens. However, further analysis on lichen species composition could reveal that both stand age and disturbance have more impact than reflected here. For example, studies that followed changes in lichen species composition immediately following different disturbances (and therefore different stand ages) and at regular intervals thereafter would likely find changes this study could not.

2.5.4 Management and Conservation Implications

Management and conservation are important issues in northwestern Quebec, where further development is planned. According to this study, if preserving lichen diversity is a goal, then lichen management and conservation efforts should include a substantial amount of Spruce Bogs and Uniform Bogs. Among Spruce and Uniform Bogs, however, those with more occurrences of peat, snag, tree, and sapling microhabitats should be given priority conservation status. However, Uniform Fens should be searched for rare species before being developed. This study also suggests that water movements have an impact on lichen diversity in peatlands, in that flooding can reduce the microhabitat availability and therefore lichen diversity. This means that construction, such as of roads, that can change water flow and cause flooding in adjacent peatlands should be avoided or mitigated. The correlation between high lichen diversity and relative air humidity, potentially with some interaction with temperature, also suggests that peatland lichens are at risk from climate change, since these are both factors projected to change under altered climate regimes (Brown, de Beurs, and Marshall, 2012). Further monitoring to track peatland lichen diversity response to climate changes would help to confirm this and to develop responses.

With the possible exception of *Peltigera*, this study did not reveal a peatland type that was clearly more important for particular lichen species than the others. Further replication could find that some of the lichen species recorded only once or twice are indeed dependent on one of the three peatland types, but it could also turn out that they are not that specific. Therefore, I cannot make any explicit recommendations for management based on species composition among the peatland types. Considering the increased lichen richness, greater emphasis on management for lichens in the northern sections of northwestern Quebec should be considered.

CHAPTER III

GENERAL DISCUSSION

My study shows beta scale differences in lichen diversity between peatland types are influenced by alpha scale environmental factors. Lower lichen diversity in fens was linked to less microhabitat availability, particularly of peat and snags. In turn, the reduced number of peat and snags as microhabitats was hypothesized to be a result of more frequent inundations of water. Gamma scale changes in lichen diversity in peatlands across a region, however, are influenced by gamma scale trends in environmental factors. As lichen diversity increases south to north, the time spent at higher relative air humidity increases as well. High temperatures are also less frequent further north along the transect, but how influential this factor is, is unclear. The significantly higher lichen diversity of one site, Renard, was due to microhabitat availability (i.e., rocks) however.

The main take-away from species composition is that there are still many possibilities for further questions and study. My data suggest that species from the genus *Peltigera* may be found exclusively in Spruce Bogs, but this is a pattern that would need to be confirmed. If confirmed, the environmental factors that promote *Peltigera* growth in Spruce Bogs would also need to be investigated. All of the species found only a few times could be targeted to see if they indeed occur in only one or two of the peatland types or sectors, and under what circumstances.

Understanding these patterns can help conservationists and natural resource managers in the preservation of lichen diversity. This study suggests not only that Uniform Bogs and Spruce Bogs should be a higher priority for lichen conservation, but that peatlands with more snags and peat microhabitats are important to peatland lichens. However, development – such as roads – that changes the flow of water and causes flooding could still impact lichen diversity in these peatlands even if they are preserved. This study also suggests that changes in climate, particularly changes in precipitation and humidity, may affect lichen diversity in peatlands.

APPENDICES

APPENDIX A. Table A4. Description of the Three Study Sectors.

	Casa Berardi	**Whabouchi**	**Renard**
Average temperature, June-September[a]	14.8°C±8.50SD	13.5°C±9.85SD	11.8°C±10.25SD
Avg. Relative Humidity[a]	80.7±20.89SD	83.2±21.02SD	87.2±16.58SD
Avg. Minimum Stand Age[b]	124±22.89SD	184.2±30.89SD	190.5±50.31SD
Avg. Peatland Depth (in cm)[c]			
Uniform Fens	201.9±71.40SD	166.9±52.30SD	105.9±40.99
Uniform Bogs	81.9±108.82SD	165.8±72.73SD	113.4±41.76SD
Spruce Bogs	162.4±66.24	118.1±61.23SD	65.5±29.94SD
Percentage of Total Peatlands in each Study Sector[d]			
Uniform Fens	5.6	4.1	32.4
Uniform Bogs	30.5	50.0	8.3
Spruce Bogs	49.3	24.9	4.2
Other	14.6	21	55
Personal Observations	Outside of peatlands forest	Surrounding land is very open and heavily impacted	Undergrowth of forests outside the peatlands is very

Suite - Appendix A.

	and underbrush is thicker	by previous fires; peatlands themselves seem smaller and more fragmentary	open often with a thick carpet of terricolous lichens

a = Average temperature and relative humidity was calculated from the data collected on each transect in individual peatlands; values for Renard are based on only three data loggers, whereas Casa Berardi are based on 12 each (see Methodology for further details).

b = Average minimum stand age was calculated from tree cores taken from at least three saplings and/or trees in each peatland; only Spruce Bogs and Uniform Bogs were included in these calculations as there were not enough saplings or trees encountered on transect lines in the Uniform Fens (see Methodology for further details).

c = data courtesy of Marc-Frédéric Indorf. Measurements were collected every ten meters from a central point to the edge of the peatland.

d = data produced by Groupe - Conseil Forchemex Ltée for 10,000 km^2 areas centered around each mine, or 30,000 km^2 total. Percentage calculated as total number of peatland in each type / total number of peatlands.

APPENDIX B. Table B5. List of All Lichen Species Identified in the Eeyou Istchee Region of Northwestern Québec, Canada, including Full Name, Abbreviation, and Number of Times Recorded in Total

Lichen Species Identified	**Abbreviation**	**# Times Recorded at Casa Berardi**	**# Times Recorded at Whabouchi**	**# Times Recorded at Renard**	**Total # Times Recorded**
Alectoria sarmentosa	Ale_sar	0	0	7	7
Arctoparmelia centrifuga	Arc_cen	0	0	3	3
Bryoria americana	Bry_ame	69	97	111	277
Bryoria furcellata	Bry_fur	174	169	120	463
Bryoria fuscescens	Bry_fus	6	28	33	67
Bryoria nadvornikiana	Bry_nad	2	6	19	27
Bryoria pikei	Bry_pik	0	6	1	7
Bryoria simplicior	Bry_sim	7	44	43	94
Bryoria trichodes	Bry_tri	37	32	26	95
Bryoria vrangiana[a]	Bry_vra	0	3	5	8

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Lichen Species Identified	**Abbreviation**	**# Times Recorded at Casa Berardi**	**# Times Recorded at Whabouchi**	**# Times Recorded at Renard**	**Total # Times Recorded**
Cetraria ericetorum	Cet_eri	0	0	1	1
Cetraria ericetorum ssp ericetorum	Cet_eri_eri	0	11	13	24
Cetraria ericetorum ssp reticulata	Cet_eri_ret	0	5	3	8
Cetraria islandica	Cet_isl	0	0	5	5
Cetraria islandica ssp crispiformis	Cet_isl_cri	0	7	26	33
Cetraria islandica ssp islandica	Cet_isl_isl	0	4	9	13
Cladonia arbuscula ssp mitis	Cla_arb_mit	13	31	35	79
Cladonia bacilliformis	Cla_bac	7	6	13	26
Cladonia borealis[a]	Cla_bor	0	0	9	9

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Lichen Species Identified	**Abbreviation**	**# Times Recorded at Casa Berardi**	**# Times Recorded at Whabouchi**	**# Times Recorded at Renard**	**Total # Times Recorded**
Cladonia botrytes	Cla_bot	11	11	5	27
Cladonia carneola	Cla_car	9	14	19	42
Cladonia cenotea	Cla_cen	55	27	41	123
Cladonia chlorophaea group	Cla_chl_grp	44	22	40	106
Cladonia coccifera[a]	Cla_coc	0	1	3	4
Cladonia coniocraea	Cla_con	6	2	6	14
Cladonia cornuta	Cla_cor	0	3	3	6
Cladonia cornuta spp cornuta	Cla_cor_cor	3	4	17	24
Cladonia crispata	Cla_cri	2	1	4	7
Cladonia crispata var crispata	Cla_cri_cri	13	36	53	102

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Lichen Species Identified	**Abbreviation**	**# Times Recorded at Casa Berardi**	**# Times Recorded at Whabouchi**	**# Times Recorded at Renard**	**Total # Times Recorded**
Cladonia cristatella	Cla_cri2	17	24	9	50
Cladonia cyanipes	Cla_cya	2	0	14	16
Cladonia deformis	Cla_def	24	22	32	78
Cladonia digitata	Cla_dig	13	7	15	35
Cladonia gracilis ssp elongata	Cla_gra_elo	0	0	1	1
Cladonia gracilis ssp turbinata	Cla_gra_tur	14	8	13	35
Cladonia grayi	Cla_gra	36	20	27	83
Cladonia macilenta	Cla_mac	5	0	0	5
Cladonia macilenta var bacillaris	Cla_mac_bac	1	0	3	5
Cladonia macrophylla	Cla_mac2	0	1	1	2
Cladonia multiformis	Cla_mul	2	0	0	2

Suite – Appendix B.

Lichen Species Identified	**Abbreviation**	**# Times Recorded at Casa Berardi**	**# Times Recorded at Whabouchi**	**# Times Recorded at Renard**	**Total # Times Recorded**
Cladonia norvegica[a]	Cla_nor	2	1	2	5
Cladonia pleurota	Cla_ple	8	1	10	19
Cladonia pyxidata	Cla_pyx	1	0	2	3
Cladonia rangiferina	Cla_ran	68	76	49	193
Cladonia rei	Cla_rei	0	1	0	1
Cladonia stellaris	Cla_ste	9	25	53	87
Cladonia stygia	Cla_sty	20	24	75	119
Cladonia subfurcata	Cla_sub	0	0	1	1
Cladonia sulphurina	Cla_sul	33	33	53	119
Cladonia uncialis	Cla_unc	0	3	17	20
Cladonia wainioi	Cla_wai	0	0	3	3
Crustose	Cru	177	165	204	546
Evernia mesomorpha	Eve_mes	219	174	90	483

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Lichen Species Identified	**Abbreviation**	**# Times Recorded at Casa Berardi**	**# Times Recorded at Whabouchi**	**# Times Recorded at Renard**	**Total # Times Recorded**
Hypogymnia bitteri	Hyp_bit	1	7	56	64
Hypogymnia incurvoides	Hyp_inc	10	30	14	54
Hypogymnia physodes	Hyp_phy	151	157	104	412
Hypogymnia tubulosa	Hyp_tub	0	1	0	1
Icmadophila ericetorum	Icm_eri	4	9	15	28
Imshaugia aleurites	Ims_ale	198	215	166	579
Imshaugia placorodia	Ims_pla	17	31	17	65
Melanelia hepatizon	Mel_hep	0	0	2	2
Melanohalea septentrionalis	Mel_sep	0	3	0	3
Mycoblastus spp	Myc_spp	119	140	119	378
Parmelia sulcata	Par_sul	17	30	22	69
Parmeliopsis ambigua	Par_amb	60	90	78	229

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Lichen Species Identified	**Abbreviation**	**# Times Recorded at Casa Berardi**	**# Times Recorded at Whabouchi**	**# Times Recorded at Renard**	**Total # Times Recorded**
Parmeliopsis capitata	Par_cap	204	136	183	523
Parmeliopsis hyperopta	Par_hyp	230	210	272	713
Peltigera neopolydactyla	Pel_neo	0	0	1	1
Peltigera polydactyla	Pel_pol	0	1	0	1
Peltigera scabrosa	Pel_sca	2	0	0	2
Platismatia glauca	Pla_gla	0	0	1	1
Stereocaulon spp	Ste_spp	0	1	3	4
Tuckermanopsis americana	Tuc_ame	150	149	106	405
Tuckermanopsis orbata	Tuc_arb	11	8	1	20
Tuckermanopsis sepincola	Tuc_sep	91	70	75	236
Umbilicaria hyperborea	Umb_hyp	0	0	3	3
Umbilicaria meuhlenbergii	Umb_meu	0	0	1	1

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Lichen Species Identified	**Abbreviation**	**# Times Recorded at Casa Berardi**	**# Times Recorded at Whabouchi**	**# Times Recorded at Renard**	**Total # Times Recorded**
Usnea spp	Use_spp	68	98	33	199
Vulpicida pinastri	Vul_pin	229	199	218	646

a = awaiting further analysis by TLC

APPENDIX C. Lichen Species Richness Models Tested.

Table C6. Lichen Species Richness Among Microhabitats. Candidate models for species richness among microhabitats and the AIC values used to determine the most parsimonious model.

Model	**AIC**
Richness ~ Microhabitat + Transect + Site + Type + Disturbance + (1|Wetland_ID/Transect)	8784.566
Richness ~ Microhabitat + Transect + Site * Type + Disturbance + (1|Wetland_ID/Transect	8780.095
Richness ~ Transect + Microhabitat * Site * Type + Disturbance + (1|Wetland_ID/Transect	8660.786
Richness ~ Microhabitat + Transect + Site * Type + (1|Wetland_ID/Transect	8784.84
Richness ~ Microhabitat + Transect + Site + Type + (1|Wetland_ID/Transect	8784.744
Richness ~ Microhabitat + Transect + Site + Type + Per_Canopy_Open + (1|Wetland_ID/Transect	7746.503
Richness ~ Microhabitat + Transect + Site * Type + Per_Canopy_Open + (1|Wetland_ID/Transect	7745.143[a]

a = final model used

Table C7. Lichen Species Richness Among Sectors and Peatlands. Candidate models for species richness among sectors and peatlands and the AICc values used to select the most parsimonious model.

Model	**AICc**
Type_tot_sqrt ~ Site + Peatland_Type + Disturbance + Per_Canopy_Open	65.40249
Type_tot_sqrt ~ Site * Peatland_Type + Disturbance + Per_Canopy_Open	109.5787
Type_tot_sqrt ~ Site * Peatland_Type + Disturbance	95.47042
Type_tot_sqrt ~ Site * Peatland_Type + Per_Canopy_Open	51.35113
Type_tot_sqrt ~ Site + Peatland_Type	31.52736[a]
Type_tot_sqrt ~ Site * Peatland_Type	46.346

a = final model used

APPENDIX D. Canopy Openness and Minimum Stand Age

Canopy Openness

The only significant difference observed was between the Spruce Bogs and the other peatland types. Spruce Bogs had significantly more closed canopies than both Uniform Bogs ($p = 0.0007$) and Uniform Fens ($p = 0.00001$). It is possible that the more closed canopy in Spruce Bogs could affect species composition. However, the species that occurred exclusively in Spruce Bogs were found so few times it is difficult to make any definitive conclusion. No significant differences were shown between canopy openness at the different sites.

Minimum Stand Age

The minimum stand age was significantly higher in Whabouchi than at Casa Berardi ($p = 0.01$), which does not follow any other patterns in lichen species richness or composition considered in this study. No other tests between sites or peatland types showed any significance. A linear regression of species richness including minimum stand age as a variable was also tested to be certain, but minimum stand age did not show a significant influence ($p = 0.72$).

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