ARBOREAL LICHEN COMMUNITY STRUCTURE AND DIVERSITY ON YELLOW BIRCH (*BETULA ALLEGHANIENSIS*) AND BALSAM FIR (*ABIES BALSAMEA*) IN THE AVALON FOREST ECOREGION IN NEWFOUNDLAND, CANADA

By

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ABSTRACT

Lichens are present in virtually all terrestrial ecosystems. However, the mechanisms driving lichen community structure are not well understood. I compared lichen community composition on yellow birch (*Betula alleghaniensis*) and balsam fir (*Abies balsamea*) in the Avalon Forest Ecoregion in Newfoundland, Canada. I examined that the tree-level and stand-level habitat variables that influence lichen community structure varies between these two tree species. To evaluate how survey methods can affect community inventory data, I compared small subplot richness values for a subset of yellow birch trees to larger tree plot richness values. Currently, on the Avalon, yellow birch populations are under threat due to moose over browsing and illegal harvest. These results will be able to direct management efforts to identify areas of high conservation value.

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1. Introduction and overview

For 3.5 billion years the Earth's ecosystems have been evolving, resulting in diverse and complex biological communities (Franco 2013). These communities provide humans with food, water, clean air, energy, medicine, and recreational enjoyment. Earth's biodiversity is important for the well-being of our planet, increasing ecosystem productivity, contributing to climate stability, decreasing the risk of extinction from reduced gene pools, and much more. Over the past century humans have taken advantage of these resources, allowing our population to grow to over seven billion. As a result, the environmental conditions that fostered this growth are now at risk of over-exploitation and extinction. Global biodiversity is decreasing at an alarming rate, and many organisms' survival have become more important than ever.

The concept of biodiversity, or biological diversity, was coined in 1985 by Walter G. Rosen from the National Research Council/National Academy of Science (NRC/NAS) while planning a forum on biological diversity (Franco 2013). Since that time, there has been considerable concern among both scientists and society about conserving the diversity of life (Franco 2013). Increased rates of habitat destruction have accelerated extinction rates beyond evolutionary processes. When biodiversity became a key research area for scientists in the late 1980s, it solidified the formation of the field of conservation biology (Soulé 1985). This field was influenced by ecologists MacArthur and Wilson's work on the theory of island biogeography, attempting to predict the number of species that could exist on an island. They noted that the number of species on an island often varies according to island size, and the distance from larger land masses, showing that

remote islands are home to fewer species, receiving fewer immigrants but have the same amount of extinctions (Figure A.1) (MacArthur and Wilson 1967).

For epiphytic species, the plants they grow on represent a type of island, although whether patterns of epiphytes on trees follow patterns predicted by island biogeography theory is not fully known (Southwood and Kennedy 1983; Patiño et al. 2018). The size, age, and proximity to other islands of this nature determine the community structure of the epiphytes. Lichens include arboreal species that colonize a variety of tree species. Early succession in many terrestrial habitats starts with these pioneer species, determining the ultimate stability and longevity of that environment (Hale 1974). They may play an important role in the forest water cycle (Knops et al. 1996) and in forest nutrient cycling (Pike 1978; Boucher and Nash 1990). In boreal forests, lichens account for 8-10% of biomass and biodiversity, making a distinct contribution to ecological processes (Nash 2008). They lack a root system and obtain their nutrients from the atmosphere, precipitation that washes over them, and take up nutrients from the substrate they are found on (Richardson 1974). These nutrients are then reintroduced into the ecosystem as they deteriorate and fall to the forest floor (Reiners and Olson 1984). Although they only represent 2.2-2.8% of total above ground litterfall, in a mixed spruce-fir system in British Columbia this accounts for 11.5% of the total N input from canopy litterfall (Campbell et al. 2010).

The role of lichen epiphytes in forest nutrient cycling is not limited to the forest floor. The presence of N-fixing lichens can be associated with epiphyte community succession, facilitating the establishment of other arboreal species (Affeld et al. 2008), such as bryophytes (Benner 2011). During different stages of succession, their biomass

and composition changes, contributing to forest ecosystem dynamics in natural and managed systems (Esseen et al. 1996; Berryman and McCune 2006). Their rate of turnover influences the presence of other organisms, including forest dwelling animals. Birds and small mammals use them as nesting material (Hayward and Rosentreter 1994; Young et al. 2002), while other organisms, such as insects, mites, and gastropods use them for shelter and forage (Richardson, 1974). They are also an important food source for caribou (Richardson, 1974). Lichens form close relationships with many invertebrates that positively correspond to lichen biomass (Henderson and Hackett 1986; Stubbs 1989; Gunnarsson et al. 2004). They also increase microhabitat complexity, facilitating the coexistence and diversity of tree-dwelling micro-fauna (Shorrocks et al. 1991).

Although we have a broad understanding of the growth and reproduction of arboreal lichens, less is known about their ecology. There is debate about what drives and maintains the structure of arboreal communities in forests. At the scale of a tree, the physical and chemical structure of the bark, humidity levels and available sunlight are often determined to be the main controls of lichen community structure (Figure A.2). These variables are influenced by factors such as changing bark properties with the age, lean and tree species. Lichens have a relatively slow growth rates compared with the trees they inhabit, subsequently the age of a tree (or other substrate) is important to allow time for colonization and growth (Richardson 1974; Nascimbene et al. 2012). The north and south side of trees also differ - the sun-facing side will have more variable moisture then the shaded side (Nascimbene et al. 2012). Different tree species provide unique microhabitats for arboreal species (Brodo et al. 2001a; Loppi and Frati 2004; Ellis 2012). Many conifers are evergreens, dropping needles sporadically throughout the year,

whereas most deciduous trees lose their leaves annually, creating yearly variations in light exposure. Which a few exceptions, coniferous trees also tend to be more acidic and host a different lichen community than the more alkaline deciduous trees (Brodo et al. 2001a). In the boreal forests of Canada, cold-tolerant conifer species, such as *Abies, Larix, Picea*, or *Pinus*, dominate while deciduous trees such as *Populus* and *Betula* are found in lower abundance (Brandt et al. 2013).

Canada's boreal zone occurs from the Yukon and northern British Columbia to Newfoundland & Labrador, covering 552 million hectares and accounting for 28% of the world's boreal zone (Brandt et al. 2013). One hundred percent of the forested land in Newfoundland, Canada, is boreal. Here, the island is further subdivided into nine ecoregions based on variation in soil, climate, and vegetation (Figure 1-2). The Avalon Forest Ecoregion (AFE) is in the central part of the Avalon Peninsula in Newfoundland (Figure 1-3) (South 1983). The AFE covers approximately 500 km^2 within the boreal shield ecozone of Canada, with balsam fir (*Abies balsamea*) dominated, and in wet areas black spruce (*Picea mariana*), forests (South 1983). Climate on the Avalon Peninsula is characterized by long, cold winters, and short, cool summers, heavily impacted by the Atlantic Ocean. Annual average temperatures in the Avalon forest ecoregion range between 14˚C in the summer and -1˚C during the winter (Beersing et al. 1992). Precipitation levels are high, averaging 1350 mm of rainfall and 125-225 cm of snow annually (Beersing et al. 1992). Past glaciation formed a ribbed moraine topography with low, steep sided hills separated by small lakes and bogs (Beersing et al. 1992; Hättestrand and Kleman 1999). The diversity in moisture regimes creates microclimates similar to a river valley, lending to a large variety of vegetation types (South 1983). The unique

vegetation pattern of the central part of the Avalon Peninsula separates it from other parts the island despite its small size (South 1983). Slope aspect is an important variable in determining vegetative composition on moraines, with north-facing slopes dominated by *Abies-Betula* (fir-birch) forests, and south facing slopes dominated by *Abies-Picea mariana* (fir-spruce) forests (South 1983; Government of Newfoundland and Labrador 2016). On more productive sites, mature conifers are generally 10-12 cm in diameter, although larger trees are not uncommon (South 1983). Other tree species in the central part of the Avalon Peninsula include white birch (*Betula papyrifera*), eastern larch (*Larix laricina*), and rarely trembling aspen (*Populus tremuloides*) (Government of Newfoundland and Labrador 2016). Ground vegetation is dominated by *Dryopteris spinulosa* var. *americana* on northern slopes, and a variety of *Sphagnum* species and *Taxus canadensis* on southern slopes (South 1983).

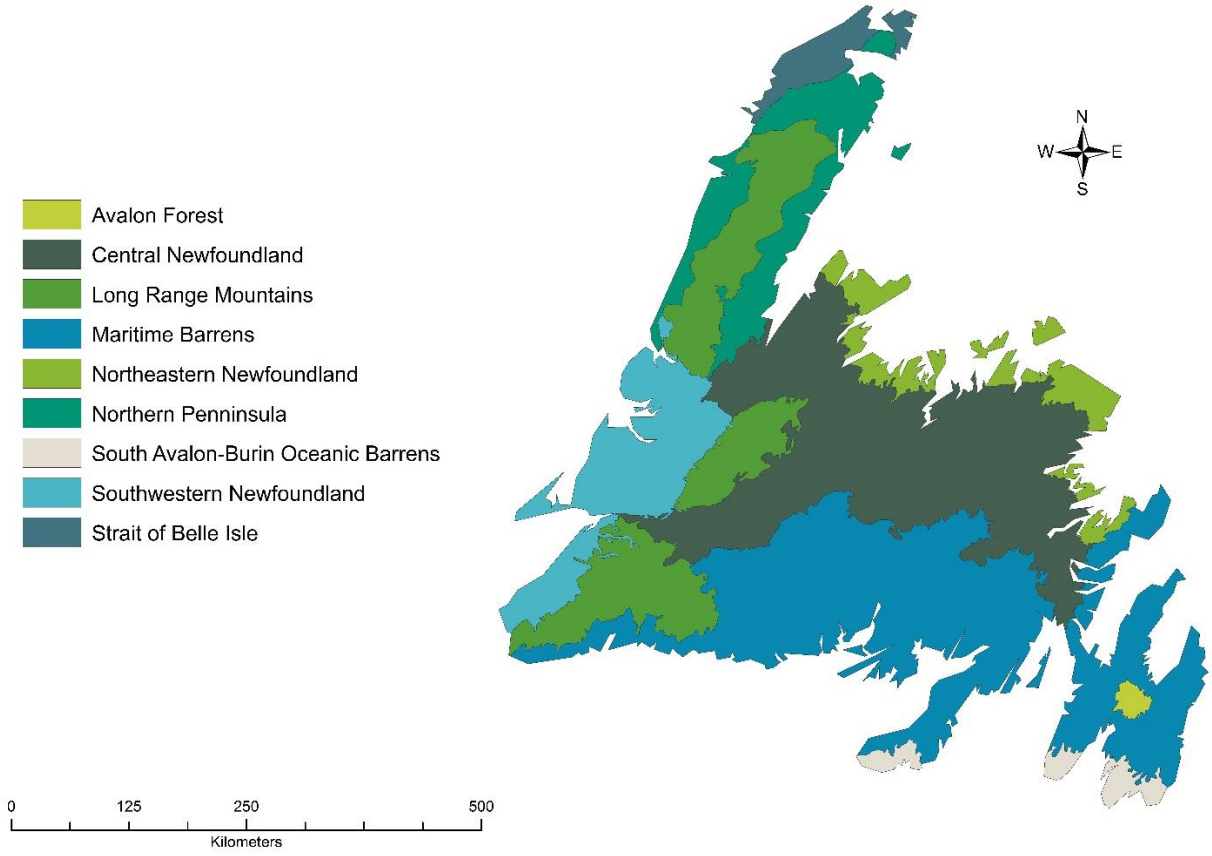

Figure 1-1. The island portion of Newfoundland, Canada, divided into nine ecoregions based on distinctive patterns of climate, vegetation and soil development. The Avalon forest ecoregion, approximately 500km^2, is the focus area for this study.

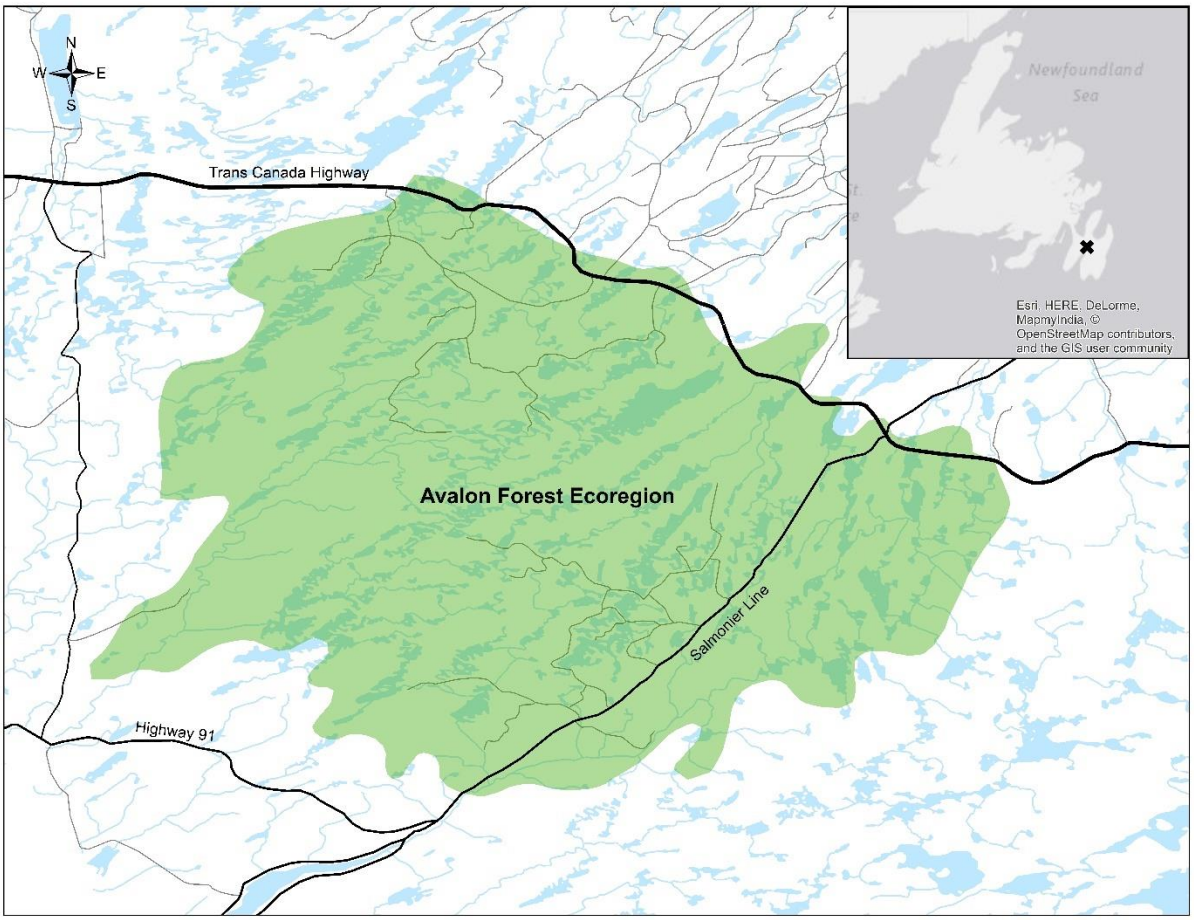

Figure 1-2. The Avalon Forest Ecoregion located in the central portion of the Avalon Peninsula in Newfoundland, Canada.

The combination of closed stand characteristics and frequent dense fog (South 1983) provides conditions for the colonization of lichens. For lichen, a series of events must occur during propagule dispersion to allow for successful colonization of a new substrate (Bailey 1976). Certain species require deciduous tree hosts and others require coniferous hosts (Nash 2008). Although there are strict forestry management plans in place for industry, illegal tree harvest is of growing concern in Newfoundland. In the Avalon forest ecoregion, hardwoods are selectively cut, including the locally rare yellow birch (*Betula alleghaniensis*) trees. The regeneration of this species is hampered by moose browsing on saplings (Bergerud and Manuel 1968; McLaren et al. 2004).

The consequences of losing yellow birch trees in the Avalon Forest Region are not fully understood. In order to aid conservation efforts, a sound understanding of this ecosystem is required. In my study, I will address several knowledge gaps in our understanding of this ecoregion. In chapter two, I will determine which lichen species are unique to yellow birch and balsam fir, and which variables are most important for their colonization, establishing baseline data that can be used to monitor changes caused by moose browse and selective harvesting. Diversity data will be collected using small plots placed on yellow birch and balsam fir trees, with abundance measured as the number of thalli present for each species within a plot. I will visually estimate percent cover in each plot on a scale from 0-100%. Comparison between host species and across sites is an important aspect of community diversity assessment.

Biodiversity counts are used to determine the richness and evenness of taxonomic groups across a variety of ecosystems. However, the effectiveness of chosen survey methods is rarely demonstrated. It is common to use methods that are standard in a

discipline, often adjusted according to project goals and target communities. A researcher examining lichen communities of the forest floor would take a different approach to that of a researcher examining lichen communities growing on trees, or on rocks (Will-Wolf et al. 2004). Even the location, in a global sense, can impact the methods a researcher uses to assess their local lichen community. This can be due to the complex nature of conducting research in different environments, such as alpine zones on mountain tops forests, or deserts. As a result, lichenologists have adapted ecological community survey methods to suit the needs of individual assessments of community diversity (Will-Wolf et al. 2004).

It is common practice to use small plots (<1 m^2) representative to capture diversity (Barabesi and Fattorini 1998), however, these methods are limited by a small area and may result in incomplete species lists (Newmaster et al. 2005). The use of small plots to survey lichen communities versus less-restricted surveys, that encompass larger areas, has been debated (McCune et al. 1997a; Will-Wolf et al. 2004). An advantage to using small plots is repeatability for greater quantitative precision, they are known as subplots or subsamples (McCune and Lesica 1992; Hauck et al. 2012; Giordani and Brunialti 2015). McCune and Lesica (1992) compared three ground cover lichen abundance sampling methods ranging from small to large and single to multiple plots. They captured a higher proportion of species in large, single-plot surveys compared to multiple micro-plots, but cover estimates for species were less accurate (McCune and Lesica 1992). Overall, the size of the plots should be small enough that the whole plot can be viewed at one time with individual organisms easily discernable within (McCune and Lesica 1992).

A good sampling design finds a balance between representativeness of the study area and a cost-effective sampling effort (Giordani and Brunialti 2015). In chapter three, I assessed two arboreal lichen diversity survey techniques, one involving the use of repeated subplots within a site, compared to the use of one large plot per site. I will discuss the advantages and disadvantages of each method, outlining when their use is most appropriate. There have been many lichen surveys done using larger plots (for example, a hectare in size) in comparison to the size of plots examined here (Will-Wolf et al. 2004, Berryman and McCune 2006). However, large plots such as these were not explored further in this study.

My thesis will provide a better understanding of how spatial drivers shape lichen community patterns. Future studies on arboreal diversity will be able to use these results to aid in selecting appropriate diversity survey methods. My results are also able to direct management efforts in identifying areas of high conservation value on the Avalon.

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1.2 Co-authorship statement

This research was co-supervised by Dr. Yolanda Wiersma of Memorial University Biology Department, and Dr. R. Troy McMullin of the Canadian Museum of Nature in Ottawa, Ontario. As the primary author, I was responsible for the majority of thesis writing, all of the data collection for the two data chapters (i.e., Chapter 2 and 3), and majority of the data analysis (approximately 90%). In addition to myself, Chapter 2, titled "Drivers of arboreal lichen community structure and diversity across scales", is co-authored by Dr. Yolanda Wiersma, Dr. R. Troy McMullin and Dr. André Arsenault. Dr. Wiersma helped refine the hypotheses being tested and assisted with the revision of the overall thesis. Dr. McMullin provided insight and assistance with lichen identification, lichen ecology, experimental design, and revision of the overall thesis. Dr. Arsenault provided information on the Avalon Forest Ecoregion, helping to guide site selection. Similarly, Chapter 3, titled "Comparing two different survey methods for arboreal lichen diversity surveys", is co-authored by Dr. Yolanda Wiersma, Dr. R. Troy McMullin and Dr. André Arsenault. Dr. Wiersma, along with Dr. McMullin, helped develop the hypothesis and experimental design. Dr. Arsenault helped with the analysis of lichen data. All three assisted with manuscript revision prior to final thesis submission. I plan to submit chapter 2 and 3 to peer-reviewed journals in the coming weeks. I will submit chapter 2 to the *Journal of Vegetation Science* and chapter 3 to *The Bryologist*.

2. Drivers of arboreal lichen community structure and diversity across scales

2.1 Introduction

Lichen biomass is known to be variable both among and within tree species (Schmitt and Slack 1990; Bates 1992; Liu et al. 2000; Benner 2011; Kiebacher et al. 2016; Wang et al. 2016). Both inter- and intra- specific differences in chemical and physical features of bark and variation in crown structure create distinct conditions for arboreal lichen establishment on individual trees (Nascimbene et al. 2012; Kiebacher et al. 2016). However, the position of the tree within a stand and the characteristics of the stand may also be important. The factors influencing lichen community patterns occur at different spatial scales, and the scale of observation determines what patterns will be noted (Kuusinen and Penttinen 1999; Will-Wolf et al. 2006; Nascimbene 2013).

At the scale of the tree, humidity, heterogeneous light levels, and physical and chemical properties of the bark have been shown to be the main controls of lichen diversity (Bates 1992; Király and Ódor 2010; Benner 2011; Ellis 2012). The lean, size and age of a tree are important factors affecting the chemistry and structure of bark (Adams and Risser 1971; Cáceres et al. 2007; Hauck and Javkhlan 2009; Nascimbene 2013). Bark pH is a recognized predictor for lichen colonization and the successful reproduction of some species requires a certain degree of alkalinity or acidity (Brodo 1973; Cáceres et al. 2007). Bark pH may have a negative relationship with tree circumference (Bates 1992; Kuusinen 1994), and/or age (Ellis and Coppins 2007), or a positive relationship with circumference (Jüriado et al. 2009) and/or tree age (Fritz et al.

2009). Other characteristics of the substrate, including texture (Hale 1974; Nash 2008) and nutrient status (Purvis 2000) influence the establishment of lichen.

At a coarser scale, stand and landscape variables act to influence arboreal lichen communities. Lichen species richness at the stand scale is hypothesized to be driven by four key processes: environmental heterogeneity, area, isolation, and continuity. Here, habitat heterogeneity is related to variation in tree age, tree species diversity, and tree age diversity within a stand (Hale 1974; Nash 2008; Ellis 2012). Available resources, moisture levels, and the size of a forest stand determine which tree species will be present. Similarly, lichen richness has been shown to increase with the area of the forest stand (Jönsson et al. 2011). The continuity of a forest stand over time leads to increased surface area of host trees, expanding the niche occupied by epiphytes. The occurrence of water bodies, variation in topography, and the altitude/exposure of the stand also modifies the structure of lichen communities (Nash 2008; Ellis 2012). Many arboreal lichens reproduce asexually and are limited by diaspore dispersal (Bailey, 1976), and thus their presence is affected by temporal continuity of the stand. The distance between isolated patches of trees (or single tree species isolated from conspecifics) can negatively affect the richness of arboreal lichens (Johansson et al. 2003; Buckley 2011; Kiebacher et al. 2017). The maintenance of stand features over time may determine the ultimate success of the arboreal lichen community.

In environments where tree species diversity is limited, one can hypothesize that less common tree species might be an important host for locally uncommon lichen. In the conifer-dominated boreal forest, the different bark conditions of broad-leaved trees make them important contributors to arboreal species diversity (Kuusinen and Penttinen 1999).

Here, these deciduous trees offer a less acidic surface to colonize, often with more variability in bark structure (Kuusinen and Penttinen 1999). However, these hardwood trees are also highly sought after by humans for recreational purposes, including bridges and ramps for off-road vehicles, and fire wood.

The large extent of the Canadian boreal forest, and its circumpolar distribution, make it difficult to closely monitor forestry practices, particularly on un-leased crown land. Of the 552 million ha of boreal forest in Canada, only 8% (45 million ha) is protected within national and provincial parks, reserves, and other protected areas (Brandt et al. 2013). The Avalon Forest Ecoregion is a 500 km^2 section of the boreal forest on the island of Newfoundland, Canada (with no protected lands), where lichens account for 8-10% of the biodiversity and biomass (Nash 2008). Frequent precipitation and dense fog, average annual temperatures of 5°C, and dense, closed stand forests create the ideal habitat for lichens (South 1983). Here, yellow birch (*Betula alleghaniensis*) is a unique host for lichen species in a balsam fir (*Abies balsamea*) dominated forest. This host is under threat due to illegal harvest, and their recovery is hampered by the effect of moose over-browsing saplings (McLaren et al. 2004).

The rarity of deciduous trees in the Avalon forest ecoregion highlights their importance as a unique local host for lichen communities. Here, I describe lichen species composition on yellow birch and balsam fir in the Avalon Forest Ecoregion (AFE) of Newfoundland, Canada. I hypothesize that yellow birch and balsam fir trees represent different habitats for lichen colonization, and therefore will have a different community of lichen growing on their trunks. I aim to determine what environmental variables are influencing the lichen communities at both the tree and stand scale. I hypothesize that the

variables at the tree scale will be different between balsam fir and yellow birch, leading to differences in lichen community composition. I also hypothesize that stand-scale variables will have a different effect on the tree species, and therefore lead to different effects on the lichen communities found on each tree. Given that many of the variables measured at the stand scale influence variables at the tree-scale, I expect there to be complex interactions between drivers across scales. Understanding the environmental factors that maintain lichen diversity can help us improve forest biodiversity conservation in the study region.

2.2 Methods

Site selection

Due to their rarity in this region, I focused site selection on the presence of yellow birch. I chose 21 sites (Figure 2-1) based the following search criteria. Suitable yellow birch trees had a diameter at breast height (DBH) between 13-35 cm, allowing space and time for lichen colonization (Adams and Risser 1971). Within 25 m of each birch tree, I selected a balsam fir that was ±5 cm DBH of the yellow birch. Each site contained two trees for examination, with a minimum of 500m between sites. The diameter range was chosen due to the limited availability of yellow birch, and smaller average size of balsam fir in the region. I selected trees based on similar exposure to sun, position on the slope, and proximity to the surrounding bog/water sources, allowing equal opportunity for lichen colonization. I avoided trees that had a lean of more than 15˚ as this can lead to excessive moisture levels and variable sun exposure on the tree bole. I recorded longitude and latitude coordinates for every tree using a Garmin 76 Global Positioning System (GPS) with ± 4-5 m resolution.

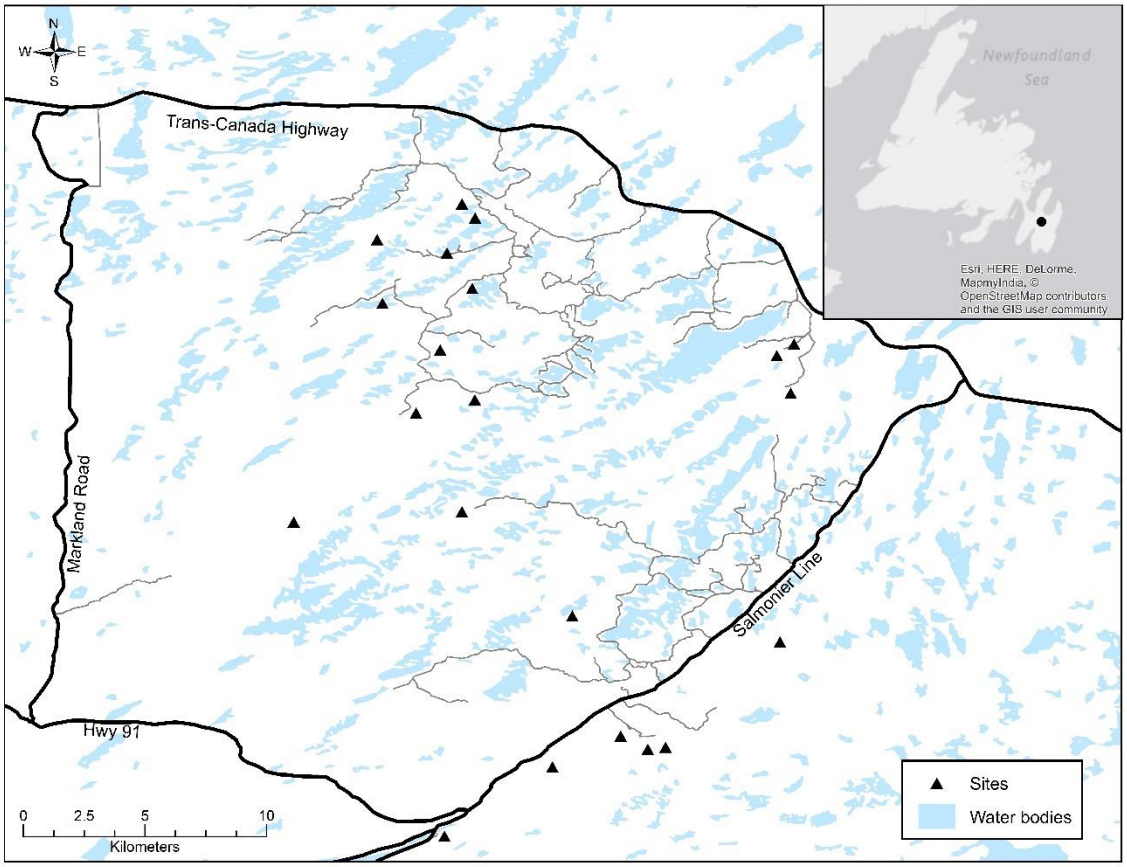

Figure 2-1. Map of study sites in the Avalon Forest Ecoregion in Newfoundland Canada.

Stand-scale measurements

I measured the distance between the two chosen trees in a site, marking the half-way point as the site centre. Here, I measured slope and aspect of the site using a Suunto clinometer and a Suunto compass set with a declination of 17° W. Aspect was later adjusted to a scale of 0-180° for statistical meaning (0 being north and 180 being south). Tree position on the stand was noted as either upper slope, mid slope, lower slope, toe, or level. Due to the high number of trees in this region, I recorded stand density using the point-quarter method (Bonham 1989). I split sites into four quadrants, measuring 10 m out from the site centre, making a division in each cardinal direction. Within each of the four quadrants, I placed a 1 m^2 quadrat and counted the percent of ground covered by the following: herbaceous plants (identified to species), grasses, sedges, lichens, duff (e.g., leaf-litter), fine woody debris, fern, moss, and fungi. This information was used to examine differences between sites. I calculated the average percent cover value across all four quadrants for the final ground cover measurement in each site. I measured stand-level canopy cover at the center of the site, and around each tree, before leaf senescence using a spherical crown densiometer.

Tree-scale measurements

I visually assessed bark texture on a scale of 1-3, where 1 is relatively smooth, 2 is moderately ridged, 3 is deeply and heavily ridged. Bark samples were collected from each tree and dried for a minimum of two weeks. Any lichens or other arboreal species and debris were scraped off the bark samples, while trying to maintain the top layer of the bark. Assuming only the immediate surface pH is important for lichens since atmospheric humidity and water running down the trunk are their main sources of nutrients (Hale

1974; Nash 2008), I ground the top layers of these bark samples using a small coffee bean grinder. I mixed the ground sample with 10 mL of distilled water, recording the pH after two hours using an ExStik Waterproof pH Meter.

Using an increment borer, I extracted tree cores as close to the base of the tree as possible, following the recommendations of government foresters with local knowledge (André Arsenault personal communications). I mounted the tree cores into grooves on a piece of wood using wood glue. Starting with 120 grade sand paper, and working up to 400 grade, I sanded the cores until tree rings were neatly visible. I then counted the tree rings to get a minimum age estimate for each tree. I measured the heights of each tree using a clinometer and measuring tape, and measured diameter at breast height (DBH) using a DBH measuring tape.

Lichen diversity

I made "lichen ladders" of 4 mm thick polypropylene rope and 5 mm wood to measure lichen abundance and percent cover (Figure B.1). Each ladder was divided into five 10 cm by 10 cm subplots hung in a vertical row, so I could pin them to the trees at a height of 160 cm. Lichens are composed of undifferentiated vegetative tissue, often called a thallus. I pinned the ladders on both the north and south side of each tree and recorded the number of individual thalli (i.e., abundance) and percent cover (visual estimate) of all lichen species within each of the five subplots. An individual was any thallus differentiated from any other thalli of the same species. I used a 10x magnification hand lens to help identify and count individual thalli in the field.

I began field work in May 2017 and concluded in autumn of the same year. I collected samples of unknown species for laboratory identification. Chemical spot tests

included Lugol's iodine, para-phenylenediamine in ethyl alcohol, sodium hypochlorite, and 10 and 20% potassium hydroxide (Brodo et al. 2001). For species that I could not identify using chemical spot tests, thin layer chromatography was used in adherence to Culberson and Kristinsson (1970) in solvents A, B and C. Voucher specimens have been deposited in the Canadian Museum of Nature (CANL).

Statistical analyses

Lichen percent cover and abundance data were combined across the subplots and sides for each tree, providing one abundance and one percent cover value for each lichen species on each tree, as sampled across a 10 cm by 50 cm transect along the trunk. I relativized all lichen community data to each species maximum at all sites (i.e., most abundant value is one, least abundant is 0, with all other values for a species falling between). I did this prior to analysis to eliminate the influence of highly abundant species, and removed species occurring in only two or less sites. To compare the similarity of ground cover across the sites, I used a permutational multivariate ANOVA (Anderson 2001) on the percent coverage for every species and species group at each site.

I explored the relationships between arboreal lichen community structure and measured environmental variables on both yellow birch and balsam fir trees using canonical correspondence analysis (CCA). This analysis is a guided ordination that orders sites based on patterns of covariance in a response matrix, constrained by multiple linear regression on variables in a second matrix (i.e., environmental variable matrix) (McCune and Grace 2002). I chose this method as it ignores community structure that is unrelated to the measured environmental variables, and my data fit the required unimodal distribution. To maintain strong constraints on the axes, I limited the number of variables

in each CCA to three (McCune and Grace 2002). As the number of variables is increased, and approaches the number of samples, the ordination becomes weaker (McCune and Grace 2002). McCune and Grace (2002) suggest three be the maximum number of variables included in a CCA. After each run, I interpreted the variables most strongly correlated with the axes. I ran site and tree level variables with high correlation coefficients ($r > 0.60$) separately. I used forward selection and Monte Carlo permutations to identify a subset of site and tree level variables that exerted significant effects on lichen distributions in each scenario.

To further examine the difference between the lichen communities on yellow birch and balsam fir trees, I used a perMANOVA with 999 permutations using the 'vegan' package in RStudio (version 1.0.153; R Core Team 2016). To help distinguish the degree of similarity between the two lichen communities, I analysed rank abundance scores using PC Ord software (McCune and Mefford 2011), where species are ranked in order from most abundant to least abundant (i.e., from 1 to *n* species, 1 being the most abundant). PC Ord is unable to handle categorical variables in CCA ordination, so the categorical variables of position on the slope and bark texture were assessed separately. Differences between these variables were analyzed using boxplots of the variables against species abundance, and the variables against site totals (i.e., total number of occurrences for each category per site).

2.3 Results

Taxonomic composition and biomass

Species groups that were difficult or impossible to distinguish in the field were grouped by genus instead of species, resulting in *Biatora, Bryoria, Cladonia, Lepraria,*

Loxospora, Ochrolechia, and usnic acid containing fruticose species groups. Thirty-six lichen species or species groups (hereafter collectively referred to as "species") were found on both host tree species (Table B.1). There was higher species richness on the yellow birch than on the balsam fir trees, with a total of 31 and 27 species found respectively. *Coccocarpia palmicola, Hypogymnia vittata, Lecanactis abietina, Lepra waghornei, Leptogium cyanescens, Lobaria pulmonaria, L. scrobiculata, Nephroma laevigatum,* and *Violella fucata* were only found on yellow birch trees. *Buellia erubescens, Lecidea albofuscescens, Mycoblastus sanguinarioides, Opegrapha varia,* and *Parmeliella parvula* were only found on balsam fir trees. The mean lichen species richness on the balsam fir and yellow birch was 11.9 ± 2.86 and 9.86 ± 3.26, respectively. Richness values varied more across sites than between tree species (i.e., if lichen richness was high on balsam fir, it was also high on nearby yellow birch, but if richness was low on one tree species, it was similarly low on the other tree in the same site). Lichen species were present on both tree species, although the cover for each species differed. Differences in species rank and total abundance (number of thalli) on each tree species are shown in Table 2-1. Ground cover (vascular plants to species, all other variables in broad categories are outlined in methods) composition differed significantly between the sites ($R^2 = 0.66542$, df = 20, p-value = 0.001).

Table 2-1. Rank abundance data for lichen species on both the balsam fir and yellow birch trees.

Species on balsam fir	Rank	*N*	Species on yellow birch	Rank	*N*
Parmelia squarrosa	1	814	*Thelotrema lepadinum*	1	395
Bryoria spp.	2	721	*Platismatia norvegica*	2	307
Ochrolechia spp.	3	331	*Lopadium disciforme*	3	283
Mycoblastus caesius	4	279	*Sphaerophorous globosus*	4	273
Thelotrema lepadinum	5	261	*Coccocarpia palmicola*	5	241
Platismatia glauca	6	254	*Ochrolechia spp.*	6	201
Lopadium disciforme	7	180	*Mycoblastus caesius*	7	146
Sphaerophorous globosus	8	165	*Lobaria scrobiculata*	8	144
Lepraria spp.	9	114	*Lobaria pulmonaria*	9	121
Biatora spp.	10	106	*Loxospora spp.*	10	96
Hypogymnia incurvoides	11	85	*Graphis scripta*	11	60
Pertusaria amara	12	85	*Parmelia squarrosa*	12	51
Cladonia spp.	13	83	*Bryoria spp.*	13	50
Opegrapha varia	14	81	*Arthonia leucopellea*	14	42
Usnic acid containing fruticose species	15	71	Usnic acid containing fruticose species	15	42
Hypogymnia physodes	16	66	*Leptogium cyanescens*	16	24
Loxospora spp.	17	40	*Biatora spp.*	17	21
Hypogymnia tubulosa	18	13	*Pertusaria amara*	18	19
Bacidia schweinitzii	19	7	*Lecanactis abietina*	19	17
Buellia erubescens	20	7	*Hypogymnia incurvoides*	20	16
Platismatia norvegica	21	7	*Lepra waghornei*	21	16
Parmeliella parvula	22	7	*Hypogymnia physodes*	22	14
Pertusaria macounii	23	6	*Hypogymnia vittata*	23	7
Mycoblastus sanguinarioides	24	5	*Bacidia schweinitzii*	24	6
Graphis scripta	25	4	*Hypogymnia tubulosa*	25	5
Lecidea albofuscescens	26	4	*Platismatia glauca*	26	5
Arthonia leucopellea	27	2	*Lepraria spp.*	27	4
			Cladonia spp.	28	2
			Nephroma laevigatum	29	2
			Pertusaria macounii	30	1
			Violella fucata	31	1

Lichen community drivers

Table 2-2 shows the mean and standard deviation for the variables measured on each tree species and in each site. Correlations between explanatory variables are in the supplementary information (Figure B.2). Height was strongly correlated with DBH and was excluded from further calculations based on the assumption that the diameter of the tree was more influential than the height in relation to the lichen community being examined.

Table 2-2. a) Means (± SD) of tree-level variables at all sites and different tree species in the Avalon Forest.

	Tree species	
	Balsam fir	Yellow birch
DBH (cm)	24.54 ± 6.10	28.93 ± 6.61
Canopy cover (%)	74.66 ± 9.66	80.14 ± 13.87
Height (m)	7.92 ± 1.69	9.20 ± 1.87
Bark pH	4.77 ± 0.11	5.14 ± 0.22
Age (years)	56.14 ± 21.71	114.57 ± 44.55

b) Means (± SD) of site-level variables at all sites in the Avalon Forest.

Slope (%)	12 ± 3.43
Aspect (˚)	90.9 ± 57.4
Canopy cover (%)	73.8 ± 18.8
Density (trees/m^2)	0.15 ± 0.12

The results from the main CCAs for yellow birch and balsam fir are shown in Table 2-3. The rank abundance curves complement the results of the ordination analysis, showing differences in lichen communities between balsam fir and yellow birch (Figure 2-2). For the comparison of the lichen communities on the two tree species, the first axis of the CCA was negatively correlated with bark pH. The two *Lobaria* species and *Platismatia glauca* had a positive correlation with bark pH. The second axis was positively correlated with tree diameter. Crustose species (*Graphis scripta, Mycoblastus caesius,* and *Ochrolechia* species) had high positive scores on the second axis. The third axis was negatively correlated with tree age. Forward selection with Monte Carlo permutation tests was applied to build the most parsimonious model, which identified pH as the main factor influencing variation in the lichen communities between each tree species. The results from the perMANOVA indicate a significant difference between the lichen communities on each tree species ($R^2 = 0.1393$, df = 1, p-value = 0.001).

Table 2-3. Summary of main ordination analyses. For all of the factors (tree variables and site variables) CCA was performed to determine the explained variance in lichen community composition on the balsam fir and yellow birch trees. Only the first and second axes are shown. P-value was calculated based on Monte Carlo test for all canonical axes.

Yellow birch and balsam fir				
	Tree canopy cover, DBH, age		Tree age, DBH, bark pH	
Axes	1	2	1	2
Eigenvalues	0.282	0.166	0.281	0.14
Percentage variance explained	8.6	5.1	8.6	4.3
Species-environment correlations	0.788	0.728	0.786	0.692
Sum of all canonical eigenvalues	0.532		0.501	
P-value	0.0751		**0.0325**	

Yellow birch						
	Aspect, density		Slope, DBH, density		Slope, density	
Axes	1	2	1	2	1	2
Eigenvalues	0.189	0.165	0.239	0.184	0.189	0.155
Percentage variance explained	8.0	7.0	10.1	7.7	8.0	6.5
Species-environment correlations	0.801	0.776	0.852	0.868	0.855	0.737
Sum of all canonical eigenvalues	0.354		0.423		0.344	
P-value	0.3175		0.191		0.0765	

Balsam fir						
	Bark pH, DBH, density		Tree canopy cover, bark pH, DBH		Bark pH, DBH, tree age	
Axes	1	2	1	2	1	2
Eigenvalues	0.18	0.113	0.199	0.095	0.181	0.136
Percentage variance explained	9.6	6.0	10.6	5.1	9.6	7.2
Species-environment correlations	0.833	0.760	0.848	0.609	0.834	0.806
Sum of all canonical eigenvalues	0.347		0.378		0.373	
P-value	0.188		0.1185		0.1	

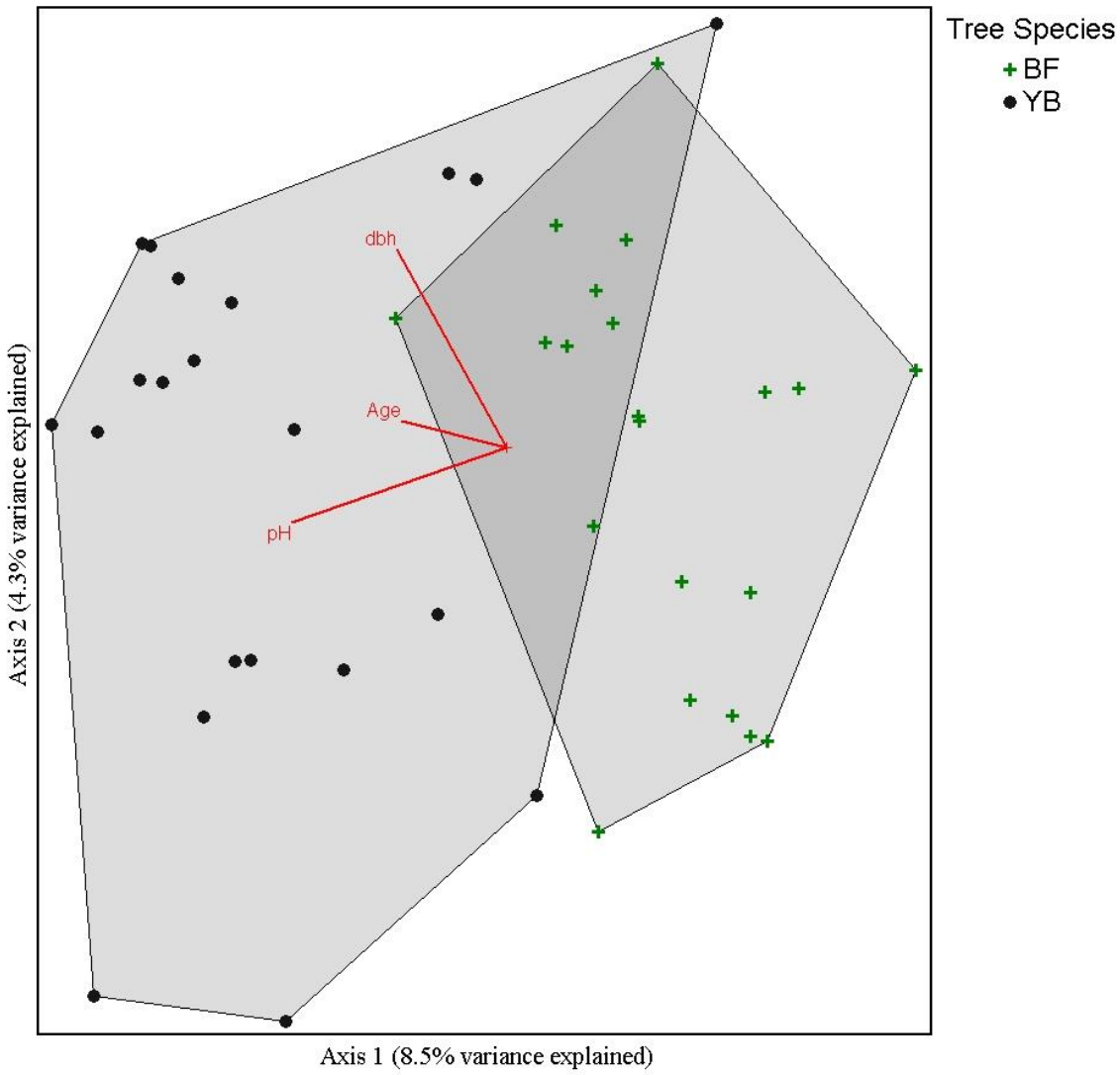

Figure 2-2. Canonical correspondence analysis of lichen abundance in relation to site, and tree species. Correlations between habitat variables and the first two canonical axes are represented by the length and angle of the red lines. Trees at each site are denoted by black circles (yellow birch) and a green plus sign (balsam fir). Forward selection with Monte Carlo permutation tests was applied to build the parsimonious model, which identified pH as the major influential factor contributing to the variation in the lichen communities between each tree species.

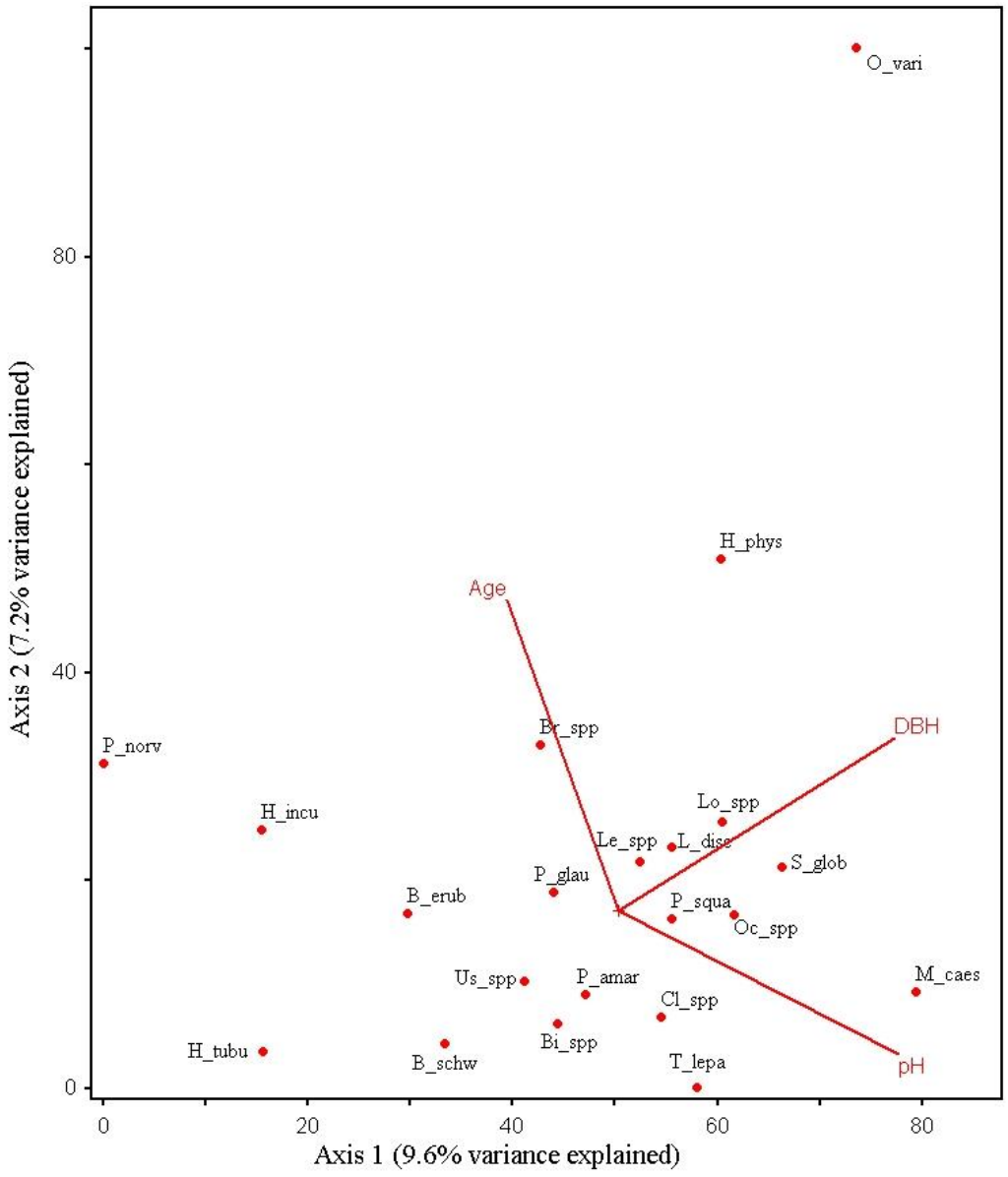

Figure 2-3. Canonical correspondence analysis of lichen abundance on balsam fir trees in the Avalon Forest Ecoregion. Lichen species are indicated red circles. Correlations between habitat variables and the first two canonical axes are represented by the length and angle of the red lines.

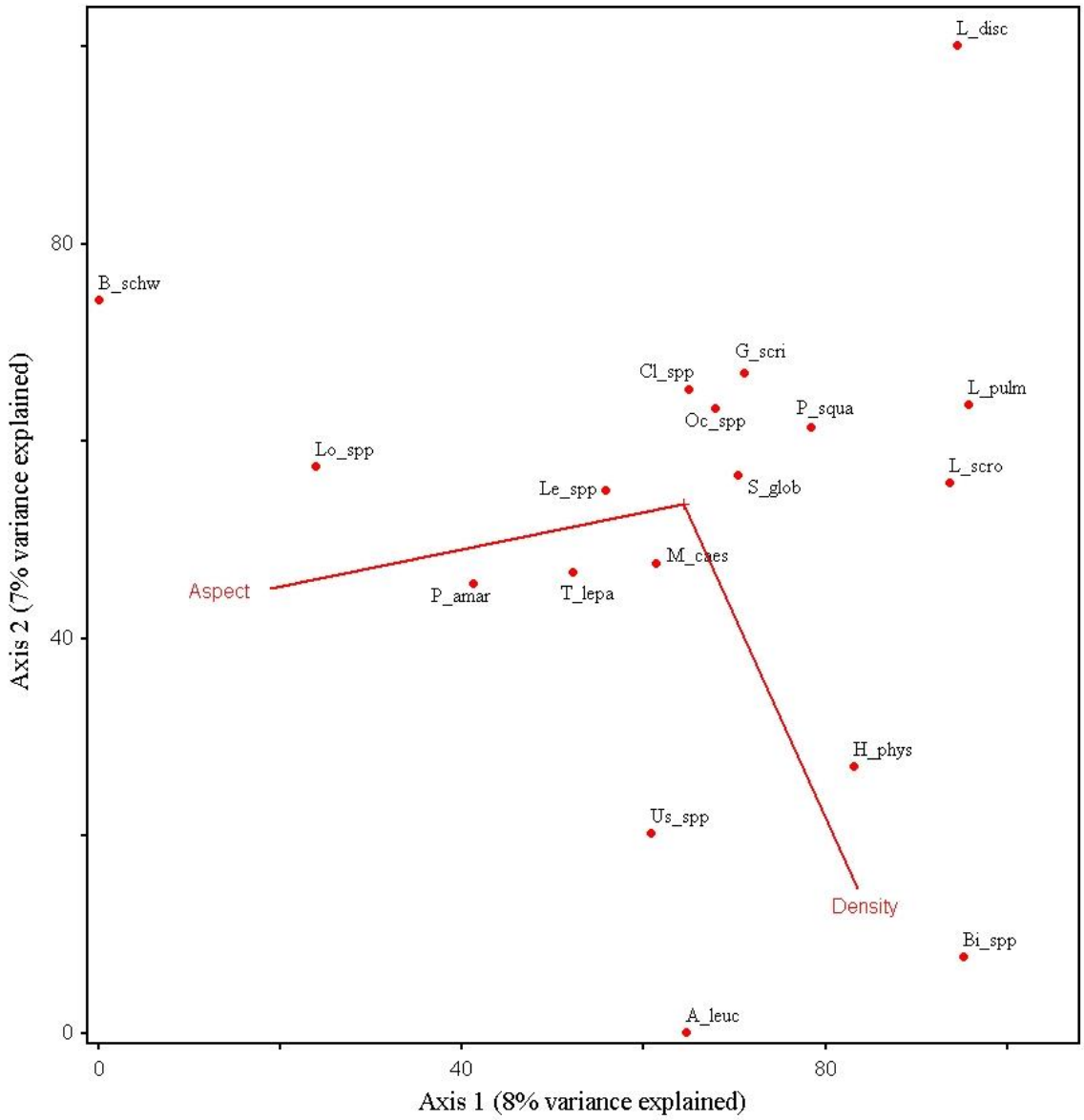

Figure 2-4. Canonical correspondence analysis of lichen abundance on yellow birch trees in the Avalon Forest Ecoregion, including the habitat variables aspect and density. Lichen species are indicated by red circles. Correlations between habitat variables and the first two canonical axes are represented by the length and angle of the red lines.

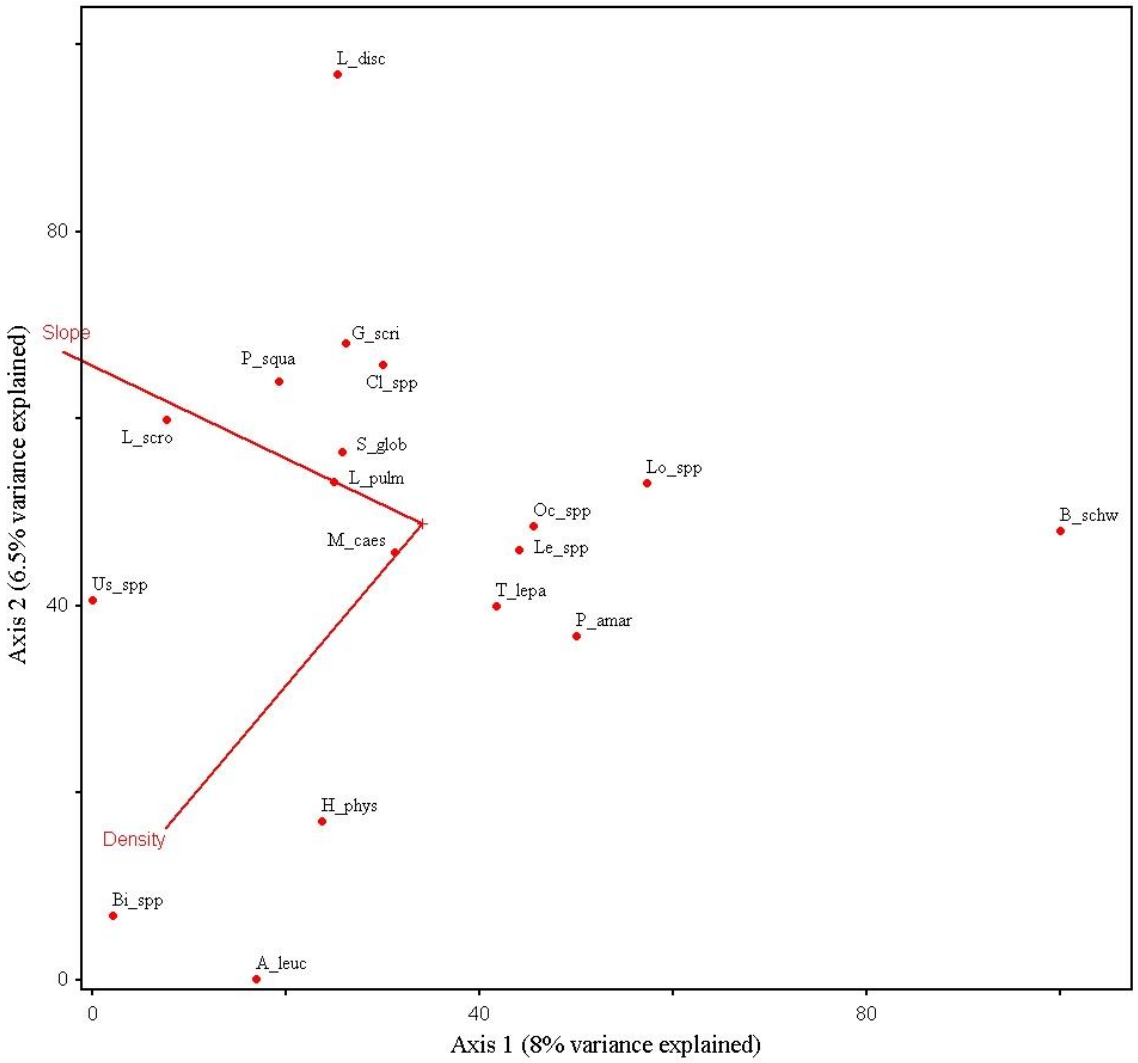

Figure 2-5. Canonical correspondence analysis of lichen abundance on yellow birch trees in the Avalon Forest Ecoregion, including the habitat variables slope and density. Sites are indicated by black triangles and lichen species by smaller red circles. Correlations between habitat variables and the first two canonical axes are represented by the length and angle of the red lines.

The CCA axes for balsam fir communities had the strongest correlations with the tree-level variables (age, DBH, and bark pH). In the top CCA result, tree diameter and bark pH were positively correlated with the first axis (Figure 2-3). *Mycoblastus caesius* had a strong positive correlation with the first axis, while *Hypogymnia incurvoides* and *Platismatia norvegica* had a weak, negative correlation with the first axis. Tree age was strongly correlated with axis 2, while tree diameter was weakly correlated with axis 2. The lichen species *Opegrapha varia* and *Hypogymnia physodes* were weakly correlated with this axis. Both bark pH and tree age had strong, negative correlations with the third axis. There were no species with a correlation to axis three stronger than r = 0.3.

The results for the CCAs comparing lichen communities across all yellow birch trees showed that the variation in the communities was mainly affected by the site-level variables slope, aspect, and density. There were two main CCAs used to describe the relationship between birch lichen communities and habitat variables as slope and aspect are correlated, and therefore not included in the same CCA. The first CCA (Figure 2-4) includes aspect, having a strong, negative correlation with axis 1, and density, having a strong negative correlation with axis 2. *Bacidia schweinitzii* and *Loxospora* spp. had a weak correlation with axis 1, while *Arthonia leucopellaea* had a weak, negative correlation with axis 2. The second top CCA (Figure 2-5) included slope, having a strong, negative correlation with axis 1, and a strong positive correlation with axis 2, and density having a strong, negative correlation with axis 2. *Bacidia schweinitzii* had a weak correlation with axis 1, while *Arthonia leucopellaea* had a weak, negative correlation with axis 2.

In every CCA, the usnic acid containing fruticose species group was positively correlated to *Sphaerophorus globosus*. There were no other significant correlations between other species in the dataset. There was no apparent relationship between lichen species composition at the different levels of bark texture and positions on the slope.

2.4 Discussion

The difference in lichen communities on the two tree types was mainly influenced by differences in bark pH, with balsam fir having a more acidic bark (i.e., lower pH) than yellow birch. Bark acidity, known to vary within and among tree species, has a strong influence on the composition of arboreal lichens (Adams and Risser 1971; Bates 1992; Hauck and Javkhlan 2009; Király et al. 2013). There was one tree from each species that was outside the normal range of bark pH for their species in this study (yellow birch with a pH of 4.5, balsam fir with a pH of 5.01), leading to lichen communities that did not match the pattern seen on their conspecifics. There has been speculation that the proximity to other tree species can alter the chemical properties of a trees bark to be more similar to the other species in the stand (Goward and Arsenault 2009; Hauck 2011). In the humid forests of south-central British Columbia, a "dripzone effect" has been proposed, in which the pH of conifers is altered due to nutrients leaching off nearby *Populus* trees (Goward and Arsenault 2009). The trees are close enough in proximity that their crowns overlap, and water flowing from the *Populus* branches travels down onto the nearby conifer branches, affecting bark pH (Goward and Arsenault 2009). This created an optimal microhabitat for *Lobaria* species and other cyanolichen in these stands (Goward and Arsenault 2009). The structure and composition of a stand may play a role in altering the chemical properties of the trunk, affecting the composition of epiphytes occurring.

The two abnormal trees in my dataset were found in stands that may have altered bark chemistry. The yellow birch was found in a balsam fir-dense stand, whereas the more basic balsam fir was found in an open, mixed-wood stand containing numerous yellow birch and white birch (*Betula papyrifera*). Lichen species commonly found on balsam fir in this study, such as *Hypogymnia physodes* and *Lopadium disciforme*, were found on this abnormally acidic yellow birch. In this case, it appears bark pH was a strong determinant for the differences between the lichen communities on these two-tree species.

When comparing the same tree species across sites, however, the mechanisms influencing lichen communities vary depending on the tree species itself. Lichen communities on balsam fir were strongly influenced by the attributes of the tree itself, including tree size, age, canopy cover and bark pH. Whereas, lichens on yellow birch were mainly influenced by the attributes of the stand where the trees were found, including slope, aspect, and density.

Given that balsam fir are the dominant species in these forests, it's not surprising that lichen communities were strongly affected by the attributes of the trees themselves. As these stands grow, senesce, and are replaced, there is little change in species composition. Changes are mainly represented in physiognomic differences on the trees, such as chemical and physical properties of the bark that are altered with age (Hilmo 1994; Farrar 1995; Nascimbene et al. 2009). For example, young conifer bark is relatively smooth, resinous, and non-absorbent compared to old bark of the same species (Barkman 1958). These forests have been heavily impacted by logging and natural disturbances such as fire, strong winds (e.g., Hurricane Igor in 2010), leading to an

average maximum age of 73 years (COSEWIC 2009). Balsam fir quickly regenerate in these areas, with seedlings from surrounding undisturbed parent stock, leading to a short stage of secondary succession (Bergerud and Manuel 1968). The short turnover time of the balsam fir forests is mirrored in the dynamic structure of the arboreal lichen community. Different lichen species prefer hosts at different successional stages (Barkman 1958; Sillett et al. 2000) resulting in variable species composition across the same tree species (Brown 1948; Hale 1950, 1952; Armstrong 1988; Uliczka and Angelstam 1999; Király et al. 2013; Rosabal et al. 2013). Large numbers of balsam fir in this forest mean a close source of spores from residual individuals or adjacent fir stands, leading to similarity in balsam fir arboreal richness across stands regardless of stand attributes (Lang et al. 1980).

The yellow birch trees are a different type of substrate for epiphytes in a conifer-dominated forest. This is reflected in the differences in lichen communities found on the bole of these trees compared to balsam fir in similar stands. Yellow birch have soft, thin bark that sloughs off at a decreasing rate with age (Schmitt and Slack 1990). This sloughing-off of the bark leads to the loss of arboreal lichen species (Schmitt and Slack 1990). However, as the yellow birch age, their bark becomes more rigid and coarse, decreasing the rate of sloughing, and increasing microtopographic variability and moisture holding capacity (Farrar 1995), increasing the availability of microhabitats for lichen colonization. The average age of yellow birch trees in this study was approximately 115 years old, all presenting heavily ridged bark. This allows for another explanation as to why the lichen communities differed between tree species. Johansson (2008) noted the importance of old growth stands as a host for unique lichen species that

are often rare and red-listed species. Certain species depend on old growth stands, such as *Lobaria* spp. (Sillett et al. 2000), found only on older yellow birch trees in this study. However, these yellow brich may be remnant trees that survived previous cutovers, where balsam fir was harvested for building materials. If this is true, the lichen on these birches may have experienced different environmental conditions, such as increased sunlight, leading to a different lichen community compared to the post-cutover grown balsam fir. Although species richness is known to increase with time (Fritz et al. 2009), unique species can be found at all stand ages, highlighting the importance of maintaining landscape level diversity in the boreal forest ecosystem (Johansson 2008).

Given the similar physical and chemical structure of the yellow birch trees examined, it is not surprising that stand-level variables had a stronger influence on the lichen communities. Birch trees senesce their leaves (Farrar 1995), changing the influx of light in the winter, a factor which has been shown to influence the arboreal communities on deciduous trees (Loppi and Frati 2004). The amount of sunlight that reaches the bole of a tree can be influenced by the characteristics of the stand, such as slope, aspect and density. Similarly, these characteristics can impact dispersal limited lichen species, hindering their dispersal abilities in dense stands, or stands with a steep slope, facing a direction opposed to wind-flow. Adjacent tree harvesting may increase solar radiation, wind, temperature, and remove potential sources of lichens, which could negatively affect the lichen communities found on yellow birch. It was not uncommon to find stands where yellow birch had been selectively harvested. The lack of yellow birch trees is the region that fit the search criteria meant a lower number of sites than originally anticipated.

If there had been more yellow birch of a suitable size, with no to little lean, I believe the number of lichen species found would have increased overall. There were many instances where trees were too large to be included, as the balsam fir in the sites did not grow large enough for comparison. Future similar studies should conduct surveys on a wider variety of tree species within these stands to provide more support for the patterns observed in these studies.

Increasing the plot and sample size may have increased the number of lichen species found, as shown in other studies (McCune and Lesica 1992). With a larger plot, I would be able to reach higher on the trees and access a microhabitat more strongly influenced by the structure of the crown. Future studies should consider increasing the sample number, as well as increasing the size of the plots used. For example, instead of a 10 cm by 50 cm plot, a 10 cm by 100 cm plot may be more appropriate, as used in previous studies (Wiersma and McMullin 2018).

Conclusion

My results are similar to that of previous studies indicating different tree species host different lichen communities as a result of variation in microhabitat features (Brown 1948; Hale 1950, 1952; Clauzade et al. 1985; Uliczka and Angelstam 1999; McMullin et al. 2010; Király et al. 2013; Rosabal et al. 2013; Lendemer et al. 2013). This includes physical and chemical variation in bark, and variable humidity and light levels. Interestingly, the features that act to maintain and influence the lichen communities were variable between the tree species. In environments where host species are threatened, it is important to understand what features in the environment maintain lichen community

diversity. Using this information, stands to be selected for harvest, and the type of harvest method that is most appropriate, can be determined. This will maintain biodiversity levels while allowing the harvest of natural resources in a sustainable manner.

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3. Comparing two methods for surveying arboreal lichen diversity

3.1 Introduction

Several methods have been developed to analyze and quantify biodiversity to describe the ecological value of a given environment. Simple descriptions of community diversity, such as richness, evenness, and the difference between repeated measures of these values, form the basis of many ecological models of community structure (MacArthur and Wilson 1967; Purvis and Hector 2000). Evaluating species richness involves counting the total number of species in a given area, and the relative abundance of each species is referred to as species evenness (Whittaker 1972; Gotelli and Colwell 2001). Knowing the community structure of one site or region provides limited understanding; data across sites, groups, or time is required for meaningful comparisons (Purvis and Hector 2000). The richness of one community may be equal to another, but the number of each species (i.e., abundance) can differ between environments (i.e., unequal evenness). Understanding these differences allows conclusions to be drawn about habitat diversity and the role of community structure in maintaining ecosystem function (Leibold et al. 2004; Verhoef and Morin 2010). However, given the simple nature of these metrics, ecologists often overlook the variable results that different methods of diversity sampling produce.

Community structure is variable and sampling techniques in one environment are not always appropriate for another (Ellis 2012). Compounding this is the variability across scales, as what acts to influence lichen community structure at a small extent, such as bark chemistry, may have less influence at the site level (Ellis 2012). Each

environment warrants a specific type of sampling method depending on the question being asked. Requirements for repeatability, researcher expertise, and search effort also need to be considered (Will-Wolf et al. 2004). For example, if the goal is to find the location of rare individuals, searching habitats that fit into a range of known suitable characteristics for those species is recommended (Bowering et al. 2018). If the goal is to compile a complete lichen list, a survey method with less restriction is required, allowing more microhabitats to be examined. If the goal is to collect lichen species abundance data, plots are recommended for repeatability and comparison across space and time (Will-Wolf et al. 2004). However, even among plots there are many variables to consider regarding size, shape, and within-site repetition. As a result, lichenologists have adapted ecological community survey methods to suit the needs of individual assessments of community diversity (Will-Wolf et al. 2004).

The use of small plots to survey lichen communities versus less-restricted surveys, that encompass larger areas, has been debated (McCune et al. 1997a; Will-Wolf et al. 2004). For arboreal lichen surveys, researchers regularly use small plots pinned to the tree bole, sometimes repeating measurements on several sides of one tree, and on many trees in one site (Scheidegger et al. 2002; Will-Wolf et al. 2004). These plots are often further divided into a vertical row of subplots, giving them the common name of lichen ladders (Nimis et al. 1991; Scheidegger et al. 2002; Stofer et al. 2003; Castello and Skert 2005; Nascimbene et al. 2010; Giordani and Brunialti 2015; McMullin et al. 2017; Wiersma and McMullin 2017; Wolseley et al. 2017). With these plots, a standardized diversity survey method can be applied across space and time. However, these methods

are bounded by a relatively small sample area and may result in an incomplete species list (Newmaster et al. 2005).

For example, I had the opportunity to measure lichen species richness levels on yellow birch trees (*Betula alleghaniensis*), using ten subplots per tree (see chapter 2), in Newfoundland, Canada for the purposes of another study. I do not believe these methods provided me with complete species richness values due to the restriction of the plot size. There were microhabitats I missed sampling, such as knots and knolls outside of the plots, and species I could physically see that were not within the plot boundaries. In order to determine if any species were missed during my original survey, I expanded the plot size to encompass a large portion of the tree bole and resurveyed the yellow birch trees at several sites. I hypothesize that with this increased survey area I will find more lichen species on each tree.

Repeating plots within one site can not only help determine most common species, but also increase chances of detecting the presence of less common species (Ravera and Brunialti 2013). However, Nascimbene and others (2010) noted the collection of redundant information by placing a lichen ladder on each of the four cardinal directions of every tree for diversity assessment. Lichen species are found on all sides of a tree, therefore I hypothesize that collecting species diversity data on both the north and south sides of trees will lead to the collection of redundant information. The information is redundant due to sampling of the same species more than once on the same substrate. Overall, the size of the plots should be small enough that the whole plot can be viewed at one time with individual organisms easily discernable within (McCune and

Lesica 1992). A good sampling design finds a balance between representativeness of the study area and a cost-effective sampling effort (Giordani and Brunialti 2015).

The surface of a tree represents its own unique landscape (Wiersma and McMullin 2018; Patiño et al. 2018), with vertical and horizontal micro-variation, such as moisture retaining scars, creating habitats for specialized lichen species (Bässler et al., 2016; Brodo, 1973; Jeseberger & Sheard, 1973; Richardson, 1974; Yarranton, 1967). For example, lichen species may occur in regions of the tree that vary based on ambient nutrient status (Seaward & Coppins, 2004; Wirth, 2010), or vertically vary based on reoccurring hydrological disturbance (Beckelhimer & Weaks, 1986; Timoney & Marsh, 2004). Similar to the many microhabitats on a rock surface (John & Dale, 1991), microtopographic variation occurs throughout the surface of a tree, but it is often examined on the bole (Jeseberger & Sheard, 1973; Wiersma & McMullin, 2018; Yarranton, 1967). The texture of the bark, or the scars of old branches can provide variable levels of moisture, sun and wind exposure, hosting specialized suites of lichen (Brodo et al., 2001). The original plots used in chapter 2 excluded a large portion of tree bole. To more accurately capture lichen species richness, the variety of microhabitats need to be included. I reassessed my original sampling methods, comparing them to another less-restrictive method of measuring arboreal lichen species richness. I wanted to know which survey method, subplot-based or tree-based, most accurately captured species richness, while examining the advantages and disadvantages of each. Rarefaction curves can be used to assess sampling methods, plotting the number of species as a function of the number of samples. A plateau in the curve indicates saturation, capturing

all or most of the species in the given environment. My aim was to determine the estimated species richness for each survey method and calculate the saturation point.

3.2 Methods

Location

This study took place on the island of Newfoundland, on the Avalon Peninsula within the Avalon Forest Ecoregion (AFE). This region is characterized by ribbed moraine topography with bog and swamp areas interspersed with forested hills (South 1983). These forests are dominated by balsam fir (*Abies balsamea*), with a moderate amount of black spruce (*Picea marina*), larch (*Larix laricina*) and white birch (*Betula papyrifera*) (South 1983). Less common is yellow birch (*Betula alleghaniensis*), found scattered throughout Newfoundland, with a cluster of the island's population occurring on the Avalon Peninsula (A. Arsenault, personal communication). Known yellow birch locations were used to locate trees for the original survey (A. Arsenault personal communication). Climate here is characterized by long, cold winters, and short, cool summers, heavily influenced by the Atlantic Ocean. Annual average temperatures range between 14˚C in the summer and -1˚C during the winter (Beersing et al. 1992). Precipitation levels are high, averaging 1350 mm of rainfall and between 125-225 cm of snow annually (Beersing et al. 1992). The relatively low variation in climate, coupled with frequent dense fog and closed stand forests create an ideal habitat for a variety of diverse lichen communities (South 1983; Beersing et al. 1992).

Lichen richness survey

In the fall of 2017, I revisited 10 sites that had been previously surveyed to reassess lichen species richness on yellow birch trees (Figure 3.1). The original survey consisted of 10 x 50 cm^2 sampling plots divided into five 10 x 10 cm^2 subplots (Figure B.1), placed on the north and south side of each tree, with the top of the plots at 160 cm above the ground. Total species richness for each tree was calculated as the total number of species (tree-level alpha diversity) within both plots on the north and south sides of a tree. I referred to these as subplot-based alpha-diversity values. I resurveyed along all sides of 10 of the original trees, searching from 0.6 m to 2 m along the bole, avoiding the lower portion where excess ground evaporation alters the community and stopped at a height past which I could not practically access. I referred to this richness as tree-based alpha diversity values. Species that were indistinguishable, or difficult to determine in the field were grouped by their genus alone. Samples of unknown specimens were collected for laboratory identification with microscopy and chemical spot tests with Lugol's iodine, para-phenylenediamine in ethyl alcohol, sodium hypochlorite, and 10 and 20% potassium hydroxide (Brodo et al. 2001b). For species that could not be identified using chemical spot tests, thin layer chromatography was used in adherence to Culberson and Kristinsson (1970) in solvents A, B′ and C. Voucher specimens have been deposited in the Canadian Museum of Nature (CANL).

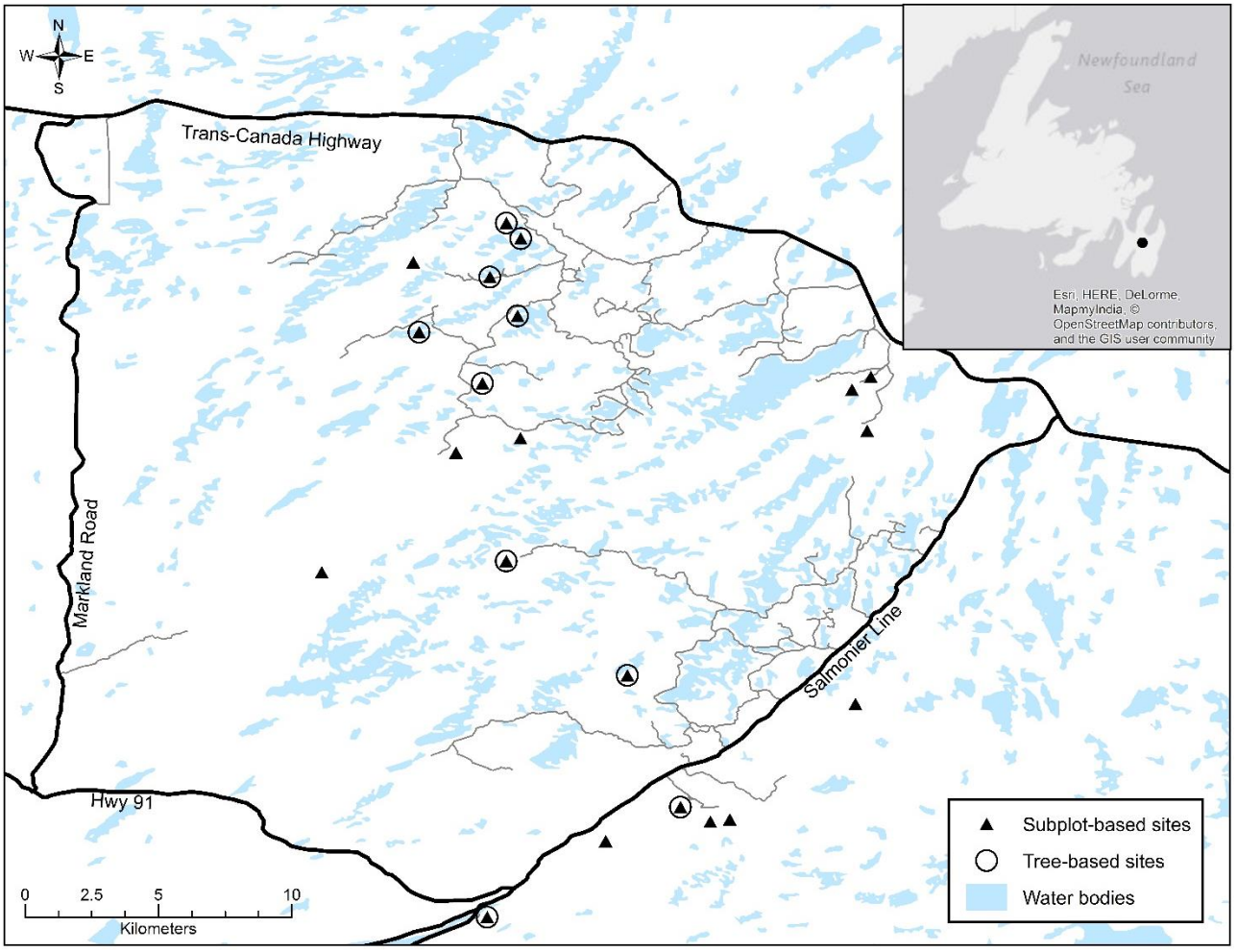

Figure 3-1. Location of sites in the AFE from both the original subplot-based surveys and tree-based surveys. Inset map: an closed circle marking the location of the AFE on the island of Newfoundland, Canada.

The diameter at breast height (DBH) of each tree was recorded. The time spent searching each tree was recorded from the start of the search period until I felt I had exhaustively searched all the microhabitats within this region of the bole. This includes tree knots, scars and any other variation on the bole of the trees (Yarranton 1967; Jeseberger and Sheard 1973). I recorded the name of every lichen species found for both foliose, fruticose and crustose (i.e., macro and micro) growth forms.

Statistical analysis

I calculated subplot-based species richness for the north side of the trees, the south sides, and then both the north and south sides combined per tree. Species rarefaction curves for the north and south lichen species richness were used to visually assess the redundancy of collecting diversity from both sides of the trees. The rarefaction curve was then used to examine whether species richness for the environment was fully saturated. The software program EstimateS (Colwell 2013) was used to estimate the Chao2 value for species richness and to produce and extrapolate the rarefaction curve data to 42 sites for both the subplot-based and tree-based incidence data. Extrapolating beyond double or even triple the original sampling size is not advised as results become less reliable (Colwell et al. 2012).

Subplot richness values for each tree were compared to the new, less restricted, tree-based richness values using a t-test. I used linear regression to assess the relationship between time spent searching and the number of lichen species found. Similarly, time spent searching and the size (DBH) of the trees was compared using regression to examine the relationship between the search area and search time. I used linear regression

to test for an effect of increased species richness on each tree with increased size of survey (cm^2). Similarly, the order in which sites were surveyed was compared to species richness using linear regression to test if there was a relationship between experience gained from searching sites and the number of species found.

3.3 Results

A statistically significant difference in tree-level alpha diversity was detected using the subplot-based versus tree-based methods; species richness was always higher using the tree-based method (Figure 3-2) (t = -8.5393, df = 9, p-value = 1.31e-05). Six species of lichens (*Anisomeridium polypori, Bacidia schweinitzii, Lobaria querzicans, Mycoblastus fucata, Opegraphia varia,* and *Parmeliella parvula*) were only found during the tree-based survey method (Table 3-1). Figure 3-3 and 3-4 show the comparison of the species accumulation curves produced by the analytical formula and simulation by randomizing the samples with EstimateS (Colwell 2013). Using the species richness estimator Chao2 the mean number of species on the north side of the tree was 44 ± 12, and 30 ± 5 for the south sides of the trees (Figure 3-3). An overlap in species richness estimator confidence intervals for the north and south lichen data implies there is no significant difference between north and south incidence data. Using the species richness estimator Chao2, the mean number of species in the original sub-plot survey of 21 sites was 35 ± 4, and 46 ± 10 for the tree-based surveys (Figure 3-4). Time spent exhaustively searching each tree, rounded to the nearest minute, ranged from 16 minutes to 36 minutes, with a mean of 26 ± 7.4 minutes. Species richness for the subplot-based method ranged from 5 to 16 with a mean of 8.6 ± 3.3 species per tree, whereas richness for the

tree-based method ranged from 9 to 24, with a mean of 14.3 ± 4.6 species per tree. The size of the trees examined ranged from a DBH of 16 cm to 34.9 cm, with an average of 26.42 ± 7.3 cm.

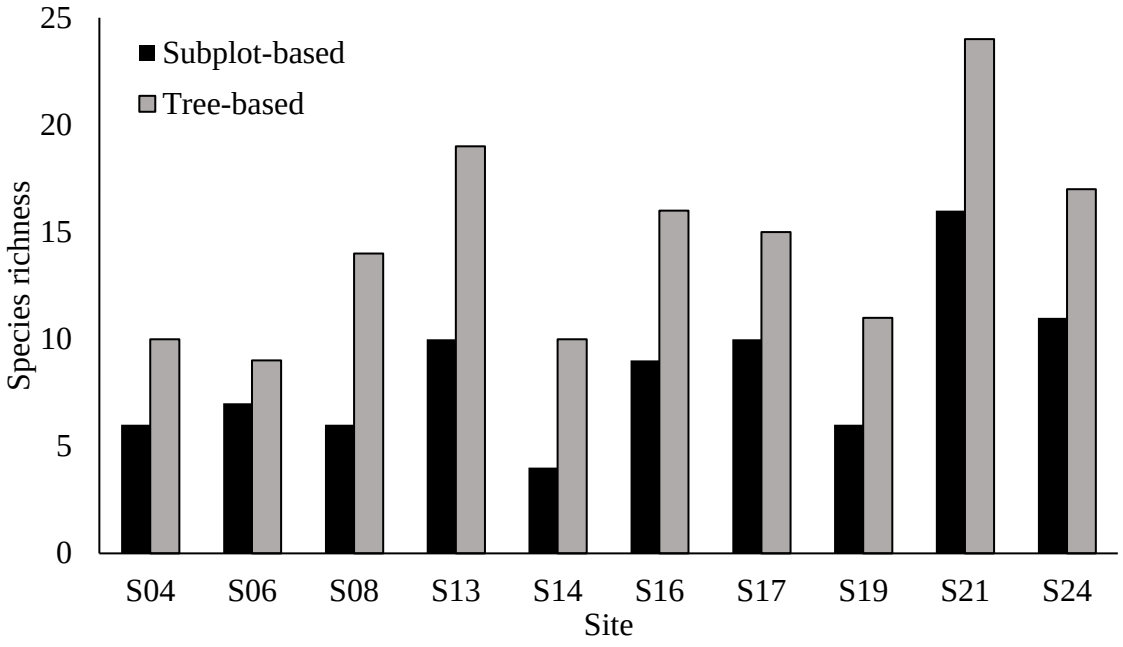

Figure 3-2. Species richness values from the ten yellow birch trees. Subplot richness refers to the original lichen richness values determined using the subplot-based method (i.e., 10 cm x 50 cm plots hung from 160 cm to 110 cm up the bole on both the north and south side). Tree-based richness refers to the number of species found on the bole of each tree from 0.6 m to 2 m.

Table 3-1. Complete list of lichen species found on yellow birch in both surveys.

Species	Total number of trees found on	Number of times found on North only	South only	Both
Alyxoria varia *	-	-	-	-
Anisomeridium polypori *	-	-	-	-
Bacidia schweinitzii	2	1	1	0
Biatora spp.	1	1	0	0
Bryoria spp.	1	0	1	0
Cladonia spp.	10	3	3	4
Felipes leucopellaeus	1	1	0	0
Graphis scripta	5	1	1	3
Hypogymnia incurvoides	1	0	1	0
Hypogymnia physodes	2	1	0	1
Hypogymnia tubulosa	1	0	1	0
Hypogymnia vittata	1	0	0	1
Lecanactis abietina	1	1	0	0
Lecanora spp. *	-	-	-	-
Lepraria spp.	9	0	1	8
Lepra waghornei	1	1	0	0
Leptogium cyanescens	1	1	0	0
Lobaria pulmonaria	3	0	1	2
Lobaria scrobiculata	3	0	1	2
Lobaria querzicans *	-	-	-	-
Lopadium disciforme	1	0	0	1
Loxospora elatina	5	3	2	1
Mycoblastus caesius	6	2	2	2
Mycoblastus fucata *	-	-	-	-
Nephroma laevigatum	1	0	1	0
Ochrolechia spp.	5	0	2	3
Parmelia squarrosa	4	0	3	1
Parmeliella parvula *	-	-	-	-
Pertusaria amara	4	2	1	1
Platismatia glauca	1	0	0	1
Platismatia norvegica	1	0	1	0
Ropalospora viridis *	-	-	-	-
Sphaerophorus globosus	2	0	1	1
Thelotrema lepadinum	10	0	1	9
Usnea spp.	1	0	1	0
Violella fucata	2	1	0	1

*Note: * indicates species that were found only during the tree-based survey*

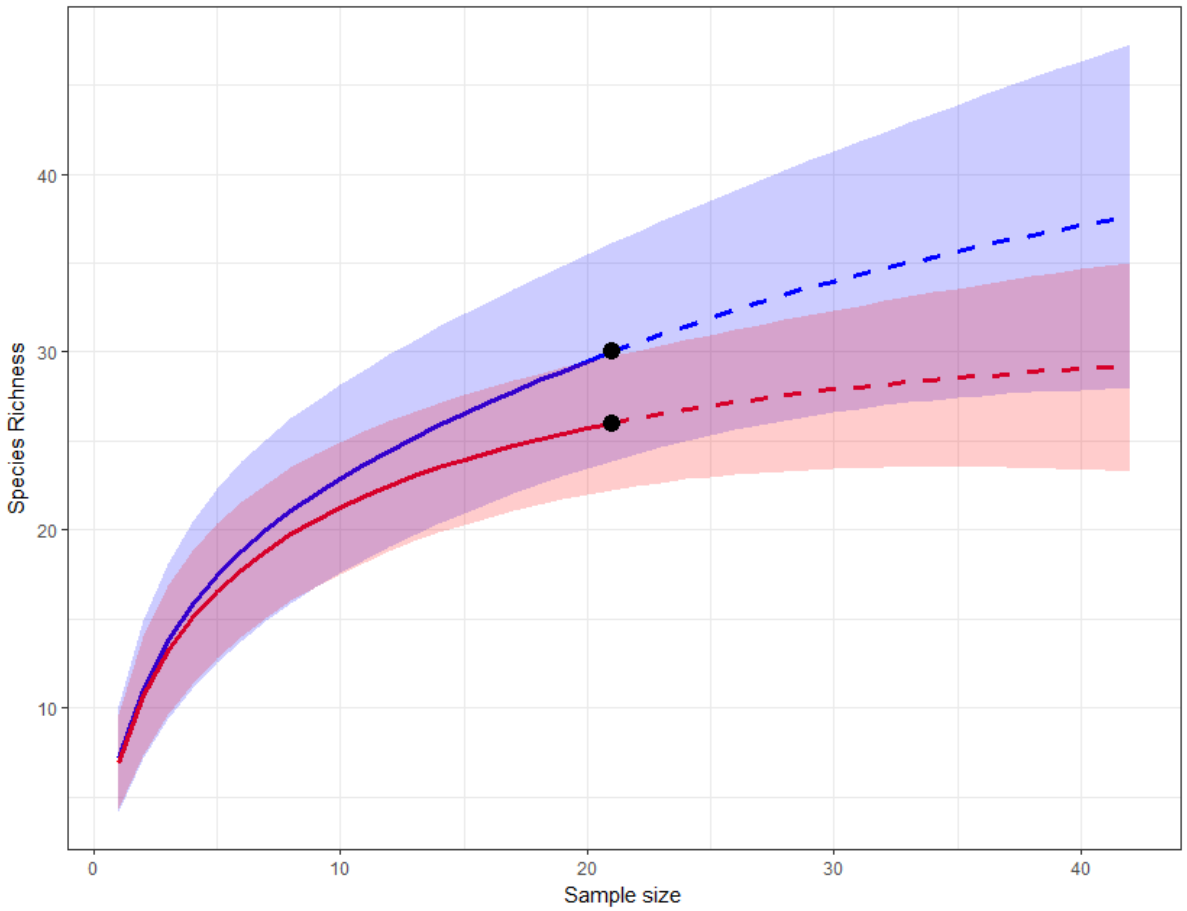

Figure 3-3. Species accumulation curve for subplot-based incidence data for the north side (blue) and south side (red) of all the yellow birch trees. Dotted lines represented data that were extrapolated using EstimateS.

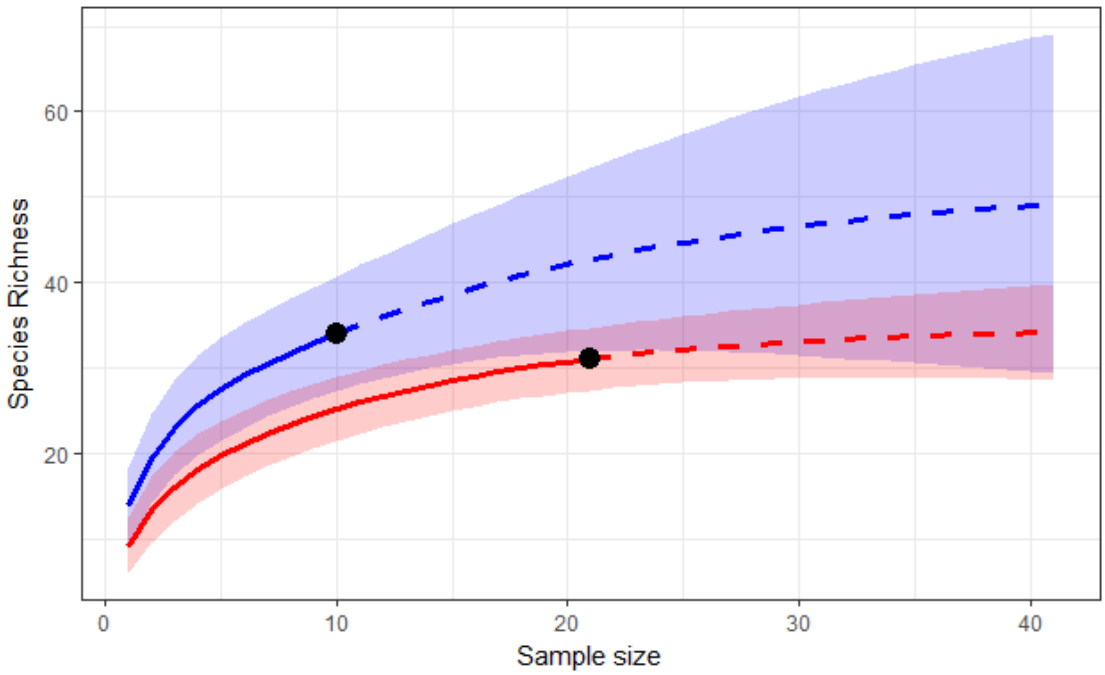

Figure 3-4. Species accumulation curve for subplot-based (red) and tree-based (blue) incidence data. Dotted lines represent data that were extrapolated using EstimateS.

There is a positive relationship between the tree-based species richness and search time (R^2 = 0.5596, df = 8, p-value = 0.007769). There was no relationship between the size (DBH) of the trees and search time (R^2 = -0.09785, df = 8, p-value = 0.6683) or size of the trees and tree-based richness values (R^2 = -0.1246, df = 8, p-value = 0.9597). A general linear model with tree richness as the response variable showed the same results, with an effect of time spent searching (df = 8, p-value = 0.01165) and no relationship with tree size (df = 7, p-value = 0.55896). Species richness-survey area regression lines are shown in Figure B.3 for the combined subplot- and tree-based surveys. There is a significant relationship between the area searched and species richness for each site (Table 3-2). There is no statistically significant relationship between the order in which a site was surveyed and species richness for that site (R^2 = 0.05581, df = 19, p-value = 0.156).

Table 3-2. Regression results between species richness and area of the surveys (cm^2). Visually represented in figure B.3.

Site code	R^2	df	p-value
S04	0.509	1	0.01
S06	0.4737	1	0.02
S08	0.8683	1	< 0.001
S13	0.9047	1	< 0.001
S14	0.7871	1	< 0.001
S16	0.6312	1	0.003
S17	0.8932	1	< 0.001
S19	0.8599	1	< 0.001
S21	0.5682	1	0.007
S24	0.521	1	0.01

3.4 Discussion

There is a difference between the number of lichen species (tree-level alpha diversity) found in the two survey methods used. Not surprisingly, there were more species found during the less restricted tree-based survey, where a larger portion of the tree bole was examined. However, every species was not located during either survey on their own. The species accumulation curves I present have not yet reached an asymptote, which suggests that there is a strong chance I did not find all the lichen species in that environment. I would have needed to double the number of sites sampled in order to reach the estimated species richness using the lichen ladders. This alludes to the complexity of lichen diversity studies, where it is difficult to determine if species richness is fully saturated, or if you have missed species and need further sampling. However, as sample size increased, the number of species captured also increased. Future studies should consider testing sampling methods on a subset of sites using a species richness estimator to predict the number of sites required to reach species saturation. This will aid in selecting an appropriate number of sites, with the acknowledgement that it may be difficult collect a complete species list as increasing sample size may result in a considerable increase to the number of species present.

During similar assessments, researchers often have difficulty reaching the level of species richness saturation that can be seen in other organismal studies in the plateau of a rarefaction curve (Gotelli and Colwell 2001; Newmaster et al. 2005; Affeld et al. 2008). To illustrate, on a sample of *Arthonia leucopella*, I noticed a calicioid, *Chaenothecopsis dibbleandersoniarum*, which was only visible under a microscope. It is an extremely

small and rarely collected non-lichenized, parasitic calicioid fungus traditionally treated with lichens. Although non-lichenized (photobiont absent) it would not have been noticed had I not taken that sample back to the laboratory to examine. There are similar lichenized calicioids that are extremely difficult to locate and identify in the field (Selva 2013, 2014) increasing the chances of missing them during diversity assessments. It is also impossible to determine the difference between some species without examining chemistry. For example, thin layer chromatography is required to distinguish between *Ochrolechia androgyna* and *O. mahluensis*. This can complicate diversity assessments, leading to misidentification and inaccurate diversity measurements, even when a researcher is experienced. Missing species is a concern when using restrictive plots such as lichen ladders. For example, *Lobaria querzicans* was only found during the tree-based surveys, always higher in the tree than where the subplot-based surveys were established. It is a particularly important species to capture as its presence helps indicate the age and integrity of the forest (Hale 1957).

Microclimates that host specific lichen species can be at the scale of vertical zones on a tree. Wiersma and McMullin (2018) noted differences in humidity at different heights on trees in the Avalon forest of Newfoundland. Although the difference was not directly related to the lichen community they examined, it suggests vertical variation is occurring, which has been known to influence lichen communities in other environments (Brodo et al. 2001a; Bässler et al. 2016; Kiebacher et al. 2016). Further up a tree, the crown is known to represent a unique environment, where different levels of moisture, light, wind and seasonal variability in crown structure can lead to the colonization of

different lichen species (Sillett et al. 2000; Kiebacher et al. 2016). For example, *Tuckermanopsis* is a lichen genus often only occurring on the branches of trees (Hilmo et al. 2009). I observed that the species found only during the tree-based surveys were often higher on the tree than the ladder surveys reached. This can perhaps be attributed to runoff from branches, as water dripping from the leafless crown of the deciduous tree would run down the branches first (Brodo et al. 2001a; Bässler et al. 2016). Coupled with closer proximity to sunlight, the pre-crown portion of a tree is unique microhabitat for the colonization of different lichens (Sillett et al. 2000; Bässler et al. 2016). Alternatively, under the exposed roots of some tree species, such as yellow birch, exists another microclimate inhabited by specific lichen species. This low-lying surface contains more moisture and is shaded from environmental effects such as light and wind. I avoided these regions during my study because they are different environments from the bole (Brodo 1973), which I originally measured.

Sampling effort and researcher expertise can alter occurrence data, although the amount of training in order to be considered an expert, or experienced enough to complete a survey, is not always explicitly stated (Kinnunen et al. 2003; Casanovas et al. 2013; Britton et al. 2014; Vondrák et al. 2016; Bowering et al. 2018). Although I felt I had been trained enough to measure the diversity of arboreal lichen in my sites, there is a possibility species were overlooked. Even the experience I gained from the original survey could have increased my chances of finding species during the second survey, as I was more knowledgeable about the lichen species found, and the microhabitats they were found in. Although there was no significant relationship between the species richness and

the order in which a site was surveyed, there appeared to be a positive relationship between these variables. It can be difficult to determine the role that search effort and expertise have on the data gathered, but researchers can prepare an appropriate sampling method using these metrics as a guideline. More experienced individuals are able to identify and count species at a quicker rate, allowing them to increase their sample size. They are also more aware of the microclimates where specific lichens are found, and during whole site surveys they are more likely to reach full species richness saturation. However, these metrics need to be contrasted with the goal of the study to choose an appropriate sampling design.

There was no significant difference between species richness on the north and south sides of the trees during the original survey, leading to redundancy in the dataset. Thus, it would be possible to reduce survey effort per tree by sampling on one side only. I recommend future studies in the Avalon Forest Ecoregion that compare diversity data between trees of variable size measure richness on the north side of the trees, as higher richness was commonly found on the north side of trees in this study. This has the benefit of increasing sample size. However, if a researcher is interested in collecting detailed floristics information, they should examine all sides of a tree. A potential explanation for increased richness on the north side is the effect of sunlight, as in the northern hemisphere the sun shines mainly on the south side of the trees, allowing higher moisture retention on the north side. Aspect has been shown to influence other arboreal species, such as the endangered orchid *Lepanthes eltoroensis* in Yunque National Forest, Puerto Rico (Tremblay and Castro 2009).

A sound sampling design follows a clear definition of the research objective and a proper understanding of the target population (Giordani and Brunialti 2015). The target population is the total group the researcher is sampling. Both subplot-based and tree-based sampling methods can be applied to different situations, and certain environments warrant different approaches to answering the same question. Sampling a larger portion of the tree provided a more complete list of the species as I was able to examine a wider variety of microhabitats. This included different directions (east and west) as well as more imperfections along the bark that offer microtopographic variability for lichen colonization. This approach was appropriate and efficient for measuring lichen species richness on yellow birch tree boles across many sites. However, it would have been more time consuming and less accurate to measure species abundance in this manner due to inconsistencies in the size and shape of trees. For diversity data, a standardized sampling strategy is important to ensure comparable results across sites (Giordani and Brunialti 2015).

Every diversity sampling method has advantages and disadvantages, with trade-offs in repeatability, precision, species capture, and survey effort (Will-Wolf et al. 2004). When choosing a sampling design, researchers must consider the environment, microvariability in the habitat, researcher expertise, search effort, and the need for comparability and repeatability across sites. Outlining goals and objectives clearly in the beginning will provide an appropriate sampling procedure, while acknowledging that it is difficult to find a sampling design that is suitable for each situation.

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4. Summary

Our world is rapidly changing, and the future of many species is uncertain (World Wildlife Fund 2016). In order to maintain biodiversity levels and habitat quality, we must develop a clear understanding of how ecosystems are structured. This involves studying the organisms present, their inter- and intra-specific interactions, and the features in their habitat that influence them. With this information we are able to understand how communities change over time, and the features within a habitat that are important for their survival.

In chapter one, I showed the significance of a range of tree and stand characteristics for arboreal lichen community structure. The abundance and richness of species was related to the tree species they were found on, and the attributes of the stands where the trees were found. For lichens on balsam fir, the attributes of the trees were important. A diverse range of tree characteristics are needed to support a diverse range of lichen species in a conifer-dominated forest such as this. Lichens on yellow birch, however, were more strongly influenced by the attributes of the stands they were found in. This indicates certain stands are more suitable to host a unique community of lichens than others. These results can information and land managers on the Avalon, recommending selective cutting of balsam fir to maintain a diverse community structure and harvest of yellow birch trees in sites that are less optimal for lichen growth. This includes low sloping sites facing north, or sites where balsam fir trees vastly outnumber yellow birch, leading to birch trees with more conifer-like bark characteristics. Several of the sites encountered may be considered less optimal sites for lichen.

Lichen diversity data can be used to help determine the relative importance of the lichens in an ecosystem (Aptroot 2001). When lichen biomass contribution is relatively low, it is assumed that the species has a greater ecological role in that environment (Wessels and Wessels 1991). On the opposite end of the spectrum, extremely complex lichenological communities can have individual thalli or species exploiting niches that are influenced by a range of microenvironmental factors, but their significance in the ecosystem is not as self-evident (Aptroot 2001). For example, a single *Elaeocarpus* tree in Papua New Guinea was found to have more than 175 species of lichens growing on it (Aptroot 2001). Understanding the relative contribution each species has in this environment can be difficult. Whereas, in low lichen diversity environments, such as city centres or regions closer to pollution sources, it is easier to distinguish the role a species may have (Kaffer et al. 2011). For example, photosynthesis in *Parmelia sulcata* has been positively correlated with pollution levels (Von Arb et al. 1990), contributing clean air to polluted environments. Lichens are also known to be passive collectors that incorporate atmospheric pollutants, such as heavy metals, into their diamagnetic matrix over long periods of time (Chaparro et al. 2013), decreasing atmospheric pollution levels.

Lichen diversity data can also be used to gather information about an environment. The presence, or absence, of pollution tolerant or intolerant species and the variability in their abundance levels can provide information on pollution levels (Nimis et al. 1991; Conti and Cecchetti 2001; Degtjarenko et al. 2016; McMullin et al. 2016), forest age and stage of succession (Hedena and Ericson 2000; Hilmo et al. 2009), history of the stand (Jönsson et al. 2011), and health of invertebrate communities (Stubbs 1989; Pettersson et al. 1995; Richardson et al. 2004). For example, communities composed of

single lichen species (monospecific communities), or of a limited number of species, are often indicators of polluted environments (Wessels and Wessels 1991). The most diverse site I found, with 24 species of lichen, was host to *Lecanactis abietina*, and several *Lobaria* spp., indicators of old woodland habitats (Johansson and Gustafsson 2001). Throughout the project, *Lobaria* spp. were only found on large, old yellow birch trees. Large trees are very important to *Lobaria* and other species of lichen (Edman et al. 2008; Boch et al. 2013). Environmental disturbances, such as selection cutting have been shown to strongly affect the abundance, frequency and fertility of *Lobaria* spp. (Edman et al. 2008). The conservation of these old trees in forest management is important for the continuity of arboreal lichen communities (Johansson 2008; Boch et al. 2013).

Similar studies have shown the importance of stand diversity and continuity in supporting diverse arboreal species assemblages (Király and Ódor 2010; McMullin et al. 2010; Boch et al. 2013; Ardelean et al. 2015). A variety of tree species, ages, and variable ground cover species create a range of conditions suitable to host arboreal lichens in that environment (Boch et al. 2013). Changes to the forest, even in small or selective ways, can both positively and negatively affect the abundance and diversity of lichen (Cameron et al. 2013). During my field work, it was not uncommon to find stands almost completely harvested of yellow birch, an important local host for lichen species in this conifer-dominated forest. Arboreal species, including lichens, are among the most sensitive components of the forest biota to habitat change (Király et al. 2013). Here in the boreal, the lichen diversity comprise 8-10% of total biodiversity of the forests in the Avalon Forest Ecoregion (Nash 2008). By opportunistically harvesting the old yellow birch trees, lichen biodiversity on the Avalon is threatened. Understanding the variables

that maintain these communities is important for determining their survival. This information can be used to help identify areas of high conservation concern on the Avalon.

Conservation goals often include maximizing species richness locally and regionally. Species richness, evenness and the difference across sites can be used to describe the conservation value of particular species and their environments (Bock et al. 2007). Without a proper assessment of diversity, we are unable to acknowledge the species that are present or fully understand their importance in ecosystem function. Knowing what species are found in a region, and the best sampling technique to accurately assess them, will benefit future projects that focus on the conservation of lichen communities. In chapter three, I demonstrated how different sampling methods can produce variable results in the same environments. Increasing survey area led to an increase in lichen species richness on the same trees. However, it becomes difficult to compare and contrast between sites when plot size is not the same. Measuring within the lichen ladders was useful for contrasting community diversity to habitat variables to determine what influences the lichen community. I could compare sites more accurately using a consistent plot size. However, if the goal of a study is to gather a complete list of arboreal lichen species, a larger portion of the bole should be surveyed. There may also be instances where information from a whole-tree survey may correlate more strongly with the environmental drivers.

The crown of the tree should also be considered when sampling, as this region is known to host a large diversity and abundance of lichen species (Sillett et al. 2000; Brodo et al. 2001a; Kiebacher et al. 2016). I avoided measuring the crown structure for two

reasons both related to sampling techniques. The first reason is that the majority of the trees examined would have been dangerous to climb and transporting a ladder to these sites to examine the crown was not possible. Climbing the trees or using a ladder are the main methods used to directly measure the lichen diversity in the crown portion of a tree (Kantvilas et al. 1989; McCune and Lesica 1992; McCune et al. 1997b; Esseen and Renhorn 1998; Sillett et al. 2000; Will-Wolf et al. 2004; Esseen 2006; McMullin et al. 2017). Secondly, measuring fallen branches would only give a stochastic representation of the tree crown diversity. It cannot be confidently determined when those branches fell, the tree they fell from, or if they are representative of the crown diversity (McMullin et al. 2017).

When choosing a sampling design, researchers must consider the environment, microvariability in the habitat, researcher expertise, search effort, and the need for comparability and repeatability across sites. A mixed-wood forest with scattered trees will need to be approached differently than a dense, coniferous forest. This is a result of differences in stand structure and composition diversity. Different tree species at different successional stages warrant different methods for lichen diversity assessments. Uniform stands may require less plots per stand as species diversity is limited due to the amount of host variety (Ellis 2012). Whereas, a mixed wood forest provides a diverse range of microhabitats for lichen species to colonize, and a larger variety of species may be found here, indicating that more plots are required per site (McMullin et al. 2010; Király et al. 2013).

In Europe, the European Committee for Standardization (CEN, Comité Européen de Normalization) has developed a standardized sampling protocol for lichen diversity

assessments (EN 16413 2014). It considers the complexity of the survey area and the distribution of trees to be sampled in order to determine which sampling design is appropriate. All of these factors need to be considered in relation to the goals of a study, when determining an appropriate method to measure lichen community diversity.

Ecosystems are shaped by a diverse range of species occupying a large spectrum of ecological niches. The loss of even one species, no matter how miniscule it seems, can have cascading effects for an ecosystem (Paine 1966; MacArthur and Wilson 1967), highlighting the importance of diverse microhabitats and the balance of variables within an ecosystem. Determining the mechanisms driving these communities is important for their management and conservation. In the boreal forest, little is known about the cumulative effects of forest change on species (Venier et al. 2014). Regional studies, such as the present study, can be used to inform management strategies at local and national levels, where other tree species are facing different threats.

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Appendix A

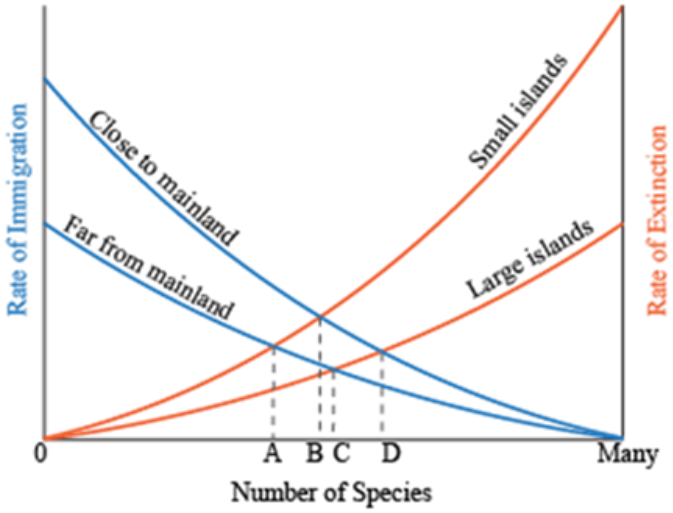

Figure A.1. The island equilibrium model describes the number of species on an island based on the immigration and extinction rates of species on that island. The island will reach equilibrium when extinction rates equal immigration rates. That is the A, B, C, and D in the graph above, which are different depending on size and distance. Taken from MacArthur and Wilson (1967).

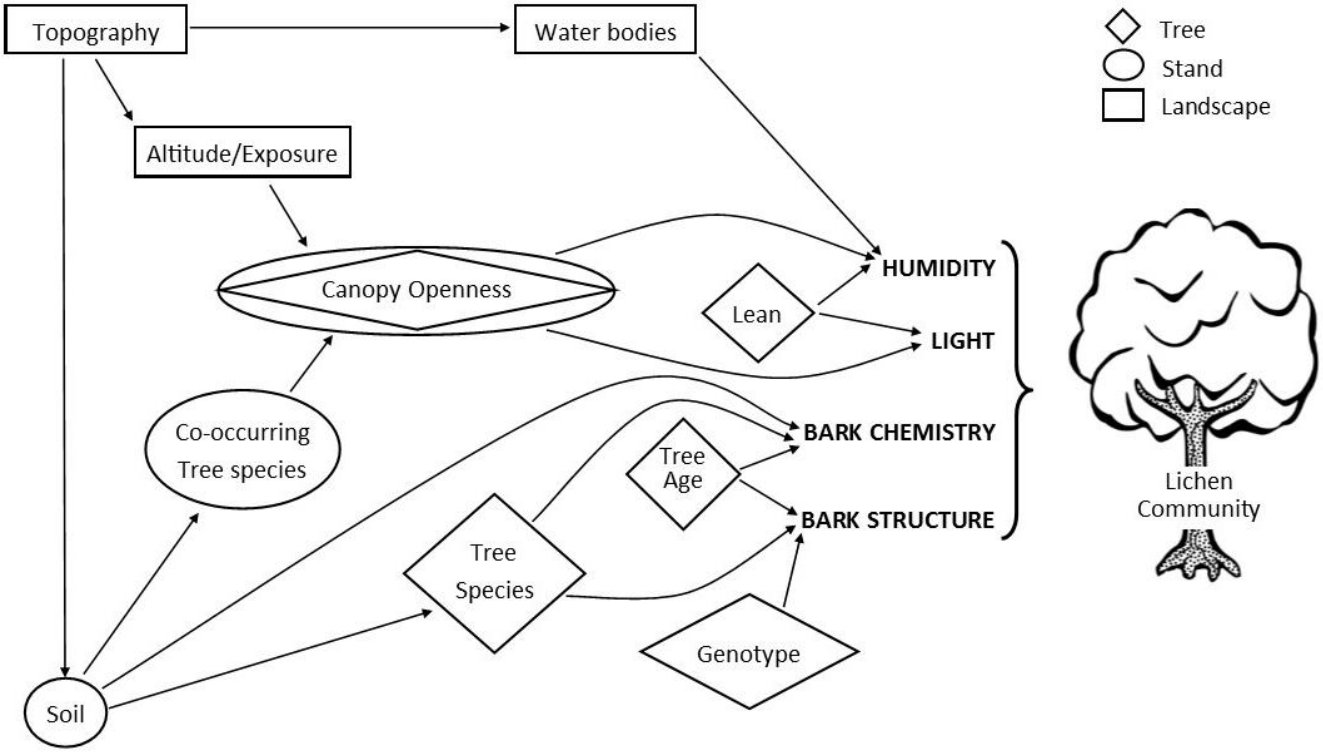

Figure A.2. A broad summary of documented environmental controls on epiphyte community composition, acting across three main scales: tree, stand, and landscape. Adapted, from Ellis, C.J. (2012).

Appendix B

Figure B.1. A lichen ladder, which was used to establish plots in Chapters 2 and 3 to measure arboreal lichen diversity on tree trunks.

Table B.1. List of species found on both balsam fir and yellow birch trees in the Avalon Forest Ecoregion. Species codes are referenced in statistical analyses. Yb and Bf refer to yellow birch and balsam fir respectively.

Species	Code	Found on	
		Yb	Bf
Alyxoria varia (Pers.) Ertz & Tehler	O_vari		x
Bacidia schweinitzii (Fr. ex Tuck.) A. Schneider	B_schw	x	x
Biatora spp. Fr.	Bi_spp	x	x
Bryoria spp. Brodo & D. Hawksw.	Br_spp	x	x
Buellia erubescens Arnold	B_erub		x
Cladonia spp. P. Browne	Cl_spp	x	x
Coccocarpia palmicola (Sprengel) Arv. & D. J. Galloway	C_palm	x	
Felipes leucopellaeus (Ach.) Frisch & G. Thor	A_leuc	x	x
Graphis scripta (L.) Ach.	G_scri	x	x
Hypogymnia incurvoides Rass. (McCune et al. 2006)	H_incu	x	x
Hypogymnia physodes (L.) Nyl.	H_phys	x	x
Hypogymnia tubulosa (Schaerer) Hav.	H_tubu	x	x
Hypogymnia vittata (Ach.) Parrique	H_vitt	x	
Lecanactis abietina (Ach.) Körber	L_abie	x	
Lecidea albofuscescens Nyl.	L_albo		x
Lepraria spp. Ach.	Le_spp	x	x
Lepra amara (Ach.) Hafellner	P_amar	x	x
Lepra waghornei (Hult.) Lendemer & R.C.Harris	V_wagh	x	
Leptogium cyanescens (Rabenh.) Körber	L_cyan	x	
Lobaria pulmonaria (L.) Hoffm.	L_pulm	x	
Lobaria scrobiculata (Scop.) DC.	L_scro	x	
Lopadium disciforme (Flotow) Kullhem	L_disc	x	x
Loxospora spp. A. Massal.	Lo_spp	x	x
Mycoblastus caesius (Coppins & P. James) Tønsberg	M_caes	x	x
Mycoblastus sanguinarioides Kantvilas (Spribille et al. 2011b)	M_sang		x
Nephroma laevigatum Ach.	N_laev	x	
Ochrolechia spp. A. Massal.	Oc_spp	x	x
Parmelia squarrosa Hale	P_squa	x	x
Parmeliella parvula P. M. Jørg.	P_parv		x
Pertusaria macounii (I. M. Lamb) Dibben	P_maco	x	x
Platismatia glauca (L.) W. L. Culb. & C. F. Culb.	P_glau	x	x
Platismatia norvegica (Lynge) W. L. Culb. & C. F. Culb.	P_norv	x	x
Sphaerophorus globosus (Hudson) Vainio	S_glob	x	x
Thelotrema lepadinum (Ach.) Ach.	T_lepa	x	x
Usnic acid containing fruticose spp.	Us_spp	x	x
Violella fucata (Stirton) T. Sprib.	V_fuca	x	

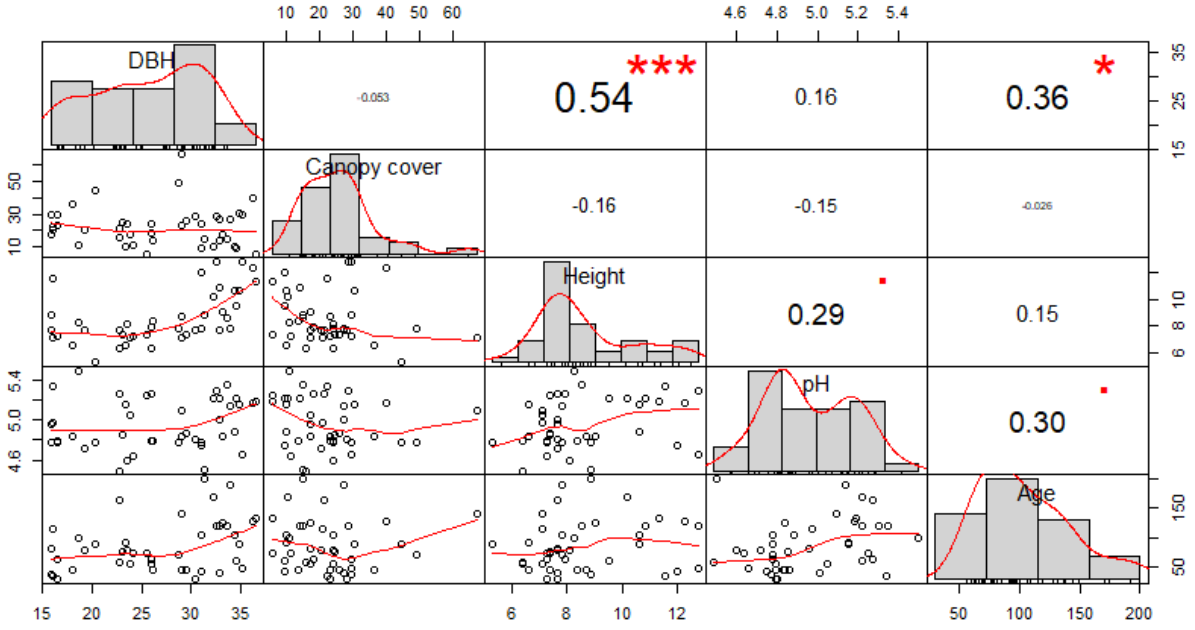

Figure B.2. a) Correlations between tree-level continuous explanatory variables for both balsam fir and yellow birch. Red asterisks and large font size indicate stronger correlation between variables.

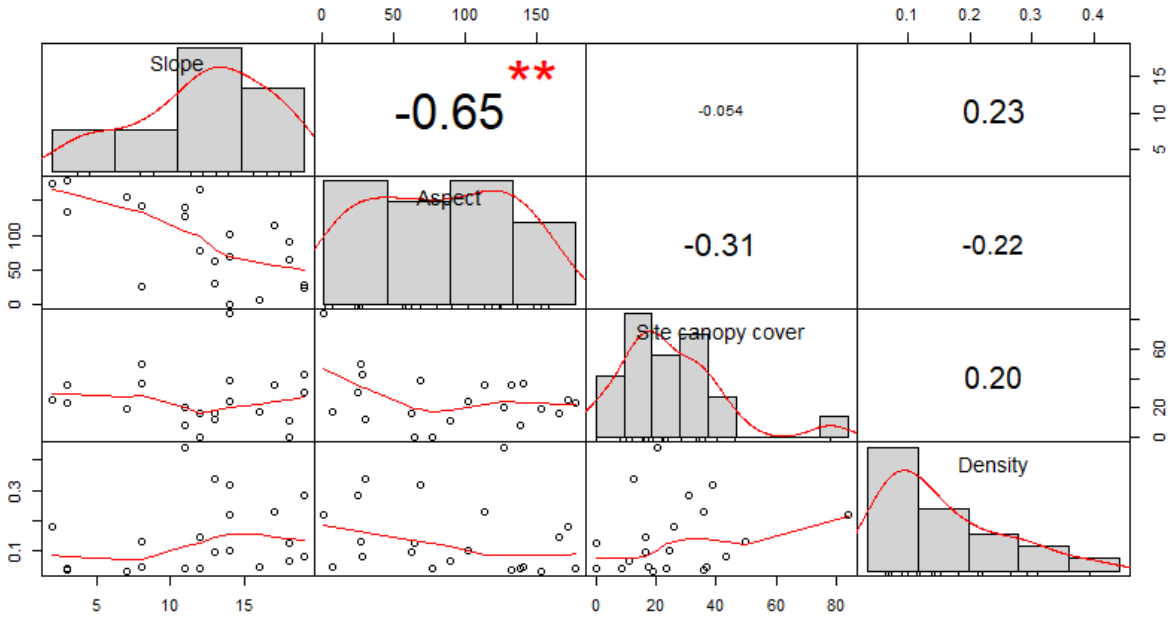

Figure B.2. b) Correlations between site-level continuous explanatory variables. Red asterisks and large font size indicate stronger correlation between variables.

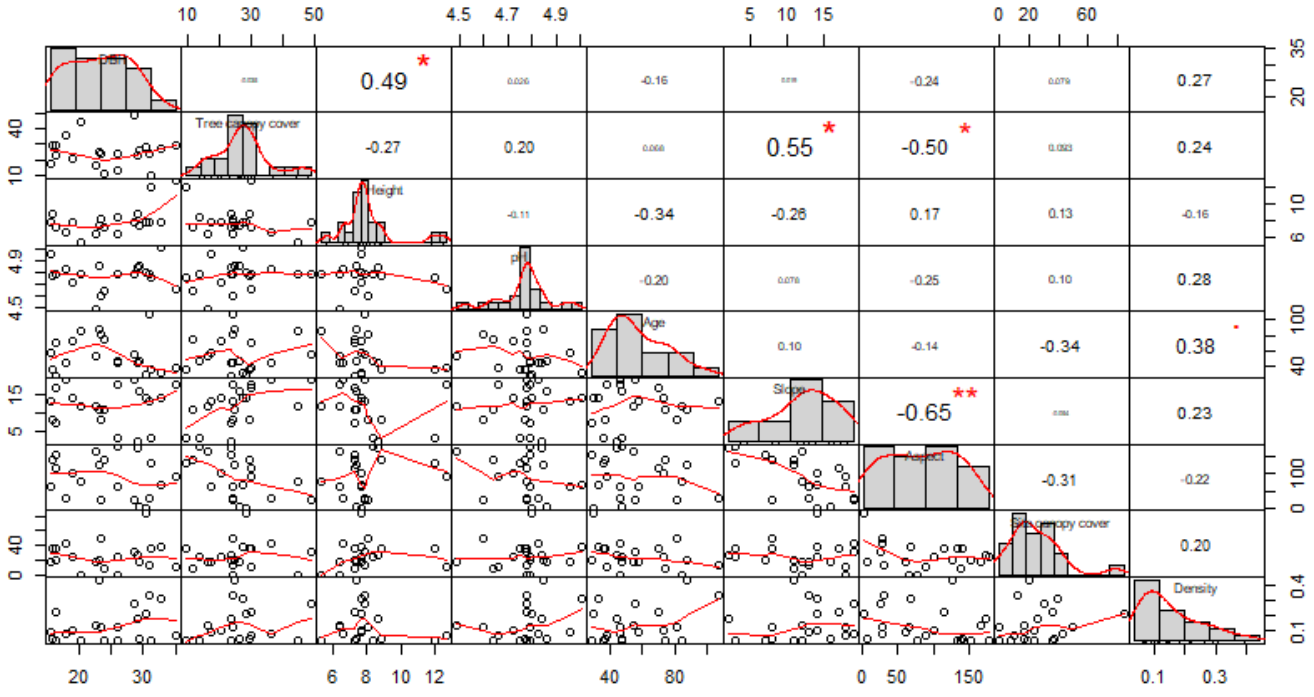

Figure B.2. c) Correlations between tree-level and site-level continuous explanatory variables for balsam fir. Red asterisks and large font size indicate stronger correlation between variables.

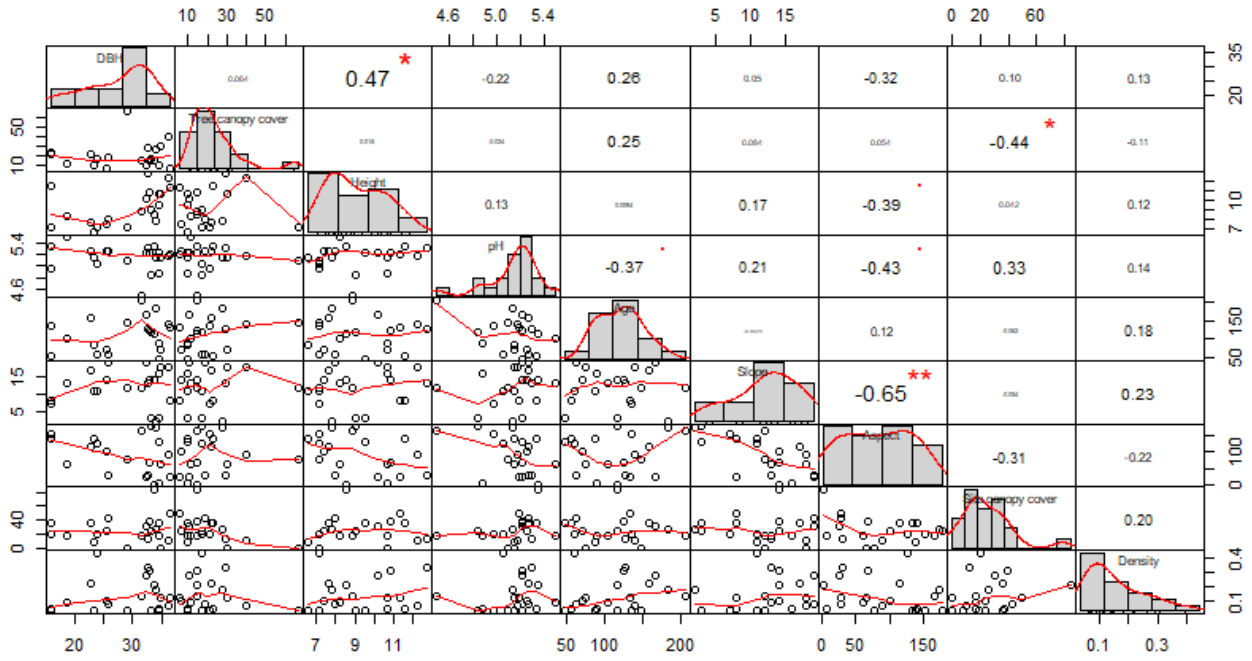

Figure B.2. d) Correlations between tree-level and site-level continuous explanatory variables for yellow. Red asterisks and large font size indicate stronger correlation between variables.

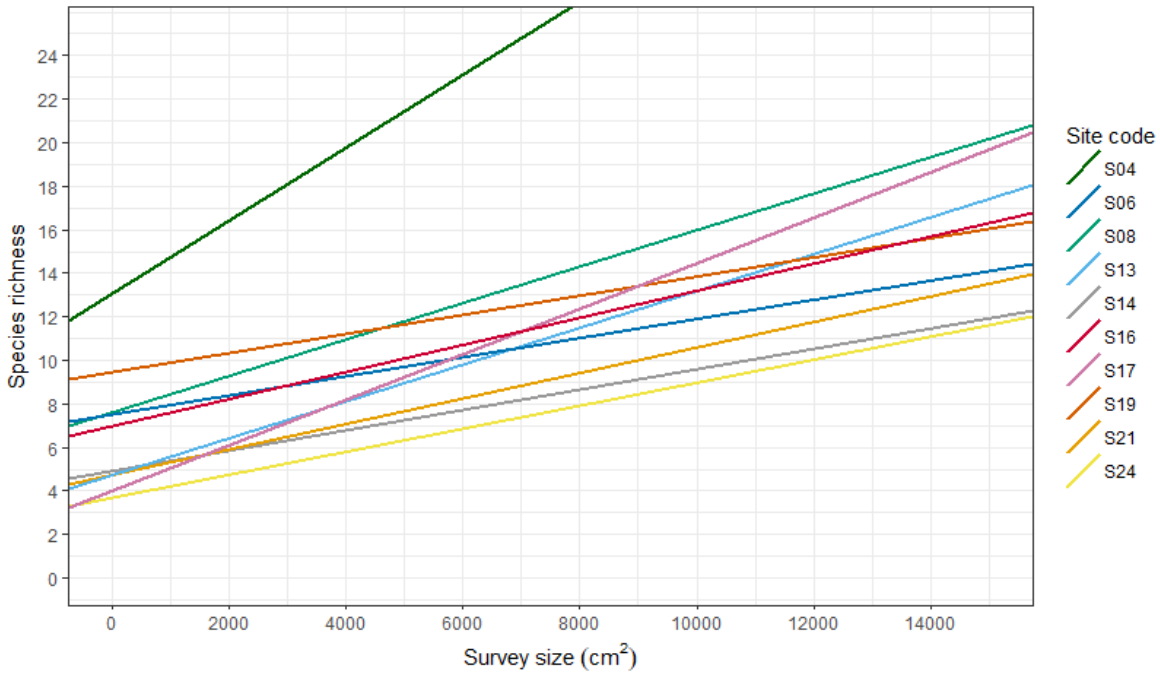

Figure B.3. Regression lines between species richness and area sampled (cm^2) in the 10 study sites. Each regression is based on 11 points of data from each site, 10 for the subplots and one for the tree-based richness values. The corresponding table shows the results of the regressions.