An effective detection strategy and determining critical habitat characteristics for Boreal Felt Lichen (*Erioderma pedicellatum*) in Newfoundland, Canada

By

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Abstract

Boreal felt lichen (*Erioderma pedicellatum*) is a rare lichen that is listed as critically endangered by the IUCN. On the island of Newfoundland, Canada, the Central Avalon Forest Ecoregion is a hotspot for this species. The population in this region is relatively abundant, providing an opportunity to study its habitat requirements. I used occupied and unoccupied plots (each 5 m radius) to test critical habitat for boreal felt lichen. To ensure I effectively detected lichens in our plots, I developed a decoy lichen experiment to test the detection probability of these lichens. I applied the results from the decoy experiment to the habitat study. Although I could not consider time in the study, I discussed how the shortened lifespan of the host tree may constrain the temporal niche of boreal felt lichen. I identified critical habitat for boreal felt lichen, which will contribute to informed land use to help protect this population.

Acknowledgments

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1 Introduction and Overview

Cyanolichens are a group of lichens that are often rare on the landscape and are rather sensitive to various threats. Although they can be locally abundant, their rarity at larger extents is documented (Allen & Lendemer 2016, Scheidegger 2003). These lichens are often used as indicators of habitat quality, due to their specificity of habitat requirements (Juriado et al. 2017). When considering the conservation of rare lichen species, it is important to determine what these habitat requirements are and thus define “critical habitat” for use in setting aside lands to protect, or which lands should be explored for new occurrences (Pearson et al. 2018). This study is carried out in the Avalon Forest Ecoregion, which is a hotspot for many rare lichens (McMullin & Arsenault 2019). In the Avalon Forest Ecoregion, boreal felt lichen (*Erioderma pedicellatum* (Hue) P.M. Jørg) is locally abundant. This provides the opportunity for a robust quantitative habitat analysis that is otherwise impossible for species that are locally infrequent. Since this lichen is listed as critically endangered on the IUCN Redlist (Scheidegger 2003), it is important for us to better determine its critical habitat to help us understand where we could find new populations in the future.

1.1 Species’ Description

The island of Newfoundland is home to a diverse community of lichen species, with the Avalon Peninsula (easternmost region of the island) being a hotspot for rare lichens. Cyanolichens can be distinguished from other lichens due to the presence of cyanobacteria within the thallus (Rikkinen 2015). Lichens excluded from this group use green algae as their photobiont and contain no cyanobacteria. Tripartite lichens, here included in the cyanolichen group, have green algae and cyanobacteria, with the cyanobacteria housed in structures called cephalodia. The cyanobacteria can fix nitrogen within their heterocysts using the enzyme nitrogenase (Richardson & Cameron 2004). This ability to fix nitrogen is important for the survival of these lichen species. Nitrogenase is sensitive to sulfur dioxide in the air, and therefore cyanolichens are rarely found in environments with significant air pollution (Richardson & Cameron 2004).

In the present study, I will examine the rare species boreal felt lichen (*Erioderma pedicellatum* (Hue) P.M. Jørg). Boreal felt lichen, is listed globally as Critically Endangered on the International Union for Conservation of Nature (IUCN) red list (Scheidegger 2003). The boreal population in Newfoundland is listed as Special Concern (COSEWIC 2014) in the Canadian Species at Risk Act (SARA). Boreal felt lichen is not listed under the US Endangered Species Act. Boreal felt lichen (Figure1.1) is grey when dry, with a white underside that is usually visible as the lobes curl upwards, giving the appearance that the margins are paler (McMullin & Anderson 2014). When wet, the grey thallus becomes bluish-green. Mature boreal felt lichen have reddish-brown apothecia. The apothecia are dispersed throughout the thallus and are between ~1-10mm in diameter.

Figure 1.1. Photograph of boreal felt lichen (*Erioderma pedicellatum*) Credit: P. Lauriault

1.2 Threats to Cyanolichens

Erioderma pedicellatum is declining globally (Scheidegger 2003). The preferred habitat for this species is old-growth forests and deforestation is their main threat causing declines in Canada (Cameron et al. 2013). On the island of Newfoundland, Canada, most known occurrences are found on public Crown land. There is no formal protection of habitat for boreal felt lichen except for a few disjunct sites found on Nature Conservancy of Canada land, the Avalon Wilderness Reserve, Salmonier Nature Park and possibly within Fitzgerald's Pond Provincial Park. Threats to the species inlude road and cabin development, habitat loss and air pollution. Natural threats include blow down of their host trees and herbivory of host trees by moose (*Alces alces*) and direct herbivory of the lichen by slugs. These are discussed in more detail below.

Road and trail development could have ambiguous impacts on boreal felt lichen habitat as it allows easy access to more remote locations. This would permit the discovery of new individuals since it would be easier for surveyors to access areas that are less explored. However, it could also increase the incidence of illegal logging in remote forests (Wigle 2018). Road and trail development are usually accompanied with cabin development in this region which requires clearing forest to build infrastructure and could lead to further habitat loss. Forest clearing activities create gaps that may expose previous internal forest to high winds, with windstorms projected to increase in the future (Dale et al. 2001). Less direct threats include air pollution. Cyanolichens are very sensitive to air pollution (Richardson & Cameron 2004). In Newfoundland, the air quality is quite clean, but regional point sources of pollution upwind from the study region are the Come by Chance oil refinery and the Long Harbour Nickel Processing Plant. Internal reports relating to the environmental impact of these facilities exist but are not available to the public. These anthropogenic threats to cyanolichens such as boreal felt lichen could put pressure on this population in the future.

Along with the anthropogenic threats to boreal felt lichen, there are also natural pressures involved as well. Moose herbivory is a threat in Newfoundland as they inhibit forest regrowth (Charron & Hermanutz 2016), which includes balsam fir, the host tree species for *E. pedicellatum*. If moose densities decrease, herbivory pressure on balsam fir would decrease and allow trees to reach a size that is favourable for boreal felt lichen colonization. Some natural disturbances such as windstorms (Arsenault et al. 2016), or spruce budworm outbreaks (McCarthy & Weetman 2007) may also affect the populations of lichen (COSEWIC 2014). In some regions where boreal felt lichen occurs, there is evidence that slug herbivory may also be exerting pressure on populations (Clyne et al. 2019). Boreal felt lichen likely have life history strategies to cope with natural disturbances, but their ability to persist with natural and anthropogenic pressures is unknown (Maas & Yetman 2002).

1.3 Avalon Forest Ecoregion Description

The landscape of the Avalon forest ecoregion contains ribbed moraines from glaciation (Meades & Moores 1994, Hattestrand & Kleman 1999). These moraines have forest cover dominated by balsam fir (*Abies balsamea*), but also contain black spruce (*Picea mariana* (Mill.) BSP), yellow birch (*Betula alleghaniensis* Britt.), tamarack (*Larix laricina* (Du Roi) K. Koch) and the occasional white pine (*Pinus strobus* L.) (South

1983). Between moraines is mostly bog with scattered small open bodies of water (Beersing et al. 1992). This landscape is highly heterogeneous, making the forest stand patches relatively small compared to other boreal forest regions.

The climate of this ecoregion is characterized by relatively mild temperatures and high humidity throughout the year (many days of fog). The average daily temperature in this ecoregion is approximately 15°C in the summer months (June-August) and in peak winter months (December-February) the average daily temperature is -2.2°C (Environment Canada 2020). The length of winter weather is highly variable but can extend, conservatively, from November until April. The level of precipitation in this ecoregion is high, with an average annual rainfall of averaging 1350 mm and nearly 200 cm of snow (Beersing et al. 1992). Fog is frequent in this ecoregion, particularly in the summer. These conditions are favorable to supporting a high diversity of lichens (McMullin & Arsenault 2019, McMullin & Wiersma 2017). Having this much rainfall, the high prevalence of bogs between moraines and the relatively low summer temperatures indicate that the water in this system evaporates or drains slowly, causing soil water saturation to be high for extended periods.

1.4 Thesis Objectives

There have been previous studies on boreal felt lichen that have tried to predict suitable habitat for this lichen (Cameron et al 2013; Wiersma & Skinner 2011; Power et al. 2018). These studies mainly focused on larger spatial extents to predict habitat for boreal felt lichen. Since populations are projected to continue declining, there is a need to sharpen our understanding of what exactly critical habitat is for boreal felt lichen. The focus of my research is on more fine scale patterns of boreal felt lichen that would complement these previous, larger scale studies by examining variation otherwise lost at coarser resolutions (Oyana et al. 2014). Improving our understanding of critical habitat is important in making management decisions about which forest stands to protect from harvest or development to help ensure that this lichen population can persist.

To look at finer scale habitat characteristics, I needed to devise a survey protocol to ensure the reliable detection of boreal felt lichen when it is present. This became the objective of Chapter 2, where I used a decoy lichen experiment to test the detectability of cryptic epiphytic lichens, a group of which boreal felt lichen is a part of. Decoy organisms have been used in the past to assess the accuracy of abundance measures as a function of survey method (Bowering et al. 2018; Dennett et al. 2018). The objective in our experiment was to determine the amount of search effort required to detect at least one thallus when they were present, rather than measuring abundances. I used density of lichen within the plot as a treatment, as well as the maximum time spent searching to assess how this affected the rate of false absences. A survey method with a high false absence rate risks under-estimating critical habitat, and also risks making the conclusion that habitat attributes which are in fact suitable for boreal felt lichen, are not.

I used the results from Chapter 2 to set up pairs of occupied-unoccupied plots in the Avalon forest ecoregion to begin testing what constitutes critical habitat. While I was setting up the plot pairs in the Avalon forest ecoregion in 2018, I noted a pattern where boreal felt lichen tends to occur on balsam fir trees that appeared quite unhealthy. This observation inspired Chapter 3, which proposes a conceptual framework for understanding the lichen-fir dynamics. There is some accompanying data exploration that examines how time constrains the window of substrate quality. This lichen is slow growing, which means that the tree condition degrades over this time, creating a natural tension between the lichen and the tree. However, since I only had one field season, I did not have sufficient data to really test these ideas, but I do highlight some important future research needs for boreal felt lichen.

After I established the plots in the Avalon forest ecoregion, I measured habitat variables that could be important predictors to where boreal felt lichen occurs. In Chapter 4, which is the main data chapter in the thesis, I identified habitat characteristics at three different levels: (1) the tree level, where we measured habitat variables pertinent to this level for five trees in each plot, (2) habitat variables constrained within the 5 m plot radius were considered "plot level", (3) some habitat variables that could be important to boreal felt lichen but were often located outside of the plot area were grouped in a beyond plot level. I used three separate response metrics: the presence and absence of boreal felt lichen; their abundance; and the reproductive output of adult thalli, which was quantified by number of apothecia per cm of thallus width. Ranking habitat variables at each level, I highlight the characteristics that constitute critical habitat for boreal felt lichen that can later be applied to predictive habitat modelling and conservation of ecologically important forest stands.

Building an understanding of critical habitat for boreal felt lichen requires a multi-step approach. Before I can determine critical habitat, I needed to delineate areas where the lichen was present and confirm areas that it was not currently occupying. The unoccupied sites provide a reference that allowed for statistical tests of why the lichen occurs in some places but not others. In Chapter 2, I determined the search effort required to detect lichens when they are present, and thus be confident that no detection means they are truly absent. This provided the grounds for an in-depth habitat analysis for Chapter 4, which statistically compares habitat attributes at sites where the lichens are present to where they are absent. Once I established that the lichen was present, I was able to use abundance and reproductive output as proxies for how well the lichen are doing at the various levels as a further inference of what constitutes critical habitat. The habitat characteristics modelled in Chapter 4 are static, and we acknowledge that the habitat of boreal felt lichen is a dynamic system where the habitat quality changes as it progresses through time. In Chapter 3, I conceptualized these habitat dynamics. I included some preliminary data where I attempt to use thallus width and tree health as proxies for the respective time-states of the lichen and the host tree. These variables proved to be an insufficient representation of substrate quality for the lichen as it and the host tree are progressing through their respective life-history stages. However, this paper was intended mainly as a conceptual piece with the aim of provoking thought and inspiring long term-studies where the changes in habitat may be directly observed over time. Overall, through carrying out this thesis research, I succeeded in delineating some habitat characteristics that may constitute critical habitat, and I considered how time might enact changes in the habitat quality at the tree level, despite this research being constrained to a single field season.

1.5 References

Allen, J. L., Lendemer, J. C. 2016. Climate change impacts on endemic, high-elevation lichens in a biodiversity hotspot. *Biodiversity Conservation* 25: 555-568.

Arsenault, A., LeBlanc, R., Earle, E., Brooks, D., Clarke, B., Lavigne, D., Royer, L. 2016. Unravelling the past to manage Newfoundland's forests for the future. *The Forestry Chronicle* 92: 487-502.

Beersing, A. K., Blouin, A., Rogers, A., Ullah, W. 1992. Water resources atlas of Newfoundland. St. John's, Newfoundland.

Bowering, R., Wigle, R., Padgett, T., Adams, B., Cote, D., Wiersma, Y. F. 2018. Searching for rare species: A comparison of Floristic Habitat Sampling and Adaptive Cluster Sampling for detecting and estimating abundance. *Forest Ecology and Management* 407: 1–8.

Cameron R., Goudie I., Richardson D. 2013. Habitat loss exceeds habitat regeneration for an IUCN flagship lichen epiphyte: *Erioderma pedicellatum*. *Canadian Journal of Forest Research* 43: 1075-1080.

Charron L., Hermanutz L. 2016. Prioritizing boreal forest restoration sites based on disturbance regime. *Forest Ecology and Management* 361: 90-98.

Clyne, A. B., Cleavitt, N. L., Fahey, T. J. 2019. Terrestrial gastropod grazing on macrolichens in a northern broadleaf-conifer foreest. *Northeastern Naturalist* 26(2): 261-274.

COSEWIC. 2014. COSEWIC assessment and status report on the boreal felt lichen *Erioderma pedicellatum*, boreal population and Atlantic population, in Canada. *Committee on the Status of Endangered Wildlife in Canada, Ottawa*.

Dale V. H., Joyce L. A., McNulty S., Nelson R. P., Ayres M. P., Flannigan M. D., Hanson P. J., Irland L. C., Lugo A. E., Peterson C. J., et al. 2001. Climate change and forest disturbances. *BioScience* 51: 723-734.

Dennett, J. M., Gould, A. J, Macdonald, S. E., Nielsen, S. E. 2018. Investigating detection success: lessons from trials using decoy rare plants. Plant Ecology 219: 577–589.

Environment Canada. 2020. Canadian climate normal (Holyrood weather station). Retrieved February 3, 2020 from Government of Canada: https://climate.weather.gc.ca/climate_normals/results_1981_2010_e.html?stnID=6658&autofwd=1

Hattestrand, C., Kleman, J. 1999. Ribbed moraine formation. *Quaternary Science Reviews* 18: 43-61. DOI: 10.1016/S0277-3791(97)00094-2

Juriado, I., Kaasalainen, U., Rikkinen, J. 2017. Specialist taxa restricted to threatened habitats contribute significantly to the regional diversity of *Peltigera* (Lecanoromycetes, Ascomycota) in Estonia. *Fungal Ecology* 30: 76-87.

Maass W. F. G., Yetman D. J. 2002. COSEWIC assessment and status on the boreal felt lichen *Erioderma pedicellatum* in Canada. *Committee on the Status of Endangered Wildlife in Canada* Ottawa 1-50.

Meades W. J., Moore L. 1994. Forest site classification manual. A guide to the Damman forest types of Newfoundland 2nd ed. *Forest Resource Development Agreement Report* 003.

McCarthy, J. W., Weetman, G. 2007. Stand structure and development of an insect-mediated boreal forest landscape. *Forest Ecology and Management* 241(1): 101-114.

McMullin T., Anderson F. 2014. Common lichens of northeastern North America: A field guide. *The New York Botanical Garden Press*, Bronx NY, USA.

McMullin, R. T., Arsenault, A. 2019. Lichens and allied fungi of Hall's Gullies: A hotspot for rare and endangered species in Newfoundland, Canada. *Northeastern Naturalist* 26(4): 729-748.

McMullin, R. T., Wiersma, Y. F. 2017. Lichens and allied fungi of Salmonier Nature Park, Newfoundland. *The Journal of the Torrey Botanical Society* 144(3): 357-369.

Oyana, T. J., Johnson, S. J., Wang, G. 2014. Landscape metrics and change analysis of a national wildlife refuge at different spatial resolutions. *International Journal of Remote Sensing* 35(9): 3109-3134.

Pearson, K., Cameron, R., McMullin, T. R. 2018. Habitat associations and distribution model for *Fuscopannaria leucosticta* in Nova Scotia, Canada. *The Lichenologist* 50(4): 487-497.

Power, T. D., Cameron, R. P., Neily, T., Toms, B. 2018. Forest structure and site conditions of boreal felt lichen (*Erioderma pedicellatum*) habitat in Cape Breton, Nova Scotia, Canada. *Botany* 96(7): 449-459.

Richardson D. H. S., Cameron R. P. 2004. Cyanolichens: their response to pollution and possible management strategies for their conservation in northeastern North America. *Northeastern Naturalist* 11(1): 1-22.

Rikkinen J. 2015. Cyanolichens. *Biodiversity Conservation* 24: 973-993

Scheidegger, C. (Lichen Specialist Group) 2003. *Erioderma pedicellatum*. *The IUCN Red List of Threatened Species 2003*: e.T43995A10839336.

South, G. 1983. Biogeography and ecology of the Island of Newfoundland, 1st edition. *Dr. W. Junk Publishers, The Hague*.

Wiersma, Y. F., Skinner, R. 2011. Predictive distribution model for the boreal felt lichen *Erioderma pedicellatum* in Newfoundland, Canada. *Endangered Species Research* 15: 115-127.

Wigle, R. D. 2018. Arboreal lichen community structure and diversity on yellow birch (*Betula alleghaniensis*) and Balsam Fir (*Abies balsamea*) in the Avalon Forest Ecoregion in Newfoundland, Canada. *Master's Thesis, Memorial University of Newfoundland*.

1.6 Coauthorship Statement

This research was supervised by Dr. Yolanda F. Wiersma of Memorial University of Newfoundland. As the primary author, I, Patrick Norman Lauriault was responsible for the greater construction of this thesis that included contributing the most to the study design, all of the data collection and subsequent analyses and the writing for Chapter 2, Chapter 3 and Chapter 4. Dr. Yolanda F. Wiersma contributed to the initial study design for Chapter 2 and set up the trials in field for seeker detections. Dr. Wiersma also contributed significantly to revisions of Chapter 2, titled “Reducing the rate of false absences of cryptic species in inventory and sampling work” that has been published in *The Bryologist*. Citation: Lauriault P., Wiersma Y.F. 2019. Reducing the rate of false absences of cryptic species in inventory and sampling work. *The Bryologist* 122: 578-585. Dr. Wiersma is a co-author on Chapter 3: “Substrate dynamics over time influences the rarity of tree-dwelling cyanolichens” that has been through two review cycles and has been granted the option to resubmit at *The Lichenologist*. Potential citation: Lauriault P., Wiersma Y.F. 2020. Substrate dynamics over time influences the rarity of tree-dwelling cyanolichens. *The Lichenologist*. Chapter 4 of this thesis has been through two review cycles with the option to resubmit at *The Bryologist*. I am the primary author of this chapter, building the experimental design and outlining the statistical approach for characterizing boreal felt lichen habitat. Dr. Yolanda F. Wiersma is a co-author on this chapter, helping refine hypotheses, sampling design, providing guidance in the narrative and assisting with revisions. Potential Citation: Lauriault, P., Wiersma Y.F. 2020.

Identifying critical habitat for boreal felt lichen (*Erioderma pedicellatum*) in Newfoundland, Canada. *The Bryologist*.

2 Reducing the rate of false absences of cryptic species in inventory and sampling work

2.1 Abstract

When doing inventory for cryptic and rare species, it can be difficult to determine with great confidence that a sampled area has no occurrences of the target species. Boreal felt lichen (*Erioderma pedicellatum* (Hue.) P.M.Jørg.) and vole ears lichen (*Erioderma mollissimum* (G.Sampaio) Du Rietz) are two rare species of cyanolichens that have several populations in North America, including Nova Scotia, Newfoundland and Alaska. These lichens occur in small numbers and are difficult to spot with the untrained eye; therefore, they are likely to be overlooked in standard sampling protocols. In this paper, we examined the relationships between detectability and known target species abundance, within the context of different search efforts and surveyor experience of a determined plot size. This was done to help reduce our false absence rates (i.e., an absence of detections indicates an absence of the target lichen species and is not a false absence). On 50 sites, we randomly assigned “decoy lichen” treatments (small pieces of felt that resemble boreal felt lichen) and three seekers with different survey experience and time limits carried out their respective searches for these decoys. Using circular sample plots of 5 m in radius, we determined that 20 minutes is the required search effort to detect at least one rare and cryptic lichen individuals within the plot. We also found that decoy density on a plot had a strong influence on decoy detectability, regardless of seeker experience. Detection reliability was greater for the two seekers with prior cryptic

survey experience compared to the seeker with none. High confidence in the “true absence” rate is useful for comparative studies of optimal and non-optimal habitat, and the methods here are useful to estimate detection rates for other cryptic organisms.

2.2 Introduction

Many statistical approaches compare “used” and “unused” or “available” habitat to understand what abiotic and biotic factors make an area suitable for establishment and persistence of a particular species (e.g., in Resource Selection Functions, see Manly et al. 2002). For plants and sessile animals, rigorous surveys can confirm occupied plots (i.e., the species of interest is present) or unoccupied. However, since the absence of evidence is not evidence of absence, such approaches can be confounded by the complication of finding sites that are considered a false absence, i.e., the plot is a false absence because the species was not detected, but is present (Mackenzie et al. 2003). If unoccupied plots are false absences because the species was present but undetected, resultant analyses of habitat may be compromised. Here, we develop an experimental approach to estimate how much survey effort in a plot is necessary to minimize the probability of reporting false absences of our target species of interest, rare arboreal lichens. This allows us to standardize a search protocol to sufficiently survey the plot and determine with high confidence that our target lichen species is truly absent within the plot.

Our wider research project focuses on two globally rare species, the boreal felt lichen (*Erioderma pedicellatum*) and the vole ears lichen (*E. mollissimum*). Both are small grey to deep-green foliose lichens that specialize on balsam fir (*Abies balsamea*) trees in our region (Avalon Forest Ecoregion, Newfoundland, Canada). *Erioderma* *pedicellatum* is IUCN Red-Listed, and within Canada, the population we study is listed by the Federal Committee on the Status of Endangered Wildlife in Canada (COSEWIC) as “Special Concern” (COSEWIC 2014). *Erioderma mollissimum* is listed as “Endangered” by COSEWIC (COSEWIC 2009). Within our region, both species have been the focus of numerous surveys (summarized in Bowering et al. 2018) and one attempt to predict habitat for *E. pedicellatum* only (Wiersma & Skinner 2011). Due to their cryptic coloration, small size and rarity, they are overlooked in surveys. To develop more rigorous models to predict suitable habitat, data comparing *Erioderma* occupied and *Erioderma* unoccupied plots are required. For these data to be reliable for modeling, we need to develop and experimentally test a sampling protocol to provide a high degree of confidence that unoccupied plots are true absences (MacKenzie & Royle 2005).

There are a number of variables that may influence detectability of epiphytic lichens to consider when conducting surveys. The thallus density within a plot may influence the detectability of arboreal lichens (specifically those dwelling on the trunks of trees). The probability of finding lichens increases as the thallus density increases, regardless of the survey method (McCarthy et al. 2013; Miller et al. 2017). Tree density also influences detectability; search effort needs to be increased in sites with higher tree density simply because there is more surface area within a given space that could have lichens. Our goal is to determine a standardized time of search effort required to sample the plot regardless of differences in tree density or thallus density. Light exposure (time of day) and water saturation are other factors that could influence the detection of lichens. Many lichens change appearance when wet vs. dry. For example, when *E. pedicellatum* becomes saturated, its color changes from a grey to a greenish colour, which makes it much more distinctive on the trunk of the tree. The light exposure to the thallus increases visibility simply because it is more difficult to spot cryptic lichens in the shade. A further factor in determining if a plot is truly unoccupied is the surveyor's experience (Bornand et al. 2014). Studies have shown a high degree of inter-seeker variability based on the surveyor's experience (Britton et al. 2014). Time spent searching will change detection reliability; the longer a surveyor spends time in a given area, the higher the likelihood of detecting an individual if it is present.

Our experimental approach makes use of "decoy lichens," an approach that has been used previously to determine the proportion of lichens detected vs. how many lichens are present on the site (Bowering et al. 2018). This approach requires a hider to place artificial lichens on trees in the study plot that the seeker(s) later survey. In this study, we are not testing abundance accuracy measurements of the seeker; rather we use decoy lichens to determine the search effort required to confirm true absence at a plot (or conversely, to detect the presence of at least one decoy in the plot). The advantage of using decoy lichens is that the hider knows the true abundance/presence and allows us to measure false absence rates. A false absence is a survey where the seeker records no decoys detected on the plot when, in fact, there are decoys present. Reporting false absences is a common challenge when surveying for rare species (Mackenzie & Royle 2005). Here our main objective is to establish a minimum search time required to reduce the occurrence of false absences.

In this field experiment, we test how detecting decoys is affected by three variables: 1) search time; 2) thallus density; and 3) seeker experience. Increased search time is expected to increase the probability of detecting a cryptic species. However, as surveying is a costly and time-consuming activity, it is important to determine the minimum required search effort to ensure lichen detection. Increased thallus density (in this case manipulated with an increased number of decoy lichens) is expected to increase the chance of detecting at least one individual (i.e., minimize false absence rate). Because time and experience can improve detection, we also expect that more experienced seekers will have a lower false absence rate.

2.3 Methods

We established 50 plots across four different sites within the St. John's, Newfoundland area (**Fig. 2.1**). These sites include Pippy Park, in the Three Ponds Barrens area (**Fig. 2.1A**, *n* = 21 plots), Rotary Park off Thorburn Road (**Fig. 2.1B**, *n* = 17 plots), the Memorial University Botanical Gardens (**Fig. 2.1C**, *n* = 4 plots) and Freshwater Bay Pond (**Fig. 2.1D**, *n* = 8 plots) located about 10 minutes south of the city centre. We selected the plots based on tree stand age (older stands preferred), where balsam fir was the dominant species, and lichen density was high. These conditions replicate the habitat found in the Avalon Forest Ecoregion, which is the main lichen "hotspot" for *Erioderma pedicellatum* and *E. mollissimum*. The plots were not distributed evenly across all four sites because of differences in the amount of suitable habitat at each location.

Once the 50 plots were selected and georeferenced, the hider, went to each site and placed decoy lichens at each plot by stapling them to the trees in a manner to mimic their natural setting. The majority of the decoy lichens were placed on living balsam fir trees. However, a few were randomly attached to dead trees or black spruce as *Erioderma* lichens are known to occasionally be found on other species and dead trees.

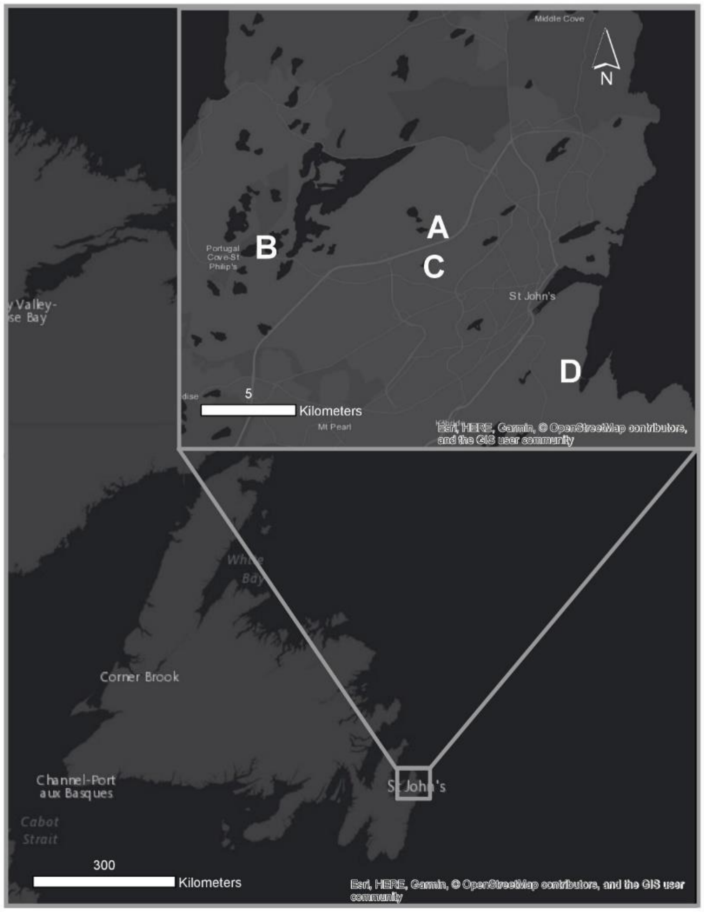

Figure 2.1 The locations of the experimental sites in St. John's, NL, Canada. Site A includes 21 plots at Three Ponds Barrens of Pippy Park, Site B is Rotary Park down Thorburn Road, which contains 17 plots, Site C is the MUN botanical gardens with 4 plots and Site D is Freshwater Bay Pond with 8 plots. There is a total of 50 plots across these four sites.

The decoy lichens are small (~1 cm × 3 cm) pieces of slate blue felt that we cut into ragged ovals (**Fig. 2.2A**). Decoy lichens were hidden following one of ten treatment options, each of which was replicated five times. The treatments included lichen abundances of zero, one, two, three, six, and ten per plot. The plots that had more than one decoy in abundance had separate conditions: either one decoy per tree on a plot or all the decoys placed on a single tree. This was done to prevent pattern recognition and bias of the seekers. We randomly assigned the treatments to each plot using a random number table. Once all experiments were set up, we sent out "seekers" to mimic a lichen survey. The lead author (Seeker C) was the first seeker, and to test for inter-seeker variability, and to determine how many surveyors are required to determine true negatives, we repeated the trials with two additional seekers. Both seekers were briefed in the search protocol by the first author. One of the seekers (Seeker A) had no prior experience searching for rare lichens, while the other (Seeker B) had the same amount of experience as the first author, gained in a field season working in an *Erioderma* hotspot. The hider completed setting up the plots by April 15th and the seekers surveyed the plots opportunistically between April 15 and June 30, 2018.

Figure 2.2. A piece of “decoy lichen” (inside the white circle) stapled to a balsam fir tree as part of a plot treatment, note the visibility of this fabric compared to that of *E. pedicellatum* (B) (Credit: Tegan Padgett) and *E. mollissimum* (C).

Each seeker independently navigated to the waypoint corresponding to the plot centre (which had been flagged by the "hider" and was a randomly chosen tree within five metres of all hidden lichens). The seeker had a 5 m rope tied to the centre tree, which served as a check that trees were in or out of the plot. The seeker then began systematically searching the trunks of all trees within the plot from approximately 50 cm from the base of the trunk to 2 m from the ground and recorded time spent searching with a stopwatch.

The seekers recorded the time of the initial detection, as well as the total number of decoy thalli found and the total search time. The seekers stopped searching when they felt an adequate search of the plot was complete. We implemented a ten-minute cap as we predicted this time to be adequate for surveying a 5 m radius sample plot. One seeker had a 20-minute time limit to provide insight into how differences in search time can influence the successful detection between two seekers of similar experience levels. In one case, the seeker detected lichens in the plot just as they were leaving the plot (i.e., just after the allotted survey time had expired). We counted this as a detection since in a real survey, such an event would have resulted in us classifying that plot as a "present" given that we did spot the target species. To ensure that a thallus was not counted twice, we placed a pin or flagging tape as close to the fabric as possible to show that it was counted. The pins and flagging tape were removed once each seeker completed the search. The seekers were permitted to revisit trees during their timed search if they felt it was necessary. The seekers conducted their surveys at different dates, such that one person only occupied a plot at a time. In addition, we surveyed any trees near or on the plot boundary, as it is important to know if *Erioderma* thalli will be found immediately outside of the plot boundary.

We used logistic regression mixed models (with α threshold = 0.05) to test whether confirmation of the presence of decoy lichens at plots is a function of the lichen density on the plot, with the inclusion of plot as a random effect. The model form used here is $SDa = e^{\mu} + Binomial\ error$. Where $SDa =$ Successful Detection of Decoy Lichen by Seeker A (low experience and a 10-minute time limit) and $\mu = \beta 0 + \beta \mathrm{DD}_{\mathrm{DD}} + \beta \mathrm{RP}_{\mathrm{RP}}$, where β_0 is the intercept and DD is the Decoy Density on the plot, RP is the model term for the random plot effect. This model form is repeated for SDb (Seeker B- high experience, 10-minute time limit) and SDc (Seeker C- high experience, 20-minute time limit). These models were separated by seeker to demonstrate the inter-seeker variability of survey efficacy. The fourth logistic regression model has the form of $SDa = e^{\mu} + Binomial\ error$, where $\mu = \beta 0 + \beta \mathrm{DD}_{\mathrm{DD}} + \beta \mathrm{S}_{\mathrm{S}} + \beta \mathrm{RP}_{\mathrm{RP}}$. In this model, S is for the seeker as a fixed effect. We carried out all modeling in R (version 3.4.1) using the lme4 package: Linear Mixed-Effects Models using ‘Eigen’ and S4 (Bates et al. 2015). A successful detection at a plot is the occurrence where at least one decoy is found at a site where they are present. We also compared the frequency of false absences by seeker to further assess inter-seeker effects.

2.4 Results

Seeker A (low experience/10-minute limit) had nine false absences out of 45 plots with decoys present. Seeker B (high experience/10-minute limit) had five counts of false absences out of 45 plots with decoys. Seeker C (high experience/20-minute limit) had one false absence count out of 45 plots with decoys.

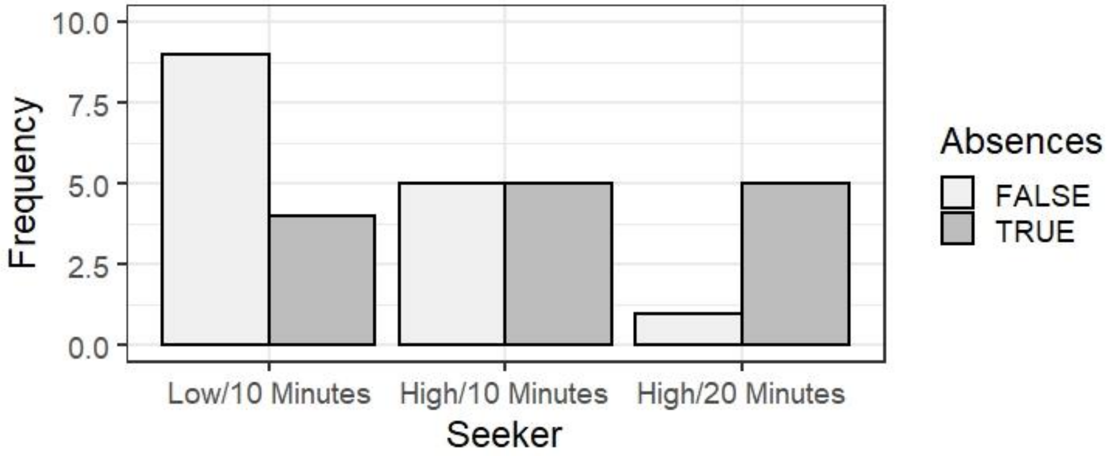

Figure 2.3 The frequency of false absences between an inexperienced seeker and an experienced seeker. It also shows the decrease in frequency of false absences between two experienced seekers where seeker B (middle) had a ten-minute search-time limit and seeker C (right) who had a 20-minute search-time limit. The mean number of thalli missed was 1.67 thalli per plot when a false absence was recorded.

Logistic regression models significantly predicted the relationship between decoy lichen abundance on plots and the successful detection of at least one individual on that plot (**Fig. 2.4**) for all plots where we placed decoy lichens (45 of the 50 plots). The threshold of decoy lichen abundance before a successful detection varied by seeker and was highest for the least experienced seeker, which required a decoy density on the site of at least three to consistently avoid false absences, however the model for seeker A was insignificant (**Fig. 2.4A**, $\beta = 0.92$, SE = 0.52, $p = 0.08$). Seeker B improves on the detection reliability of Seeker A, where they need greater than two decoys on the plot (**Fig 2.4B**, $\beta = 21.70$, SE = 8.10, $p = 0.007$). Seeker C (the most experienced seeker with the most search time) required the lowest decoy density, which was one decoy per plot (**Fig. 2.4C**; $\beta = 2204.40$, SE = 70.39, $p<0.001$). We tested the ability to identify a site as a true presence as a function of number of decoy lichens on a sample plot. Across all three seekers, we found a significant trend of lower detectability with fewer decoy lichens in a plot (**Fig. 2.4D**, $\beta = 8.02$, SE = 3.41, $p = 0.02$). We included a predictive curve derived from these data of all three seekers to show a generalized result of lichen detectability without considering seeker experience or the two search time limits (**Fig. 4D**). When there were at least three lichens in a plot, the successful detection rate was nearly 100%.

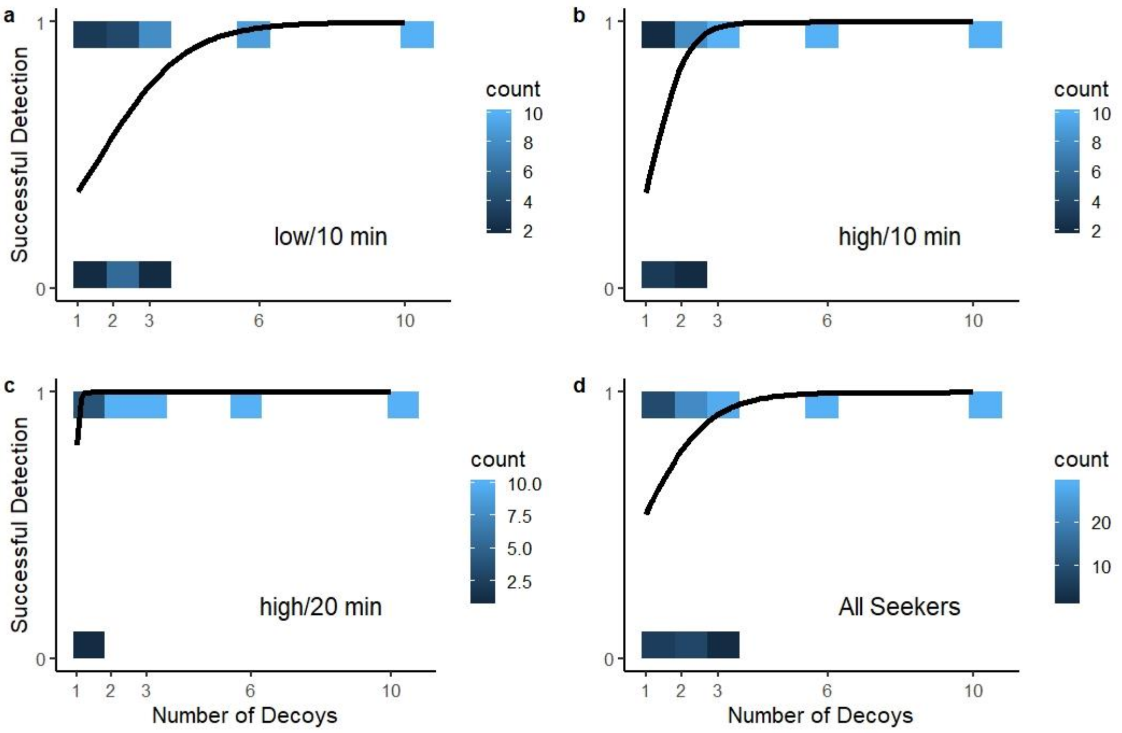

Figure 2.4 Binary logistic regression models for each seeker were made to see how lichen detectability within a plot as a function of thallus density varied among seekers. Seeker A (far left) had the least amount of survey experience. Seeker B and C (middle and right respectively) had equal survey experience for lichens. However, seeker C had a time limit of 20 minutes whereas seeker B had a time limit of ten minutes. A binary logistic regression model is also included (d) showing the likelihood of having a successful detection of decoy lichens on a plot as a function of the total number of thalli hidden within the plot pooled for all three seekers.

2.5 Discussion

Seeker experience has a major impact on the ability to detect decoys. The frequency of false absences is high for Seeker A who began this experiment with no prior lichen survey experience and a ten-minute search time limit. The frequency of false absences falls with a more experienced seeker (B) who has one field season of survey experience. However, even with greater survey experience, ten minutes is not enough time to ensure a lower rate of false absences (five false absences out of 45 occupied plots). Seeker C has equivalent field experience to seeker B but a twice the search time limit. This amount of time drops the frequency of false absences to a low level (one in 45 sample plots, or 0.02 false absence rate; **Fig. 3**). The models we present illustrate that seekers with more experience can detect rare lichens better. The seeker with low experience and a short time limit requires more thalli on a plot to reliably detect plot occupancy (~three decoys for consistent detection, **Fig. 4A**). Reliable detections, as seen in **Fig. 4**, continue to shift towards lower decoy density as we examine the seekers with more experience and search time (**Fig. 4A, B, C**, respectively).

Our findings suggest that 20 minutes of search effort, using small survey plots (5 m radius), allow for more reliable detection of rare lichens than in larger, more conventional study plots (Zhang et al. 2014). The total area of these plots is roughly 78 m^2, which enables the collection of high-resolution habitat data and species abundances within a defined space. The small plots also reduce the amount of search time required to determine if a species is truly absent from the plot, making them a more manageable unit when dealing with presence/absence data. If a more common survey protocol, such as a

~400 m^2 circular plots (Kaufmann et al. 2017; Miller et al. 2018) is applied, at least four times more search time (i.e., 80 minutes) would be required to sample as rigorously as we do, given that the probability of overlooking a tree with the target species remains constant. If we were to scale up our plot size to mimic a survey protocol such as the Forest Inventory Analysis (0.4 hectares; 4000 m^2), the search time required to determine with confidence that no lichen are in the plot would be 17 hours. Spotting a lichen in a plot in the 17th hour would require the surveyor to reject it as an unoccupied plot, find a new location and start the search effort over again. Bowering et al. (2018) found that between 20 and 30 percent of decoys were detected in one hectare plots. Using smaller plots will further improve abundance estimates within the defined space as well as baseline detection rates (Zhang et al. 2014). However, using a 5 m radius plot is inadvisable if the goal is to find the target species that have no historical occurrences in the region of interest. When looking for new populations, it is important to cover large swaths of land rather than focusing on small pockets of forest.

The focus for seekers was to detect the presence of the decoy lichens. Using decoys in defined sample plots has been done before to test abundance estimates for lichens (Bowering et al. 2018) and detecting the presence of vascular plants (Dennett et al. 2018). In previous work done with decoy lichens, Bowering et al. (2018) compare the abundance measures across two sampling protocols: adaptive clustering sampling (Thompson 1990) and floristic habitat sampling (Newmaster et al. 2003). The Bowering et al. (2018) decoy test methods required the seekers to keep searching until they felt they had surveyed all the trees and record the total number of thalli, whereas our experiment made use of a time-limit aimed only at assessing the presence, not abundance of decoys. To ensure proper estimates of abundance, further work is required. The effect of seeker experience on detectability could be better understood by replicating this experiment with more seekers; time and resource limitations did not allow this here. However, future studies that explicitly test survey protocols might improve their experimental design with a broader range of seekers.

A potential critique with using “decoys” (e.g., Dennett et al. 2018) is that decoy plants/lichens might stand out and hence their detectability is unnaturally high. We argue that the grey-blue felt used here (**Fig. 2.2A**), although it mimics the colour of a dry *Erioderma* thallus, is arguably more difficult to detect among real lichens than both *E. pedicellatum* and *E. mollissimum*. Both of these species have light upturned undersides, giving a contrasting margin to the thallus (**Fig. 2.2B**); the apothecia of *E. pedicellatum* are red, and *E. mollissimum* is usually quite sorediate. The visual complexity of these two species would make them easier to detect in the field compared to the fabric once the surveyor has an established search image for them. Thus, our estimates of error are likely conservative compared to the real-world detectability for these two species.

There are some challenges that elapsed between the time of the hider placing the decoy lichens at the plot and the seeker searching the plot that could influence the results. Balsam fir has shallow root systems (Farrar 2009), and the frequency of extreme wind events in this region caused blow down of two trees in two of our plots that contain decoy lichens (at plot 3 and 15). At plot three, a large tree fell directly through the site, making the search for decoy lichens much more challenging. There are also bark dwelling birds (woodpeckers, creepers and nuthatches) and red squirrels present that are capable of picking fabric off trees, although this behavior was not observed directly during this experiment. These stochastic events may have slightly influenced our results by making detectability of decoys more difficult in this experiment. If detecting decoys is more difficult, then our results are even more compelling since we are trying to maximize detectability of cryptic lichens regardless of random events such as windfall and animal interference; all of which impede detection of real lichens.

2.6 Conclusion and Future Recommendations

We found that a search time of 20 minutes yielded, for an experienced seeker, consistent and reliable detection of decoys when they are occupying a plot. At this amount of time spent searching a 5m plot, we have a high level of confidence that failure to detect a rare lichen at a plot means that it contains no lichen. However, if the goal of the survey is to report new species in a forest stand, larger plots are recommended because area coverage is key in these surveys. Searches for rare/cryptic species in other forest types may need to adjust the search time accordingly. However, a simple experiment with decoys such as presented here could be an effective way to estimate the optimal search time.

2.7 Literature Cited

Bates, D., Mächler, M., Bolker, B., Walker, S. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67(1): 1-48.

Bornand, C. N., M. Kery, L. Bueche & M. Fischer. 2014. Hide-and-seek in vegetation: time-to-detection is an efficient design for estimating detectability and occurrence. Methods in Ecology and Evolution 5: 433–442.

Bowering, R., R. Wigle, T. Padgett, B. Adams, D. Cote & Y. F. Wiersma. 2018. Searching for rare species: A comparison of Floristic Habitat Sampling and Adaptive Cluster Sampling for detecting and estimating abundance. Forest Ecology and Management 407: 1–8.

Britton, A. J., R. J. Mitchell, J. M. Potts & D. R. Genney. 2014. Developing monitoring protocols for cost-effective surveillance of lichens. Lichenologist 46: 471–482.

COSEWIC. 2009. COSEWIC assessment and status report on the vole ears *Erioderma mollissimum* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa.

COSEWIC. 2014. COSEWIC assessment and status report on the boreal felt lichen *Erioderma pedicellatum,* boreal population and Atlantic population, in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa.

Dennett, J. M., A. J. Gould, S. E. Macdonald & S. E. Nielsen. 2018. Investigating detection success: lessons from trials using decoy rare plants. Plant Ecology 219: 577–589.

Farrar J. L. 2009. Trees in Canada. Fitzhenry and Whiteside Limited, Markham, Markham, Ontario 84–85.

Kaufmann, S., M. Hauck & C. Leuschner. 2017. Comparing the plant diversity of paired beech primeval and production forests: Management reduces cryptogram, but not vascular plant species richness. Forest Ecology and Management 400: 58–67.

MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson & A. B. Franklin. 2003. Estimating site occupancy, colonization and local extinction when a species is detected imperfectly. Ecology 84: 2200–2207.

Mackenzie, D. I. & J. A. Royle. 2005. Designing occupancy studies: general advice and allocating survey effort. Journal of Applied Ecology 42: 1105–1114.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald & W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies, 2nd edition. Kluwer Academic Publishers, Dordrecht.

McCarthy, M. A., J. L. Moore, W. K. Morris, K. M. Parris, G. E. Garrard, P. A. Vesk, L. Rumpff, K. M. Giljohann, S. Camac, S. S. Bau, T. Friend, B. Harrison & B. Yue. 2013. The influence of abundance on detectability. Oikos 122: 717–726.

Miller, J. E. D., H. T. Root & H. D. Safford. 2018. Altered fire regimes cause long-term lichen diversity losses. Global Change Biology 24: 4909–4918.

Miller, J. E. D., J. Villella, G. Carey, T. Carlberg & H. T. Root. 2017. Canopy distribution and survey detectability of a rare old-growth forest lichen. Forest Ecology and Management 392: 195–201.

Newmaster, S. G., R. J. Belland, A. Arsenault & D. H. Vitt. 2003. Patterns of bryophyte diversity humid coastal and inland cedar-hemlock forests of British Columbia. Environmental Review 11: S159–S185.

Thompson, S. K. 1990. Adaptive Cluster Sampling. Journal of the American Statistical Association 85: 1050–1059.

Wiersma, Y. F. & R. Skinner. 2011. Predictive distribution model for the boreal felt lichen *Erioderma pedicellatum* in Newfoundland, Canada. *Endangered Species Research* 15: 115–127.

Zhang, J., S. E. Nielsen, T. N. Grainger, M. Kohler, T. Chipchar & D. R. Farr. 2014. Sampling plant diversity and rarity at landscape scales: importance of sampling time in species detectability. *PLoS ONE* 9(4): e95334.

3 Substrate dynamics over time influence the rarity of tree-dwelling cyanolichens

3.1 Abstract

Most conservation reports indicate that habitat loss is the primary concern when trying to manage species-at-risk. For epiphytic lichens, their habitat is a living organism that has a limited lifespan itself. When dealing with epiphytic lichens that are rare on the landscape, it is especially important to consider that the substrate is dynamic and living. Here we conceptualize the tension between the (critically endangered) boreal felt lichen (*Erioderma pedicellatum* (Hue) P.M.Jørg) and its host tree species in Newfoundland, balsam fir (*Abies balsamea* (L.) Mill.), as they progress through their respective lifecycles. We did not find a significant pattern between thallus size measurements and categorical tree health conditions ($X^2 = 1.09$, $p = 0.78$). Different response metrics other than thallus width may better capture the pattern of thallus age relative to tree condition. We note a pattern where the number of trees that host mature lichens decrease as tree health condition is rated lower ($X^2 = 19.74$, $p < 0.001$). This trend may indicate the degeneration of habitat quality for these lichens as the lichen-balsam fir life cycle progresses, suggesting that the links between lichen and host life cycles merit further research.

3.2 Introduction

Boreal felt lichen (*Erioderma pedicellatum* (Hue) P.M. Jørg) is a species red-listed by the International Union for Conservation of Nature (IUCN) that occurs in three geographically isolated populations within North America (Scheidegger 2003). One population is in Alaska, USA (Nelson et al. 2009) and two east coast populations are divided into the Atlantic population (Nova Scotia and New Brunswick, Canada) and the boreal population (island of Newfoundland, Canada). The Atlantic population is listed under Schedule 1 of the Canadian Species-at-Risk Act (SARA) as “Endangered”; the boreal population is considerably larger than the Atlantic population and listed as “Special Concern” by SARA (COSEWIC 2014). Despite its listing as Special Concern, Boreal felt lichen is a cryptic species and occurs at low densities even in pristine habitat (Scheidegger 2003). This lichen is often quite small, rarely exceeding 5 cm in width, and has an overall dark colouration that blends in well with the bark of its host tree, which is balsam fir (*Abies balsamea* (L.) Mill.) in this region. The most recent population model predicts a decline over time (Goudie et al. 2011). Here we propose a conceptual framework to explain why boreal felt lichen has consistent population declines and is rare the landscape.

We posit that the micro-habitat of boreal felt lichen has a temporal aspect which plays a large role in restricting the abundance of this species at finer scales (Fig. 3.1). Studies on boreal felt lichen often look at broader scale habitat of the species (Cameron et al. 2013; Wiersma & Skinner 2011). At finer scales, the life cycle of boreal felt lichen is intertwined with the life cycle of the balsam fir, the main substrate for boreal felt lichen in eastern North America (Maass and Yetman 2002). Here we discuss some of the mechanisms that reduce the viability of host trees for boreal felt lichen, including relative lifespans, lichenization requirements and the water stress of host balsam fir.

When considering trees as lichen substrates, they are often suitable for much less time compared to lichens that grow on rocks or ground. Throughout much of its range, balsam fir has an average maximum lifespan of nearly 150 years (Farrar 2009), but in this ecoregion the maximum average lifespan is roughly 70 years (Arsenault et al. 2016). The condition of trees will certainly change over this short lifespan. Within this time frame, boreal felt lichen spores must disperse to the tree and undergo lichenization (Purvis 2010). For lichenization to occur, the spores must land on a balsam fir that also has free-living cyanobacteria in the *Rhizonema* genus (Cornejo et al. 2016). A commonly associated liverwort, *Frullania asagrayna* (Fig. 3.2) provides the substrate *Rhizonema* (Cornejo & Scheidegger 2016). It is suggested that enrichment from a nearby deciduous tree (the “dripzone hypothesis”) is an important factor for conifer-dwelling cyanolichens to establish, but there is uncertainty about the mechanism (Arsenault & Goward 2000; Campbell et al. 2010). The need for spores to land on the right species of tree, which also has the cyanobacterium present in an already-established liverwort, along with the needed enrichment from a nearby deciduous tree, are all limiting factors that likely lend to the overall rarity of this species (Fig. 3.1).

After the boreal felt lichen has established, it faces another set of challenges over time as it reaches reproductive maturity. The average reproductive age of an adult boreal felt lichen is estimated at 30 years (COSEWIC 2014). Although there is variability with this length to reproductive maturity, it is a significant amount of time relative to the lifespan of balsam fir, especially in this region. This creates a temporal tension between the lichen and the host tree. The balsam fir trees on which boreal felt lichen tends to occur are most often near wetlands (Wiersma & Skinner 2011; Power et al. 2018). Though balsam fir is somewhat tolerant of hydric soils, it is susceptible to root-rot when it has roots in chronically saturated soils (Whitney 1995). The susceptibility to rot limits the life span of the tree, yet boreal felt lichen tend to colonize these compromised trees. This tendency likely occurs because wetter environments enable prolonged periods of turgidity for boreal felt lichen, which is beneficial to the lichen as it needs to be water saturated to photosynthesize (Gauslaa 2014). However, the reduced lifespan of the host tree, due to the high soil moisture content, will limit the chance of the lichen colonizing and growing to reproductive maturity. This shrinks the temporal extent of the habitat to a point where the lichen remains rare, sensitive and at risk of further population declines on the landscape.

The above-described life history of the boreal felt lichen means that it must survive a suite of challenges to reach maturity. These challenges are not only to the lichen itself, but rather to its host. Windthrow events can occur at any point during the post-lichenization stage of the lichen-balsam fir lifecycle. Strong windstorms are a common occurrence in the Central Avalon Forest Ecoregion and lead to frequent blowdown events due to the shallow soil and thin roots (likely exacerbated by root rot) of the conifers (Arsenault et al. 2016). The lichen microhabitat is no longer suitable if the host tree is not upright since the habitat conditions change considerably due to exposure. This lichen does not appear to colonize balsam fir recruits. We did not detect boreal felt lichen on balsam fir below 5 cm diameter at breast height (DBH) and other researchers (Wiersma and Skinner 2011) have not found the species on younger trees. This becomes a concern when intensive moose browsing of balsam fir saplings prevents new tree recruitment in the region (Charron & Hermanutz 2017). Moose are currently at atypically high densities in Newfoundland because of the absence of a natural predator (Gosse et al. 2011).

We suspect that micro-habitat dynamics through time greatly restrict the abundance of boreal felt lichen, which is rare even in known hotspots (Scheidegger 2003). Logistical limitations constrained our ability to test the effect of time on niche dynamics for boreal felt lichen. Thus, we have conceptualized how the boreal felt lichen is temporally constrained and we supply some preliminary data to illustrate the concept. We hypothesize that the water level requirements for good quality boreal felt lichen habitat is also a stressor for balsam fir host trees they occupy, thus reducing the chance the lichen will reproduce before its substrate is no longer suitable. We attempt to use lichen size relative to the tree health. We tested this with two different approaches: 1) If boreal felt lichen tend colonize water-stressed trees, we predicted that thallus size (which we use as a proxy for time spent in these conditions) increases as the tree health degrades (a proxy for water stress). Our assumption here that larger lichen thalli have existed longer than smaller thalli. 2) If boreal felt lichen tend to colonize trees that may be water stressed, but still healthy, then we predicted to see more host trees that are healthy. The abundance of host trees will decrease as tree health class transitions from good towards death, this would also indicate that the tree capacity for lichenization is also degrading as tree health decreases.

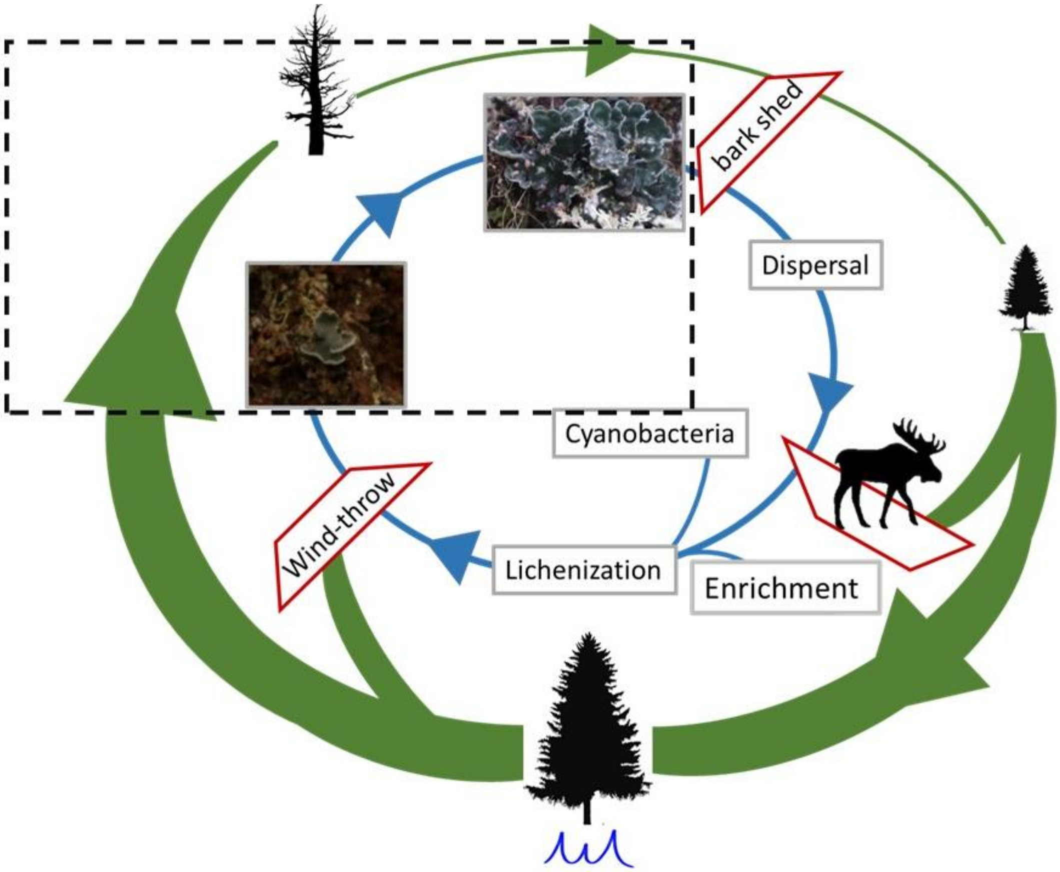

Figure 3.1. Conceptual figure showing micro-habitat dynamics of boreal felt lichen along with host tree species balsam fir. The inner circle represents the life cycle of boreal felt lichen, and the outer circle represents the life cycle of balsam fir, the habitat for the lichen. The trapezoids indicate frequent natural disturbance events that affect the host tree and consequently disrupt the lichen's life cycle. The width of the line on the tree life cycle indicates the relative overall habitat quality for the lichen through time. For the scope of this study, we are considering only the component that falls within the hatched box.

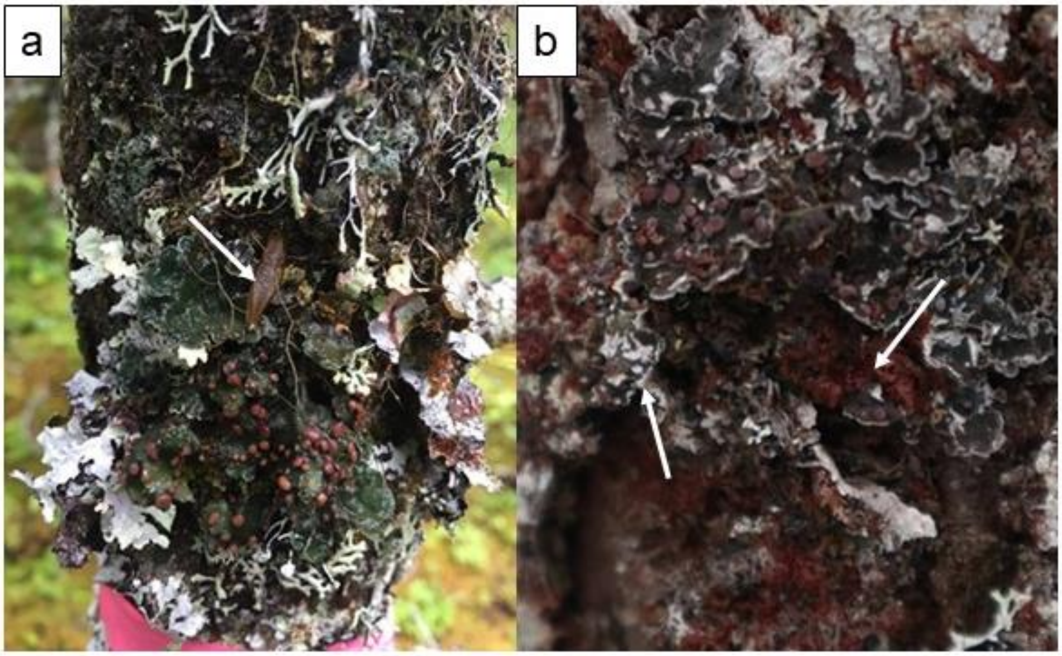

Figure 3.2. Boreal felt lichen (*E. pedicellatum*) found on its host tree, balsam fir (*A. balsamea*). (a) water-saturated boreal felt lichen with the tree slug (*Lehmannia marginata*) found on the thallus (indicated with white arrow). (b) A dry thallus that is closely associated with the *Frullania* (red liverwort indicated by right-hand arrow) and which shows grazing scars from tree slugs (indicated by left-hand arrow). Grazing scars are detectable as the white medulla contrasts with the dark grey upper cortex. Fig. 3.2a Courtesy of B Ronayne

3.3 Methods

We carried out this study in the Central Avalon Forest Ecoregion of Newfoundland, Canada. This ecoregion is found directly in the centre of the Avalon Peninsula, and is characterized by having a post-glacial ribbed moraine landscape structure with intermittent peat bogs. The area immediately surrounding the moraines to the moraine crest is predominantly occupied by balsam fir trees, with spruce, larch, white birch, and yellow birch as occasional species (Meades & Moore 1984). There are patches of old growth balsam fir that appear to have high lichen loads in certain pockets of forest (McMullin & Arsenault 2019). The average annual rainfall here is approximately 1500 mm, but with the high proportion of area covered by bog, and relatively low annual temperatures (~10°C) this water is retained in the soil for extended periods of time. The study area is described in more detail in chapter 1.3 of the thesis.

Surveys for lichens were opportunistic, using an intelligent meandering method (Mueller-Dombois & Ellenberg 1974; Minnesota DNR 2013) between the 15th of May and the 13th September 2018. We selected areas that appeared to be ideal boreal felt lichen habitat in the ecoregion, which consisted of stunted-growth balsam fir stands that are either in close proximity to a wetland, or are found on ground that had flat topography at the bottom of a moraine, thus would be chronically water saturated. Within this area we surveyed the boles of balsam fir trees from the ground to about 2 m up the bole.

When we detected a boreal felt lichen, we took the location coordinates of the host tree, the width of the thallus and categorized tree health. To classify the health of the tree, we adapted Zemaitis & Zemaite's (2017) crown health classes to include 4 categories with their descriptors to improve repeatability. The four categories were: 1) “good” trees have no crown decay; 2) “moderate” trees have signs of compromised health that include crown decay, but it was not clear that mortality was imminent; 3) “Poor” trees have advanced crown decay, sometimes with flaking bark and with tree mortality very likely to occur shortly; and 4) “Dead” trees no longer have any needles and the bark is either loose or partially shed. The most stressed trees will be found in the poorest condition, which is a relative category assignment within the suite of trees sampled; nearly all balsam fir trees found in low lying areas near wetlands appear much less healthy than upland balsam fir trees, which were not considered in this present study.

In our analyses, we used the largest boreal felt lichen thallus on each tree to test the relative growth of lichens vs. tree condition decay. We chose thallus width to see if we can use it as an approximation for time spent on the host tree. We used the Kruskal-Wallis non-parametric test ($\alpha = 0.05$) to test the thallus width in response to tree health. We also tested the number of host trees with at least one mature thallus associated with tree health using a 1-sample chi square test with $\alpha = 0.05$ (R Core Team 2019).

3.4 Results

There was no significant pattern of thallus size in response to tree health decline. The Kruskal-Wallis rank sum test across all four treatment groups found no significance for thallus width in response to tree health (Fig. 3A: $X^2 = 1.09$, $p = 0.78$). The mean thallus width and standard deviations for the largest thalli per tree are as follows: Trees in good (mean thallus width = 3.64 cm, SD = 2.64) and moderate (mean thallus width =

3.53 cm, SD = 1.57) health, and poor (mean thallus width = 3.94 cm, SD = 1.75) to dead (mean thallus width = 3.55 cm, SD = 2.78).We did find a significant difference between the number of trees that host at least one mature thalli at each health group using a 1-sample chi square test (Fig. 3B: $X^2 = 19.74$, $p < 0.001$). As seen in Figure 3.3B, the prevailing pattern is the number of trees hosting at least 1 thallus declines as tree health decreases.

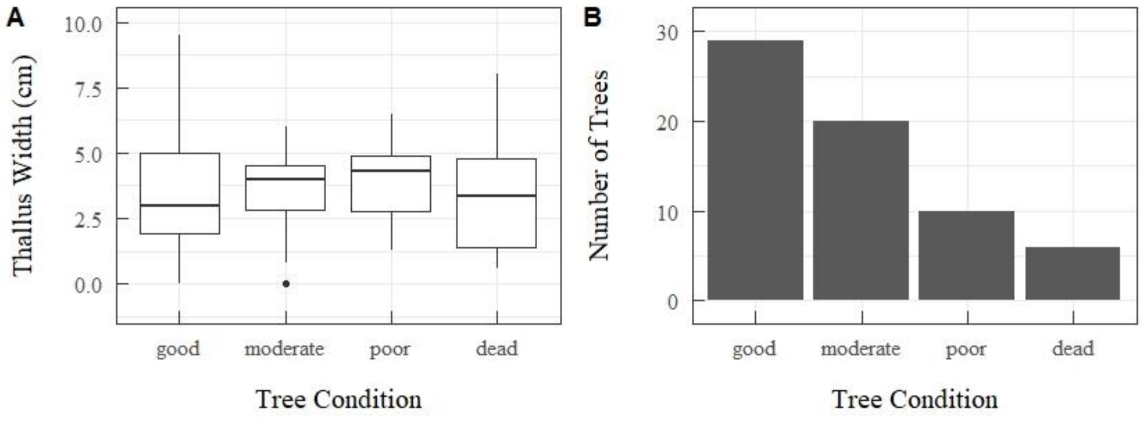

Figure 3.3. Distribution of thallus width of largest lichen per tree (panel A) and number host trees with at least 1 mature thalli (panel B) in response to the condition of the host balsam fir tree. (A) Includes the largest thalli found on each tree only. (B) The number of Trees with at least one mature thallus separated by tree health.

3.5 Discussion

Our data showed no pattern of the thallus width changing relative to tree health. There are two confounding factors when examining these data: 1) *Erioderma* will reach reproductive maturity on average in 30 years after lichenization (Goudie 2009b as cited in COSEWIC 2014). With that considered, the assumed growth rate is ~0.08 mm/year in diameter given that we consistently detect apothecia once a thallus is at least 2.5 cm diameter. If the growth rate is indeed this slow, the statistical signal for thallus size as a function of current tree health is going to be inherently minute and difficult to detect. 2) Lichen colonization is continuous through time, and may occur later in the life of the host tree, regardless of condition. These considerations add significant noise to the data that is not possible to quantify currently. With these considerations, coupled with the results of the study, we suggest that using thallus size as a proxy for time spent on tree is not adequate.

When looking at the number of host trees with one or more mature thalli occupying it, we can see a clear pattern that the number of trees at each tree health category decreases. This could indicate that the relative substrate quality of the tree is decreasing as the tree health declines, however we would suggest a more thorough exploration of these patterns in future studies. The detectability of this lichen across tree health classes are quite similar, and we used a survey method that has been demonstrated to minimize missed detections (Lauriault & Wiersma 2019). Abundance is important in quantifying habitat quality for boreal felt lichen, but the time factor can be confounding as we only have the snapshot of present sampling effort and cannot yet backtrack to date colonization events. Knowing the minimum tree age at which lichens can colonize would be useful but would require careful monitoring of young trees to detect when a lichen appears, along with knowledge of the tree age. However, we never found boreal felt lichen on trees less than 5 cm DBH, suggesting that the species does not colonize trees until they reach a certain age. Work with dendrochronologists might help us better infer what age trees in this ecoregion are when they attain a girth of at least 5 cm. Another recent study successfully aged the host trees and found that the thalli per tree peaked at around 80 years (Tagirdzhanova et al. 2019), which is beyond the maximum age of most balsam fir in our study region. Due to the sensitivity of the habitat in Newfoundland, and the fact that most of these trees are rotten, we were unable to obtain ages of the sampled trees

We quantified tree health groups in this study by visual inspection of the apparent tree crown health, the trees categorized as being in good condition are likely already experiencing rot but do not yet exhibit crown decay. Tree health is a proxy for water stress, and future studies could examine the hydrodynamics of the soil. The rarity of this lichen on the landscape, we suggest, is tightly associated with the micro-habitat conditions required for them to complete their life cycle. We established permanent sampling plots in 2018 and will continue to monitor these in the future for both new thalli and disappearance of existing ones, to provide a high temporal resolution of boreal felt lichen dynamics.

Boreal felt lichen, as well as some other cyanolichens, have a strong preference for growing in very moist environments (Cameron & Richardson 2006). This preference for moist environments creates a natural tension between the lichen and their host tree. Tree species have a tolerance limit of hydric soils before they exhibit some form of a stress response (Rodriguez-Gonzalez et al. 2010). Our study species is boreal felt lichen, but the results seen here may be pertinent to the broad group of rare cyanolichens, as well as any other rare lichen species that require wet environments (which would mean their host tree is likely growing in a waterlogged soil). When lichens grow on the balsam fir in this environment, their habitat has a limited lifespan, and this will affect their ability to persist in the landscape. Generalist lichens that can colonize and grow on a variety of tree species (particularly more long-lived trees) and survive highly variable conditions will have more available habitat than specialist lichens such as boreal felt lichen.

Balsam fir trees are mildly tolerant of hydric soils, but if the soil moisture remains high, then root rot is more likely to take hold (Whitney & MacDonald 1985). Balsam fir becomes more susceptible to windthrow as the decay in the roots reduces the stability of the host tree (Whitney 1995). Windthrow is a significant natural disturbance in the Avalon Forest Ecoregion (Arsenault et al. 2016), and with further monitoring of the frequency of windthrow patterns we would be able to assess the threat to potential host balsam fir trees. Balsam fir that host *Erioderma* are particularly susceptible to rot and windthrow since these trees are normally found near wetlands, which maintain water saturated soils for prolonged periods throughout the years. The trees sampled are all balsam fir that has not yet experienced a windthrow event but could be at future risk. Little work has been done related to wind disturbance in Newfoundland, but other studies have indicated concern of wind throw as a concern for habitat loss in boreal forests

(Peltola et al. 2010; Schlyter et al. 2006). Related to this is the inter-relationship between tree age, tree condition, and proximity to wetland. Trees will naturally senesce as they age, but condition will be confounded by location relative to wetland. Our trees were all located on average within ~15 m of open wetlands, and we noted a general trend of trees closer to wetlands being smaller, and in poorer condition than upland trees (PL, Pers Obvs). Considering these multiple dynamics that affect lichen micro-habitat, a multi-factorial analysis might be required.

Lichens are extremely slow growing, and often need decades to reach reproductive capacity. This time-sensitive tension between the lichen of interest and its substrate will contribute to the susceptibility of lichen to changing conditions. Stochastic events such as blowdown due to windstorms further contribute to the population declines of rare lichens such as the boreal felt lichen. Powerful windstorms are projected to be more frequent due to changing climatic conditions (Dale et al. 2001). More windthrow events, coupled with cyclical disturbances such as spruce budworm outbreaks, would further strain the boreal felt lichen population as its host tree health is further compromised (Solomon et al. 2003). We can think of two potential mechanisms to consider for why we see these patterns: 1) these lichens are extremely moisture loving so will occur on balsam fir in regions that are highly water saturated for long periods over their lifecycle. The limited tolerance of balsam fir for saturated soils, coupled with the moisture requirements of boreal felt lichen, makes it a challenging long-term substrate. Long-term monitoring would be necessary to test this hypothesis; 2) the balsam fir, like most trees, responds chemically to the water stress/root rot related to being stressed from chronic water saturation in soil (Rocha et al. 2018; Kreuzwieser & Rennenberg 2014). The tree response to the water stress may promote its quality as a substrate for lichenization of boreal felt lichen. Many lichens have some level of host specificity, thus there likely are chemical interactions between the tree and lichen that have not yet been found, that promote or inhibit lichenization of certain species. However, this is under-documented in lichen-host tree studies, and such an investigation was beyond the scope of our study. Understanding these relationships between the lichen and its substrate will be important in considering future management practices for endangered lichen species.

Understanding the relationship between lichen and substrate of boreal felt lichen may help us better understand why these lichens are rare on a local, and global scale. The linkage between the life cycle of the lichen and its host tree (Fig. 1) is also relevant framework for other rare epiphytic lichens (Scheidegger & Werth 2009). This tension between the mutualistic counterparts is present in epiphytic lichen-tree relationships but greater in those that have more specific habitat requirements and is important to consider in future management practices for endangered lichens.

3.6 References

Arsenault, A., Goward, T. 2000. The drip zone effect: new insights into the distribution of rare lichens. *Proceedings of Biology and Management of Species and Habitats at Risk* 15-19.

Arsenault, A., LeBlanc, R., Earle, E., Brooks, D., Clarke, B., Lavigne, D., Royer, L. 2016. Unravelling the past to manage Newfoundland's forests for the future. *The Forestry Chronicle* 92: 487-502.

Cameron, R., Goudie, I., Richardson, D. 2013. Habitat loss exceeds habitat regeneration for an IUCN flagship lichen epiphyte: *Erioderma pedicellatum*. *Canadian Journal of Forest Research* 43: 1075-1080.

Cameron, R.P., Neily, T. 2008. Heuristic model for identifying the habitats of *Erioderma pedicellatum* and other rare cyanolichens in Nova Scotia, Canada. *The Bryologist* 111: 650-658.

Cameron, R. P., Richardson, D. H. S. .2006. Occurrence and abundance of epiphytic cyanolichens in protected areas of Nova Scotia, Canada. *Opuscula Philolichenum* 3:5-14.

Campbell J., Bradfield G. E., Prescott C. E., Fredeen A. L. 2010. The influence of overstory *Populus* on epiphytic lichens in subboreal spruce forests of British Columbia. *Canadian Journal of Forest Research*. 40: 143-154.

Charron, L., Hermanutz, L. 2017. Simplicity is key: restoration protocols for nonregenerating forests degraded by overabundant herbivores. *Restoration Ecology* 25(3): 432-441.

Cornejo, C., Nelson, R. P., Stepanchikova, I., Himelbrant, D., Jorgensen, P. M., Scheidegger C. 2016. Contrasting pattern of photobiont diversity in the Atlantic and Pacific populations of *Erioderma pedicellatum* (*Pannariaceae*). *The Lichenologist* 48 (4): 275-291.

Cornejo, C., Scheidegger, C. 2016. Cyanobacterial gardens: the liverwort *Frullania asagrayana* acts as a reservoir of lichen photobionts. *Environmental Microbiology Reports* 8: 352-357.

COSEWIC. 2014. COSEWIC assessment and status report on the boreal felt lichen *Erioderma pedicellatum*, Boreal population and Atlantic population, in Canada. *Committee on the Status of Endangered Wildlife in Canada. Ottawa* p. Xiv-66.

Dale, V. H., Joyce, L. A., McNulty, S., Nelson, R. P., Ayres, M. P., Flannigan, M. D., Hanson, P. J., Irland, L. C., Lugo, A. E., Peterson, C. J., et al. 2001. Climate change and forest disturbances. *BioScience* 51: 723-734

Farrar, J.L. 2009. Trees in Canada. Fitzhenry and Whiteside Limited 84-85.

Gauslaa, Y. 2014. Rain, dew, and humid air as drivers of morphology, function and spatial distribution in epiphytic lichens. *The Lichenologist* 46(1): 1-16.

Gosse, J., Hermanutz, L., McLaren, B., Deering, P., Knight, T. 2011. Degradation of boreal forests by non-native herbivores in Newfoundland's national parks: recommendations for ecosystem restoration. *Natural Areas Journal* 31: 331-339.

Goudie, I. 2009b. Compendium of studies of the boreal felt lichen (*Erioderma pedicellatum*) funded by Vale Inco Newfoundland and Labrador Limited in Eastern Newfoundland, 2005 to 2008. LGL Report No. SA992/SA1003 Supplement. Prepared for Vale Inco Newfoundland and Labrador Limited, St. John's, NL. 7 + appendices.

Goudie, R. I., Scheidegger, C., Hanel, C., Munier, A., Conway, E. .2011. New population models help explain declines in the globally rare boreal felt lichen *Erioderma pedicellatum* in Newfoundland. *Endangered Species Research* 13:181-189.

Kreuzwieser, J., Rennenberg, H. 2014. Molecular and physiological responses of trees to waterlogging stress. *Plant, Cell & Environment* 37(10): 2245-2259.

Lauriault, P., Wiersma, Y. F. 2019. Reducing the rates of false absences of cryptic species in inventory and sampling work. *The Bryologist* 122(4):578-585.

Maass, W. S. G., Yetman, D. 2002. COSEWIC assessment and status report on the boreal felt lichen (*Erioderma pedicellatum*) in Canada. *Committee on the Status of Endangered Wildlife in Canada, Ottawa ON.*

McMullin, R. T., Arsenault, A. 2019. Lichens and allied fungi of Hall's Gullies: A hotspot for rare and endangered species in Newfoundland, Canada. *Northeastern Naturalist* 26(4): 729-748.

Minnesota Department of Natural Resources. 2013. A handbook for collecting vegetation plot data in Minnesota: the relevé method, second ed. Minnesota Biological Survey, Minnesota Natural Heritage and Nongame Research Program, and Ecological Land Classification Program. *Department of Natural Resources, St. Paul, MN Biological Report* 92.

Mueller-Dombois, D., Ellenberg, H. 1974. Aims and methods of vegetation ecology. *John Wiley & Sons, New York.*

Nelson, P., Walton, J., Roland, C. 2009. *Erioderma pedicellatum* (Hue) P. M. Jorg., New to the United States and western North America, discovered in Denali National Park and Preserve and Denali State Park, Alaska. *Evansia* 26:19-23.

Peltola, H., Ikonen, V. P., Gregow, H., Strandman, H., Kilpelainen, A., Venalainen, A., Kellomaki, S. 2010. Impacts of climate change on timber production and regional risks of wind-induced damage to forests in Finland. *Forest Ecology and Management* 260:833-845.

Purvis, W. 2010. Lichens. *The Natural History Museum of London*.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.r-project.org/.

Rocha, G. A., Romanatti, V., Oliveira, F. M., da Cunha Neto, A. R., Pereira F. J., Polo, M. 2018. Ecophysiology of the tree species *Cedrela fissilis* Vell. (Meliacaea) submitted to flooding. *Cerne* 24(4): 323-333.

Rodriguez-Gonzalez, P. M., Stella, J. C., Campelo, F., Ferreira, M. T., Albuquerque, A. 2010. Subsidy or stress? Tree structure growth in wetland forests along hydrological gradient in Southern Europe. *Forest Ecology and Management* **259**: 2015-2025.

Scheidegger, C. (Lichen Specialist Group). 2003. *Erioderma pedicellatum*. The IUCN Red List of Threatened species 2003. e.T43995A10839336. http://dx.doi.org/10.2305/IUCN.UK.2003.RLTS.T43995A10839336.en

Scheidegger, C., Werth, S. 2009. Conservation strategies for lichens: insights from population biology. *Fungal Biology Reviews* 23: 55-66.

Schlyter, P., Stjernquist, I., Barring, L., Jonsson, A. M., Nilsson, C. 2006. Assessment of the impacts of climate change and weather extremes on boreal forests in northern Europe, focusing on Norway spruce. *Climate Research* 31: 75-84.

Solomon, D. S., Zhang, L., Brann, T. B., Larrick, D. S. 2003. Mortality patterns following spruce budworm infestation in unprotected spruce-fir forests in Maine. *Northern Journal of Applied Forestry* 20(4): 148-153.

Tagirdzhanova, G., Stepanchikova, I. S., Himelbrant, D. E., Vyatkina, M. P., Dyomina, A. V., Dirksen, V. G., Scheidegger, C. 2019. Distribution and assessment of the conservation status of *Erioderma pedicellatum* in Asia. *The Lichenologist* 51(6): 575-585.

Wiersma, Y.F., Skinner, R. 2011. Predictive distribution model for the boreal felt lichen *Erioderma pedicellatum* in Newfoundland, Canada. *Endangered Species Research* 15: 115-127.

Whitney, R.D. 1995. Root-rotting fungi in white spruce, black spruce, and balsam fir in northern Ontario. *Canadian Journal of Forest Research* 25:1209-1230.

Whitney, R. D., MacDonald, G. B. 1985. Effects of root rot on the growth of balsam fir. *Canadian Journal of Forest Research* 15: 890-895.

Zemaitis, P., Zemaite, I. 2018. Does butt rot affect the crown condition of Norway spruce trees? *Trees* 32: 489-495.

4 Identifying critical habitat for boreal felt lichen (*Erioderma pedicellatum*) in Newfoundland, Canada

4.1 Abstract

In conservation management, outlining critical habitat is an important factor to consider when making recommendations. Our study adopts a multi-scale approach to determine critical habitat characteristics for boreal felt lichen (*Erioderma pedicellatum* (Hue.) P. M. Jørg.). The boreal felt lichen in the Avalon Forest Ecoregion of Newfoundland nearly exclusively inhabits balsam fir in old-growth forest stands. However, other factors still need to be determined to better understand what constitutes “critical habitat” in this region, i.e., what are the characteristics of the best quality forest stand for boreal felt lichen? We tested multiple working hypotheses at three levels: 1) At the tree-level, we examined tree morphometrics to determine substrate quality within the lichen habitat; 2) At the plot-level we assessed habitat characteristics and variation in landscape characteristics that can be captured within the 5 m plot radius; 3) We also measured habitat variables beyond the 5 m plot radius, these variables included distance from gaps of various types, elevation and distance from deciduous donor trees. In our study site, we compared plot pairs at 25 sites, where one plot contained at least one boreal felt lichen thallus and the other contained none. Our findings suggest that characteristics at each level are important when determining critical boreal felt lichen habitat. The tree-level models indicate that boreal felt lichen is likely to occur on trees with a small diameter (5-12 cm). The plot-level models show that north facing slopes are an important habitat

characteristic. The beyond plot analysis suggests an interaction with distance to deciduous trees, however findings were not consistent with the dripzone hypothesis. The findings of this study will help streamline future survey efforts and guide important criteria in protecting critical habitat.

4.2 Introduction

Sensitive epiphytic lichen species are declining worldwide due to anthropogenic changes to the environment (Rubio-Salcedo et al. 2017). Among these changes, habitat loss is a threat to many epiphytic lichens (Pykälä 2019), particularly timber harvesting (Cameron et al. 2013). Many species of lichens are naturally rare, which increases their vulnerability to threats. In this study, we examine the critical habitat of a rare and sensitive cyanolichen, boreal felt lichen (*Erioderma pedicellatum* (Hue.) P.M. Jørg.).

Boreal felt lichen is a circumboreal species that is listed as “critically endangered” by the International Union for the Conservation of Nature (IUCN). There are three populations in North America, in Alaska (Nelson et al. 2009), Nova Scotia and Newfoundland (Maass 1983). On the island of Newfoundland, there are two sub-populations, in the Bay D’Espoir region and the Central Avalon Forest Ecoregion (Fig. 4.1). The Avalon forest is a small ecoregion, just under 500 km^2, but has a relatively large population of boreal felt lichen. In this region, boreal felt lichen is abundant compared to other regions, where extreme population declines have been reported (COSEWIC 2014). This provides the opportunity to quantitatively test which characteristics may be the most important for “critical habitat”, to help inform future predictive habitat models.

The life history of the boreal felt lichen contributes to its restricted distribution. The reproductive structures (apothecia) disperse only the fungal component of the lichen symbiosis between mycobionts and photobionts. For boreal felt lichen to grow, the fungal spore needs to land on a suitable substrate that contains the cyanobacteria *Rhizonema*, which is associated with common liverwort *Frullania asagrayana* (Cornejo & Scheidegger 2016). It has also been posited that colonization for some cyanolichens on conifers may require calcium enrichment from neighboring deciduous trees (Arsenault & Goward 2000). However, this proposed mechanism between the deciduous trees enriching the coniferous substrate hasn’t been adequately tested for boreal felt lichen, particularly because carbon compounds have also been shown to be important in this process (Campbell et al. 2010).

Past studies on boreal felt lichen have examined population dynamics over time (Goudie et al. 2011) and island-scale habitat predictive models were developed for Newfoundland (Wiersma & Skinner 2011) as well as Nova Scotia (Cameron and Neily 2008). The island-scale habitat suitability model developed by Wiersma and Skinner (2011) has high accuracy for predicting unsuitable habitat but performed poorly when predicting where boreal felt lichen might occur (i.e., critical habitat). The Nova Scotia work (Cameron & Neily 2008; Power et al. 2018) found that boreal felt lichen would be found on more northerly facing slopes (steeper slopes are better) in old growth forests, and that hardwoods are important habitat for some rare lichens. However, it is important to note that the forests in Newfoundland are not directly comparable to Nova Scotia as the climate is different, one notable difference is that the forest is discontinuous and nearly exclusively found on moraines (Chapter 1.3 for NL description). Most spatial models do not include finer-scale variables (i.e., tree level) that would contribute to error rates when not considered. This is the level at which processes that drive lichen colonization occurs and should be considered in habitat analyses.

When examining the critical habitat of boreal felt lichen, multiple levels need to be considered, from microhabitats to landscapes. Having empirical evidence at smaller scale resolutions helps fill the data gaps that are lost at coarser resolutions (Hijmans et al. 2005); the level at which most management activities takes place Critical habitat can be determined based on several indicators: the presence of the lichen, the relative abundance of the lichen (places with more thalli are assumed to be higher quality habitat) and the reproductive output (highest quality habitat is assumed to provide the resources the lichen needs to invest in reproductive structures (spore-bearing apothecia). These indicators would have different sensitivities (abundance in a plot would be more variable than presence or absence in a plot) so there may be a more appropriate metric to use at different scales.

The purpose of our study is to better define critical habitat for boreal felt lichen in the Avalon forest ecoregion. Since Wiersma and Skinner (2011) was better suited at predicting unsuitable habitat for boreal felt lichen at the provincial scale, we propose that determining critical habitat characteristics at stand and tree-level may be more successful. Using an information-theoretic approach, we devised multiple competing hypotheses at each level to test which parameters are most important in determining critical habitat for boreal felt lichen. These hypotheses, along with the underlying mechanisms and our predictions are summarized in Table 4.1. These hypotheses have been grouped by level, but they target three underlying mechanisms: 1) Stability and protection of the microclimate (e.g., Gap distance, canopy closure); 2) topographic features that influence hydrodynamics in soil, and subsequently humidity, water retained at lichen level (e.g., elevation, aspect, slope); and 3) Colonization, tree age, surface area for available habitat (e.g., donor distance, tree density, snag density).

Table 4.1. List of working hypotheses to be used in the AIC(c) analyses grouped by scale. In this table, boreal felt lichen is abbreviated as BFL, the predictions are the direction of habitat suitability (positive: more suitable, negative: less suitable) as the hypothesized factor increases. Suitability will be indicated by presence/absence of BFL, abundance and reproductive output.

Level	Variable name	Mechanism	Prediction	References
Beyond	Gap distance	BFL sensitive, requires forest shelter from extreme wind, solar radiation, polluted air etc.	Positive	Benson & Coxson 2002
Beyond	Donor distance	BFL requires enrichment from nearby donor trees to establish	Negative	Arsenault et al. 2000, Campbell 2010
Beyond	Elevation from bog	Plots that are more elevated relative to wetland will be better drained, less favourable to BFL	Negative	Wiersma & Skinner 2011
Beyond	Elevation sea level	Drainage in lower elevation lands poorer, water retained in soil longer	Negative	Wiersma & Skinner 2011
Plot	Aspect	Northerly facing slopes receive less solar radiation, evaporation is delayed and lichen can photosynthesize longer	Negative (0=N, 180=S)*	Wiersma & Skinner 2011, Cameron et al. 2013
Plot	Slope	steeper angle is more sheltered from sunlight/water remains in system longer (N)	Positive	Cardos et al. 2017, Radies et al. 2009
Plot	Tree density	Higher density trees has more surface area for lichen colonization	Positive	Moroni & Harris 2010
Plot	Snag density	Snags indicate stand age, older sites more likely to have BFL	Positive	Moroni & Harris 2010
Tree	Diameter of tree	Larger trees are older/have more surface area for lichen colonization	Positive	Cameron & Neily 2008

Tree	Canopy closure	Level of light that reaches thallus will increase photosynthetic activity, but also evaporation	Goldilocks**	Benson & Coxson 2002
Tree	Tree height	Taller trees are older, and provide more shelter from sunlight, wind	Positive	Cameron & Neily 2008, Benson & Coxson 2002

*Normalized aspect for 0 being more northerly and 180 being more southerly, so as the plot is located on more southerly slopes (increase in value) then the habitat in the plot is less suitable for BFL.
** Goldilocks here refers to thresholds: Completely closed canopy will not let in enough sunlight for optimal photosynthesis, too much exposure to open canopy will dry out lichen due to higher levels of solar radiation, making conditions too harsh to persist.

4.3 Methods

4.3.1 Study area

The Avalon forest ecoregion is found in the centre of the Avalon peninsula of the island of Newfoundland. It is characterized as having a ribbed moraine landscape structure (Hattestrand & Kleman 1999) and mild summer and winter temperatures (Environment Canada 2020). The forest is dominated by balsam fir, but includes black spruce, white birch, yellow birch and tamarack. Forests are mostly restricted to the raised moraines with areas between moraines being classified as bog wetlands (Beersing et al. 1992).

The boreal felt lichen population is mostly found within a restricted area called Halls Gullies in the Avalon Forest Ecoregion, but we wanted to capture habitat outside of this space as this is where the population would expand to in the future. This reduced our sample size considerably because large proportions of highly aggregated lichen individuals were excluded from the study. However, it provides better spatial coverage of the entire Avalon forest boreal felt lichen population. At each level, we tested our model sets against three different response variables: presence/absence, abundance and the mean reproductive output of adult boreal felt lichen, quantified by number of apothecia per cm thallus width. Adult thalli were categorized by either being greater than 2.5 cm in thallus width or by having apothecia present. Fieldwork was carried out from May 1st 2018 to September 15th 2018.

4.3.2 Data collection

We used circular plots with a 5 m radius to sample habitat characteristics that may be critical features for boreal felt lichen. Plots were paired based on occupancy; one plot had no boreal felt lichen and the other contained at least one thallus. To ensure this criteria, two surveyors searched all trees in each plot for 20 minutes as this is the search effort required to minimize false absence rates for one surveyor (Lauriault & Wiersma 2019/Chapter 2). Plot pairs were positioned proximal (mean 22 m between plot edges) to maintain tree stand similarities, to find small signals in habitat differences. This also reduces the confounding effect of short-range dispersal as a confounding factor for occurrence. If the unoccupied plot is closer to the occupied plot, the assumption of ruling out dispersal distance as the reason for the lichen being absent becomes stronger (Werth et al. 2006), so its absence can be attributed to unsuitable habitat. One plot pair occurred on each moraine sampled, making our sampling less prone to follow the aggregated pockets of the boreal felt lichen population (PL, Pers. Obs.).

Our tree level data was collected using an adaptation of the point-quarter method, constrained to the plot boundaries (Krebs 1989). We sampled five trees per plot for tree morphometrics. The trees selected for data collection were all balsam fir. More information on sampling can be found in Appendix C. In the occupied plots, host trees were preferentially selected when possible, but unoccupied trees were confirmed and measured as well. We measured tree diameter at breast height (1.3m), the height of the tree (using a clinometer) and canopy closure (using a spherical densitometer). We also noted the positional measurements of the lichens on the tree that include height from ground, and the side of the tree they were found on.

The plot level data collection included the slope aspect, which was measured using a handheld compass. We then normalized the data to 0 for north, to 180 for south to fit the data to a linear model. The slope steepness was measured using a clinometer for a degree value. We counted the number of trees and standing snags within plot boundaries to characterize horizontal density. These measurements were carried out on both occupied and unoccupied plots.

Using the paired plot approach, some of the habitat variables measured exceeded the constraints of the plot area, which we grouped into the beyond plot level model set. Variables considered here include the distance to the nearest donor tree, which is a measure from the centre of the plot to the nearest deciduous tree, which was frequently found outside of the plot. The deciduous trees included in our study were mostly white birch (*Betula papyrifera* (Marsh.)), with the occasional yellow birch (*Betula alleghaniensis* (Britt.)), and pin cherry (*Prunus pensylvanica* (L. f.)). We measured distance from gap, while classifying the gap type by three different categories: windthrow, bog, and anthropogenic gap. Other characteristics quantified at the beyond plot level were absolute elevation and relative elevation, which is elevation relative to the elevation of neighbouring wetlands (since the ribbed moraine landscape is highly variable in elevation). Relative elevation was calculated by subtracting the elevation of the nearest wetland to the plot from the absolute elevation of the plot.

We used three different response metrics (presence/absence, abundance, reproductive output), where reproductive output is defined as # of apothecia/cm for adult thalli at each level (tree level, plot level and beyond plot level) to test habitat quality for boreal felt lichen (top findings are summarized in Figure 4.2). We used an array of response metrics to observe if the sensitivity of the response variable will change based on the level that is assessed. Since we had three response metrics and three separate levels tested, we devised 9 model sets.

4.3.3 Statistical Analyses

In each model set, we determined the top explanatory parameter using an information-theoretic approach (Anderson 2008), where we ranked competing models using AIC, or AICc when the sample sizes were < 30 (Burnham & Anderson 2002). We used logistic regressions to test the relationship among habitat variables and presence/absence data at each level (tree, plot, beyond) and checked each model for assumptions and fit. We tested the model additions and interactions of up to two habitat variables at a time and then used AIC($_c$) to rank the competing models. For abundance and reproductive output metrics, we used GLMs and ranked these models using AIC_C. The data for abundance and reproductive output were sub-sectioned from the host trees and plots that had boreal felt lichen present only. At the tree level, we used AIC instead of AIC_c to rank models, since our sample size was much larger (n = 125) and models for pretending variables were removed following Leroux (2017) throughout.

All statistical models were carried out in base R version 3.4.1 (R Core Team 2019) and the models were illustrated using the ggplot2 package (Wickham 2016). To assess how well these models predict, we extracted the β coefficient along with the model variance (Pseudo R^2 or R^2 scores) and checked for significance of the top models against $\alpha = 0.05$. Comparing the model results at each level post hoc, we highlighted which top model scored the best at each level (dark themed graphs).

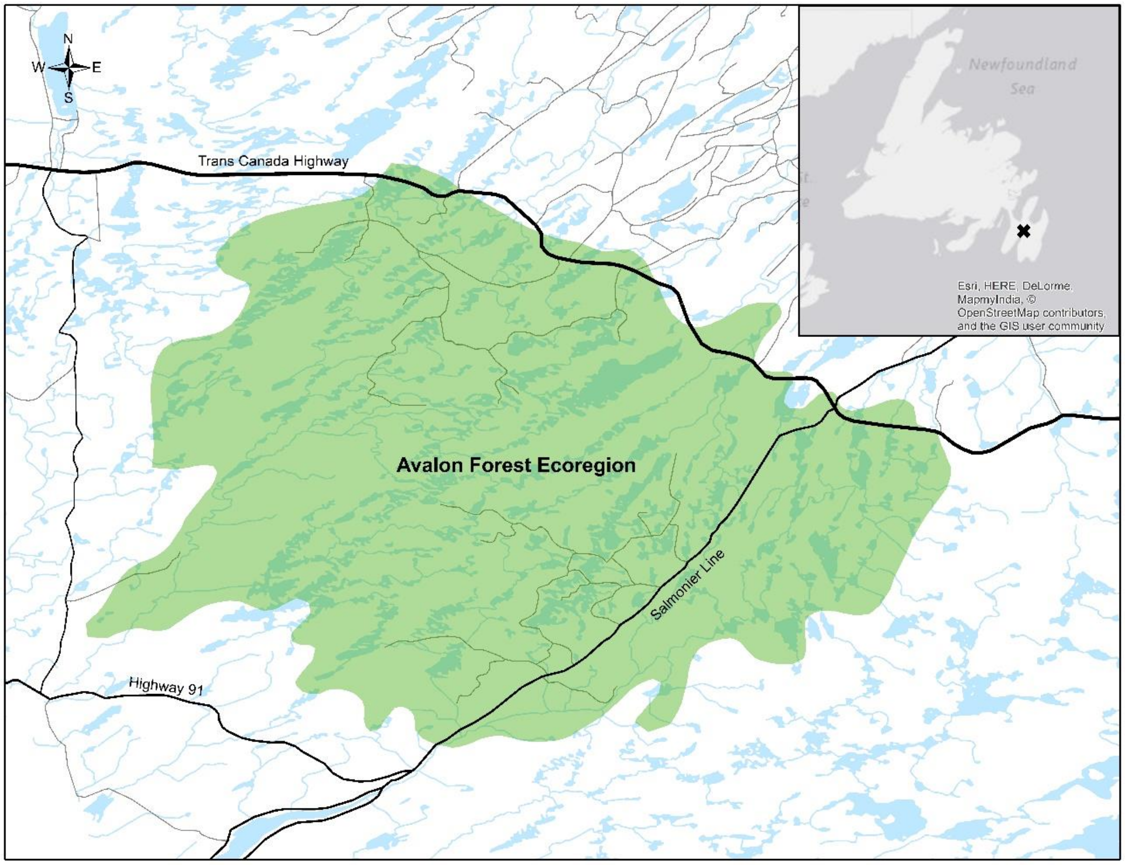

Figure 4.1. A map of the Central Avalon Forest Ecoregion with an inset map showing the island of Newfoundland Canada (Credit: R. Wigle). This ecoregion contains a ribbed moraine landscape structure and is in a lower elevation respective to surrounding land.

4.4 Results

At each level (tree, plot, and beyond plot), a different response metric (either presence/absence, abundance, or reproductive output) gave us the best model fit for the top models displayed. We noted some interesting spatial distributions of boreal felt lichen on the tree, but they did not fit our model framework (Appendix B). At the tree level, the response variable that provided the best model fit was reproductive output, however the presence absence/response was nearly as good of a fit. The top model out of the tree-level model set was tree diameter after removing pretending variables of tree height and canopy cover (Table A.1), with likelihood of having boreal felt lichen present decreasing with tree diameter (Table A.1; β = -0.15, SE = 0.06, pseudo-R^2 = 0.06, p = 0.01 Fig. 4.A).

At the plot level, boreal felt lichen abundance was the response variable that gave the best model fit. The normalized aspect model ranked the highest (after removing the model with the pretending variable of snag density; Table A.2), which showed that boreal felt lichen abundance decreases from north-facing to south-facing slopes (β = -0.02, SE = 0.009, R^2 = 0.13, p = 0.04, Fig. 4.2E).

Beyond the plot level, the presence/absence of boreal felt lichen was the most effective response metric (Table A.3). The top model indicated that probability of boreal felt lichen presence increases with distance from donor tree (β= 0.05, SE = 0.022, pseudo-R^2 = 0.15, p = 0.02 Fig. 4.2C). These models performed the best out of all model sets and will form the major basis for the following discussion.

The top models for the rest of the response-predictor pairs were partially consistent in their predictor variables. However, based on the performance of the model fits, we will not discuss these in detail, save for some noteworthy comparisons. For abundance at the tree level, the model fit becomes very poor; the best-ranked model using abundance is canopy openness, where 0 is complete canopy closure, and 100 is open canopy ($\beta = 0.03$, SE = 0.02, $R^2 = 0.02$, p = 0.3, Fig. 4.2D). The tree level best model for reproductive output was the tree diameter predictor, albeit insignificant ($\beta = -0.54$, SE = 0.28, $R^2 = 0.10$, p = 0.06 Fig. 4.2G).

The normalized aspect predictor variable performed best in both presence/absence ($\beta = -0.008$, SE = 0.006, $R^2 = 0.03$, p = 0.22, Fig. 4.2B) and reproductive output ($\beta = -0.04$, SE = 0.02, $R^2 = 0.13$, p = 0.08, Fig. 4.2H). At the beyond plot level, we used abundance and reproductive output metrics to rank the model sets. For abundance we found no association for distance to nearest donor tree ($\beta = -0.04$, SE = 0.03, $R^2 = 0.08$, p = 0.17, Fig 4.2F). When using reproductive output as the response metric, the top model became elevation above sea level ($\beta = 0.07$, SE = 0.04, $R^2 = 0.09$, p = 0.13, Fig. 4.2I). The reproductive output here is the number of apothecia per cm averaged over adult thalli in the plot only.

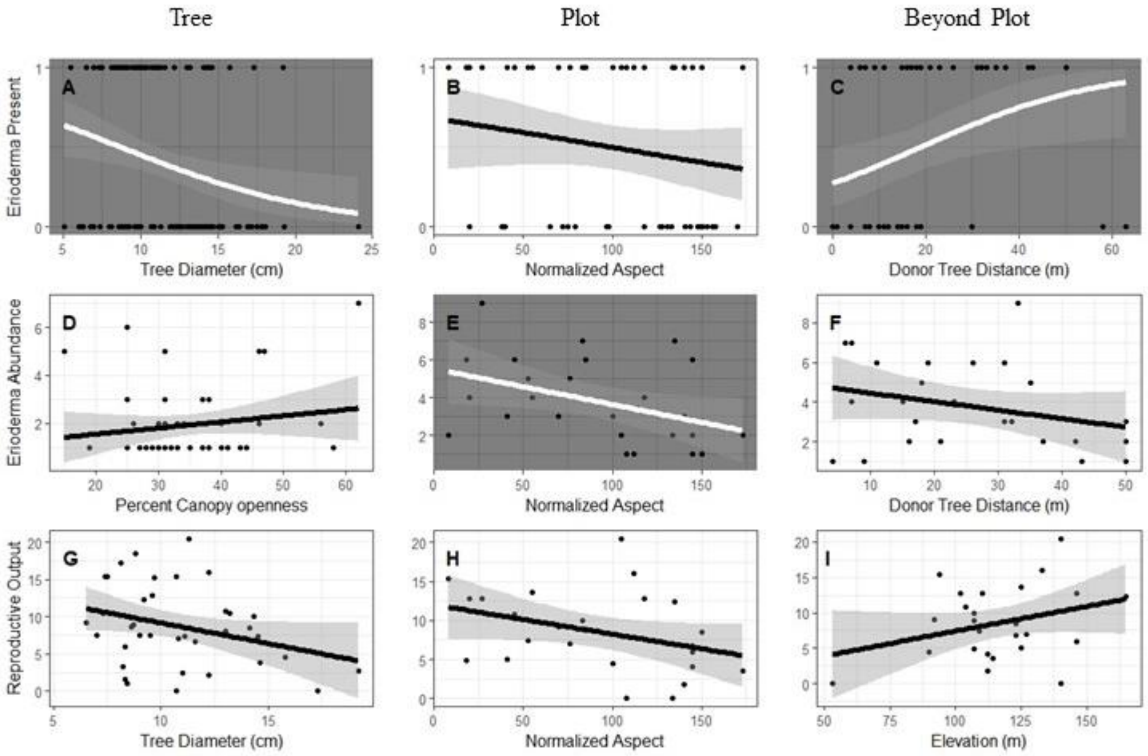

Figure 4.2. A multi-level plot showing the top ranked models for each response variable. The columns are for level (from left to right: tree level, plot level, beyond plot level). The response metrics are separated by row. The dark graphs show the best model fit out of the three response variables at each level.

4.5 Discussion

When determining critical habitat, the most important characteristics differ based on level. Overall, our results suggest that critical habitat for boreal felt lichen includes small trees, on north facing slopes where donor trees are present, but not necessarily close to the host balsam fir. These parameters ranked the highest among all models present, suggesting they are the most important that were considered at each level. The results from this study seem to indicate that habitat characteristics that are most important contribute to water retention in an area or are a result of water saturated areas. These results will help streamline survey efforts in the Avalon Forest Ecoregion and should be considered when making land management decisions to preserve “critical habitat” for these species.

At the tree level, the reproductive output of adult boreal felt lichen is best explained by tree size. We saw a relationship between smaller balsam fir host trees and more fertile adult thalli, which was opposite to our prediction that larger trees are more suitable habitat. In light of our result, we hypothesize that boreal felt lichen, which prefers habitats that are highly water-saturated, occur on trees in conditions that are suboptimal for the tree due to water stress (this is consistent with the conceptual framework presented in chapter 3). In fact, the underlying mechanism for the top models in this study seem to reflect how habitat features may retain water for longer periods. This prevents the tree from achieving a larger size over time (Kreuzwieser & Rennenberg 2014). Most of the balsam fir trees in this region tend to be small. Furthermore, additional characteristics could be considered to help refine the definition of critical habitat at the tree level since we have only looked at tree size and canopy measurements here. Tree morphometrics could influence environmental variables such as average airflow, moisture. The diversity of an individual tree's lichen community assemblages may give us a better indication of boreal felt lichen habitat in the future. These further considerations could help improve the predictive power of the tree-level models in future studies.

The plot-level analysis revealed that the aspect of the slope face, was the most important predictor, regardless of the response metric used (Fig. 4.2B, E, H). More northerly facing slopes are an important component of the critical habitat at this level, which is consistent with the island-scale model of Wiersma and Skinner (2011) and Cameron et al. (2013). North facing slopes receive lower levels of direct solar radiation than south slopes, which reduces the rate of water evaporation. This extends the length of time the lichen remains turgid, so the north slopes provide better habitat conditions. This is important since boreal felt lichen, like other cyanolichens, need to be water saturated to photosynthesize (Büdel & Lange 1991). However, there is high variation in the plot-level data, likely caused in part by the small sample size (n = 25).

The most important variable at the beyond plot level was the distance from the nearest donor tree. However, the direction of the relationship we observed did not support our prediction. We hypothesized that boreal felt lichen presence would be higher the closer the boreal felt lichen host tree was to a donor tree; Figure 4.2A shows probability of presence increasing as distance from donor tree increases. Enrichment can be challenging to measure directly; once a lichen is visible, the lichenization event likely happened more than a decade ago. Thus, the true deciduous donor tree that was responsible for the enrichment could have disappeared by the time we sampled. However, based on the trees that are currently present, our hypothesis predicting the distance to donor trees was not supported. The model likely captured the landscape structure related to deciduous trees being more prevalent on the tops of moraines and balsam fir that hosted boreal felt lichen being more prevalent at the slope bottom. Based on the relative tolerance to water saturated soils between deciduous trees and balsam fir host trees, this tendency to have separation between donor and host tree would occur.

Deciduous tree species in this region tend to occupy drier, more south-facing components of the moraine in this ecoregion due to lower tolerance of water saturated soils, relative to conifers. The host trees of boreal felt lichen usually occur on north-facing slopes close to wetlands, where the soil is more water-saturated. Thus, the minimum distance between the host tree and the donor tree is confounded by the topography. When examining this interaction using abundance measurements, we saw no relationship between donor tree distance and boreal felt lichen abundance (Fig. 4.2D). We observed that cyanolichen diversity and biomass were greater when the donor was yellow birch instead of white birch or pin cherry (PL, pers. Obs.). The potential importance of yellow birch to boreal felt lichen critical habitat warrants further investigation. Yellow birch is rare in the region and contain high and unique diversity of lichens, including cyanolichens (Wigle 2018), so their conservation value is multi-faceted.

Our results help to define critical habitat and better inform survey methods for boreal felt lichen. Boreal felt lichen tends to be on north facing slopes. At the tree level, the host balsam fir trees tend to be small (frequently < 10 cm DBH). At the beyond plot level, deciduous donor trees could be an important proximal habitat characteristic. We speculate that the donor trees are important for the initial colonization of boreal felt lichen, which is likely a challenging barrier for these species to overcome, as deciduous trees are rare locally. The presence/absence data indicated that boreal felt lichen host trees tend to be farther from a donor tree for boreal felt lichen to occur. The presence/absence data is likely capturing the landscape structure, as deciduous trees can only persist at the top of the moraine, and the host trees need to be closer to the bottom of the moraine slope, with their roots submerged in the surrounding wetland.

Understanding the habitat characteristics of boreal felt lichen is important for long-term conservation. Our results better inform management and forest harvest decisions in the Central Avalon Forest Ecoregion. Based on the results of this study, I would recommend protecting areas that have smaller balsam fir trees, that are located on the north sides of moraines through the landscape. Sufficient forest stands under this description should also be protected to allow for the “blinking on” and blinking off” nature of boreal felt lichen populations. Sound management strategies are needed because there are several threats to the critical habitat of boreal felt lichen, including illegal tree harvest and clearing for development. Sufficient land protection that contain the most important habitat characteristics for boreal felt lichen will help ensure its long term persistence.

4.6 References

Anderson, D. R. 2008. Model based inference in the life sciences, a primer on evidence. *Springer-Verlag New York.*

Arsenault A., Goward T. 2000. The drip zone effect: new insights into the distribution of rare lichens. *Proceedings of a Conference on the Biology and Management of Species and Habitats at Risk*. 767-768.

Benson, S., Coxson, D. S. 2002. Lichen colonization and gap structure in wet-temperate rainforests of northern interior British Columbia. *The Bryologist* 105(4): 673-692.

Büdel B., Lange O. L. 1991. Water status of green and blue-green phycobionts in lichen thalli after hydration by water vapor uptake: do they become turgid? *Plant Biology* 104(5): 361-366.

Burnham, K. P., Anderson, D. R. 2002. Model selection and multimodel inference: a practical information theoretic approach 2nd ed. *Springer New York*.

Cameron R., Goudie I., Richardson D. 2013. Habitat loss exceeds habitat regeneration for an IUCN flagship lichen epiphyte: *Erioderma pedicellatum*. *Canadian Journal of Forest Research.* 43: 1075-1080.

Cameron R. P., Neily T. 2008. Heuristic model for identifying the habitats of *Erioderma pedicellatum* and other rare cyanolichen in Nova Scotia, Canada. *The Bryologist*. 111:650-658.

Campbell J., Bradfield G. E., Prescott C. E., Fredeen A. L. 2010. The influence of overstory *Populus* on epiphytic lichens in subboreal spruce forests of British Columbia. *Canadian Journal of Forest Research*. 40: 143-154.

Cardos, J. L. H., Aragon, G., Martinez, I. A species on a tightrope: Establishment limitations of an endangered lichen in a fragmented Mediterranean landscape. *American Journal of Botany* 104(4): 527-537.

Cornejo C., Scheidegger C. 2016. Cyanobacterial gardens: the liverwort *Frullania asagrayana* acts as a reservoir of lichen photobionts. *Environmental microbiology reports*. 8(3): 352-357.

COSEWIC. 2014. COSEWIC assessment and status report on the Boreal Felt Lichen *Erioderma pedicellatum*, Boreal Population and Atlantic Population, in Canada. *Committee on the Status of Endangered Wildlife in Canada*. Ottawa. Xiv+66pp.

Goudie I. R., Scheidegger C., Hanel C., Munier A., Conway E. 2011. New population models help explain declines in the globally rare boreal felt lichen *Erioderma pedicellatum* in Newfoundland. *Endangered Species Research.* 13: 181-189.

Hattestrand, C., Kleman, J. 1999. Ribbed moraine formation. *Quaternary Science Reviews* 18: 43-61. DOI: 10.1016/S0277-3791(97)00094-2

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., Jarvis, A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1967-1978.

Krebs C. J. 1989. Ecological Methodology 1st ed. *Harper Collins Publishers, Inc.*

Kreuzwieser, J., Rennenberg, H. 2014. Molecular and physiological responses of trees to waterlogging stress. *Plant, Cell & Environment* 37(10): 2245-2259.

Lauriault P., Wiersma Y. F. 2019. Reducing the rates of false absences of cryptic species in inventory and sampling work. *The Bryologist* 122: 578-585.

Lauriault P., Wiersma Y. F. In Prep. Substrate dynamics over time influence the rarity of tree-dwelling cyanolichens. *The Lichenologist*.

Leroux S. J. 2019. On the prevalence of uninformative parameters in statistical models applying model selection in applied ecology. *PLOS ONE*. 14(2): 1-12.

Maass W. S. G. 1983. New observations on *Erioderma* in North America. *Nordic Journal of Botany* 3(5): 567-576.

Moroni M. T., Harris D. D. 2010. Snag frequency, diameter and species distribution input rate in Newfoundland boreal forests. *Forestry* 83(3): 229-244.

Nelson P., Walton J., Roland C. 2009. *Erioderma pedicellatum* (Hue) P.M. Jorg., new to the United States and Western North America, discovered in Denali National Park and Preserve and Denali State Park, Alaska. Evansia. 25: 19-23.

Power T. D., Cameron R. P., Neily T., Toms B. 2018. Forest structure and site conditions of boreal felt lichen (*Erioderma pedicellatum*) habitat in Cape Breton, Nova Scotia, Canada. *Botany*. 96: 449-459.

Pykälä J. 2019. Habitat loss and deterioration explain the disappearance of populations of threatened vascular plants, bryophytes and lichens in a hemiboreal landscape. *Global Ecology and Conservation*. 18: 1-18.

Radies, D., Coxson, D., Johnson, C., Konwicki, K. 2009. Predicting canopy microlichen diversity and abundance within old-growth in land temperate rainforests. *Forest Ecology and Management* 259:86-97.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.r-project.org/.

Rubio-Salcedo M., Psomas A., Prieto M., Zimmermann N. E., Martinez I. 2017. Case study of the implications of climate change for lichen diversity and distributions. *Biodiversity Conservation* 26: 1121-1141.

Werth, S., Wagner, H. H., Gugerli, F., Holderegger, R., Csencsics, D., Kalwij, J. M., Scheidegger, C. 2006. Quantifying dispersal and establishment limitation in a population of an epiphytic lichen. *Ecology* 87(8): 2037-2046.

Wickham H. 2016. Ggplot2: elegant graphics for data analysis. *Springer-Verlag New York.*

Wiersma Y. F., Skinner R. 2011. Predictive distribution model for the boreal felt lichen *Erioderma pedicellatum* in Newfoundland, Canada. *Endangered Species Research.* 15(2): 115-127.

Wigle R. D. 2018. Arboreal lichen community structure and diversity on yellow birch (*Betula alleghaniensis*) and Balsam Fir (*Abies balsamea*) in the Avalon Forest Ecoregion in Newfoundland, Canada. *Master's Thesis, Memorial University of Newfoundland*.

5 Summary

5.1 Thesis Summary

Erioderma pedicellatum (boreal felt lichen) is rare and difficult to detect, making it difficult to manage. These two factors played an important role in it being listed as Critically Endangered globally by the IUCN. This species requires greater search effort compared to species that contrast well with their surroundings before reliable detection. In any survey, the abundance of boreal felt lichen is likely to be underestimated. Another management issue is that the ideal habitat of boreal felt lichen in the Central Avalon Forest Ecoregion likely has differences compared to ideal habitat in other, geographically isolated populations. Thus, the habitat characteristics outlined as important here will need careful examination to confirm that they are consistent for each population of boreal felt lichen.

In Chapter 2, we devised a survey protocol to assess the necessary search effort for detection of difficult-to-detect lichens such as boreal felt lichen. We employed small pieces of grey felt as our target species to test for detectability. The benefits to using felt instead of trying to find natural lichens is that we conduct the survey and the hider has a guaranteed known outcome of condition. The participant who hid the felt knew the abundance and distribution of felt pieces on a plot, giving us a comparable value to what the participants who survey the plots detect. The surveyors did not have knowledge of the number of felt pieces at each plot, thus replicating real survey scenarios where true presence and abundance of rare lichens is unknown. Having a known maximum per treatment allowed us to determine detection reliability based on surveyor experience and the time limit given to the three surveyors in this study. Survey effort was limited to 20 minutes for a 5 m radius plot, we found that we had near complete detection of our decoys when they were present, giving us a satisfactory false absence rate. Ensuring that our false absence rates are near zero is important in comparative presence vs. absence plots because it gives greater confidence in assessing the fine level habitat characteristics that may dictate why a boreal felt lichen grows in some forest stands but not others. This permits us to use presence/absence of boreal felt lichen as a response metric and a more reliable abundance measurement to use for quantitative habitat analyses.

During the exploratory phase of fieldwork in the summer of 2018, our survey time was dedicated to establishing paired presence/absence plots. We recorded 124 new occurrences of *E. pedicellatum*, and 1 new occurrence of *E. mollissimum*. These new occurrences tend to occupy balsam fir trees that appear to be unhealthy, which prompted the new ideas around substrate presented in Chapter 3. Most rare cyanolichens prefer environments with high rainfall, dewfall or fog (Gauslaa 2014). The Central Avalon Forest Ecoregion receives nearly 1500 mm of rain annually (Environment Canada 2019) but since the summers are relatively cool compared to more temperate regions of the world, and because this region experiences long periods of heavy fog, water persists in the landscape for long periods. This is ideal conditions for the lichens that grow there, but not for the trees they grow on. Balsam fir is the exclusive host for boreal felt lichen in this region. This tree has mild tolerance of saturated soils, but the host trees we observed grow near the bog edges where their roots are immersed in water-saturated soils for much of their lives. This appears to stunt their growth and erodes their condition over time.

In Chapter 3, we presented a conceptual figure to highlight the ecological constraints on the lichen- host tree dynamic through time, and then we ran an analysis to demonstrate a component of this temporal tension. We concluded that using thallus width as a proxy for time spent on tree is inadequate. However, the differences in occurrence of host tree at different health classes suggests that further research is needed to explore the dynamics of the substrate and boreal felt lichen. We suggest that balsam fir in these localities are stressed by chronic soil saturation, their lifespan is reduced to the maximum average age of 70 years in this region (Arsenault et al. 2016). We opted not to core these trees as they are already subject to natural stresses that will reduce their lifespan significantly. Since this lichen appears to better colonize unhealthy trees, it has a narrow window of time to colonize, grow to maturity and release spores before the tree dies. Here we posit that boreal felt lichen better colonizes trees that are under stress, whether it is facilitated by a secondary compound the tree is producing or there is an interaction with the root rot that is taking hold are questions that could direct future research.

To better understand the threats to boreal felt lichen, we need to improve our understanding of the critical habitat for this species. Our goal for Chapter 4 was to outline the habitat variables most important for this species to occur. Using our survey specifications from Chapter 2, we surveyed habitat using a paired plot approach. In each plot pair, we had one plot with boreal felt lichen occupying at least one host tree, and in the other plot we ensured that no boreal felt lichen was present. Within the occupied plots we also collected information on boreal felt lichen abundance and the reproductive output of adult thalli to use as response metrics to a suite of habitat variables. We grouped habitat variables based on level. Tree level habitat variables measured were tree height, diameter and canopy closure. Scaling up, habitat characteristics were measured within a 5 m radius plot, which were direction of slope face, slope steepness, the number of trees and snags. Other characteristics were also considered outside of the plots, which were distance from gaps in the forest stand as well as distance to deciduous donor trees and elevation.

We ranked the best response metric-predictor variable at each of the three levels. At the tree level, our model using presence/absence provided the best model fit and the top competing predictor variable was tree diameter. Smaller diameter trees were more likely to be host trees for boreal felt lichen. Our plot level analysis indicated that north facing slopes were the most important habitat characteristic at this level. The most important characteristic beyond the plot level is the distance from the nearest donor tree, where boreal felt lichen-occupied plots were further away from donor trees. Available moisture content in the environment appears to be the underlying driver behind the variables that competed best for the occurrence of boreal felt lichen.

5.2 Limitations

Our developed methodology from Chapter 2 requires intensive, surveys over small areas, which is a tradeoff for detectability of low abundance species vs. wider area coverage. Even though this protocol has high detectability, it is not the most time-effective survey protocol as the area coverage is only 78 m^2 per 20 minutes of sampling. Other survey methods would be better for covering large areas of land, but Type 2 error would increase with area covered. I recommend my protocol for more targeted habitat surveys since it would not be logistically feasible for high-area coverage surveys; other survey methods are better suited for this (Bowering et al. 2018).

Chapter 3 highlights the needs for future research on boreal felt lichen. There is a temporal constraint by this lichen’s substrate relative to the length of the boreal felt lichen generation cycle. However, as my project had only one field season, there was no ability to directly test the way the lichen and its substrate (balsam fir) change through time. Many host trees do not appear to be healthy compared to balsam fir in more upland regions. The categorical classification of tree health specific to this area could be improved. Moreover, using thallus size as a response measure instead of true thallus age is inadequate because the thallus can grow and shrink (by necrosis, grazing or shearing) irregularly over time. Tree age was also not measured for this study as there was concern that tree health was already compromised and coring trees would further jeopardize their state. The strength of my study is how it highlights research needs for boreal felt lichen, and potentially for other endangered lichens that face similar niche restrictions.

In Chapter 4, we identified the important habitat characteristics at the three levels. This will help inform management decisions to protect specific parcels of land in the Avalon Forest Ecoregion. An important consideration here is the response metrics we used to determine critical habitat. These include abundance and reproductive output which are not commonly used in habitat analyses for lichens. The reproductive output is also measured by the number of apothecia (not considering which ones have already released spores and are no longer active). This response metric can be improved significantly for future work. An oversight that was not considered prior to the field season was the effect of commercially thinned stands on the microclimate for the lichen (Haughian & Frego 2017). While there were some thinned stands found within the Avalon forest ecoregion, collecting data related to this was not considered and may improve future efforts to quantify habitat. The results presented in this chapter are likely only specific to this population of boreal felt lichen. Generalizing our results to other boreal felt lichen populations is not recommended. This study also does not consider how the habitat changes over time as the models are static. These limitations may be problematic as boreal felt lichen is a long-lived species and the habitat around it will change over its lifespan.

With these limitations considered, we were successful in reaching our objectives of this study. In Chapter 2, we devised and tested the survey protocol to detect boreal felt lichen with minimal error. This allowed us to have true unoccupied plots to compare to the occupied plots for the habitat analysis, which we carried out in Chapter 4. However, the models in Chapter 4 were static, and we couldn't include time as a factor here, we explored the concept of how time influences boreal felt lichen habitat in Chapter 3. We suspect that the lichen-tree relationship is under temporal pressure, as the lichen needs to proceed through its life cycle before the host tree dies in its unsuitable environment. Chapter 3 outlines future research that is important for boreal felt lichen that was beyond the scope of our study. Our results from Chapter 4 can be directly applied to management decisions when designated areas that are important to protect for current, and future boreal felt lichen occurrences. Habitat to protect for boreal felt lichen includes small diameter balsam fir trees found on northern slopes, with consideration given to nearby deciduous trees.

5.3 Management Implications

Boreal felt lichen is difficult to detect. This likely contributes to their perceived rarity as they are hard to find. As the search for boreal felt lichen continues, we expect to find more populations as well as some population expansions in some regions. In Chapter 2, we devised a time-area protocol that would help ensure detection in a small area of interest, which is a useful tool when looking for previously undetected or new individuals in a population near the boundaries of their currently known range. This will help build a better picture of what the population dynamics are truly like as it is easier to see previously known lichen disappear than new colonization events of rare lichens.

There are some conservation concerns that we were unable to address directly with this study, the most important being the time dynamics of this population. Having one field season limited our ability to see changes to habitat and respectively the lichen populations over time. We tried to conceptualize this in chapter 3 where we used thallus size as a proxy for time. Ultimately this metric proved to be insufficient, but the dynamics of the habitat (both at the tree level and the forest stand level) relative to the lifecycle requires careful consideration when making management decisions. Another important factor that we noted but did not test directly was the prevalence of windthrow in the Avalon forest ecoregion. This disturbance is infrequently studied, but since this part of Newfoundland is subject to frequent high winds, this disturbance is rather common (Arsenault et al. 2016). Host trees that are blown over are no longer suitable substrate for boreal felt lichen. The prevalence of windthrow, as well as predicting the frequency of windthrow occurrence in the future, is an important consideration for future management practices.

In our habitat analysis, we were able to rank which characteristics best predicted boreal felt lichen habitat. At the tree level, we noted a trend where boreal felt lichen is more likely to occur on smaller diameter host trees. This pattern is uncharacteristic of a lichen that is presumed to occur in old growth forests (Wiersma & McMullin 2017). These lichens were also found more on north facing slopes of the moraines within the landscape. This constricts the amount of land area the lichen will be found at. We suggest that management strategies should include choosing to develop trails more on southerly facing slopes and perhaps have them cut through the upland portions of the moraine where trees are larger, and the terrain is better drained. Although our results disproved the donor tree hypothesis, there is still a relationship between deciduous trees and areas that have host balsam fir. This could either indicate a distance between the top of the moraine (where deciduous trees are more likely to be found) and the bottom (where the balsam fir is stunted from oversaturation), where the lichen is more likely to occur. Protecting small trees in water saturated soils will help preserve *Erioderma* habitat.

5.4 References

Arsenault A., LeBlanc R., Earle E., Brooks D., Clarke B., Lavigne D., Royer L. 2016. Unravelling the past to manage Newfoundland’s forests for the future. *The Forestry Chronicle*. 92(4): 487-502.

Bowering, R., R. Wigle, T. Padgett, B. Adams, D. Cote & Y. F. Wiersma. 2018. Searching for rare species: A comparison of Floristic Habitat Sampling and Adaptive Cluster Sampling for detecting and estimating abundance. Forest Ecology and Management 407: 1–8.

Environment Canada. 2019. Whitbourne weather station annual climate data. *National Climate Data and Information Archive.*

Gauslaa Y. 2014. Rain, dew, and humid air as drivers of morphology, function and spatial distribution in epiphytic lichens. *The Lichenologist* **46**(1):1-16.

Haughian, S.R., and Frego, K.A. 2017. Log moisture capacity does not predict epixylic bryophyte growth under thinned and unthinned forest canopies. Funct. Ecol. 31: 1540–1549. doi:10.1111/1365-2435.12864.

Appendices

Appendix A: AIC tables for Chapter 4 habitat analyses

The tables in this appendix are ordered firstly by the sequence they are referred to in Chapter 4 (Table A.1. to Table A.3.) since these were the main findings discussed. Tables that were not directly cited in he results of Chapter 4 were ordered by level, from tree level (Table A.4.) to beyond plot level (ending on Table A.9.). Each table corresponds to a panel in Figure 4.2 which is specified in the captions.

Table A.1. Corresponding to Figure 4.2A, the tree level AIC table that includes tests the presence/absence of boreal felt lichen, with points taken on boreal felt lichen presence plots (N = 125). "+" indicates the addition of variables to the model, ":" is the model that includes the interaction of the two variables.

Explanatory Parameters	**logLik**	**K**	**AIC**	**ΔAIC**	**w_i**
Percent canopy + tree diameter	-108.43	2	158.73	0.00	0.32
Tree diameter at breast height	-109.09	1	158.95	0.22	0.29
Global Model	-108.39	3	160.42	1.69	0.14
Tree diameter + tree height	-109.06	2	160.67	1.94	0.12
Percent canopy : tree diameter	-110.44	3	162.76	4.03	0.04
Canopy openness	-114.46	1	164.16	5.43	0.02
Tree diameter : tree height	-109.54	3	164.30	5.57	0.02
Percent canopy + tree height	-112.76	2	164.38	5.65	0.02
Tree height	-113.34	1	164.52	5.80	0.02
Percent canopy : tree height	-112.89	3	166.80	8.07	0.01
Null Model	-117.47	1	169.41	10.68	0.00

Table A.2. Corresponding to Figure 4.2E, the AIC table showing the top-ranked models out of all explanatory parameters tested for plot level using boreal felt lichen abundance as the response metric (N = 25). "+" indicates the addition of variables to the model, ":" is the model that includes the interaction of the two variables.

Explanatory Parameters	**LogLik**	**K**	**AICc**	**ΔAICc**	**w_i**
Normalized aspect + snags	-51.83	2	106.41	0.00	0.39
Normalized aspect	-53.46	1	107.67	1.25	0.21
Normalized aspect + slope steepness	-53.44	2	108.95	2.53	0.11
Normalized aspect + number of trees	-53.44	2	109.81	3.40	0.07
Global model	-51.68	4	109.99	3.58	0.06
Number of snags on site	-55.42	1	110.74	4.33	0.04
Slope steepness	-55.93	1	112.22	5.81	0.02
Number of trees on plot	-56.06	1	112.23	5.81	0.02
Null model	-56.07	1	112.25	5.83	0.02
Slope steepness + snags	-55.14	2	112.91	6.50	0.01
NumTrees + numSnags	-55.42	2	112.92	6.50	0.01
Slope steepness + numTrees	-55.91	2	114.38	7.97	0.01
Normalized aspect : number of trees	-54.01	3	114.54	8.13	0.01
Slope steepness : snags	-56.05	3	116.06	9.65	0.00
Normalized aspect : slope steepness	-54.90	3	116.14	9.72	0.00
NumTrees : numSnags	-55.84	3	116.14	9.73	0.00
Normalized aspect : snags	-55.80	3	116.31	9.89	0.00
Slope steepness : Trees	-55.84	3	116.68	10.27	0.00

Table A.3. Corresponding to Figure 4.2C, The AIC table for beyond plot analyses looking at various parameters that exceed the constraints of the plot area. This table is for the logistic regression models using presence and absence of boreal felt lichen as the response metric (N = 50). "+" indicates the addition of variables to the model, ":" is the model that includes the interaction of the two variables.

Explanatory Parameters	**LogLik**	**K**	**AIC**	**ΔAIC**	w_i
Donor tree distance	-31.24	1	64.48	0.00	0.35
Distance from gap + donor distance	-31.07	2	66.13	1.65	0.15
Elevation + donor distance	-31.24	2	66.48	2.00	0.13
Differential elevation + donor distance	-31.24	2	66.48	2.00	0.13
Elevation : donor distance	-30.84	3	67.68	3.20	0.07
Distance from gap : donor distance	-31.13	3	68.26	3.78	0.05
Distance from gap	-34.52	1	69.31	4.83	0.03
Gap type	-32.13	3	70.25	5.77	0.02
Elevation	-34.64	1	71.04	6.56	0.01
Differential Elevation	-34.66	1	71.27	6.79	0.01
Null model	-34.66	1	71.31	6.83	0.01
Distance from gap + elevation	-34.50	2	73.00	8.52	0.00
Distance from gap + dif elevation	-34.51	2	73.03	8.55	0.00
Differential elevation + elevation	-34.63	2	73.23	8.75	0.00
Differential elevation : donor distance	-34.49	3	73.26	8.78	0.00
Distance gap : dif elevation	-34.59	3	74.98	10.50	0.00
Differential elevation : elevation	-34.65	3	75.19	10.71	0.00
Distance from gap : elevation	-34.65	3	75.31	10.83	0.00
Global model	-30.61	6	75.31	10.83	0.00
Distance from gap : gaptype	-33.41	5	76.83	12.35	0.00

Table A.4 Corresponding to Figure 4.2D, the AIC rankings for the abundance response metric at tree level testing all trees measured in the occupied plots (N = 125). “+” indicates the addition of variables to the model, “:” is the model that includes the interaction of the two variables.

Explanatory Parameters	**LogLik**	**K**	**AIC**	**ΔAIC**	**w_i**
Canopy openness	-88.49	1	178.98	0.00	0.25
Tree height	-89.04	1	180.09	1.10	0.14
Tree diameter at breast height	-89.07	1	180.14	1.16	0.14
Null Model	-89.08	1	180.15	1.17	0.14
Percent canopy + tree height	-88.45	2	180.90	1.92	0.09
Percent canopy + tree diameter	-88.49	2	180.98	2.00	0.09
Tree diameter + tree height	-89.00	2	182.00	3.01	0.05
Global Model	-87.69	3	182.86	3.88	0.04
Percent canopy : tree diameter	-88.93	3	183.85	4.87	0.02
Percent canopy : tree height	-89.01	3	184.03	5.05	0.02
Tree diameter : tree height	-89.04	3	184.07	5.09	0.02

Table A.5. Corresponding to 4.2G AIC model rankings for reproductive output (number of apothecia/cm adult thallus width) as the response metric at the tree level (N = 125). “+” indicates the addition of variables to the model, “:” is the model that includes the interaction of the two variables.

Explanatory Parameters	**LogLik**	**K**	**AIC**	**ΔAIC**	$\mathbf{w_i}$
Global model	-112.33	3	225.17	0.00	0.32
Tree diameter + tree height	-113.75	2	225.79	0.62	0.23
Percent canopy + tree diameter	-113.95	2	226.53	1.36	0.16
Tree diameter at breast height	-115.06	1	226.58	1.41	0.16
Canopy openness	-116.19	1	228.76	3.59	0.05
Tree height	-117.02	1	230.25	5.08	0.02
Null model	-117.02	1	230.27	5.10	0.02
Percent canopy + tree height	-116.19	2	230.73	5.56	0.02
Tree diameter : tree height	-113.75	3	233.09	7.92	0.01
Percent canopy : tree height	-116.54	3	233.26	8.09	0.01
Percent canopy : tree diameter	-116.98	3	234.17	9.00	0.00

Table A.6. Corresponding to Figure 4.2B, the AIC set for presence/absence of boreal felt lichen at the plot level (N = 50). "+" indicates the addition of variables to the model, ":" is the model that includes the interaction of the two variables.

Explanatory Parameters	LogLik	K	AIC	ΔAIC	w_i
Normalized aspect	-33.90	1	69.80	0.00	0.19
Number of snags on site	-34.48	1	70.95	1.15	0.10
Number of trees on plot	-34.59	1	71.13	1.33	0.10
Slope steepness	-34.60	1	71.19	1.39	0.09
Normalized aspect + snags	-33.57	2	71.21	1.40	0.09
Null model	-34.66	1	71.59	1.79	0.08
Normalized aspect + slope steepness	-33.80	2	71.72	1.92	0.07
Normalized aspect + number of trees	-33.86	2	72.44	2.64	0.05
Normalized aspect : slope steepness	-33.22	3	72.58	2.78	0.05
Slope steepness + snags	-34.44	2	72.88	3.08	0.04
Number trees + snags	-34.45	2	72.90	3.10	0.04
Slope steepness + trees	-34.53	2	73.07	3.26	0.04
Normalized aspect : number of trees	-34.37	3	74.75	4.95	0.02
Slope steepness : trees	-34.39	3	74.78	4.98	0.02
Number trees : snags	-34.56	3	75.12	5.32	0.01
Normalized aspect : snags	-34.63	3	75.26	5.46	0.01
Slope steepness : snags	-34.63	3	75.27	5.46	0.01
Global model	-33.48	4	79.60	9.80	0.00

Table A.7. Corresponding to Figure 4.2H, the AIC table for reproductive output at the plot level model set (N = 25). "+" indicates the addition of variables to the model, ":" is the model that includes the interaction of the two variables.

Explanatory Parameters	**LogLik**	**K**	**AICc**	**ΔAICc**	**w_i**
Normalized aspect + snags	-73.12	2	150.49	0.00	0.22
Normalized aspect	-74.26	1	150.61	0.12	0.21
Normalized aspect + trees	-73.93	2	152.12	1.63	0.10
Normalized aspect + slope steepness	-74.22	2	152.70	2.21	0.07
Number of snags on plot	-75.40	1	152.88	2.39	0.07
Number of trees on plot	-75.42	1	152.92	2.43	0.07
Slope steepness	-75.59	1	153.27	2.78	0.05
Null model	-75.93	1	153.94	3.45	0.04
Slope steepness + snags	-74.86	2	153.98	3.49	0.04
Slope steepness + trees	-74.94	2	154.13	3.64	0.04
Trees + snags	-75.00	2	154.25	3.76	0.03
Global model	-72.76	4	154.41	3.92	0.03
Slope steepness : trees	-74.94	3	156.21	5.72	0.01
Trees : snags	-75.00	3	157.37	6.88	0.01
Normalized aspect : trees	-75.74	3	157.99	7.50	0.01
Slope steepness : snags	-75.77	3	158.06	7.57	0.00
Normalized aspect : slope steepness	-75.86	3	158.24	7.75	0.00
Normalized aspect : snags	-75.89	3	158.31	7.82	0.00

Table A.8. Corresponding to Figure 4.2F, the AIC table showing the abundance linear models for the beyond plot level analyses (N = 25). "+" indicates the addition of variables to the model, ":" is the model that includes the interaction of the two variables.

Explanatory Parameters	**LogLik**	**K**	**AICc**	**ΔAICc**	**w_i**
Donor tree distance	-54.04	1	110.26	0.00	0.20
Elevation	-54.50	1	111.17	0.91	0.13
Elevation + donor distance	-53.50	2	111.54	1.28	0.11
Differential elevation + donor Distance	-53.72	2	111.99	1.73	0.08
Differential elevation	-54.97	1	112.12	1.86	0.08
Distance from gap	-55.00	1	112.17	1.91	0.08
Null model	-55.08	1	112.34	2.08	0.07
Distance from gap + donor Distance	-53.98	2	112.50	2.24	0.07
Differential elevation + elevation	-54.45	2	113.44	3.18	0.04
Distance from gap + elevation	-54.49	2	113.52	3.26	0.04
Distance from gap + differential elevation	-54.88	2	114.30	4.04	0.03
Distance from gap : gap type	-53.73	3	114.60	4.34	0.02
Elevation : donor distance	-54.29	3	115.73	5.47	0.01
Distance from gap : donor Distance	-54.62	3	116.38	6.12	0.01
Distance from gap : differential elevation	-54.93	3	117.01	6.75	0.01
Distance from gap : elevation	-54.99	3	117.13	6.87	0.01
Differential elevation : donor Distance	-55.03	3	117.21	6.95	0.01
Differential elevation : elevation	-55.08	3	117.30	7.04	0.01
Distance from gap + gap type	-53.83	4	117.66	7.40	0.00
Global model	-51.66	7	123.91	13.65	0.00

Table A.9. Corresponding to Figure 4.2I, the AIC table for reproductive output at the beyond plot level (N = 25). “+” indicates the addition of variables to the model, “:” is the model that includes the interaction of the two variables.

Explanatory Parameters	**LogLik**	**K**	**AICc**	**ΔAICc**	**w_i**
Elevation	-74.66	1	151.43	0.00	0.18
Elevation + donor distance	-73.85	2	152.03	0.59	0.14
Distance from gap	-75.22	1	152.56	1.12	0.10
Distance from donor	-75.30	1	152.71	1.28	0.10
Distance from gap + elevation	-74.32	2	152.97	1.53	0.09
Distance from gap + donor Distance	-74.49	2	153.32	1.89	0.07
Differential elevation + elevation	-74.65	2	153.62	2.19	0.06
Differential elevation	-75.84	1	153.79	2.35	0.06
Null model	-75.93	1	153.96	2.53	0.05
Distance from gap + differential elevation	-75.10	2	154.54	3.10	0.04
Differential elevation + donor distance	-75.28	2	154.89	3.46	0.03
Distance from gap : differential elevation	-74.15	3	154.98	3.55	0.03
elevation : donor distance	-74.81	3	156.30	4.87	0.02
Distance from gap : donor distance	-75.64	3	157.96	6.52	0.01
Distance from gap : elevation	-75.75	3	158.19	6.76	0.01
Differential elevation : elevation	-75.86	3	158.41	6.98	0.01
Differential elevation : donor distance	-75.90	3	158.49	7.06	0.01
Distance from gap : gap type	-74.86	4	158.90	7.47	0.00
Distance from gap + gap type	-75.10	4	159.37	7.94	0.00
Global model	-72.24	7	162.10	10.67	0.00

Appendix B: Tree spatial distribution of boreal felt lichen

When searching for boreal felt lichen, we took positional measurements on the tree of each individual thallus so that we could map out where these lichens tend to aggregate on the tree bole. This data did not fit our model framework for chapter 4, but it is important to share for future sampling efforts of this species. There appears to be patterns on the vertical plane (Fig. B.1) where these lichens tend to aggregate most between 120-140 cm up the tree bole. This pattern may be an artefact of sampling effort, as this height range is slightly below eye level, which is where a surveyor tends to start gazing at the tree. However, below this level was searched thoroughly as well. The lesser abundance of thalli may indicate that slug grazing excludes thalli from persisting at the lower levels of the tree long term. It could also reflect the vertical pattern of chronic fog exposure to the tree bole within forest stands. Above eye level of the surveyor can be explained by sampling accessibility. The maximum height we managed to detect *Erioderma* thalli was 235 cm from the ground. Small thalli would be overlooked and anything beyond would likely be missed altogether if present. When looking at the distribution of boreal felt lichen on the side of the tree, we also note a rather interesting and thought-provoking pattern. *Erioderma* appears to have a tendency to occupy the West-North-West and the East-South-East facing sides of the trees (Fig B.2). The abundance of *Erioderma* found in this orientation is quite striking, and could have two explanations: 1) *Erioderma* grows better when it is facing to the average annual path of the sun. However, this contradicts the findings in Chapter 4, where *Erioderma* is most abundant on North facing slopes.

North facing slopes are subject to less solar radiation on average, indicating that *Erioderma* may be avoiding extreme solar radiation; 2) This pattern potentially matches the average wind direction throughout the year, signifying dispersal patterns. I find this unlikely since the high abundance is mirrored on both sides of the trees on average, rather than having an extremely high abundance on one side and the other side being nearly void of lichen thalli. Ground level wind direction in the Avalon varies a lot so it would be challenging to attribute the dispersal pattern to prevailing wind.

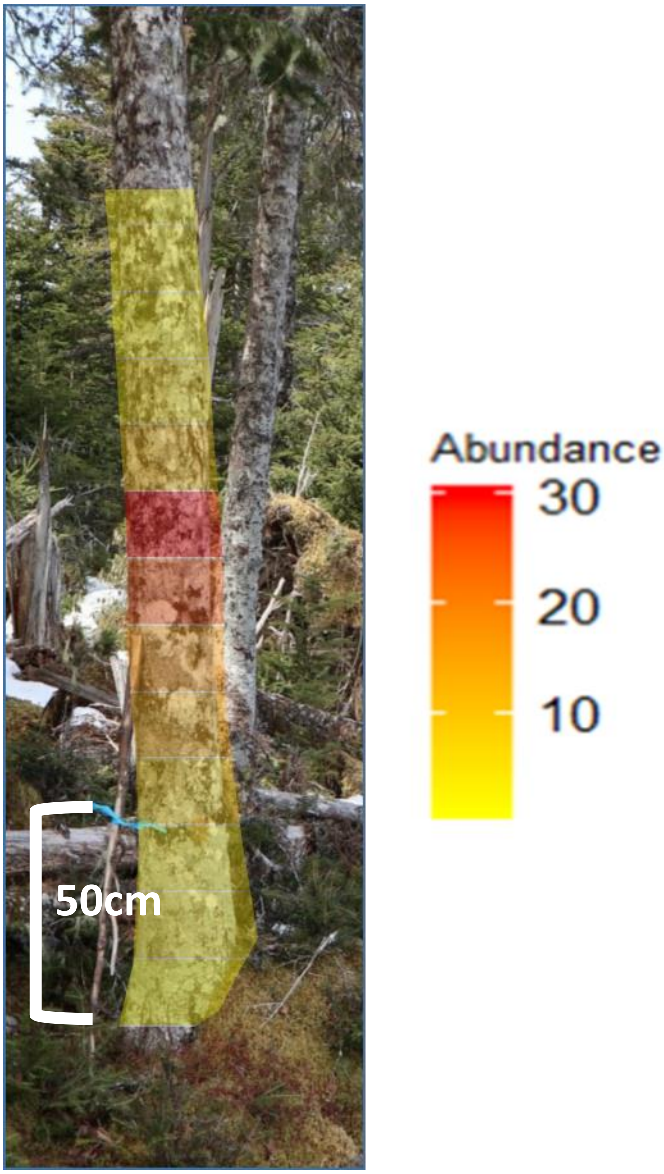

Figure B.1. A heatmap transposed over a balsam fir bole to give reference to where the boreal felt lichen (*E. pedicellatum*) to show the vertical distribution of thalli. The blue flag beside the tree represents a 50 cm interval from the ground. Detection of the lichen becomes unreliable above the limit of the heat map.

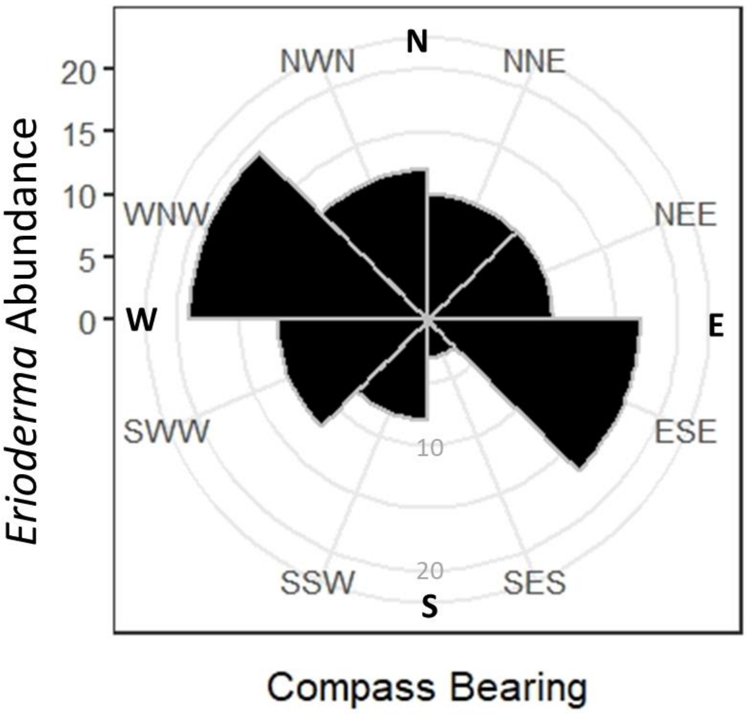

Figure B.2. Boreal felt lichen (*E. pedicellatum*) abundance measures based on the side of the tree bole they were located.

Appendix C: Protocol for Field Season 2018 (Chapter 4)

Definitions

Plot: location where surveys will take place defined by a centralized reference tree and a 5m radius, circular plot. The total area of a site is $78.54m^2$

Quadrant: A quarter piece of a site, seperated by the cardinal directions. Each quadrant takes up a total area of $19.64m^2$

Host Tree: Any Balsam fir within each plot that contains at least 1 boreal felt lichen thallus on it.

Reference Tree: The tree that is the centrepoint of the site, in boreal felt lichen occupied plots, this tree will have at least 1 boreal felt lichen thallus. In boreal felt lichen unoccupied plots, there will be no boreal felt lichen individuals on this tree.

Unoccupied Plot: The plot that is to be paired with boreal felt lichen positive plot. This site will be found within 100m of the paired positive site and will be within the same stand. This plot will contain no boreal felt lichen.

Materials

DBH measuring tape, GPS, Compass, Spherical densiometer, 50m measuring tape, rope, flagging tape various colours, brown paper bags, stopwatch, 2m folding ruler, clinometer, clipboard, data sheets.

Chapter 4 Protocol

Plot selection and construction

1) 25 plots with a boreal felt lichen will be selected using coordinates from past sightings, or completely new findings. At the centre of the plot will be the host tree. From that centre point, the plot will be delineated by measuring a 5m radius from the centre in each cardinal direction (See Figure 1). After the boreal felt lichen occupied plot is established, a neighbouring unoccupied plot are subjectively set up in close proximity (aim for <100m) and will be built in the same stand. This allows us to compare a plot that has presence to one with no boreal felt lichen found. The boreal felt lichen unoccupied plot will be centred on a balsam fir tree that is similar in size to the boreal felt lichenr occupied plot and the same procedure will be use to outline the plot. The unoccupied plot will then be sampled to ensure there are no trees with thalli found on them. To do so, each tree within the plot will be surveyed from the base up to 3 metres high. The total sampling effort on each plot will be 20 minutes, with 2 people looking for lichens.
2) One tree per quadrant will be selected and measured for the tree level measurements. For example, in plot 5, the tree that is selected in quadrant A will be labelled 5A Centre point tree will be identified as R(5A) on the negative sites, and H(5A) on the positive sites. These numbers can be converted into continuous numbers at the end for statistical analysis.
3) The reference tree will be flagged with blue flagging tape and be marked as R# (Each number will correspond to the site number the tree is found in). If a tree

was to land directly on the quadrant division, the North tree will be part of quadrant A, the East tree will be part of quadrant B, the South tree will be part of quadrant C and the West tree will be part of quadrant D.

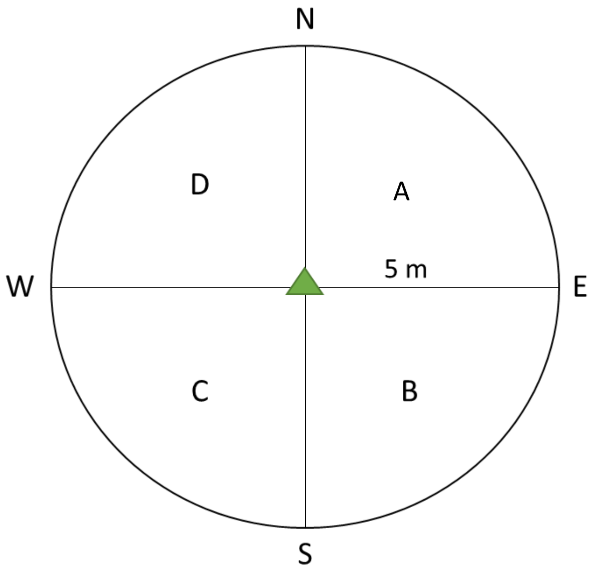

Figure C.1. Illustration of how to set up each site for sampling. The host tree (green triangle) is marked as the centre and from there we will measure out 5m and mark off the perimeter of the site at 4 points.

Survey protocol for new boreal felt lichen thalli

4) Any new boreal felt lichen trees will be recorded as has been in previous years. Data will be taken on: tree coordinates, DBH (cm), height up the tree (cm), thallus width, apothecia presence/absence, surveyer who discovered, date discovered and tree description that includes species name and condition.

Beyond plot measurements

5) Once the plots have been constructed, the plot-level data will be obtained. The first task will be to take distance measurements of both the nearest deciduous tree and the nearest gap. The nearest broadleaf tree can be either a yellow birch (*Betula alleghenensis*), red maple (*Acer rubrum*) or white birch (*Betula papyrifera*). If other broadleafs are nearby they will be noted as well but these are the three species normally found in this ecoregion. The distance from gap will be categorized as windthrow, bog (or wetland) and anthropogenic disturbance. The distances will be measured with a 50m measuring tape.

Plot Level Measurements

6) To determine the slope face aspect, I will face downslope with the compass and determine what bearing I am facing. The steepness of the slope will also be recorded using a clinometer from the peak of the slope and reading the degree level while sighting in at the surveyer’s height on a tree at the bottom of the slope. The total number of trees will be counted at each site, and the standing snags will be counted separately.

Tree level measurements

7) The Tree level measurements will be taken after the plot level measurements. The trees will be surveyed on occupied plots using the point quarter method that is constrained to the 5m radius. Including the reference tree, one tree from each quadrant will be selected for morphometric measurements (Height and DBH).

Height is measured using a clinometer, and a calculation of the slope from a distance of either 10 m, or 15m if the top of the crown is not visible from 10m. The tree will be selected based on distance from the centrepoint, it should be the closest tree to the perimeter of the plot without going outside the boundary, but if it is a host tree it will be preferentially selected. On boreal felt lichen occupied trees, the thallus width will be measured using a ruler, as well as the height up the tree the thallus is found at. The thallus will be located by the side of the tree they are found at, using a compass to get a bearing on the direction the thallus is facing. The number of apothecia will be counted for each mature thallus. Canopy openness will be determined using a spherical densiometer at the tree level, where 4 measurements are taken in one spot, but facing the four cardinal directions at arms length from the tree. These values are then averaged out and corrected for percent canopy openness. On trees with boreal felt lichen these measurements will be taken on the side of the tree the thallus is found on. On trees without boreal felt lichen, these measurements will be taken on a randomly selected side of the tree.