Drivers of change in the temperate-boreal refugium of Cape Breton Highlands National Park

by © Hannah Kosick

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Abstract

The Acadian-Maritime boreal ecotone of Cape Breton Highlands National Park contains low-elevation temperate species (Wabanaki-Acadian forest), and isolated patches of highland boreal stands at their northern and southern geographic extremes, respectively. The cumulative effects of moose herbivory, continued warming, and an imminent spruce budworm outbreak are expected to increase ecological pressures on the boreal forest, further isolating at-risk species. In addition to these stressors, climate change could induce range shifts of Acadian forests, constraining boreal species distributions. Our study identified if/where Acadian forest range shifts are occurring, examined if moose constrain species expansion, and assessed the availability of species-specific seedbeds. Despite the potential for Acadian range expansion, we did not find evidence of range shifts. Our findings suggest multiple constraints on Acadian forest range expansion, including moose herbivory and lack of suitable Acadian seedbeds at higher altitudes. We observed red maple (*Acer rubrum*) succession at moose meadows (historic boreal habitat), indicating persistent transitional stages of the boreal forest. Although range shifts have yet to occur, red maple success at moose meadow sites could facilitate Acadian forest expansion if herbivory pressures are reduced. Our research contributes to understanding Acadian-boreal forest dynamics at geographic extremes and establishes a foundation for long-term monitoring.

Key words: range shifts, refugia, Acadian forest, boreal forest, ecotone, *Acer rubrum*

General Summary

Cape Breton Highlands National Park has two main forest types: boreal and Acadian. The boreal forest predominantly consists of coniferous species. It is found in cooler climates at higher elevations in the Park. The Acadian forest has many warm-adapted deciduous trees in the valleys. Climate change, moose herbivory and insect outbreaks threaten the isolated boreal forest of this region. Rising temperatures in the area could allow Acadian species to grow at higher altitudes where, historically, boreal forests have resided. In the end, we found that Acadian species are not growing at higher altitudes despite regional warming. There are few areas at high altitudes with suitable seedbeds for Acadian seedlings to grow. If Acadian tree species did germinate, moose would likely eat them. Unlike Acadian species, red maple has been able to grow at higher altitudes. In the future, red maple could help Acadian forests expand their habitat by creating suitable seedbeds.

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Table of Contents

Abstract .... **ii**

General Summary .... **iii**

Acknowledgements .... **iv**

Table of Contents .... **vii**

List of Tables .... **ix**

List of Figures .... **xi**

List of Appendices .... **xiv**

Co-Authorship Statement .... **xv**

Chapter 1 : Introduction and thesis overview **1**

1.1 Introduction **1**

1.1.1 Forests under global change *1*

1.1.1.1 The boreal forest 1

1.1.1.2 The temperate forest 3

1.1.1.3 The Acadian forest 5

1.1.1.4 Forest refugia 7

1.1.1.5 Ecotones 8

1.1.1.5.1 The boreal-temperate ecotone 8

1.1.2 Biotic and abiotic determinants of change *9*

1.1.2.1 Topography 9

1.1.2.2 Canopy and light 10

1.1.2.3 Herbivory 11

1.1.2.4 Seedbed type 12

1.1.3 Forest range shifts *14*

1.2 Study Area: Cape Breton Highlands National Park **18**

1.2.1 Ecoregions and ecodistricts *19*

1.2.1.1 Cape Breton Highlands Ecodistrict 19

1.2.1.2 Cape Breton Hills Ecodistrict 20

1.2.2 Ecological history *20*

1.2.3 Previous boreal forest research *22*

1.3 Research significance **23**

1.4 Thesis overview and objectives **25**

1.5 Figures **27**

1.6 References **32**

Chapter 2 : Drivers of change in the temperate-boreal refugium of Cape Breton Highlands National Park **50**

2.1 Introduction **50**

2.2 Methods **52**

2.2.1 Study area *52*
2.2.2 Study Species *53*
2.2.3 Field methods *54*
2.2.3.1 Sampling Strategy 55
2.2.3.2 Plot Design and Measurements 55
2.2.4 Statistical analyses *57*
2.2.4.1 Are Acadian forest range shifts occurring in CBHNP? 58
2.2.4.2 Do moose preferentially browse on tree species at different site types? 59
2.2.4.3 Is tree species establishment limited by seedbed type? 59

2.3 Results 60
2.3.1 Are Acadian forest range shifts occurring in CBHNP? *60*
2.3.2 Do moose preferentially browse on tree species at different site types? *61*
2.3.3 Is tree species establishment limited by seedbed type? *62*

2.4 Discussion 62
2.4.1 Multiple constraints on range shifts *63*
2.4.2 The role of ungulate herbivory *65*
2.4.3. Seedling microsites inhibit temperate range expansions *67*

2.5 Recommendations 69

2.6 Conclusion 70

2.7 Tables 72

2.8 Figures 80

2.9 References 96

Chapter 3 : Summary and conclusions 114

3.1 Summary of findings 114

3.2 Study considerations and next steps 116

3.3 Management recommendations 118
3.3.1 Plan for success 119
3.3.2 Share the load 120
3.3.3 Prioritize and maximize conservation 121

3.4 Tables 123

3.5 References 124

Appendix I: Tree species identification guide 127
Appendix II: Field sites 129
Appendix III: Generalized linear model outputs 131

List of Tables

Table 2.1. Site types were used to categorize research fieldwork sites (n=28) in CBHNP 72

Table 2.2. Ungulate herbivory on different tree species in CBHNP. Using the Preference Index from Basquil and Thompson's research on ungulate herbivory in the Park in 1997, this table compares ungulate herbivory preferences from 30 years ago to what we observed in the field in summer 2022. 73

Table 2.3. Biotic and abiotic variables used for data analysis..........74

Table 2.4. Summary of results from a GLM on the seedling proportion of Acadian, boreal, and red maple seedlings present at different altitudes(m) (Figure 2.10). Altitude and species group were predictor variables with seedling proportion as the response variable. This model assumes a Gaussian distribution. Values in bold indicate a significant difference (p-value < 0.05)............76

Table 2.5. Summary of results from a GLM on the population density of Acadian, boreal, and red maple seedlings present at different altitudes(m) (Figure 2.10). Altitude and species group were predictor variables with seedling population density as the response variable. This model assumes a Gaussian distribution. Values in bold indicate a significant difference (p-value < 0.05). 77

Table 2.6. Summary of results from a two-way ANOVA on seedling proportion of seedlings present at different site types within species groups (Figure 2.11). Site type and species group were the predictor variables with seedling proportion as the response variable. Values in bold indicate a significant difference (p-value < 0.05)..........77

Table 2.7. Summary of results from a GLM on the seedling proportion of Acadian, boreal, and red maple seedlings present with Acadian canopy coverage (Figure 2.12). Acadian canopy percentage and species group were predictor variables with seedling proportion as the response

variable. This model assumes a Gaussian distribution. Values in bold indicate a significant difference (p-value < 0.05)..78

Table 2.8. Summary of results from a GLM on the seedling proportion of Acadian, boreal, and red maple seedlings present with boreal canopy coverage (Figure 2.12). Acadian canopy percentage and species group were predictor variables with seedling proportion as the response variable. This model assumes a Gaussian distribution. Values in bold indicate a significant difference (p-value < 0.05)..78

Table 2.9. Summary of results from a GLM on the proportion of herbivory on different species (Figure 2.13). Species was the predictor variable with proportion of herbivory as the response variable. This model assumes a Gaussian distribution. Values in bold indicate a significant difference (p-value < 0.05)..79

Table 2.10. Summary of results from a two-way ANOVA on the proportion of herbivory at different site types within species groups (Figure 2.14). Site type and species group were predictor variables with the proportion of herbivory as the response variable. Values in bold indicate a significant difference (p-value < 0.05)..79

Table 3.1. Biotic and abiotic mechanisms recommended to be included in regular site monitoring...123

List of Figures

Figure 1.1 A visual depiction of latitudinal forest range shifts. Climate change, in concert with biotic and abiotic mechanisms, can induce latitudinal range shifts, shifting temperate and boreal forest ranges poleward where climate is more suitable for species. 27

Figure 1.2. A visual depiction of altitudinal forest range shifts. Climate change, in concert with biotic and abiotic mechanisms, can induce altitudinal range shifts, shifting temperate forest ranges upslope into boreal stands. The expansion of temperate forests reduces the amount of habitat available for boreal species. 28

Figure 1.3. Acadian, boreal, ecotone, and moose meadow project field sites throughout CBHNP. Sites span over 400m of elevation from Chéticamp to Big Intervale (M. Kosick, 2023)........... 29

Figure 1.4. The Cape Breton Highlands Ecodistrict (210) ecological landscape analysis (Nova Scotia Department of Natural Resources, 2015a). The boreal forest patches within CBHNP are located within this ecodistrict. 30

Figure 1.5. The Cape Breton Hills Ecodistrict (310) ecological landscape analysis (Nova Scotia Department of Natural Resources, 2015b). The Acadian forest of western CBHNP is part of this ecodistrict 31

Figure 2.1. Flow chart demonstrating the biotic and abiotic mechanisms that correspond to our three research objectives, ultimately branching out from our research focus: forest health......... 80

Figure 2.2. Acadian, boreal, ecotone, and moose meadow sites (n=28) throughout CBHNP. Sites span over 400m of elevation from Chéticamp to Big Intervale (Kosick, M. 2023). 81

Figure 2.3. Altitudinal gradients visualized to delineate Acadian, ecotone, and boreal regions of CBHNP using our site selection parameters. Elevation ranges from 1.1-150m, 150.1-400m, and 400m+ illustrate Acadian, ecotone, and boreal regions, respectively (Kosick, M. 2023). 82

Figure 2.4. Moose meadow sites are present throughout the historic boreal regions of the Park, especially around North Mountain and French Mountain. These sites contain tall grasses, ericaceous heaths, and standing deadwood (typically white birch)... 83

Figure 2.5. Visuals of the four different site types in CBHNP. (A) Acadian site EMAN GA1, (B) ecotone site EMAN FC, (C) moose meadow site F2, and (D) boreal site E5............................. 84

Figure 2.6. 32m^2 circular sites (n=28) were established at Acadian, boreal, moose meadow, and ecotone sites. Our sampling design is nested; Objectives 1 and 2 occur within the entire plot, while Objective 3 occurs in quadrats within the circular plot.. 85

Figure 2.7. Levels of herbivory on deciduous white birch (B. papyrifera) and coniferous balsam fir (A. balsamea) trees. Low herbivory is characterized by intact apical meristem. Medium and high herbivory is characterized by an apical meristem that ungulates have removed. Browse severity intensifies from low to high herbivory. 86

Figure 2.8. Tree species observed at field sites in CBHNP organized by species group. Red maple, balsam fir, white birch, and sugar maple were the most observed species across field sites. 87

Figure 2.9. Tree species distribution along altitudinal gradients in CBHNP. In general, Acadian species were observed at lower altitudes, boreal species at higher altitudes, with red maple being found across all altitudinal gradients. 88

Figure 2.10. The proportion and density of Acadian, boreal, and red maple seedlings present at different altitudes. Acadian species were not observed at altitudes greater than 350m. Boreal and red maple seedlings were present across altitudinal gradients. Acadian seedling density was greater at lower altitudes, and Boreal seedling density was greater at higher altitudes. Red maple density remained relatively consistent across altitudinal gradients, with few exceptions........... 89

Figure 2.11. The proportion of Acadian, red maple, and boreal seedlings present at different site types in CBHNP. The proportion of Acadian seedlings present at Acadian sites (i.e., sites <150m elevation) is greater than at ecotone sites (i.e., sites between 150 and 400m elevation). Acadian seedlings were not observed at boreal or moose meadow sites (i.e., sites > 400m). The proportion of boreal seedlings present was greatest at boreal sites. The proportion of A. rubrum seedlings was greater at ecotone and moose meadow sites...90

Figure 2.12. The proportion of Acadian, red maple, and boreal seedlings present with different canopy coverage and type. 91

Figure 2.13. The proportion of ungulate herbivory on individual observations of different tree species categorized by species group at field sites throughout CBHNP 92

Figure 2.14. Proportion of herbivory observed at different site types within species groups. Acadian species were not observed at boreal or moose meadow sites; therefore, we could not calculate herbivory proportion for this species group at these site types 93

Figure 2.15. Most common seedbeds observed at seedling microsites in CBHNP.....................94

Figure 2.16. Most common seedbeds observed at seedling microsites within three species groups: Acadian, red maple, and boreal...95

List of Appendices

Appendix I: Tree species identification guide 127

Appendix II: Field sites 129

Appendix III: Generalized linear model outputs 131

Co-Authorship Statement

Dr. Carissa Brown is a co-author on all chapters of this thesis and contributed significantly to project conceptualization, design, analysis, and manuscript preparation. As this project's primary author and researcher, I led the literature review, research proposal, project logistics, data collection and analysis, and manuscript preparation.

Chapter 1 : Introduction and thesis overview

1.1 Introduction

1.1.1 Forests under global change

Forests are critical biomes that store carbon, produce oxygen, cycle nutrients, and create habitat for diverse species. Forests are also experiencing stresses of ongoing global change, from land use change to climate change. Predicting the outcome of those stresses on forest structure and function is key to managing and conserving these landscapes in the long term. Areas at the edge of species distributions often provide a glimpse into what may happen more broadly across a biome in the future. Here, we use the temperate-boreal forest transitions of the Cape Breton Highlands, at the southeasterly most range of the boreal forest, as a model system to understand the role of temperate species, herbivores, and ongoing climate change on the future of these remnant (or refugia) boreal forest stands.

1.1.1.1 The boreal forest

Boreal forests are important economic, cultural, and ecological systems. Economically, the boreal forest produces timber forest products in the form of lumber and paper (Gauthier et al., 2015). Culturally, the boreal forest is an integral part of indigeneity. From hunting and fishing to spiritual activities, the boreal forest is intrinsically linked to cultural identity for many Indigenous peoples (Gauthier et al., 2015; Uprety et al., 2012). At least 546 medicinal plants grow in the boreal forest of Canada (Uprety et al., 2012), some of which help treat major ailments, from physical injuries to coughs and colds. Ecologically, boreal forests provide vital habitat for species and contribute to water and energy cycling. The boreal forest is a significant carbon sink (Aalto et al., 2023; Kasischke et al., 1995) and, thus, can store and sequester carbon, reducing carbon dioxide in the atmosphere.

The boreal forest is found throughout the northern hemisphere (Kayes & Mallik, 2020) and mainly consists of coniferous tree species with scattered deciduous taxa throughout (Kayes & Mallik, 2020; Price et al., 2013; Shugart et al., 1992). Some species found within the boreal forest include white spruce (*Picea glauca*), black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), and white birch (*Betula papyrifera*) (Gauthier et al., 2015; Rowe, 1972). Wolves (*Canis lupus*), warblers (e.g., *Cardellina canadensis*), owls (Order *Strigiformes*), beavers (Genus *Castor*), bears (Genus *Ursus*), hares (Genus *Lepus*), and several species of ungulates are common residents in the boreal forest and are well-adapted to the cool climate (Kayes & Mallik, 2020). This region is characterized by long, cold winters and short, cool summers (Price et al., 2013; Stralberg et al., 2020) with freezing temperatures and snow coverage lasting anywhere from 6 to 8 months of the year (Gauthier et al., 2015).

A healthy boreal forest is a balanced ecosystem with varying aged stands (Charron et al., 2020). The forest understory mainly consists of mosses and leaf litter with some lichen (Mallik & Kayes, 2018; Nagati et al., 2020). For many boreal species (e.g., balsam fir), regeneration occurs in closed-canopy environments where trees germinate together to form a tight-knit community of saplings (Leroux et al., 2021). Disturbance regimes are a natural part of the boreal forest cycle, thus making boreal species highly adaptive and resilient (Gauthier et al., 2015). Fire and insect outbreaks are routine occurrences and significantly contribute to the overall health of the ecosystem (Gauthier et al., 2015; Johns et al., 2019; Stralberg et al., 2020).

Fire is the dominant natural disturbance driving the structure and function of the boreal forest. Many boreal species (e.g., jack pine, *Pinus banksiana*) are adapted to fire and require specific postfire conditions to release their seeds, germinate, and survive (Baltzer et al., 2021).

Fire also releases nutrients into the ecosystem and reduces soil organic matter, making it easier for seeds of fire-adapted boreal species to germinate (Baltzer et al., 2021; Kasischke et al., 1995).

In eastern and Atlantic Canada, spruce budworm (*Choristoneura fumiferana)* outbreaks are another landscape-scale disturbance regime in these balsam fir dominant boreal forests. Spruce budworms are defoliating insects and have co-evolved with balsam fir to create a cycle of disturbance and succession (Collier et al., 2022). Outbreaks coincide with ecosystem phenology, the specific climate patterns and temperature changes that occur due to the changing seasons' (Walther et al., 2002). The synchrony between budburst and larvae emergence plays a vital role in balsam fir survival (Pureswaran et al., 2019). Windthrow events are also important in boreal forests at the local scale, creating gap openings and increasing light for tree recruitment (Taylor et al., 2020).

After a natural or anthropogenic disturbance, boreal forests become an ideal habitat for fast-growing, early successional, deciduous species (Périé & de Blois, 2016), which can change the chemical and physical compositions of the forest (Mallik & Kayes, 2018). In the following decades, conditions become more favourable for conifer species, which grow much slower (Kolstad et al., 2018). The regeneration of boreal forests is complex and takes place over a significant period of time, which means there is ample opportunity for complications (i.e., additional pressures from diseases, insect outbreaks, herbivory, fire, and anthropogenic influences).

1.1.1.2 The temperate forest

Similar to the boreal forest, temperate forests significantly contribute to local economies, cultures, and ecology. Due to their geographic location, temperate forests have long-standing relationships with humans, as we have colonized extensively in the temperate region (Gilliam, 2016). Over the centuries, we have exploited the bounties of this ecosystem for economic purposes, mainly forestry, and thus, have left substantial ecological footprints on this forest type. Due to consistent, repeated logging, less than 1% of global temperate old-growth forests (> 150 years old) remain (Gilliam, 2016; Millar & Stephenson, 2015). A significant anthropogenic presence in the temperate region has resulted in diverse cultural relationships with temperate forests. Worldwide, temperate forest plant species are used in dyes, as material for shelters or crafting, and for consumption by Indigenous peoples (Barreau et al., 2016). A healthy and sustainable forest ecosystem promises that future generations will have access to this environment's economic and cultural riches for years.

Temperate forests are diverse and are predominantly made up of hardwood deciduous taxa with scattered conifers. Maples (*Acer* spp.), oaks (*Quercus* spp.), birches (*Betula* spp.), and American beech (*Fagus grandifolia*) are some of the most common deciduous species, with spruces (*Picea* spp.), firs (*Abies* spp.), pines (*Pinus* spp.), and hemlocks (*Tsuga* spp.) as the most common coniferous species (Gilliam, 2016; McCarragher & Rigg, 2020). These conifers are primarily present in extreme environmental conditions as they are more resilient to cold, wind, salt, and infertile soils than deciduous taxa (Gilliam, 2016). Temperate forests are subject to natural disturbances such as insects, windthrow, and occasionally fire (Keddy & Drummond, 1996).

As their name suggests, temperate forests have moderate climates and can be found worldwide in mid-latitude regions (McCarragher & Rigg, 2020). Three different types of temperate forests exist; temperate deciduous forests, temperate coniferous forests, and temperate mixed forests (McCarragher & Rigg, 2020). All temperate forests are characterized by distinct seasons with humid, mild summers and dry, cold winters (McCarragher & Rigg, 2020); however, forests are regionally influenced by topographic elements (i.e., mountains) and aquatic features (i.e., oceans), which have unique effects on local climates (Gilliam, 2016).

The temperate forest understory varies and can consist of moss, lichen, and leaflitter seedbeds, which are suitable for coniferous and deciduous species (McCarragher & Rigg, 2020). Seedlings can spend years living in low-light conditions under towering deciduous canopies. Thus, many temperate deciduous species are shade tolerant; however, a consistent increase in anthropogenic disturbance has led to more shade-intolerant species establishing themselves in the understory (Keddy & Drummond, 1996).

1.1.1.3 The Acadian forest

The Wabanaki-Acadian forest is a temperate mixed forest unique to the Maritime provinces and the north-eastern United States. This forest is found throughout Mi'kma'ki, the traditional, unceded territory of the Mi'kmaw, Maliseet (Wolastoqey), Passamaquoddy, and Penobscot peoples (The Nashwaak Watershed Association, 2021). Today, the Wabanaki-Acadian forest is more commonly known as the Acadian/New England forest or simply the Acadian forest, named for the Acadian peoples, who were some of the earliest European colonizers of the area. This forest has significantly influenced Mi'kmaw and Acadian culture, particularly in the form of traditional medicines (Cormier-Boudreau, 1992; Deschênes, 1992; B. Jones, 2020). Some widespread examples of ethnomedicines in the Acadian forest include Chaga (*Inonotus obliquus*) (Brydon-Williams et al., 2021), wild sarsaparilla (*Aralia nudicaulis*) (Arseneau, 2019.; B. Jones, 2020), several species of birch (MacLeod et al., 1976), and St. John's Wort (*Hypericum perforatum*) (B. Jones, 2020).

A diverse ecosystem with regionally distinct assemblages, old-growth, mixed Acadian forests are some of the oldest forests in eastern Canada. Some of the oldest, yet few, remaining

Acadian forest stands are over 150 years old, with some individuals at protected sites (e.g., Kejimkujik National Park) are recorded as over 350 years old (Fulton et al., 2023; Mosseler et al., 2003). The Acadian forest region exhibits similar characteristics as the Great Lakes-St. Lawrence forest region and the boreal forest region (Rowe, 1972). Generally, Acadian forests are a transition between temperate and boreal biomes, placing species at their southernmost or northernmost geographic range (Taylor et al., 2017, 2020; Vaughn et al., 2021). Balsam fir (*Abies balsamea*), yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), and American beech are prevalent in this mixed forest, and in many cases, red spruce (*Picea rubens*) is also present (Neily & Parsons, 2017; Rowe, 1972). Similar to boreal and temperate forests, the Acadian forest is prone to disturbances such as fire, windthrow, and insect outbreaks (Mosseler et al., 2003; Neily et al., 2017).

Like other temperate forests, the Acadian forest has warm, humid summers and cold winters with distinct seasonal changes in climate (McCarragher & Rigg, 2020; Mosseler et al., 2003; Swift et al., 2006.). Some Acadian species need between 40 and 90 days near freezing to ensure seeds are released and are able to germinate in spring (Vaughn et al., 2021, 2022; Vaughn & Taylor, 2022). Snow depth is also important as it helps insulate seeds and seedlings during winter. As the Acadian forest is dominated by a deciduous overstory, species within the Acadian forest are typically shade tolerant or shade intermediate (Neily & Parsons, 2017; Vaughn et al., 2021a), meaning they can survive in low light conditions. In most places, Acadian forests have medium nutrient-rich, well drained soils (Neily et al., 2017) which is ideal for deciduous species with specific nutrient requirements (e.g., sugar maple) (Collin et al., 2016).

1.1.1.4 Forest refugia

Tree species are resilient; however, there comes a point when a species reaches its physiological limit. As climate change affects forest ecosystems, species ranges may shift, with small populations remaining in forest refugia. These climate change-resistant landscapes act as "stepping stones" (Hannah et al., 2014) for species range shifts (Stralberg et al., 2020). Unlike refuges, which provide temporary refuge for an individual, refugia can support small species populations for extended periods (Ashcroft, 2010).

There are two types of refugia: macrorefugia and microrefugia. Refugia size is influenced by a hierarchy of processes with latitude, continentality, and elevation producing larger macrorefugia and finer-scale processes such as surficial geology, landform and lake effects, and ecological inertia producing smaller microrefugia (Stralberg et al., 2020). Macrorefugia are larger ecosystems with expansive spatial, climate, and temporal gradients at the regional scale (Ashcroft, 2010; Stralberg et al., 2018). In contrast, microrefugia house smaller populations of species nestled within microclimates decoupled from local climate conditions (Ashcroft, 2010; Hannah et al., 2014; Stralberg et al., 2018). Human land-use can exacerbate refugia by fragmenting population distribution (Ashcroft, 2010). Further, physical features can influence thermal differences in the landscape, carving out microrefugia (Estevo et al., 2022; Stralberg et al., 2018). For example, ecological features such as mountains, interior plateaus, lakes, and coastal regions are frequently associated with boreal refugia as they exacerbate boreal environmental conditions (Stralberg et al., 2020).

Refugia are also defined as being *in situ* or *ex situ* (Ashcroft, 2010). An *in situ* refugia refers to a landscape that continues to be a suitable habitat for a species, whereas in an *ex situ* refugia, climatic conditions are periodically unfavourable for that species (Ashcroft, 2010).

Generally, refugia are valuable ecosystems when faced with global change (Stralberg et al., 2018). *Ex situ* microrefugia are particularly resilient as they remain even if there is a shift in regional climatic patterns causing the disappearance of macrorefugia (Ashcroft, 2010). In extreme cases, microrefugia become places where "tailing-edge populations" (Gilbert et al., 2022) make their last stand if they cannot shift their distributions.

1.1.1.5 Ecotones

As one forest ecosystem transitions to the next, ecological communities converge along gradients creating a unique, integrated habitat called an ecotone. These regions are influenced by ecological stress as habitat and climate become more favourable for different species types (Goldblum & Rigg, 2010). Ecotones can have distinct transitions, such as the shift from prairie to a forest or more subtle transitions between forest types (Goldblum & Rigg, 2010). These constantly shifting ecological edges can tell us much about species' resilience and ecological integrity.

1.1.1.5.1 The boreal-temperate ecotone

In regions throughout the northern hemisphere, as the latitude increases, average annual temperatures decrease, creating more favourable conditions for boreal species. At more southern latitudes, the temperature is milder, creating suitable conditions for temperate species establishment. Between temperate and boreal forests lies the boreal-temperate ecotone, a transitional area where the ecosystems converge to form mixed forest landscapes (Evans et al., 2020; Goldblum & Rigg, 2010). As climate change progresses, the boreal-temperate ecotone will be subject to warming temperatures and increased precipitation, potentially altering species distribution (Evans & Brown, 2017a).

As latitude and altitude increase, viable seed availability decreases (Frei et al., 2018) making it more challenging for temperate-deciduous species to germinate. Mechanisms such as climate, substrate, precipitation, drainage, soil nutrients, and physical soil properties influence what species can survive and thrive throughout environmental gradients (Goldblum & Rigg, 2010).

1.1.2 Biotic and abiotic determinants of change

The combined effects of biotic and abiotic mechanisms influence what species can grow and where (Evans & Brown, 2017a). Some of these mechanisms include overstory, seedbed, herbivory (biotic), altitude, and light (abiotic), which together can inhibit or facilitate seedling growth.

1.1.2.1 Topography

Landscape topography plays a significant role in determining what species can grow and where. From oceanic and lake influences to mountains and highlands, topography can put seedlings under stress (e.g., salt spray, wind, lower temperatures), making germinating and surviving challenging for some species. Topographic changes are often linked to changes in climate (Goldblum & Rigg, 2010), such as wind velocity, temperature, and precipitation. Topography can also influence species richness. For example, higher elevations are typically associated with lower species richness, as it is more challenging for some species to thrive at higher altitudes (Savage & Vellend, 2015). Lower minimum temperatures (Savage & Vellend, 2015), herbivory (Brown & Vellend, 2014), natural disturbances such as insect or pathogen outbreaks, and anthropogenic mechanisms like air pollution (Beckage et al., 2008) can make it particularly challenging for species to establish themselves at higher elevations. Within the boreal-temperate ecotone, the boreal forest dominates higher elevation sites (Beckage et al., 2008; Foster & D'Amato, 2015) where the environmental conditions are too harsh for temperate species, which prefer nutrient-rich, lower elevations (Brown & Vellend, 2014).

1.1.2.2 Canopy and light

Forest canopies can influence understory growth in many ways, including determining how much light is available for seedlings and generating species-specific seedbed conditions. Light availability is often credited as one of the main mechanisms influencing understory composition (Su et al., 2019). After a disturbance (i.e. fire, insect outbreak), more light is available in the understory, creating favourable vascular plant growth conditions. As the forest matures, light availability decreases, and understory composition shifts, becoming more favourable for non-vascular plants such as mosses and lichens. A decrease in light availability increases understory resource competition and limits vascular plant growth and regeneration (Su et al., 2019). Canopies also influence seedbed typing. For example, in a predominantly deciduous canopy, trees are exposed to a season of dormancy where they lose their leaves (McCarragher & Rigg, 2020). These leaves are deposited on the forest floor and become nutrient-rich seedbeds.

The boreal forest mainly consists of coniferous species (i.e. white spruce, black spruce, balsam fir) with several deciduous species (e.g., white birch) scattered throughout (Neily et al., 2017). These trees significantly influence the amount of light available for understory plants. Balsam fir trees, in particular, grow in dense stands with thick overstory canopies, which can influence seedbed quality and seedling survival rates (Leroux et al., 2021). Depending on the species, some seedlings are more shade tolerant than others. For example, white spruce is considered intermediately tolerant to shade, whereas white birch is very shade-intolerant (Robert et al., 2012).

Within temperate and Acadian forests, canopies are not remarkably diverse (Keddy & Drummond, 1996); however, the understory below is where species vie for space and light beneath the light-inhibiting canopy. Tree species within temperate and Acadian forests can range from shade tolerant to intolerant (Keddy & Drummond, 1996).

1.1.2.3 Herbivory

Herbivory shapes forest composition by altering seedling growth rates and forest succession pathways, increasing competition among species (Kolstad et al., 2018; Vuorinen et al., 2020). In some circumstances, herbivory can reduce (Kain et al., 2011) or enhance species richness and diversity, and thus plays a critical role in the successional trajectory of a boreal forest in the early stages of post-disturbance. For example, herbivory frequently occurs alongside disturbances (e.g., insect outbreaks), delaying seedling regeneration and having long-lasting effects on forest composition (Kolstad et al., 2018; Leroux et al., 2021).

Due to their height, ungulates can have the most profound herbivore effect on plant structure (Vuorinen et al., 2020). Ungulate browsing has direct and indirect effects on the successional trajectory of boreal forests, including selective browsing of seedlings and saplings, trampling and modification of seedbeds, and herbivory itself (Ellis & Leroux, 2017; C. M. A. Franklin & Harper, 2016; Leroux et al., 2021). Herbivory leads to many other mechanisms that influence forest recovery, including removing shade for seedlings and saplings and increasing the amount of light availability, which raises soil temperatures (Kolstad et al., 2018). Herbivory can influence climate in many ways. For example, herbivory can increase surface albedo, thus causing climate cooling, and limit carbon sequestration by reducing the number of trees present, causing the climate to warm (Salisbury et al., 2023).

Herbivory resilience varies by plant species (Vuorinen et al., 2020). Boreal species such as white birch and balsam fir are essential to a moose's diet and, therefore, often exposed to browsing pressures. White birch is the preferred browse species for moose; however, as it is deciduous, forage is primarily available for moose in the spring and summer months. Therefore, balsam fir, a coniferous species that retains its needles year-round, is an essential staple for a moose's fall and winter diet (C. M. A. Franklin & Harper, 2016).

Ungulates preferentially forage where they will receive high quantities of nourishment for little energy (Ellis & Leroux, 2017; Kuijper et al., 2009). Forest gaps are suitable for foraging as trees have greater light availability for growth and are more accessible for large herbivores (Kuijper et al., 2009). Forest gaps become foraging hotspots for ungulates which are likely to re-browse (Mathisen et al., 2017) previously visited sites, producing shrub-like seedlings (Ellis & Leroux, 2017). Rebrowsing benefits herbivores as they can return to the same sapling or shrub at an accessible height with new shoots to forage on (Mathisen et al., 2017). Rebrowsing in forest gaps post disturbance can result in moose meadows, also known as moose spruce savannahs, a grassland like habitat with sporadic and less palatable spruce regeneration (Noonan et al., 2021). Where removing browsing pressures aids in forest recovery, active management is required to revert forest structure and composition to its historic state (Noonan et al., 2021).

1.1.2.4 Seedbed type

Seedbeds and established seedling microsites promote germination and growth and produce healthy seedlings and saplings (Collier et al., 2022; Mallik & Kayes, 2018). Different species have different seedbed preferences (i.e., species-specific seedbeds) that depend on tree type (deciduous or coniferous), seed size, and germination method. Species-specific seedbeds create an environmental buffer for seedlings allowing them to thrive with non-optimal conditions (e.g., high quantities of precipitation) (Clark & D'Amato, 2023). Where some research shows seedbed type does not constrain germination (Bélanger & Chaput-Richard, 2023), some species have niche seedbed requirements (e.g., sugar maple) and thus are more limited (McCarragher et al., 2011).

Seedbeds are edaphic, meaning they are influenced by soil composition and nutrient availability. Temperate and boreal species have unique seedbed and soil requirements. Boreal seedbeds (i.e., needle litter) and soils tend to be more acidic, which is unsuitable for temperate species establishment (Bélanger & Chaput-Richard, 2023). In contrast, leaf litter decomposition produces carbon and nutrient-rich soil, which is ideal for temperate species (Bélanger & Chaput-Richard, 2023; McCarragher & Rigg, 2020). Mosses and lichen seedbeds create a thick carpet layer on the forest floor which can be challenging for some seedlings to germinate both physically and chemically; however, some species may benefit from the moisture retention properties of these seedbeds (Clark & D'Amato, 2023; Mallik & Kayes, 2018).

Research on boreal species suggests that black spruce, white spruce, balsam fir, and white birch show a preference for moss seedbeds over lichen and leaf litter seedbeds (Leroux et al., 2021; Mallik & Kayes, 2018). Moss seedbeds retain moisture levels and have a much lower soil temperature than leaf litter seedbeds, which is favourable for boreal seedling germination. Interestingly, Nagati et al. (2020) identified that balsam fir had similar survival rates on moss and leaf litter seedbeds. Balsam fir seeds are much larger than black spruce, white spruce, and white birch seeds, which could contribute to their success on both seedbeds; however, in most circumstances, leaf litter seedbeds are not available for balsam fir seeds. Regardless, the research community has yet to agree on the defining characteristics of optimal seedbeds for balsam fir (Robert et al., 2012).

In addition to soil organic layers, woody debris and herbaceous shrubs influence seedbed quality and seedling germination (Gilliam, 2007; C. E. Jones & Landhäusser, 2018). Low-growing species such as bunchberry (*Cornus canadensis*) are commonly found along the forest floor where boreal species grow (Leroux et al., 2021). Ericaceous heaths, a community of plants that prefer acidic soil, impede tree growth and have been known to limit tree recruitment (Mallik & Kayes, 2018; Nagati et al., 2020). Some researchers have hypothesized that the presence of logs (e.g., nurse logs) can provide additional protection for seedlings and increase the probability of germination (C. E. Jones & Landhäusser, 2018).

Topography, forest overstory, light availability, herbivory, and seedbed type collectively influence species distribution across temporal and environmental gradients. In addition to these biotic and abiotic mechanisms, climate change can exacerbate non-optimal growing conditions for seedlings, altering succession pathways and changing forest dynamics. More specifically, climate change can induce forest range shifts, expanding or contracting species ranges as they respond to warming temperatures, droughts, or other environmental changes (Simmons & Thomas, 2004).

1.1.3 Forest range shifts

When faced with environmental changes, species have one of three options: adapt, move, or die (Aitken et al., 2008; Price et al., 2013). Naturally, adaptation and shifts in distribution are the preferred responses of species under change. Some species have niche requirements making adapting to a changing environment challenging; however, some species are resilient and adaptable, making species range shifts attainable. Environmental changes within ecotones can create favourable conditions for the species of one ecosystem, allowing them to expand their ranges into another, causing a contraction of the latter species' range (Zhu et al., 2012). These range shifts can occur along latitudinal or altitudinal gradients as species shift poleward, equatorward, upslope, or downslope depending on their climate and environmental preferences (Figure 1.1; Figure 1.2). Ultimately, the direction of range shifts is context specific (Savage & Vellend, 2015), and the extent is influenced by a species' environmental niche requirements and available niche space (Boisvert-Marsh et al., 2020; Solarik et al., 2020). Over time, individual species range shifts can collectively lead to community ecotonal shifts, where the forest shifts its entire distribution. Range shifts are natural and expected as species respond to disturbance events and climatic and ecological changes (Chen et al., 2011). Anthropogenic climate change, however, has expedited range shifts (Beckage et al., 2008; Iverson & Prasad, 2002; Marquis et al., 2021; McCarragher & Rigg, 2020; Walther, 2010). Forest range shifts within ecotones can dramatically alter forest ecosystems, having long-lasting effects on resident species (Brice et al., 2020; Evans & Brown, 2017a; Walther, 2010). Loss of habitat and resources provided by forests can cause a bottom-up trophic cascade, resulting in regional extinctions (Aitken et al., 2008).

Several mechanisms influence species range shifts, including topography, climate, and disturbance regimes. Topography facilitates or inhibits range shifts by creating physical gateways and barriers for species migration (Brice et al., 2020; Estevo et al., 2022; Stralberg et al., 2018). Plant communities shifting upslope may sometimes reach their limit at the mountain summit (Grabherr et al., 1994). This results in a 'shrinking' of habitat for species (Savage & Vellend, 2015). Thus, species ranges contract at lower latitudes and altitudes, with limited expansion potential at high latitudes and altitudes (Zhu et al., 2012). Where upslope range shifts are common, downslope migration of species is also possible (Foster & D'Amato, 2015). Many environmental mechanisms can cause range shifts. Although non-climatic mechanisms greatly influence range shifts (Brown & Vellend, 2014), treelines influenced by warming, particularly winter warming, are more apt to advance (Harsch et al., 2009; Leithead et al., 2010). Range shifts occur episodically and are often linked to climate and disturbance events (Walther et al., 2002). Although climate significantly influences forest transitions, natural and anthropogenic disturbances are the primary facilitator of range shifts (Brice et al., 2020). Therefore, forest history and regional environmental mechanisms dictate range shift potential, which can then be exacerbated by climate change. Post-disturbance treefall gaps may permit southern seedlings to colonize habitat, facilitating range shifts (Brice et al., 2020; Leithead et al., 2010); however, if the seedbed is poor, if there is competition among species, or if herbivory is high, range shifts are constrained. Each species responds differently to these biotic and abiotic mechanisms dependent on their niche requirements and has a unique range limit (Beckage et al., 2008; Goldblum & Rigg, 2010); therefore, range shift responses are species-specific (Boisvert-Marsh et al., 2014; Sittaro et al., 2017) and regionally defined (Collier et al., 2022; Harsch et al., 2009). Regrettably, anthropogenic climate change has increased the frequency and severity of natural disturbances (e.g., fire), putting additional pressure on vulnerable forests (Pureswaran et al., 2019; Stralberg et al., 2020). Species cannot adapt instantaneously to changing climate conditions (Harsch et al., 2009; Walther et al., 2002). Trees are sedentary species and have long lifespans, which means maladapted species could remain present in an area well after climate conditions have changed (Boisvert-Marsh et al., 2014; Harsch et al., 2009; Périé & de Blois, 2016; Price et al., 2013; Solarik et al., 2020). This decoupling of species and climate could influence forest health, productivity, and its successional trajectory (Taylor et al., 2020). When disturbances are combined with other biotic and abiotic mechanisms, boreal forests could experience alternate successional trajectories that could degrade these vital landscapes (Kolstad et al., 2018; Walther, 2010).

Temperate-boreal range shifts have become a prominent point of discussion in literature in the last decade (Brice et al., 2020; Brown & Vellend, 2014; Evans & Brown, 2017a; Leithead et al., 2010; Périé & de Blois, 2016; Sittaro et al., 2017; Solarik et al., 2020). Range shifts within the temperate-boreal ecotone can result in borealization, a decline in temperate tree species and an increase in favourable conditions for boreal species, or the antithesis, deborealization (Noseworthy & Beckley, 2020; Taylor et al., 2017). At latitudes south of 60 degrees N, temperatures have risen with mean annual increases between 0.5 and 3.0°C warming (Price et al., 2013). Continued warming of boreal forest ecosystems at geographic extremes combined with regionally specific biotic and abiotic mechanisms has caused temperate forest range shifts and, in some circumstances, has led to deborealization (Boisvert-Marsh et al., 2014; Harsch et al., 2009; Iverson & Prasad, 2002; Leithead et al., 2010). As climate conditions become more favourable for temperate Acadian species, we can expect they will migrate poleward, which could further constrain boreal forests (Kellman, 2004). When preferred habitat becomes available for temperate Acadian species, their range shift potential increases (Thomas et al., 2001). Not only do temperate species have an advantage over boreal species due to their climate preferences, boreal species are slower growing and are less tolerant to drought and heat making them even more vulnerable (Brice et al., 2020; Goldblum & Rigg, 2010). Although, temperate species range expansion into boreal stands is expected, there are many biotic and abiotic barriers (e.g., "blocking effects") temperate species will face, making recruitment challenging in some circumstances (Solarik et al., 2020; Taylor et al., 2017).

Generally, range shifts are challenging to quantify and document (Sittaro et al., 2017). Recent research in this field calls for studies to explore the intricate connections between range shifts, regional distributions, and biotic and abiotic mechanisms that might influence the expansion or contraction of species ranges (Chen et al., 2011; Sittaro et al., 2017; Walther, 2010). In northeastern North America, Atlantic Canada is expected to become a refugium for boreal species at their most southern geographic range as climate change continues to provide nonoptimal growing conditions for boreal species (Collier et al., 2022; D'Orangeville et al., 2016). One such refugium threatened by temperate Acadian range expansions is the boreal forest of Unama'ki (Cape Breton Island), Nova Scotia.

1.2 Study Area: Cape Breton Highlands National Park

Cape Breton Highlands National Park (CBHNP) is located in northern Nova Scotia on Cape Breton Island, also known as *Unama'ki*, the unceded territory of the Mi'kmaq (Figure 1.3). Cape Breton Island is ecologically and culturally diverse and deeply rooted in Mi'kmaq, Acadian, and Gaelic cultures (Parks Canada, 2022). Hundreds of thousands of sightseers visit CBHNP annually, significantly contributing to the local economy (Neily et al., 2017; Parks Canada, 2022). Many of these visitors come to the island to drive the Cabot Trail. This scenic route winds through the rolling hills of CBHNP, where visitors can see ocean views, experience local culture and marvel at natural wonders. With nearly 1000 km^2 of protected area from the east to the west of Cape Breton Island, CBHNP is a rare boreal-temperate forest refugia with isolated old-growth Acadian forests and patchy remnants of historic boreal forests in the western and central region of the Park (D'Orangeville et al., 2016). In this section, we will discuss the topography, climate, and ecology of the Cape Breton Highlands and Cape Breton Hills Ecodistricts found in CBHNP, review the ecological history of the National Park, and highlight current climate change influences on forest ecology.

1.2.1 Ecoregions and ecodistricts

There are two ecoregions in western CBHNP: Cape Breton Highlands and Nova Scotia Uplands ecoregions. The Cape Breton Highlands ecoregion is found at elevations 300-340 m above sea level in northern Cape Breton, where the climate, topography, and recurring disturbance events support maritime boreal ecosites (Neily et al., 2017). The Nova Scotia Uplands ecoregion is found throughout the North Shore area of mainland Nova Scotia and the western region of Cape Breton Island. A blend of highlands, steep valleys, and lowlands creates favourable habitat for Acadian ecosites. Where disturbance events are infrequent in this ecoregion, wind and ice damage heavily influence seedling and sapling success (Neily et al., 2017). Both ecoregions are heavily influenced by high winds and precipitation, mainly snowfall, with elevation and disturbance regimes being key distinctions between the two (Neily et al., 2017). Within these ecoregions, two ecodistricts support the boreal-temperate forest refugia. The Cape Breton Highlands ecodistrict (Cape Breton Highlands ecoregion) supports boreal forest habitat, and the Cape Breton Hills ecodistrict (Nova Scotia uplands ecoregion) supports Acadian forest habitat.

1.2.1.1 Cape Breton Highlands Ecodistrict

The Cape Breton Highlands ecodistrict is located at high elevations in Cape Breton and makes up most of the Cape Breton Highlands ecoregion (Figure 1.4). The Northern Plateau, an open taiga habitat, makes up the other component of the ecoregion and is found at the highest elevations in northern Cape Breton (Neily et al., 2017). The Cape Breton Highlands Ecodistrict boreal forest is mainly woodland covering over 1800 km^2, primarily found in CBHNP. The mountainous climate provides cool, short summers, long, mild winters, and late springs (Bush & Baldo, 2019). In winter, snowfall can result in 3m of snowpack, insulating seedlings and saplings

(Neily et al., 2017). In some places, strong winds blowing through the highlands result in stunted tree growth (Krummholz), which prevents trees from reaching their full height. Spruce budworm outbreaks occur every 30-40 years, meaning that stand age is typically younger than 75 years, with few exceptions (Taylor et al., 2020). At lower elevations within this ecodistrict, the boreal forest transitions into the Acadian forest habitat of the Cape Breton Hills ecodistrict, creating an isolated boreal-temperate ecotone (Bush & Baldo, 2019; Neily et al., 2017).

1.2.1.2 Cape Breton Hills Ecodistrict

Amidst the valleys and lowlands of western CBHNP lies the Cape Breton Hills ecodistrict, home to one of few protected, old-growth Acadian forests in the province (Figure 1.5). This ecodistrict is much larger than the Cape Breton Highlands ecodistrict, covering over 3000 km^2 of wooded habitat throughout Cape Breton Island (Neily et al., 2017). The Cape Breton Hills ecodistrict ranges from 150 m – 300 m above sea level (Neily et al., 2017). Like the Cape Breton Highlands ecodistrict, the Cape Breton Hills have long winters subjected to high snowfall and snowpack and have a limited, cooler growing season than elsewhere in Nova Scotia (Neily et al., 2017). Stand-wide natural disturbances are limited to spruce and fir stands within this ecodistrict. Instead, treefall gaps produced from windfall and ice damage provide opportunities for succession (Neily et al., 2017). Strong winds from the Gulf of St. Lawrence, locally referred to as 'les suêtes, ' cascade off the highland plateau at speeds upwards of 200 km/h, dramatically shaping the landscape (Neily et al., 2017).

1.2.2 Ecological history

Indigenous peoples have lived in Unama'ki as stewards of the Land for millennia (Parks Canada, 2022). Throughout this time, the Land has changed numerously and has withstood colonization and industrialization, both of which have had unique effects on the landscape. The present state of the temperate and boreal forests of CBHNP have been profoundly shaped by the region's ecological history, which has been affected by natural and anthropogenic disturbances. Over the last century, the Acadian-Maritime boreal ecotone of CBHNP has been cultivated and shaped by its largest herbivore: the moose (*Alces alces* spp.). Before colonizers arrived in the area, moose were abundant throughout Cape Breton and essential to Mi'kmaw culture and food systems (Bush & Baldo, 2019; Lefort et al., 2014). Their primary predator, the wolf, was extirpated from the Park in the mid-1800s and native moose (*Alces alces americana*) themselves were extirpated from Cape Breton around the turn of the 20th century (D'Orsay & Howey, 2020). Seven individuals of this native subspecies also referred to as "mainland moose", were reintroduced to northern Cape Breton in 1928 and 1929; unfortunately, this effort was in vain, and no moose survived to produce viable offspring (Bush & Baldo, 2019). The Cabot Trail was constructed in 1932, and shortly after that, the Government of Canada established its first National Park in Nova Scotia in Northern Cape Breton in 1936. In 1947 and 1948, a decade after CBHNP was established, Parks Canada introduced 18 moose (*Alces alces andersoni*) to the Park from Alberta (D'Orsay & Howey, 2020; Lefort et al., 2014). A similar strategy was implemented to reintroduce caribou to CBHNP in 1968 and 1969; however, this plan was unsuccessful, and all 51 introduced caribou (and their offspring) disappeared in 1972 (Dauphiné, 1974). At the time, researchers believed caribou deaths could have been caused by a meningeal worm, a common parasite of the white-tailed deer (*Odocoileus virginianus*).

In the 1970s, a spruce budworm outbreak swept through the region, leaving two-thirds of balsam fir stands completely decimated (Basquill & Thompson, 1997; D'Orsay & Howey, 2020; Smith et al., 2010). An increase in food availability post-disturbance left the landscape vulnerable to pervasive ungulate herbivory, resulting in a hyperabundant *Alces alces* *andersoni* population (D’Orsay & Howey, 2020). The lack of predatory pressure from wolves has meant that moose have been less restricted and can choose their habitat based on preferred food availability (C. M. A. Franklin & Harper, 2016; Frelich et al., 2012). Since the spruce budworm outbreak of the 1970s, moose herbivory has prolonged boreal forest succession in CBHNP (Smith et al., 2010). Ungulate rebrowsing patterns have cultivated 'moose meadow' habitat, where sections of the historic boreal forest habitat have been reduced to open grasslands with shrub-like balsam fir and white birch amidst sparse standing deadwood (D’Orsay & Howey, 2020). Today, many boreal research projects view ungulates as the antagonist; however, we cannot ignore the vital role they play in climate change mitigation and forest conservation. Vuorinen et al. (2020) argue that large herbivores can counteract non-boreal vegetation colonization. In CBHNP, moose could demonstrate a preference for deciduous species and thus limit Acadian forest range expansion into boreal stands through selective browsing. It has been 50 years since the last spruce budworm outbreak, and researchers predict another one is imminent (Johns et al., 2019). With the boreal forest in its current degraded state, the next spruce budworm outbreak could result in the local extinction of at-risk boreal species in CBHNP.

1.2.3 Previous boreal forest research

The degradation of boreal forest health in CBHNP due to a suite of a/biotic mechanisms has made this boreal refugium of conservation concern for Parks Canada since the early 2010s. In 2013, Parks Canada launched the Bring Back the Boreal Project, which involved installing exclosures in moose meadows to monitor forest regeneration, experimental planting of over 67,000 trees by volunteers and professionals, and organized moose culls in collaboration with the Unama’ki Institute of Natural Resources (UINR) (D’Orsay & Howey, 2020; Parks Canada, 2022). Up until this point, tree restoration efforts by Parks Canada have been largely unsuccessful, and quality, species-specific seedbeds have yet to be identified to determine what seedbeds are suitable for boreal species growth.

Research by Parks Canada indicates that boreal stands throughout the Park have responded differently to restoration efforts (D'Orsay & Howey, 2020). This discrepancy is likely due to the variety of biotic and abiotic mechanisms present at each site; however, long-term monitoring of these mechanisms has yet to be established. Therefore, future conservation efforts should reflect the biotic and abiotic conditions and indicators of each boreal area. There is an overwhelming consensus from researchers who study biotic and abiotic mechanisms of change that more long-term, regionally specific, and interdisciplinary research projects are developed to address the complex environmental issues ecological communities are faced with (e.g., Brown and Vellend, 2014).

1.3 Research significance

Across the boreal forest biome, local boreal forest ecosystems are threatened by the cumulative effects of global change. Climate change, land-use activities, and changes in species distributions and abundances are compounding stresses on one of Canada's defining biomes. The boreal forest fragments within Unama'ki may act as an early warning of what is to come in other regions of Canada: boreal forest degradation from overabundant herbivores, insect and disease outbreaks, and encroaching southern ecosystems. The magnitude of resources required for managing moose impacts has meant that the potential valley-up encroachment of Acadian forests is an unknown influence on boreal forest resilience within CBHNP. The lack of graduate research programs at Cape Breton institutions has meant minimal research has been conducted on boreal forests in Unama'ki, yet it is critically needed. Additionally, researchers have emphasized that more scholarship is needed around "the cumulative and interactive impact of ungulates" in concert with natural disturbances to comprehend better how boreal ecosystems respond to disturbance regimes (Charron & Hermanutz, 2016; Leroux et al., 2021; Walther, 2010).

The boreal forest stands within CBHNP are geographically unique, islands of threatened boreal forest and at-risk species surrounded by temperate Acadian forests (Neily et al., 2017). The Park lies at the southernmost and northernmost geographic extremes of boreal and Acadian forest distributions, respectively. Intense logging occurs just outside the Park boundary, and hunting is also popular in areas North and South of the Park (D'Orsay & Howey, 2020). As a protected area, the temperate-boreal microrefugia of CBHNP is a refuge for at-risk species in northern Cape Breton, where old-growth Acadian forests and sporadic boreal forests provide invaluable habitat in a time where untouched natural landscapes are scarce. More importantly, protected areas such as CBHNP provide a climate refugia for species, creating a climate buffer amidst urban development (Xu et al., 2022). This boreal refugium is particularly important as it remains the last patch of habitat for at-risk boreal species in southern Canada (Stralberg et al., 2020). Within the Park, the fragmented distribution of boreal forest habitats further isolates individuals and makes them more susceptible to ecological disturbances. Species such as the Canada lynx (*Lynx canadensis*) and American marten (*Martes americana*), regionally at-risk boreal species, are particularly vulnerable as they rely on boreal forest habitat for survival (Bush & Baldo, 2019).

Our research is relevant to both Parks Canada and Mi'kmaw conservation priorities. In the last decade, Parks Canada has collaborated on several research projects with the same overarching goal: improving boreal forest health and resiliency in CBHNP (Charron et al., 2020; D'Orsay & Howey, 2020; C. M. A. Franklin & Harper, 2016; Leroux et al., 2021; MacSween et al., 2019). L'nu also have invested interest in the health of the boreal forest in CBHNP. UINR is an Indigenous-led research and conservation non-profit in Cape Breton, and moose management is one of their primary research priorities. Parks Canada and UINR have collaborated on boreal forest restoration in CBHNP through organized moose cull events to manage the overpopulated Park as part of Parks Canada's Bring Back the Boreal Project.

Range shifts of temperate Acadian forest species upslope into boreal forest stands, in concert with other biotic and abiotic mechanisms acting within the Park, could further constrain boreal boundaries, limit viable habitat for boreal species, increase their risk of extirpation, and could potentially result in a bottom-up trophic cascade that could have severe consequences for all boreal species in Cape Breton. Therefore, learning about this boreal refugia is critical to predicting how different regions respond to climate change and other biotic and abiotic mechanisms (Stralberg et al., 2020).

1.4 Thesis overview and objectives

The purpose of this research is to assess the current state of temperate-boreal forest dynamics in the CBHNP refugia, an area that houses remote, protected Acadian and boreal species populations at their northernmost and southernmost geographic ranges. To inform future research, we wanted to quantify how specific biotic and abiotic mechanisms influence species distributions and forest transitions. The following chapter outlines our study design, including research methods and findings. More specifically, we explored how different species groups (e.g., Acadian, boreal) were affected by biotic and abiotic mechanisms in CBHNP, including the effects of altitude, canopy coverage and type, ungulate herbivory, and seedbed on species distributions. Our project objectives were as follows:

1. **Identify if and where range shifts are occurring in CBHNP**
2. **Examine if moose are a potential biotic constraint on temperate Acadian species expansion**
3. **Assess species-specific seedling microsite characteristics**

Finally, we contextualize and contemplate our findings in Chapter 3 and review some of our recommendations for future research in CBHNP and elsewhere. The cumulative effects of moose herbivory, continued warming, and an imminent spruce budworm outbreak are expected to increase ecological pressures on an already threatened boreal forest ecosystem. In addition to these stressors, climate change could induce forest range shifts, further constraining boreal stands within the Park if Acadian forests shift upslope. Data from our project contributes to this overarching body of knowledge by outlining ecotonal shifts at geographic extremes. Understanding biotic and abiotic mechanisms that facilitate or inhibit upslope elevational shifts will give us a better insight into what boreal stands require immediate attention and, thus, ensure that conservation efforts are cost-effective and concentrated on the boreal boundaries of greatest concern. Overall, this data will help inform boreal forest conservation efforts in CBHNP to protect isolated populations of boreal species in an ecologically and culturally significant region.

1.5 Figures

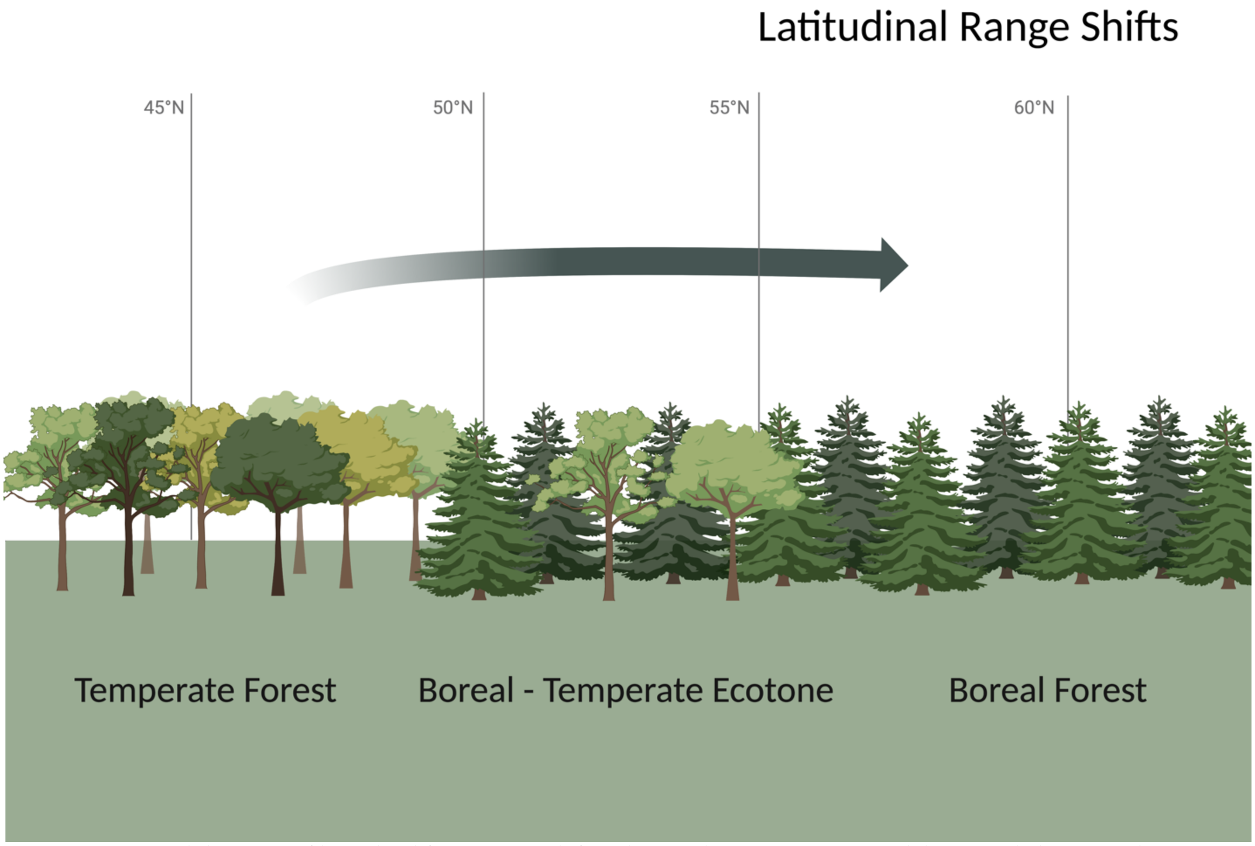


Figure 1.1 A visual depiction of latitudinal forest range shifts. Climate change, in concert with biotic and abiotic mechanisms, can induce latitudinal range shifts, shifting temperate and boreal forest ranges poleward where climate is more suitable for species.

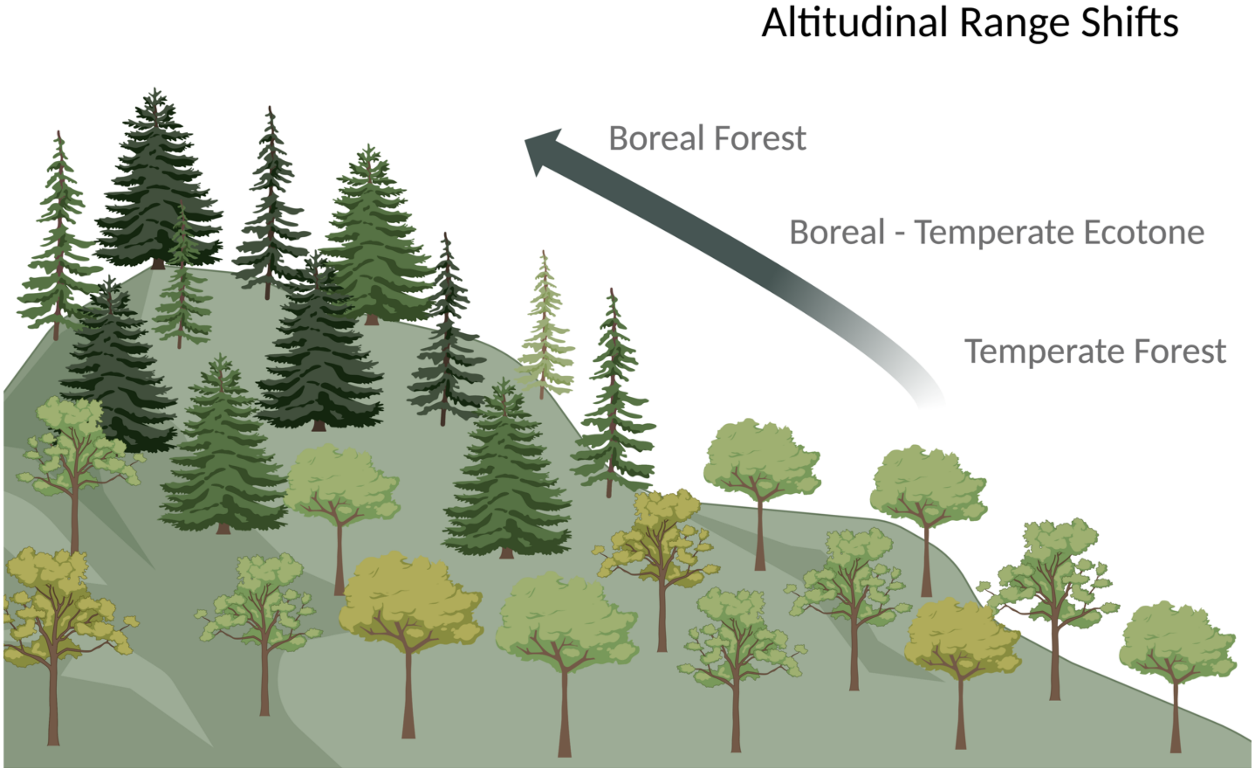


Figure 1.2. A visual depiction of altitudinal forest range shifts. Climate change, in concert with biotic and abiotic mechanisms, can induce altitudinal range shifts, shifting temperate forest ranges upslope into boreal stands. The expansion of temperate forests reduces the amount of habitat available for boreal species.

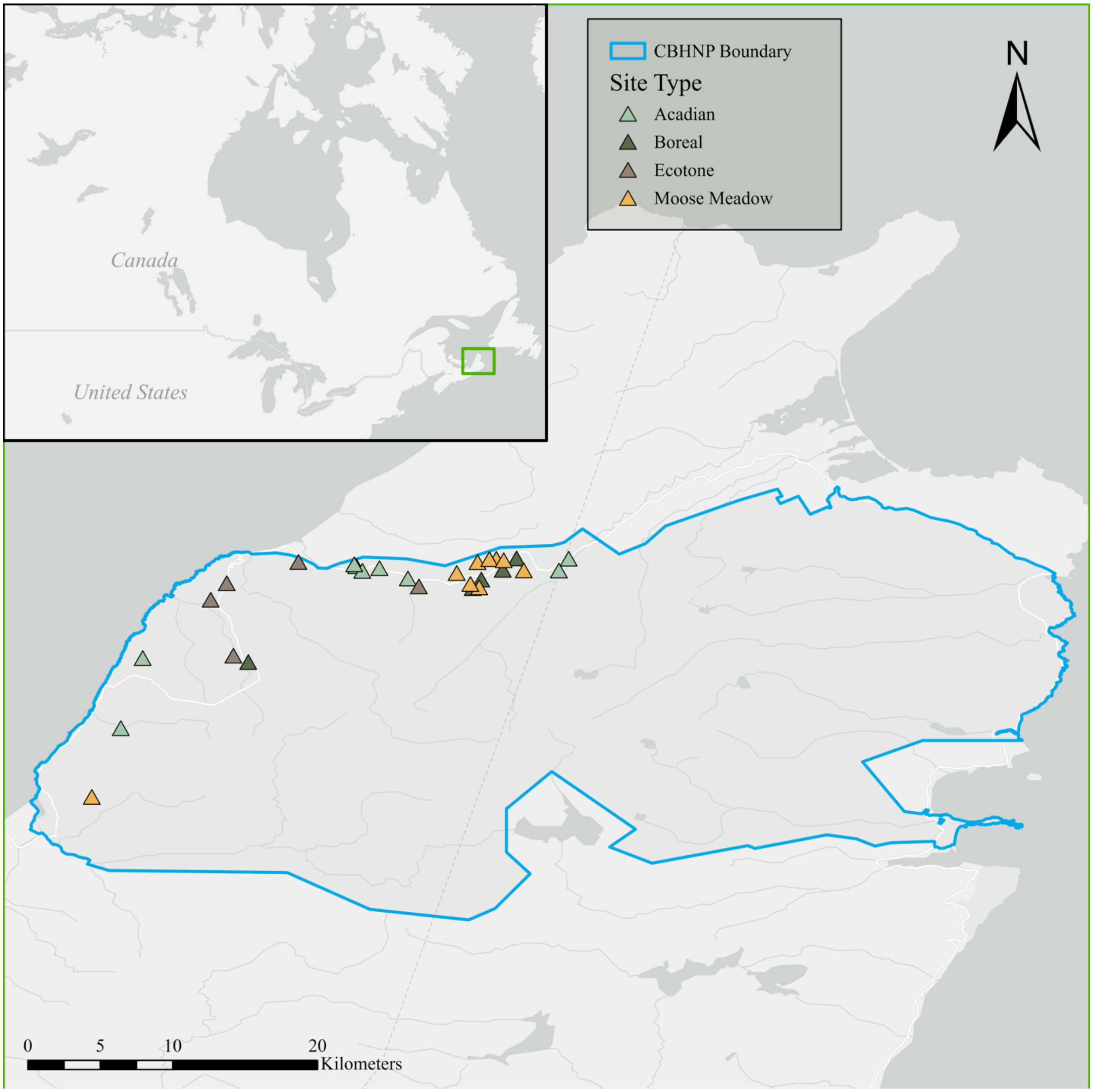
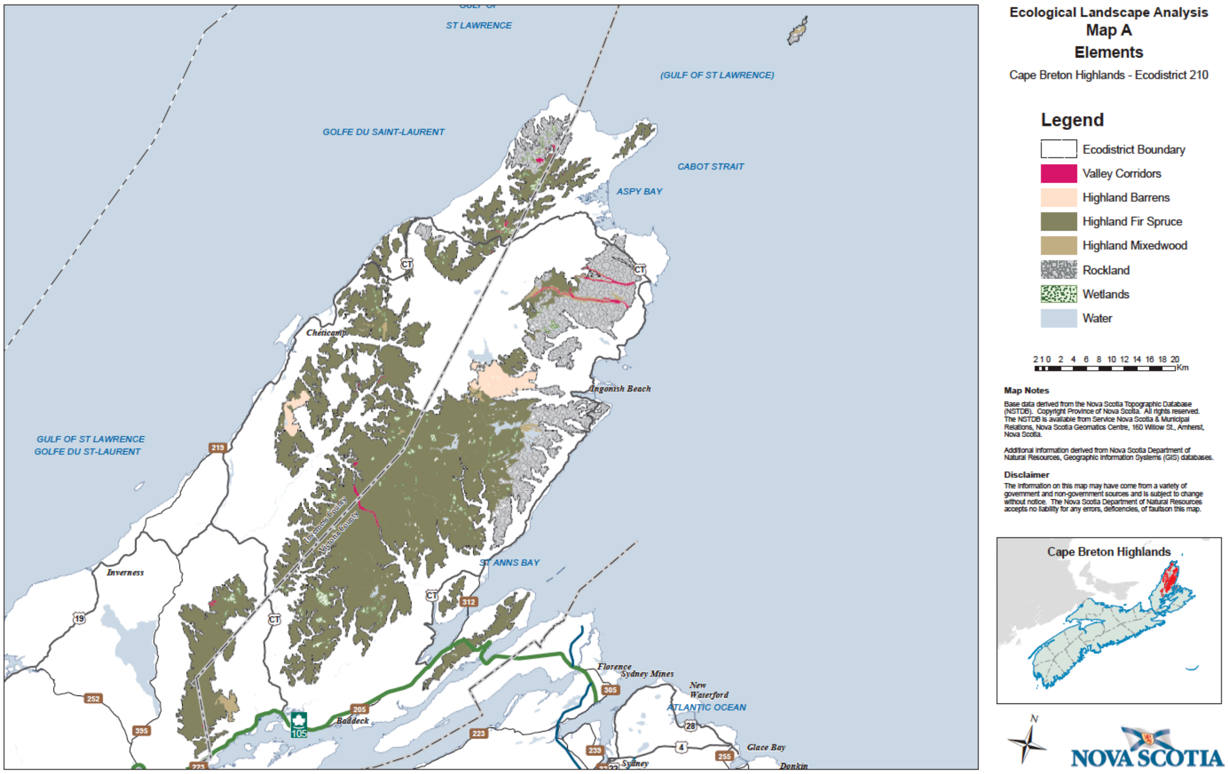


Figure 1.3. Acadian, boreal, ecotone, and moose meadow project field sites throughout CBHNP. Sites span over 400m of elevation from Chéticamp to Big Intervale (M. Kosick, 2023).



Map Notes

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Additional information derived from Nova Scotia Department of Natural Resources, Geographic Information Systems (GIS) databases.

Disclaimer

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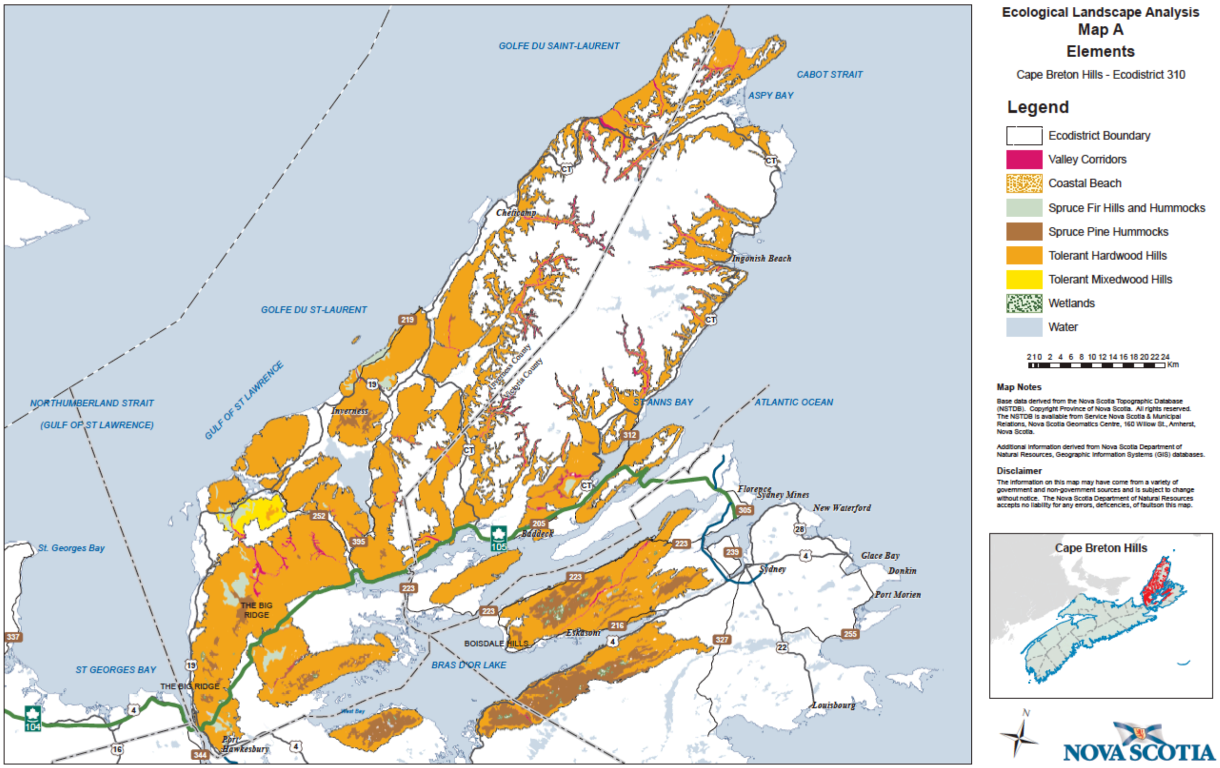
Date: 6/25/2015

Figure 1.4. The Cape Breton Highlands Ecodistrict (210) ecological landscape analysis (Nova Scotia Department of Natural Resources, 2015a). The boreal forest patches within CBHNP are located within this ecodistrict.



Map Notes

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Additional information derived from Nova Scotia Department of Natural Resources, Geographic Information Systems (GIS) databases.

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Date: 6/25/2015

Figure 1.5. The Cape Breton Hills Ecodistrict (310) ecological landscape analysis (Nova Scotia Department of Natural Resources, 2015b). The Acadian forest of western CBHNP is part of this ecodistrict

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Chapter 2 : Drivers of change in the temperate-boreal refugium of Cape Breton Highlands National Park

2.1 Introduction

The prevailing prediction that species will shift their distributions in concert with climate change has repeatedly been unsupported by observation evidence at range edges, including trees responding asynchronously to warming (Harsch et al., 2009; Walther et al., 2002). Research suggest that the expansion or contraction of forests is influenced by climate change in concert with regional, biotic and abiotic mechanisms (Beck et al., 2011; Brown & Vellend, 2014; Evans & Brown, 2017b; Foster & D'Amato, 2015; Frei et al., 2018; Silva & Anand, 2013; Vuorinen et al., 2020). Each responds differently to these mechanisms (Goldblum & Rigg, 2005); hence, range shift responses are species-specific (Boisvert-Marsh et al., 2014) and regionally defined (Harsch et al., 2009). Ecosystems are incredibly complex, and many biotic mechanisms, abiotic mechanisms and cumulative stressors contribute to ecotonal shifts. Therefore, we need to learn more about these non-climatic mechanisms alongside phenological changes to develop regional-based conservation and management strategies in response to range shifts.

Boreal species respond to changes in temperature, humidity, and precipitation, and these mechanisms can result in the expansion or contraction of forest habitat. Anthropogenic climate change is often credited as the main factor that influences species range shifts (Leithead et al., 2010); however, it is unlikely that range shifts are exclusively driven by climate. In addition to directly affecting species, climate change can facilitate or inhibit biotic and abiotic mechanisms (Figure 2.1) that influence that species' occurrence or success (Beckage et al., 2008).

Continued warming of boreal forest ecosystems at geographic extremes combined with regionally specific biotic and abiotic mechanisms could induce temperate forest range shifts, a natural and expected process at ecotones (Harsch et al., 2009; Iverson & Prasad, 2002). As climate conditions become more favourable for temperate species, we can expect these species will migrate poleward or upslope, which could further constrain southern boreal forests (Kellman, 2004). When preferred habitat becomes available for temperate species, their range shift potential increases (Thomas et al., 2001). Although temperate range shifts can lead to deborealization (Taylor et al., 2020), these mixed forests remain vital ecosystems, and their failure to shift would have ecosystem-wide consequences.

Cape Breton Highlands National Park (CBHNP) lies at Canada's most southern geographic extreme of boreal forest distributions and contains high-elevation sections of boreal forest threatened by cumulative stressors. These stressors include ungulate herbivory on boreal seedlings and saplings (D'Orsay & Howey, 2020), the legacy of historic spruce budworm outbreaks and the fact that another outbreak is emerging (C. M. A. Franklin & Harper, 2016), and climate change (Parks Canada, 2022). In addition to these mechanisms, we do not know if the potential valley-up encroachment of Wabanaki-Acadian forests (hereafter referred to as the Acadian forest) or ubiquitous species like red maple (*Acer rubrum*) is putting additional stress on boreal forests. The boreal refugium in CBHNP is particularly important as it remains the last patch of habitat for at-risk boreal species in Nova Scotia (Tomie et al., 2018).

Lack of suitable boreal forest habitat can create a bottom-up trophic cascade that could have catastrophic implications for all boreal species, including Canada lynx (*Lynx canadensis*), Bicknell's thrush (*Catharus biknelli*), and the American marten (*Martes americana*). Boreal forest refugia in CBHNP may be characteristic of refugia across the southern boreal forest of North America under ongoing global change (see Stralberg et al. 2020 for future refugia). Understanding the role range shifts, herbivory, and seedling microsites play in this environment is critical to protect and preserve this ecosystem within CBHNP and will also contribute to our forecasting of the characteristics and processes in boreal forest refugia in other regions of North America in the future. Our aim was to assess the current status of Acadian forest range expansion in CBHNP, specifically by identifying biotic (e.g., herbivory and seedbed characteristics) and abiotic (e.g., altitude, light) mechanisms that can influence temperate-boreal transitions (Evans & Brown, 2017b). We developed three research questions to explore Acadian-boreal forest dynamics in CBHNP:

Q1: Are Acadian forest range shifts occurring in CBHNP?

Q2: Do moose preferentially browse on tree species at different site types?

Q3: Is tree species establishment limited by seedbed type?

From there, we developed two hypotheses:

H1: Moose will preferentially browse on deciduous species, which will limit Acadian tree range expansion; and

H2: Acadian tree species establishment will be limited to leaf litter dominated seedbeds, and absent from grass-dominated seedbeds, like those typical of moose meadows.

2.2 Methods

2.2.1 Study area

Our research was conducted in *Unama'ki* (Cape Breton), the ancestral and unceded territory of the Mi'kmaw people (Figure 2.2; Figure 2.3). L'nu (Mi'kmaw) have lived as stewards of this Land for thousands of years and have witnessed the ecological changes of the landscape throughout its history. Additionally, our study area is an important region of the

Acadian people of Chéticamp (*Awjátúj*) and the ancestors of the families expropriated from Cap-Rouge (*Mkwesaqtuk*) when CBHNP was established in 1936.

Our research occurred in northwestern Cape Breton at two Acadian-maritime boreal transition areas within the Acadian-Maritime Boreal ecotone of CBHNP: French Mountain and North Mountain (Figure 2.2; Figure 2.3). The Acadian-boreal transition area is an area where temperate hardwoods and boreal species converge. More broadly, this is known as an ecotone (Goldblum & Rigg, 2010). Our sites spanned over 400m of elevation between Chéticamp and Big Intervale, from Acadian forests (Cape Breton Hills Ecodistrict) at lower elevations upslope towards the highland plateau's boreal forest (Cape Breton Highlands Ecodistrict). In between lies the Acadian-maritime boreal ecotone (Neily et al., 2017; Neily & Parsons, 2017).

This region is particularly significant as it encompasses the northern elevational extreme of Acadian forests and the southern geographic extreme of boreal forests. Moose spruce savannahs (also called 'moose meadows') are also present in this region (Figure 2.4). These grassland-like areas were once boreal habitat and have since changed due to the combined effects of a spruce budworm outbreak and pervasive ungulate herbivory (D'Orsay & Howey, 2020). The forests within CBHNP are exposed to various environmental phenomena, especially fire and insect outbreaks (Neily et al., 2017; Taylor et al., 2020). Heavy snowfall events and severe southeast winds (regionally referred to as 'les suêtes') profoundly impact the landscape, particularly in the extended, cold winter months (Bush & Baldo, 2019).

2.2.2 Study Species

Our study focussed on Acadian and boreal tree species found within CBHNP (Table AI.I). Identifying dominant species historically present in boreal and Acadian forests is critical to highlight indications of potential range shifts along natural edges (Evans & Brown, 2017b).

Species characteristic of the Maritime-boreal forest in Cape Breton include balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), white spruce (*Picea glauca*), American mountain ash (*Sorbus americana*), pin cherry (*Prunus pensylvanica*), and black spruce (*Picea mariana*) (Neily et al., 2017; Neily & Parsons, 2017). White birch is a preferred forage for moose in the spring and summer months. In winter, when white birch is not available, moose tend to forage on balsam fir (Basquill & Thompson, 1997).

In the Acadian forest of CBHNP, deciduous species such as sugar maple (*Acer saccharum*), Northern red oak (*Quercus rubra*), white ash (*Fraxinus Americana*), yellow birch (*Betula alleghaniensis*), and American beech (*Fagus grandifolia*) are common. Conifers such as eastern hemlock (*Tsuga canadensis*) are also present with red spruce (*Picea rubens*) being less common. Many of these deciduous species are preferred forage for moose in the spring and summer months (Basquill & Thompson, 1997).

Red maple is commonly a more ubiquitous species than those described so far, and is found in southern boreal forest communities, including CBHNP, as well as in Acadian forests (Neily et al., 2017). Because it thrives in both ecosystems, we cannot classify it as strictly "boreal" or "Acadian." For this research, we categorized species into three different species groups: Acadian, boreal, or red maple (Table AI.I). In doing so, we can compare species group responses to biotic and abiotic mechanisms and assess their success in specific environmental conditions.

2.2.3 Field methods

We selected 28 sites from Parks Canada's forest monitoring plots to quantify biotic and abiotic drivers of change. These sites align with previous Parks Canada research on boreal forest health and moose herbivory in CBHNP. We selected sites from several long-term monitoring datasets, including Acadian old-growth (AOG) plots (2006-2013), ecological monitoring and assessment network (EMAN) plots (2012-2013), vegetation survey plots (2014-2021), and boreal survey plots (2014-2021). Where most of these sites were selected to represent Acadian (i.e., AOG plots) or boreal (i.e., boreal survey plots), several vegetation survey plots were specifically chosen because they exhibit moose meadow characteristics. Further, several EMAN and AOG sites were located near the altitudinal median (approx. 200m), making them ideal for identifying range shifts along the Acadian-boreal ecotone.

2.2.3.1 Sampling Strategy

Field sites were classified into four categories: Acadian (n=9; site names labelled “A”), boreal (n=5; “B” sites), ecotone (n=5; “E” sites), and moose meadow (n=9; “M” sites). We classified Parks Canada pre-established monitoring sites into these categories based on altitude and light availability (Figure 2.5; Table 2.1; Table AII.I). Sites M3 and E2 were established in July 2022; therefore, there is no long-term monitoring data for those sites.

2.2.3.2 Plot Design and Measurements

At each monitoring site, we located the site center coordinate and inserted a stake for establishing a 32 m^2 circular sampling plot (Figure 2.6). A 3.2 m radius was used because it was large enough to represent the local variation in vegetation and small enough to be logistically feasible. Within each circular sampling plot, we conducted an exhaustive sweeping survey for seedlings and saplings as evidence of Acadian forest species range expansion. For the purpose of our analysis, we defined saplings as any tree < 3m in height based on average snowfall in the area which can result in 3m of snowpack in the winter. In practice, this meant walking behind the center-staked transect tape (i.e., plot radius) as the field crew systematically searched the ground layer for tree seedlings and saplings. We measured the height of each seedling and identified it to species.

In concert, we quantified a suite of variables (i.e., seedling proportion, seedling population density, canopy type and percentage) to see if tree range expansion varies with biotic and abiotic drivers. Seedling proportion was calculated as the number of individuals of a chosen species over the total number of individuals at a site with seedling population density as the number of individuals of a chosen species over the area of the site ($32m^2$). Canopy type and percentage was determined based on the proportion of Acadian or boreal canopy trees present in the overstory at a site.

To explore the effect of ungulates on Acadian species expansion and test hypothesis one, we identified signs of herbivory on each seedling and sapling surveyed (Table 2.2). If a site had a high density of seedlings and saplings, we only assessed herbivory on a subset (i.e., maximum eight trees) of the site (Figure 2.6). Herbivory was identified using a visual assessment of seedlings and saplings by closely examining the tree crown, branches, and buds for evidence of browsing.

Browse severity was categorized as 0, 1, 2, or 3, identified by lack of herbivory, low, medium, and high herbivory, respectively (Figure 2.7). This was based on the proportion of tree growth compared to the amount of deadwood on the tree. Trees experiencing low amounts of herbivory show healthy growth and a limited amount of dead material, whereas trees experiencing high herbivory have stunted growth and a significant amount of dead material. Trees with medium herbivory will show signs of growth and dead material. All herbivory observed was assumed to be moose, as other ungulates (e.g., white-tailed deer) are less abundant in CBHNP. Moose herbivory is easily distinguishable from other boreal herbivores, such as snowshoe hares. Hare browsing is visually identifiable by linear browsing, also called “hare-lines”, characterized by a sharp 45-degree angle bite on growth segments (Olnes et al., 2017, 2018).

To test hypothesis two, we characterized seedling microsite characteristics associated with a subset of seedlings (i.e., maximum of eight trees) within each site as follows: As the plot radius crossed each cardinal direction in the sweeping survey, the next temperate and the next boreal tree seedling intersecting the radius was selected for intensive sampling. The seedling microsite, a 30cm x 30cm area around the base of the seedling of each of these individuals, was observed, and the primary seedbed was identified (e.g., leaf litter, moss, grass, bunchberry (*Cornus canadensis*), conifer needles). Light availability was characterized at each microsite via an estimate of canopy openness using a spherical densiometer (Model A). Finally, each target seedling was measured for height and herbivory. As expected, we did not find four temperate or four boreal tree seedlings in each cardinal direction at some sites. The boreal or Acadian microsite at that cardinal direction was omitted in these cases.

2.2.4 Statistical analyses

To answer our research questions, we collected and calculated data corresponding to biotic and abiotic variables contributing to forest health in CBHNP (Table 2.3). Seedling proportion, population density, and Acadian and boreal canopy percentages were calculated in R within RStudio version 4.2.0 alongside our statistical analyses (R Core Team 2022). We used generalized linear models (GLMs), two-way ANOVAs, and Fisher's exact tests to assess the effects of seedbeds, herbivory, altitude, site type, taxon, and canopy type and percentage on tree seedling occurrence in the form of seedling proportion or population density. For the most part, our analysis looked at seedling proportion instead of population density, as seedling proportion showed a stronger statistical relationship. We combined tree species into three species groups for some of our analyses: boreal, Acadian, and red maple, in their unique category. Each species group reflects the **dominant** species of a particular forest type. This does not mean that these species are found exclusively at these site types. In creating these categories, however, we can assess similar species' responses to environmental conditions and stressors, gaining a broader picture of ecodistrict-specific ecological preferences within our dataset.

2.2.4.1 Are Acadian forest range shifts occurring in CBHNP?

Mechanisms such as altitude, species group, canopy type and percentage can significantly influence seedling proportion and seedling population density, which can ultimately contribute to species range shifts. To identify if range shifts are occurring in CBHNP, we created four GLMs to test the following relationships [response ~ predictor(s)]: 1) seedling proportion ~ altitude and species group (Table 2.4); 2) seedling population density ~ altitude and species group (Table 2.5); 3) seedling proportion ~ Acadian canopy percentage and species group (Table 2.7); and 4) seedling proportion ~ boreal canopy percentage and species group (Table 2.8). We also used a two-way ANOVA to test the relationship between 5) seedling proportion ~ site type and species group (Table 2.6).

For models 1-4, GLM (Gaussian family) was the preferred choice of analysis as these models all used continuous response variables with continuous and/or categorical predictors to explore linear relationships between variables. In contrast, we used a two-way ANOVA for model 5 when we had two categorical predictors to identify how the mean seedling proportion differs at different site types within different species groups.

2.2.4.2 Do moose preferentially browse on tree species at different site types?

As ungulates have unique herbivory preferences, different tree species experience varying proportions of moose herbivory; therefore, to assess the impact of herbivory on temperate and boreal species, we used a GLM (Gaussian family) to analyze the relationship between tree species (predictor variable) and the proportion of moose herbivory on each species as the response variable (Table 2.9).

The GLM was the preferred choice of analysis as we had a continuous response variable with a categorical predictor variable. We used a two-way ANOVA to assess species group and site type (predictor variables) effects on herbivory proportion as the response variable (Table 2.10). For this model, we had two categorical predictors; therefore, we chose to use a two-way ANOVA to identify if there are differences between the mean herbivory proportion at different site types within different species groups.

2.2.4.3 Is tree species establishment limited by seedbed type?

Different tree species thrive in different environments, and each species has unique germination and growing conditions, heavily influenced by seedbeds. To identify optimal seedling microsite conditions for different species, we used a Fisher’s Exact Test for count data to assess the effect of seedbed and species group (predictor variables) on the number of seedlings observed of each species on one of five seedbed types as the response variable. Once again, the Fisher's Exact Test was the preferred choice for this analysis as we had less than five frequencies for more than 20% of cells (e.g., Acadian species were not frequently observed on grass, bunchberry, or moss seedbeds). We conducted diagnostics to test for violations of model assumptions by testing for linearity, homogeneity, normality, and independence (Zuur et al., 2010). All models met assumptions.

2.3 Results

We observed 13 different species at field sites at varying elevations around North and French Mountain (Table AI.I). Of those species, balsam fir was the most observed species, followed by red maple, sugar maple, and white birch*,* respectively (Figure 2.8). Eastern hemlock was exclusively observed at site A4.

2.3.1 Are Acadian forest range shifts occurring in CBHNP?

Acadian species were more commonly observed at lower altitudes and boreal species at higher altitudes, with some exceptions (Figure 2.9). Acadian species, except for yellow birch, considered an ecotone species in this region, were not found at altitudes higher than 300m. In contrast, red maple, considered neither Acadian nor boreal, was found at all altitudes. To further examine if Acadian species' ranges were shifting upslope, we looked at the seedling proportion and population density of Acadian, boreal, and red maple seedlings at different altitudes (Figure 2.10). General linear models (Table 2.4; Table 2.5) indicated that greater proportions of Acadian species were predominantly found at lower altitudes ($p = 0.016$), and greater proportions of boreal species were found at higher altitudes ($p = 0.002$). The proportion and density of red maple seedlings remained relatively consistent across altitudes, with few site-specific exceptions, showing no statistical relationship between altitude and red maple seedling proportion or population density (Table 2.4; Table 2.5). Further, we did not find strong statistical evidence that the population density of Acadian and boreal seedlings depends on altitude (Table 2.5).

An ANOVA of the proportion of Acadian species present at different site types provides further evidence of Acadian species being more prevalent at lower elevations (i.e., Acadian sites) (Figure 2.11; Table 2.6). In addition, Acadian seedlings were only present at Acadian and ecotone sites and therefore were not present at higher elevations. Generally, the proportion of seedlings within species groups mirrors the site type (Table 2.6), with higher proportions of Acadian species at Acadian sites and higher proportions of boreal species present at boreal sites ($p = 0.001$).

GLMs that examined the relationships between canopy and seedling type (Table 2.7; Table 2.8) only observed a significant statistical relationship between the proportion of boreal seedlings and Acadian canopy ($p < 0.0001$). As the percentage of Acadian canopy coverage increased, the proportion of boreal seedlings present decreased (Figure 2.12). Acadian and red maple seedlings showed no statistical relationship with canopy type, nor boreal seedlings with boreal canopy coverage (Table 2.7; Table 2.8).

2.3.2 Do moose preferentially browse on tree species at different site types?

We observed herbivory on all species except for black spruce with white spruce experiencing very little herbivory (Figure 2.13). GLM analysis indicates a significant relationship between the proportion of herbivory experienced by white spruce ($p = 0.006$) and black spruce ($p = 0.014$) which highlights ungulates' avoidance for these coniferous boreal species (Table 2.9).

At boreal and moose meadow sites, an ANOVA indicated higher mean proportions of herbivory on boreal seedlings than on red maple seedlings (Table 2.10). Further, we found that the proportion of herbivory observed was significantly influenced by species group ($p = 0.023$, Table 2.10). Herbivory intensity varied on Acadian, boreal, and red maple seedlings at different site types. Acadian species were only observed at Acadian and ecotone site types, whereas red maple and boreal species were observed at all site types (Figure 2.14). Generally, Acadian species experienced greater herbivory than boreal and red maple seedlings at Acadian and ecotone sites; therefore, H1 is supported.

2.3.3 Is tree species establishment limited by seedbed type?

The Fisher's Exact Test indicated that the number of seedlings we observed was greatly influenced by the interaction between species group and seedbed type ($p = 0.0005$). Of the five seedbed categories, leaf litter and grass seedbeds were the most common at seedling microsites, with moss, bunchberry, and conifer needle seedbeds being the least common (Figure 2.15). Acadian species were only found on leaf litter seedbeds (e.g., white ash, American beech), and no Acadian species were found on grass seedbeds (Figure 2.16); thus, H2 was supported. As leaflitter seedbeds were only found at lower elevations at Acadian and ecotone sites, Acadian seedlings were limited to lower elevational sites.

Boreal species had more diverse seedbeds, mainly balsam fir, white birch, and white spruce. Only boreal species and conifers like Eastern hemlock grew on mossy seedbeds. Similarly, only boreal species grew on bunchberry seedbeds, except yellow birch, a species prevalent in the Acadian-boreal ecotone region of CBHNP. Red maple microsite seedbeds varied but were not found on mossy seedbeds (Figure 2.16).

2.4 Discussion

We found no evidence of temperate tree range shifts into boreal forest communities in CBHNP. We assessed the Acadian-Maritime boreal ecotone in a snapshot of time, and hypothesize that multiple constraints are acting on temperate forest advance and delineation of community assemblage. The southern margin of the boreal forest is where we expect to see temperate, deciduous-dominated forests shifting their distributions into boreal forest stands under ongoing climate change. In these cases, we might expect temperate forests to shift poleward along a latitudinal gradient or upslope into boreal mountains or highlands. In some instances these ecosystems are boreal refugia, which are critical as they are the last available patches of habitat for the species that depend on them. Our research in CBHNP revealed the possibility of multiple constraints on upward range expansion, including altitudinal limitations affecting species establishment, preferential browsing of temperate and deciduous species by moose, and a lack of suitable seedbeds for temperate species germination and establishment at boreal and moose meadow sites.

2.4.1 Multiple constraints on range shifts

Despite the potential for Acadian species range expansion, we did not find evidence of successful range shifts in the Acadian-Maritime boreal ecotone. Although we were unable to assess long-term trends of forest range shifts due to limited and divergent datasets, we did find that that, presently, there are likely too many limiting mechanisms (i.e., altitude, seedbed type, light availability, canopy type) in CBHNP for a successful range shift to transpire. Instead, our findings suggest that red maple and other generalist species expected to thrive under changing climate conditions in other regions of the boreal-temperate ecotone (Collin et al., 2016; Stern et al., 2022; Vaughn et al., 2021b; Wang & Ibáñez, 2022) have established themselves in post-disturbance ecodistricts within CBHNP. The continued establishment and growth of red maple populations could result in persistent transitional stages and extended periods of succession, affecting forest dynamics and composition.

At higher elevations in CBHNP, there is a cooler, wind-exposed climate, providing favourable growing conditions for boreal species, with a more temperate climate at lower altitudes suitable for Acadian species (Environment and Climate Change Canada, 2023),. These elevational-linked mechanisms likely contributed to the proportions of Acadian and boreal seedlings at different altitudes and site types. Of the four site types we examined, ecotone and moose meadow sites present the greatest opportunity for deborealization (Taylor et al., 2020).

Hypothetically, Acadian seeds can easily disperse and encroach into boreal stands from the ecotone should suitable environmental parameters (e.g., seedbed, soil composition) present themselves. Moose meadows and other sites affected by disturbance regimes also make way for Acadian species establishment, whether or not ungulate herbivory occurs. While we did not observe any evidence of range shifts in CBHNP, that does not mean that temperate range expansions are inconceivable in Cape Breton or elsewhere. It is possible that climate is suitable for temperate species at the highest elevations of CBHNP (Environment and Climate Change Canada, 2023), and with continued warming, the conditions will only become more preferable for temperate Acadian species (Natural Resources Canada, 2022). It is also possible that potential range-expanding species are dispersing seed into these higher elevation sites, but are constrained at a subsequent stage is establishment, discussed further below.

Some temperate and boreal species are limited by seedling dispersal and germination (McCarragher et al., 2011), and canopy type and coverage can significantly contribute to this. A predominantly Acadian canopy consists of mainly deciduous species that provide leaflitter seedbeds beneath them (Bélanger & Chaput-Richard, 2023; McCarragher & Rigg, 2020). Not only does canopy type and coverage influence seedbeds, it also determines when and how light is available for seedlings (Goulet & Bellefleur, 1986). In old-growth temperate forests, seedlings experience low light availability in spring, summer, and autumn. Because many temperate species are adapted to low-light conditions, these species thrive in mixed old-growth environments (Keddy & Drummond, 1996). Boreal species, however, experience greater success in open canopy environments or with a boreal overstory (Robert et al., 2012).

Typically, Acadian old-growth forests provide optimal canopy coverage and type for Acadian seedlings. In some instances, however, we observed boreal seedlings thriving in the valleys of the Cape Breton Highlands. This pattern was likely due to the surrounding topography, where cold air currents cascade down from the highland plateau (Goulet & Bellefleur, 1986). Sites with boreal canopies or open canopies (i.e., moose meadow sites) typically had higher proportions of boreal and red maple seedlings as, unlike Acadian seedling, they are less restricted by growing conditions (Collin et al., 2016; Vaughn et al., 2022). Ultimately, we only found strong statistical evidence to support the relationship between Acadian canopy and boreal seedlings. Where canopy coverage and type do not directly affect most seedling proportions in CBHNP, the subsidiary effect of providing suitable seedbeds for different species will ultimately contribute to temperate or boreal seedling success in Cape Breton and beyond.

2.4.2 The role of ungulate herbivory

It is well established that herbivory has had a significant impact on the landscape of CBHNP in the last 50 years. Leafy, deciduous trees are common in an ungulate's summer diet and are often more resilient and tolerant to browsing (Charron et al., 2020). Spruce trees are undesirable forage for ungulates (Kolstad et al., 2018); however, balsam fir is an essential food source for ungulates in winter (Basquill & Thompson, 1997). Excessive, repeated browsing of balsam fir by ungulates in the winter can result in dead saplings, prolonging the period of succession post-disturbance (Mathisen et al., 2017). Herbivory effectuates herbivory, and, in extreme cases, this behaviour results in the formation of moose meadow habitat (D'Orsay & Howey, 2020). Ungulates typically prefer browsing in forest gaps, like those observed in moose meadow habitats (Kuijper et al., 2009), which makes trees in these gaps susceptible to rebrowsing and further accentuates moose meadows without conservation intervention (i.e., population management).

In CBHNP, we found that herbivory varied across tree species and had a range of effects on seedling growth. Unsurprisingly, we did not observe herbivory on black spruce seedlings. Historically, black spruce has had a low herbivory index (0.05 in 1995) in CBHNP (Basquill & Thompson, 1997) as it is not a favourable forage by moose (Charron et al., 2020). Deciduous trees were more commonly selected by ungulates than coniferous trees, which aligns with historic herbivory preference indices (Table 2.2) (Basquill & Thompson, 1997). Although the deciduous red maple did experience herbivory, the proportion and intensity of browsing varied considerably. Moose meadow sites in particular experienced large amounts of herbivory and were likely exposed to annual rebrowsing (Mathisen et al., 2017), thus becoming an integral part of ungulate foraging patterns. The intensity and consistency of browsing on individuals of these species showcases moose preference for rebrowsing deciduous boreal species at moose meadow and boreal sites.

Overall, we found that the proportion of herbivory was heavily influenced by species group (boreal, Acadian, or red maple), regardless of site type. In CBHNP and beyond, ungulates will likely gravitate towards their preferred forage, regardless of location. Species considered less desirable by ungulates (e.g., spruce) are likely to have greater chances of success than other species in forests with overabundant ungulate populations. In some instances, red maple may experience less herbivory than boreal species, particularly at moose meadow sites, depending on the season. The resiliency of red maple makes it a formidable successional species in transitioning landscapes (Goszka & Snell, 2020; Taylor et al., 2020; Tremblay et al., 1996) such as moose meadow sites where boreal species have been struggling to recover.

2.4.3. Seedling microsites inhibit temperate range expansions

Seedling observations within species groups were significantly influenced by seedbed type. Most notably, Acadian species were not observed on grass seedbeds and rarely on boreal seedbeds (i.e., moss, bunchberry, conifer needles). In a broader context, our findings contribute to our understanding of species-specific seedbed preferences, a biotic factor that can encourage or inhibit temperate range expansions. As tree planting is a vital component of boreal forest conservation efforts in CBHNP, understanding what types of substrate the seedlings of each species thrives on will inform future restoration efforts. Further, knowing what seedbeds are absent gives insight into why certain species are not thriving.

Due to the degraded state of the boreal forest in CBHNP, fewer boreal seedbeds (i.e., moss, conifer needles, bunchberry) were observed. Higher observations of grass and leaf litter seedbeds suggest an increase in moose meadow, Acadian, and ecotone microsite conditions, providing favourable habitat for the species that thrive in those environments. The lack of preferred seedbeds could explain why some boreal species were observed less frequently or faced additional challenges. For example, black spruce typically prefers moss seedbeds with low soil organic matter (Mallik & Kayes, 2018); however, we only observed seven individuals, and those observed at seedling microsites were all on grass seedbeds. On the other hand, we observed white birch frequently at field sites; however, all our observations of white birch experienced herbivory, negatively contributing to tree health and height. Increased herbivory of white birch, non-optimal seedbed conditions, and the legacy effects of the 1970s spruce budworm outbreak combined with this species' innate response to thinning could explain why white birch populations are struggling to recover. Unlike other boreal species, white spruce was commonly found on leaf litter seedbeds at Acadian sites. White spruce seeds are larger than other boreal seeds (e.g., white birch), which increases their chance of survivorship on these seedbeds (Robert et al., 2012).

In general, boreal seedling survivorship is greater on moss seedbeds as they help seedlings retain moisture and make it easier for smaller seeds (e.g., white birch) to germinate (Charron et al., 2020; Mallik & Kayes, 2018; Robert et al., 2012). While some researchers argue that moss seedbeds are best for balsam fir (Nagati et al., 2020), there is no consensus on balsam fir seedbed preferences (Robert et al., 2012). What is widely accepted, however, is that balsam fir responds well to thinning, a process where some trees are removed, making way for new seedlings to grow (Pothier & Margolis, 1991). Thinning resilience is one of the many mechanisms that makes balsam fir capable of bouncing back post-disturbance. White birch, however, is thought to experience "thinning shock" in its second growing season after stand thinning (Pothier & Margolis, 1991). Therefore, it is possible that in the future balsam fir will be more successful at moose meadow sites than white birch as it is more resilient to thinning.

For the most part, we observed Acadian species on leaflitter seedbeds, and, as expected, we did not find Acadian species on grass seedbeds. It is very challenging for Acadian species to germinate in tall grasses, which explains why we did not observe any at that site type with those seedbed conditions. Red maple microsite conditions in CBHNP were similar to that of Acadian species. Most red maple we sampled were observed on leaflitter seedbeds; however, red maple was commonly observed at moose meadow sites with grass seedling microsite conditions. Red maple's strong presence in moose meadow habitat indicates they have the potential to establish themselves and survive despite the effects that come with being at a higher altitude, being faced with potential herbivory, and having to reside in non-optimal seedbed conditions.

The herbaceous layer is integral to temperate forest ecosystems (Gilliam, 2007). Sugar maple and many other temperate species require nutrient-rich soil to thrive (McCarragher et al., 2011). Acidic and nutrient-poor soils limit this species' ability to migrate poleward into boreal stands (Collin et al., 2016). Further, seedbed type influences temperate seedling survivorship, with Acadian seedlings demonstrating a preference for leaflitter seedbeds. Unlike most Acadian species, predominately found in lower-elevation temperate forests, red maple can thrive across altitudinal gradients, in wet, swampy environments, and in warming climates (Royer et al., 2008; Sanders-DeMott et al., 2018; Wang & Ibáñez, 2022). Many researchers expect red maple to thrive under climate change compared to other temperate-ecotone species. As a generalist species, red maple thrives in most habitats across North America, with water availability being one of its few limiting mechanisms (Vaughn et al., 2021b). Increased anthropogenic and climatic disturbance events could further benefit red maple as it thrives in open canopy environments with thinned stands (Goszka & Snell, 2020; Leithead et al., 2010).

2.5 Recommendations

Establishing consistent and accessible long-term monitoring is critical for conservation, especially when ecosystem changes can span days to decades. We need to prepare for changes as abrupt as fire to gradual climatic shifts. Understanding how an ecosystem works prior to disturbance makes us better equipped to protect and preserve habitat for species. Long-term monitoring studies are required to learn more about correlations between biotic and abiotic mechanisms, such as spruce budworm synchrony with climate patterns and herbivory correlations to treeline expansions (Charron et al., 2020; Leroux et al., 2021). Further, research conducted in conjunction with academic institutions (i.e., universities) reduces time and resource constraints on conservation, allowing key stakeholders to share the load (Charron et al., 2020).

Here, we highlight three key areas that require additional insight that could be gained through long-term monitoring: moose herbivory preferences, red maple resiliency, and climate-linked abiotic mechanisms.

As discussed, herbivory significantly contributes to species occurrence at different site types throughout CBHNP. Therefore, future research should focus on moose herbivory preferences at moose meadow rebrowsing sites (i.e., North Mountain), capitalizing on pre-existing moose exclosures. If we can identify specific moose herbivory preferences in a controlled experiment, we can formulate replanting and conservation strategies directly informed by the boreal forest's largest herbivore. As we demonstrated, red maple resiliency at moose meadow and ecotone sites indicates their potential to thrive in non-optimal conditions, potentially resulting in alternate successional trajectories of the boreal forest. Therefore, future research should examine red maple in CBHNP to identify how it might transform the landscape should it out-compete boreal species. Finally, future research should target climate-linked abiotic mechanisms such as soil moisture, temperature, and precipitation in addition to the biotic mechanisms examined here. As anthropogenic climate change continues, we expect to see emerging environmental issues accumulate. By designing consistent long-term ecological monitoring across field sites that are easy to access for annual assessment, we can ensure that we are prepared to monitor potential changes to the ecosystem and respond swiftly with conservation plans where needed.

2.6 Conclusion

The Acadian-Maritime boreal ecotone within CBHNP marks the boundary between the northernmost and southernmost ranges of Acadian and boreal forests, respectively. Presently, we detected no range shifts of Acadian species into boreal communities. We hypothesize that

Acadian range expansion is limited by species' ability to survive at higher altitudes and withstand corresponding biotic and abiotic mechanisms. Northward expansion of boreal forests, however, is simply unattainable. Perched on the precipice of the Cape Breton highlands, boreal forests make their last stand in southeastern Canada in CBHNP. With the compounding effects of climate change, the future of this vulnerable forest remains unknown.

Our research has outlined some of the defining characteristics of boreal and Acadian species establishment in this ecotone. Generally, Acadian species demonstrate a preference for lower altitudes, Acadian canopies, and leaflitter seedbeds, whereas boreal species prefer higher altitudes, boreal canopies and seedbeds, and increased light availability. We found that red maple was able to thrive in all site types under diverse ecological conditions. Unlike most species, red maple was found at several moose meadow sites, demonstrating the resiliency of this species post-disturbance. Faced with climate uncertainty, we anticipate red maple faring better than boreal and Acadian species in this region.

Ungulate herbivory has transformed the boreal landscapes of CBHNP, especially around North and French mountain. Moose management efforts in the Park have reduced herbivory pressures allowing natural succession to run its course. We anticipate that in the coming years, herbivory will have less of an impact on range shifts and ecological succession than other biotic and abiotic mechanisms, particularly those that relate to climate change (e.g., temperature, moisture availability). Long-term monitoring of forest dynamics within Cape Breton Highlands National Park will facilitate the management of this boreal forest refugium under ongoing climate change.

2.7 Tables

Table 2.1. Site types were used to categorize research fieldwork sites (n=28) in CBHNP.

Site Type	# Sampled	Characteristics
Acadian	9	Sites observed at an elevation < 150m
Boreal	5	Sites observed at an elevation > 400m
Ecotone	5	Sites observed between 150m - 400m
Moose meadow	9	Sites observed at an elevation > 400m with canopy openness greater than 90% for each recorded individual and with no mature trees present at the site.

Table 2.2. Ungulate herbivory on different tree species in CBHNP. Using the Preference Index from Basquil and Thompson's research on ungulate herbivory in the Park in 1997, this table compares ungulate herbivory preferences from 30 years ago to what we observed in the field in summer 2022.

Species	Species observations	Herbivory observations	Proportion of herbivory	Preference Index 1997	Preference Index 2022
Eastern hemlock	1	1	100	0.032	100.000
Pin cherry	4	3	75	0.336	18.750
Yellow birch	6	5	83	0.007	13.833
Black spruce	7	0	0	0.05	0.000
American mountain ash	8	7	100	3.445	12.500
White ash	12	7	63	0.593	5.250
American beech	12	11	91	0.424	7.583
Northern red oak	15	11	78	0.001	5.200
White spruce	44	2	4	0.061	0.090
White birch	88	88	100	22.52	1.136
Sugar maple	100	39	39	1.299	0.390
Red maple	146	69	47	0.966	0.321
Balsam fir	165	87	53	4.628	0.321

Table 2.3. Biotic and abiotic variables used for data analysis

Variable Name	Units	Type	Role	Description
Tree species	N/A	Categorical	Predictor	13 different canopy tree species were identified at field sites throughout CBHNP
Altitude	m	Continuous	Predictor	The altitude measurement for each site was recorded from Google Earth
Seedling proportion	N/A	Continuous	Response	The seedling proportion was calculated in RStudio as the number of individuals of a chosen species over the total number of individuals at a site.
Population density	N/A	Continuous	Response	The population density was calculated in RStudio as the number of individuals of a chosen species over the area of a site (32m2)
Species group	N/A	Categorical	Predictor	13 species were divided into three species groups: boreal, Acadian, and red maple. Species groups were created based on species commonly present in Acadian and boreal habitat. As red maple is found in both habitats, we considered it a unique species group.
Site type	N/A	Categorical	Predictor	Each field site was assigned a site typing based on mechanisms such as altitude, species occurrence, and light availability.

Acadian canopy percentage	%	Continuous	Predictor	We calculated canopy percentage using recorded canopy cover data (inverse of light availability data recorded using a densiometer) from a maximum of eight seedling microsites observed at each field site. We then took the average canopy cover percentage from the total number of microsites at the field site to determine the overall site canopy percentage. Then, using field site observations, we identified a site as having a majority Acadian or boreal canopy based on the species in the overstory.
Boreal canopy percentage	%	Continuous	Predictor	We calculated canopy percentage using recorded canopy cover data (inverse of light availability data recorded using a densiometer) from a maximum of eight seedling microsites observed at each field site. We then took the average canopy cover percentage from the total number of microsites at the field site to determine the overall site canopy percentage. Then, using field site observations, we identified a site as having a majority Acadian or boreal canopy based on the species in the overstory.
Proportion of herbivory	N/A	Continuous	Response	The proportion of herbivory was calculated in RStudio as the number of individuals of a chosen species experiencing herbivory (y/n) over the total number of individuals at a site.
Herbivory level	0, 1, 2, 3	Categorical	Predictor	The herbivory level was categorized as 0, 1, 2, or 3, identified by lack of herbivory, low, medium, and high herbivory, respectively based on previous browse surveys conducted by Parks Canada in CBHNP.
Seedbed type	N/A	Categorical	Predictor	We identified the primary seedbed cover type at each seedling microsite as moss, grass, leaf litter, needle litter, or bunchberry.

Table 2.4. Summary of results from a GLM on the seedling proportion of Acadian, boreal, and red maple seedlings present at different altitudes(m) (Figure 2.10). Altitude and species group were predictor variables with seedling proportion as the response variable. This model assumes a Gaussian distribution. Values in bold indicate a significant difference (p-value < 0.05).

	Parameter	Estimate	Std. Error	z-value	p-value
Acadian seedlings					
	Intercept	0.854	0.138	6.177	6.93e-05
	Altitude	-0.002	0.001	-2.842	**0.016**
Boreal seedlings					
	Intercept	0.219	0.125	1.762	0.093
	Altitude	0.001	0.001	3.638	**0.002**
Red maple seedlings					
	Intercept	0.243	0.111	2.183	0.041
	Altitude	0.001	0.000	0.901	0.378

Table 2.5. Summary of results from a GLM on the population density of Acadian, boreal, and red maple seedlings present at different altitudes(m) (Figure 2.10). Altitude and species group were predictor variables with seedling population density as the response variable. This model assumes a Gaussian distribution. Values in bold indicate a significant difference (p-value < 0.05).

	Parameter	Estimate	Std. Error	z-value	p-value
Acadian seedlings					
	Intercept	0.388	0.147	2.639	0.023
	Altitude	-0.001	0.001	-0.333	0.745
Boreal seedlings					
	Intercept	0.343	0.195	1.757	0.0942
	Altitude	0.001	0.001	0.596	0.5578
Red maple seedlings					
	Intercept	0.244	0.091	2.716	0.013
	Altitude	-0.001	0.001	-0.499	0.623

Table 2.6. Summary of results from a two-way ANOVA on seedling proportion of seedlings present at different site types within species groups (Figure 2.11). Site type and species group were the predictor variables with seedling proportion as the response variable. Values in bold indicate a significant difference (p-value < 0.05)

Parameter	Df	Sum Sq	Mean Sq	z-value	p-value
Site type	3	0.388	0.129	1.83E+00	0.155
Species group	2	1.095	0.5477	7.736	**0.001**
Site type : species group	4	1.674	0.419	5.912	**0.001**

Table 2.7 Summary of results from a GLM on the seedling proportion of Acadian, boreal, and red maple seedlings present with Acadian canopy coverage (Figure 2.12). Acadian canopy percentage and species group were predictor variables with seedling proportion as the response variable. This model assumes a Gaussian distribution. Values in bold indicate a significant difference (p-value < 0.05)..

	Parameter	Estimate	Std. Error	z-value	p-value
Acadian seedlings					
	Intercept	0.280	0.173	1.618	0.134
	Acadian canopy	0.004	0.002	1.802	0.099
Boreal seedlings					
	Intercept	0.787	0.058	13.599	1.45e-11
	Acadian canopy	-0.006	0.001	-4.975	**7.29e-05**
Red maple seedlings					
	Intercept	0.365	0.072	5.049	6.14e-05
	Acadian canopy	-0.001	0.001	-0.838	0.412

Table 2.8. Summary of results from a GLM on the seedling proportion of Acadian, boreal, and red maple seedlings present with boreal canopy coverage (Figure 2.12). Acadian canopy percentage and species group were predictor variables with seedling proportion as the response variable. This model assumes a Gaussian distribution. Values in bold indicate a significant difference (p-value < 0.05).

	Parameter	Estimate	Std. Error	z-value	p-value
Acadian seedlings					
	Intercept	0.625	0.117	5.339	0.001
	Boreal Canopy	-0.003	0.002	-1.418	0.184
Boreal seedlings					
	Intercept	0.597	0.079	7.550	2.82e-07
	Boreal Canopy	0.002	0.002	0.774	0.448
Red maple seedlings					
	Intercept	0.288	0.063	4.554	0.001
	Boreal Canopy	0.002	0.002	1.377	0.184

Table 2.9. Summary of results from a GLM on the proportion of herbivory on different species (Figure 2.13). Species was the predictor variable with proportion of herbivory as the response variable. This model assumes a Gaussian distribution. Values in bold indicate a significant difference (p-value < 0.05).

Parameter	Estimate	Std. Error	z-value	p-value
(Intercept)	0.667	0.188	3.552	0.001
Eastern hemlock	0.333	0.375	0.888	0.377
Red oak	0.028	0.230	0.121	0.904
Sugar maple	-0.161	0.220	-0.731	0.467
White ash	0.019	0.265	0.070	0.945
Yellow birch	0.208	0.297	0.702	0.485
Red maple	-0.133	0.200	-0.665	0.508
Balsam fir	-0.171	0.201	-0.852	0.397
White birch	0.333	0.214	1.558	0.123
Black spruce	-0.667	0.265	-2.511	**0.014**
American mountain	0.250	0.248	1.007	0.317
Pin cherry	0.083	0.297	0.281	0.780
White spruce	-0.610	0.214	-2.848	**0.006**

Table 2.10. Summary of results from a two-way ANOVA on the proportion of herbivory at different site types within species groups (Figure 2.14). Site type and species group were predictor variables with the proportion of herbivory as the response variable. Values in bold indicate a significant difference (p-value < 0.05).

Parameter	Df	Sum Sq	Mean Sq	z-value	p-value
site_type	3	0.576	0.192	1.253	0.295
species group	2	1.205	0.602	3.935	**0.023**
site type: species group	4	0.318	0.0795	0.508	0.730

2.8 Figures

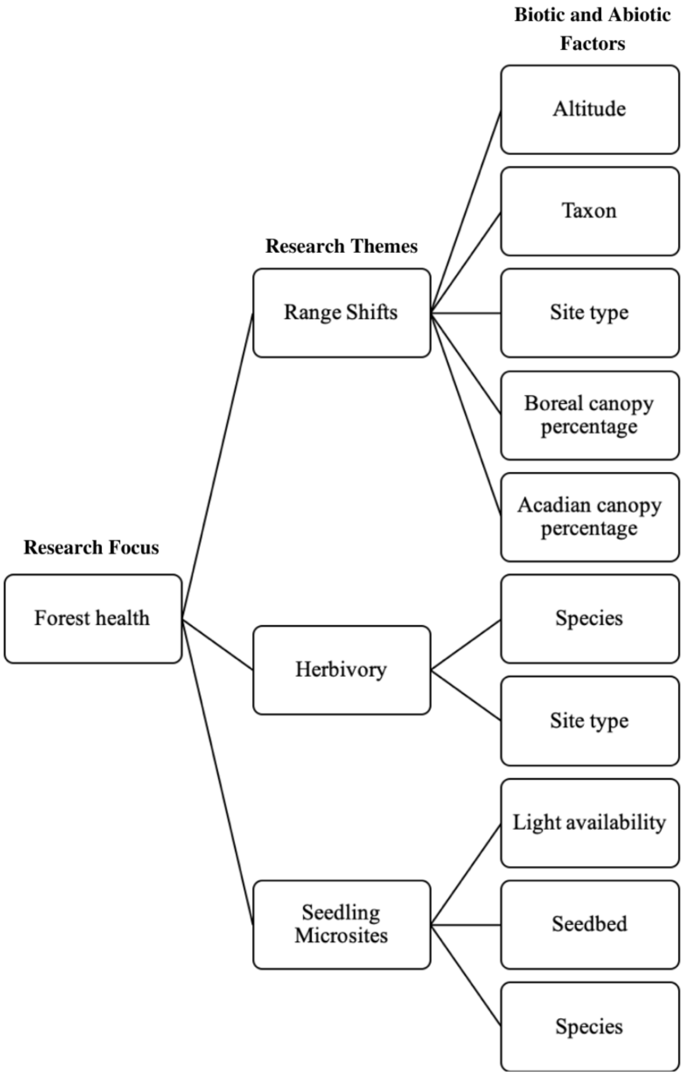

Figure 2.1. Flow chart demonstrating the biotic and abiotic mechanisms that correspond to our three research objectives, ultimately branching out from our research focus: forest health.

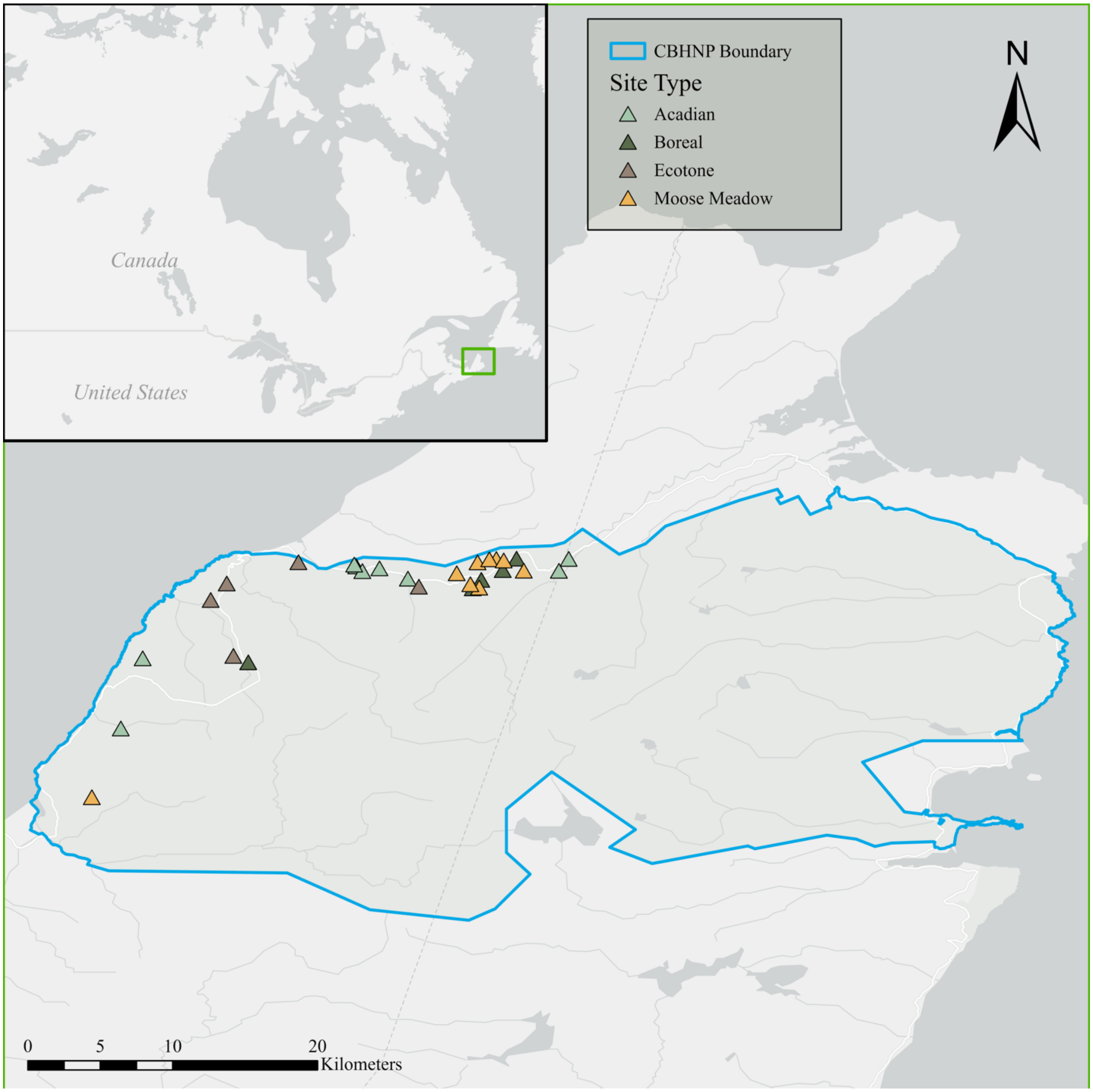

Figure 2.2. Acadian, boreal, ecotone, and moose meadow sites (n=28) throughout CBHNP. Sites span over 400m of elevation from Chéticamp to Big Intervale (Kosick, M. 2023).

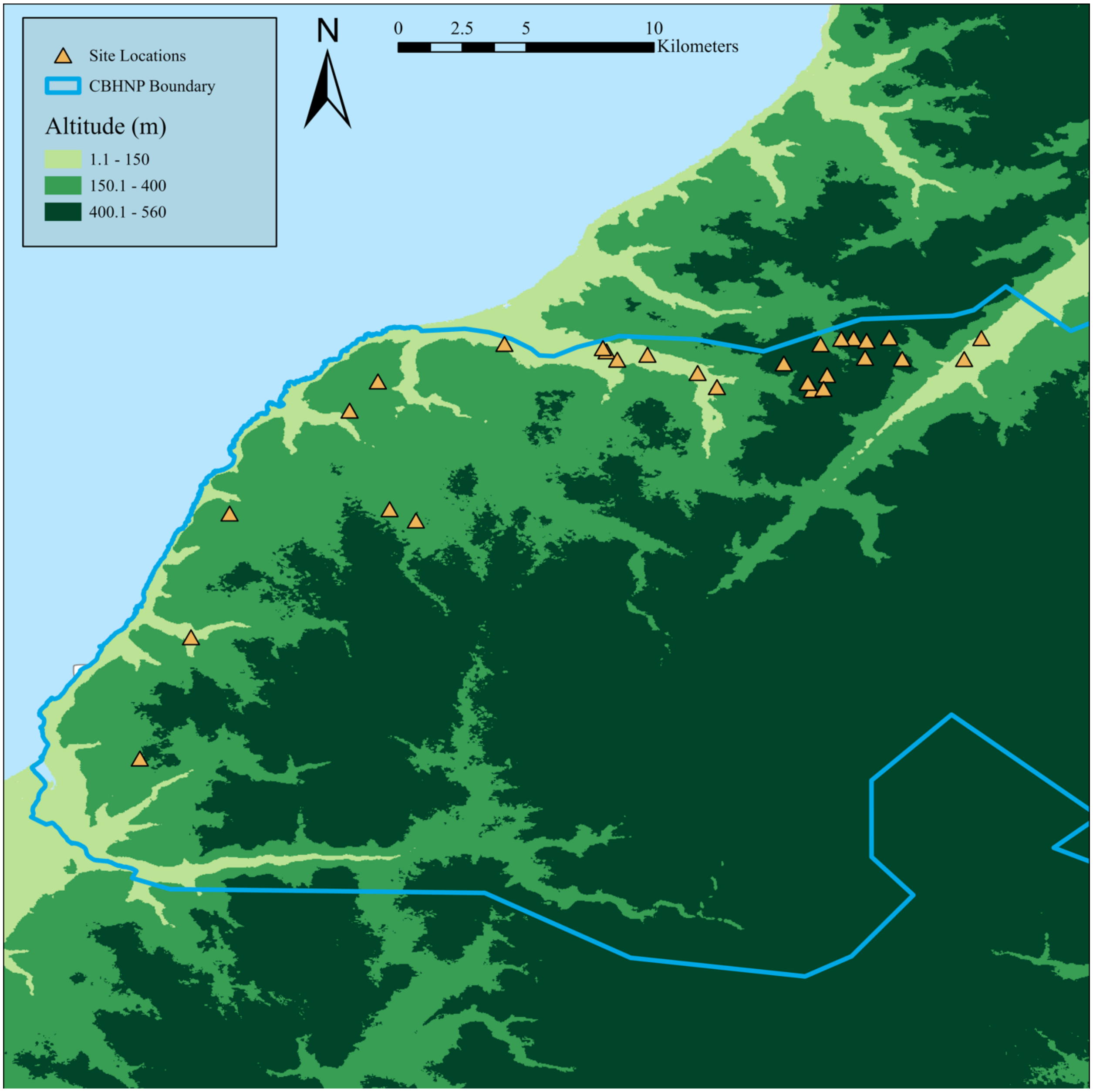

Figure 2.3. Altitudinal gradients visualized to delineate Acadian, ecotone, and boreal regions of CBHNP using our site selection parameters. Elevation ranges from 1.1-150m, 150.1-400m, and 400m+ illustrate Acadian, ecotone, and boreal regions, respectively (Kosick, M. 2023).

Figure 2.4. Moose meadow sites are present throughout the historic boreal regions of the Park, especially around North Mountain and French Mountain. These sites contain tall grasses, ericaceous heaths, and standing deadwood (typically white birch).

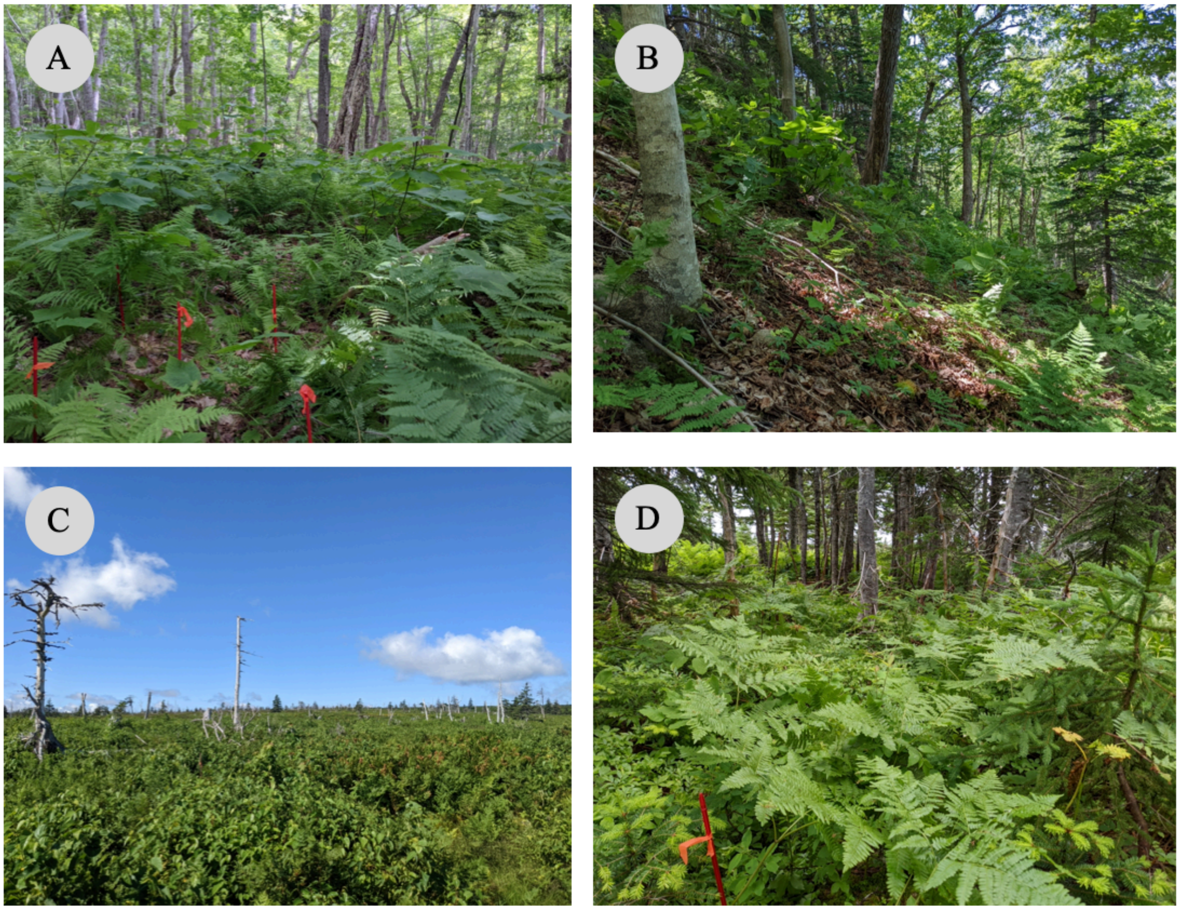

Figure 2.5. Visuals of the four different site types in CBHNP. (A) Acadian site EMAN GA1, (B) ecotone site EMAN FC, (C) moose meadow site F2, and (D) boreal site E5.

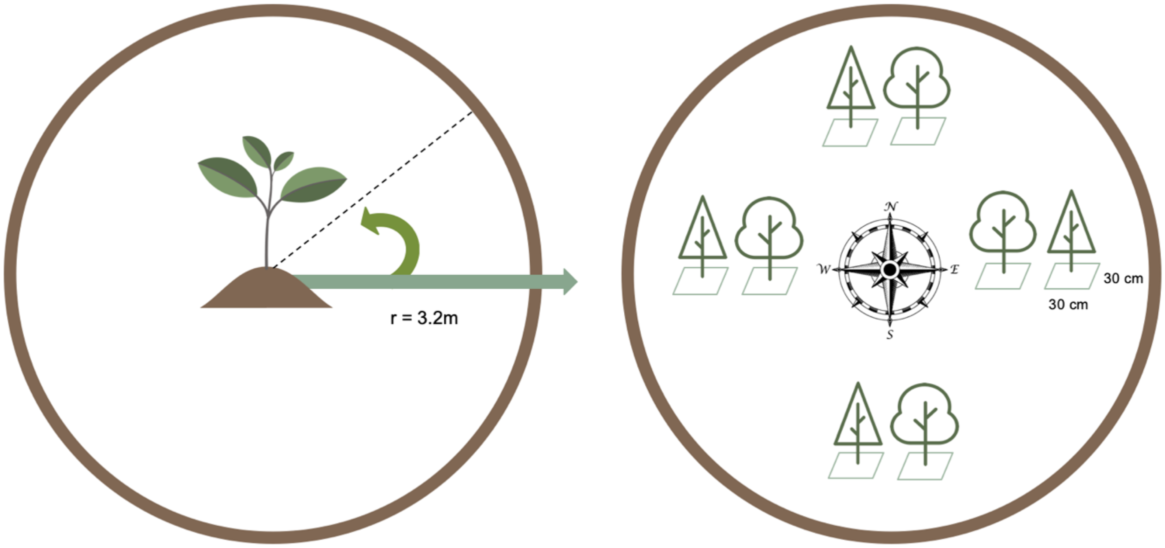

Figure 2.6. 32m^2 circular sites (n=28) were established at Acadian, boreal, moose meadow, and ecotone sites. Our sampling design is nested; Objectives 1 and 2 occur within the entire plot, while Objective 3 occurs in quadrats within the circular plot.

Figure 2.7. Levels of herbivory on deciduous white birch (B. papyrifera) and coniferous balsam fir (A. balsamea) trees. Low herbivory is characterized by intact apical meristem. Medium and high herbivory is characterized by an apical meristem that ungulates have removed. Browse severity intensifies from low to high herbivory.

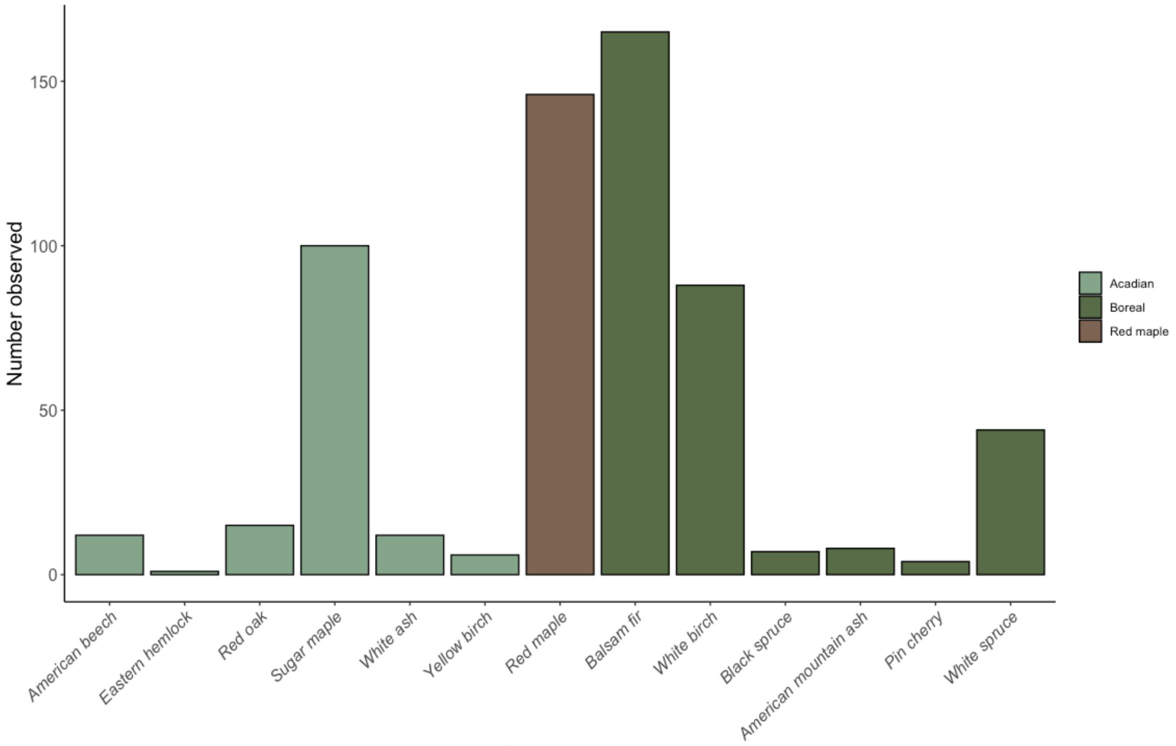

Figure 2.8. Tree species observed at field sites in CBHNP organized by species group. Red maple, balsam fir, white birch, and sugar maple were the most observed species across field sites.

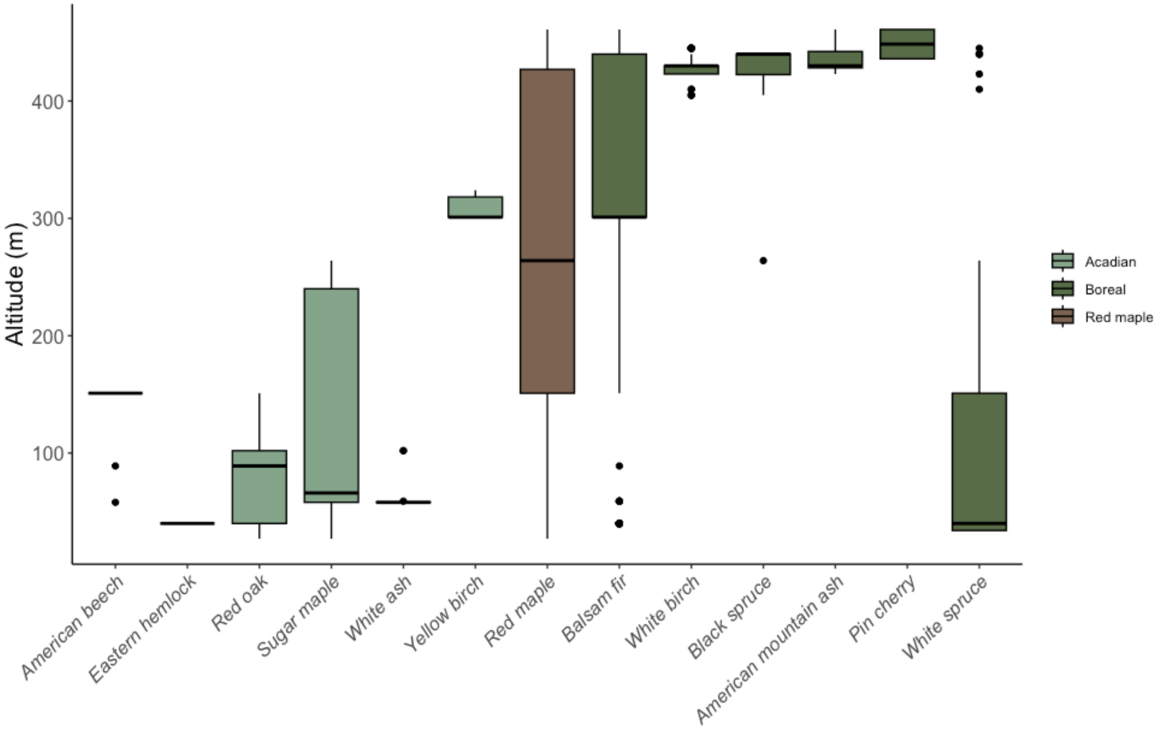

Figure 2.9. Tree species distribution along altitudinal gradients in CBHNP. In general, Acadian species were observed at lower altitudes, boreal species at higher altitudes, with red maple being found across all altitudinal gradients.

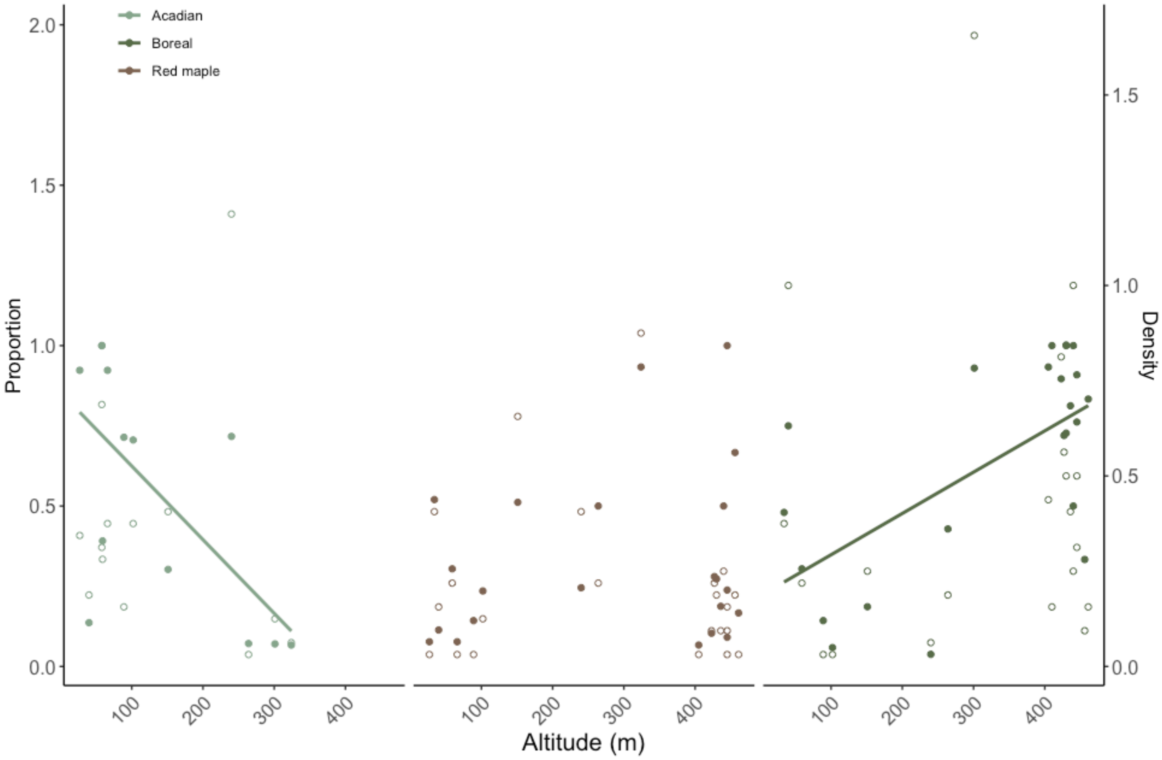

Figure 2.10. The proportion and density of Acadian, boreal, and red maple seedlings present at different altitudes. Acadian species were not observed at altitudes greater than 350m. Boreal and red maple seedlings were present across altitudinal gradients. Acadian seedling density was greater at lower altitudes, and Boreal seedling density was greater at higher altitudes. Red maple density remained relatively consistent across altitudinal gradients, with few exceptions.

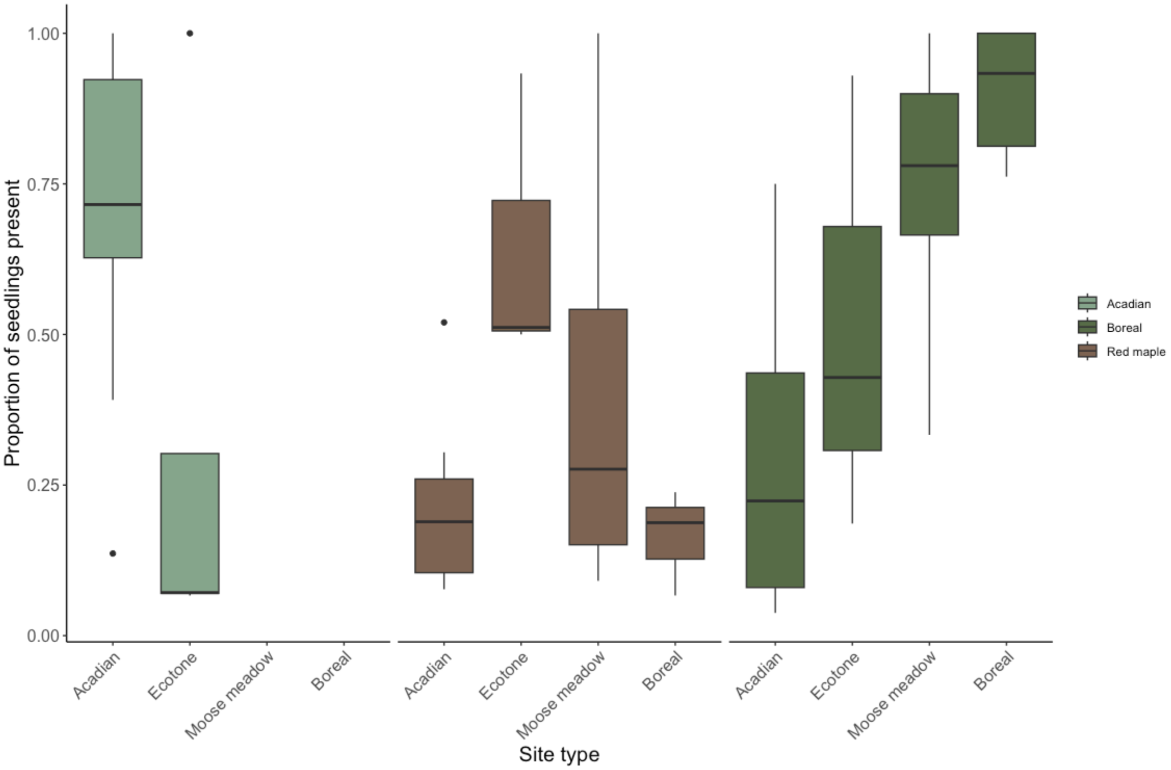

Figure 2.11. The proportion of Acadian, red maple, and boreal seedlings present at different site types in CBHNP. The proportion of Acadian seedlings present at Acadian sites (i.e., sites <150m elevation) is greater than at ecotone sites (i.e., sites between 150 and 400m elevation). Acadian seedlings were not observed at boreal or moose meadow sites (i.e., sites > 400m). The proportion of boreal seedlings present was greatest at boreal sites. The proportion of A. rubrum seedlings was greater at ecotone and moose meadow sites.

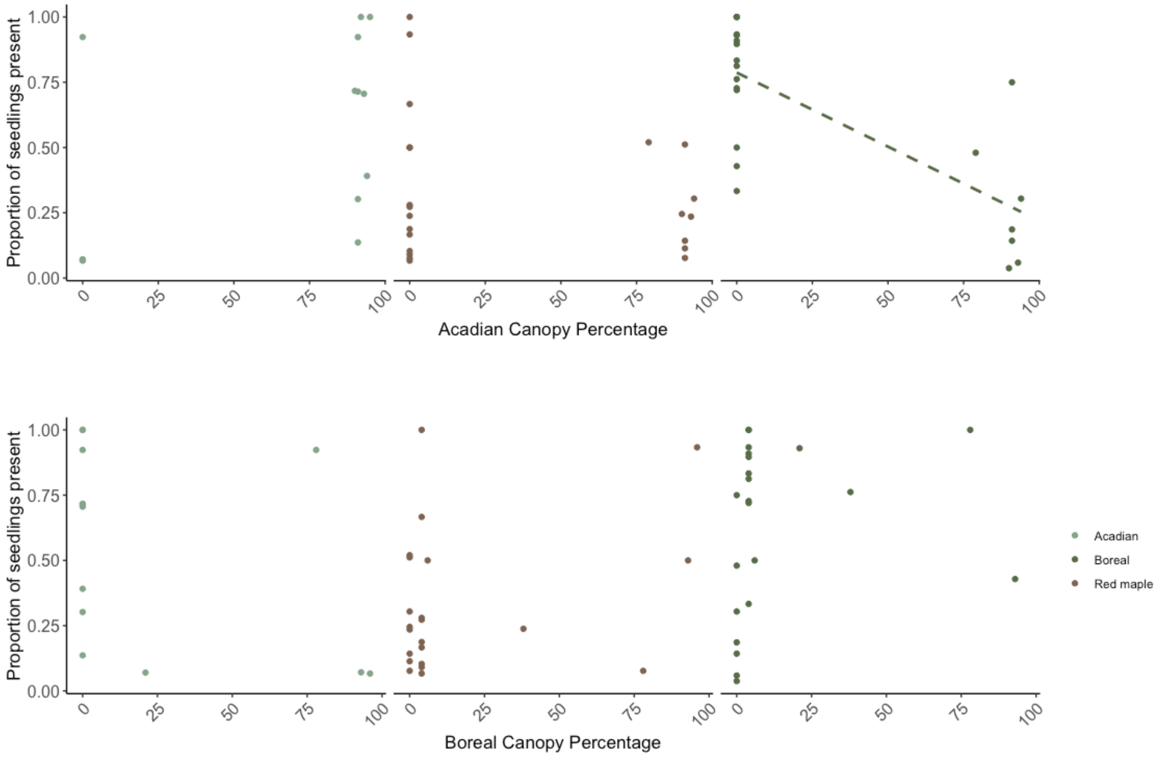

Figure 2.12. The proportion of Acadian, red maple, and boreal seedlings present with different canopy coverage and type.

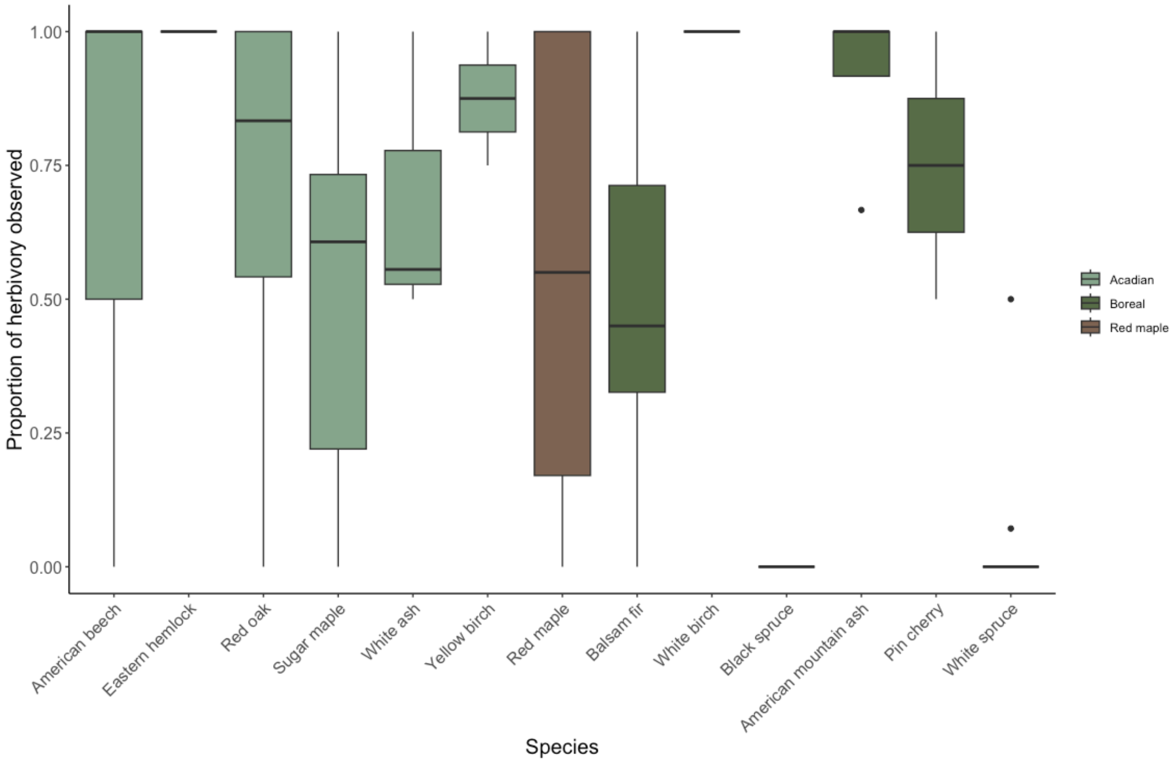

Figure 2.13. The proportion of ungulate herbivory on individual observations of different tree species categorized by species group at field sites throughout CBHNP

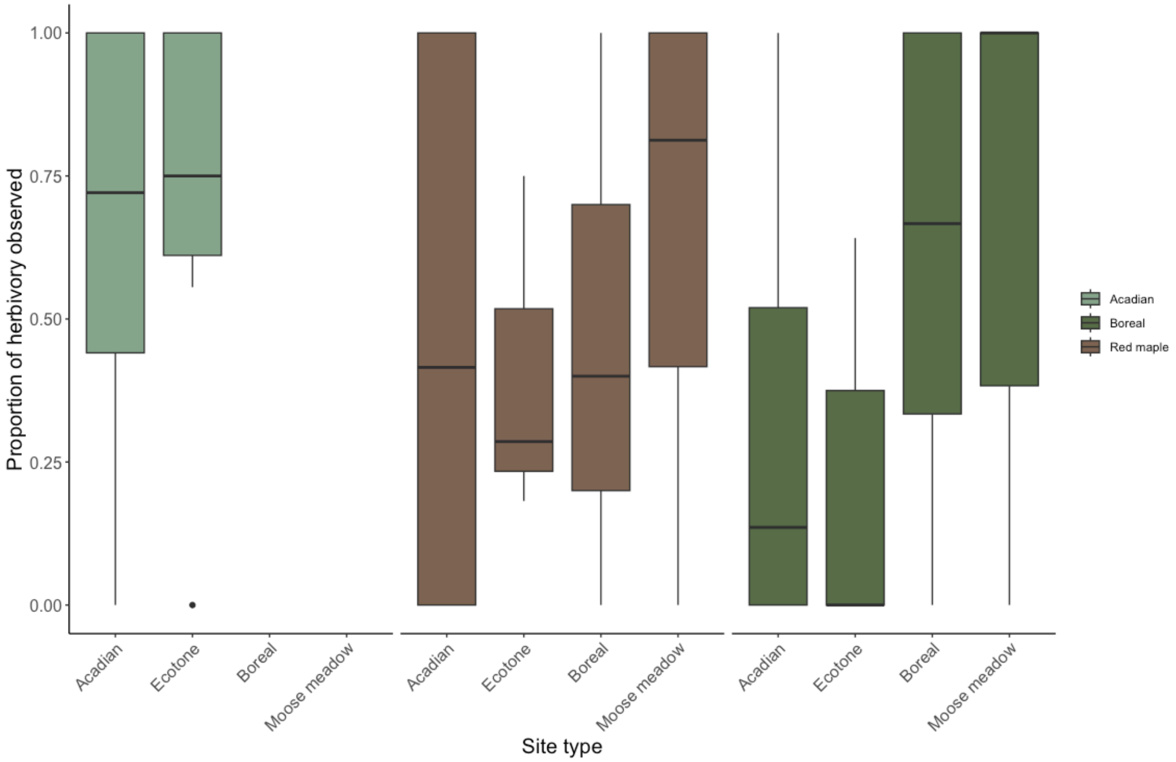

Figure 2.14. Proportion of herbivory observed at different site types within species groups. Acadian species were not observed at boreal or moose meadow sites; therefore, we could not calculate herbivory proportion for this species group at these site types

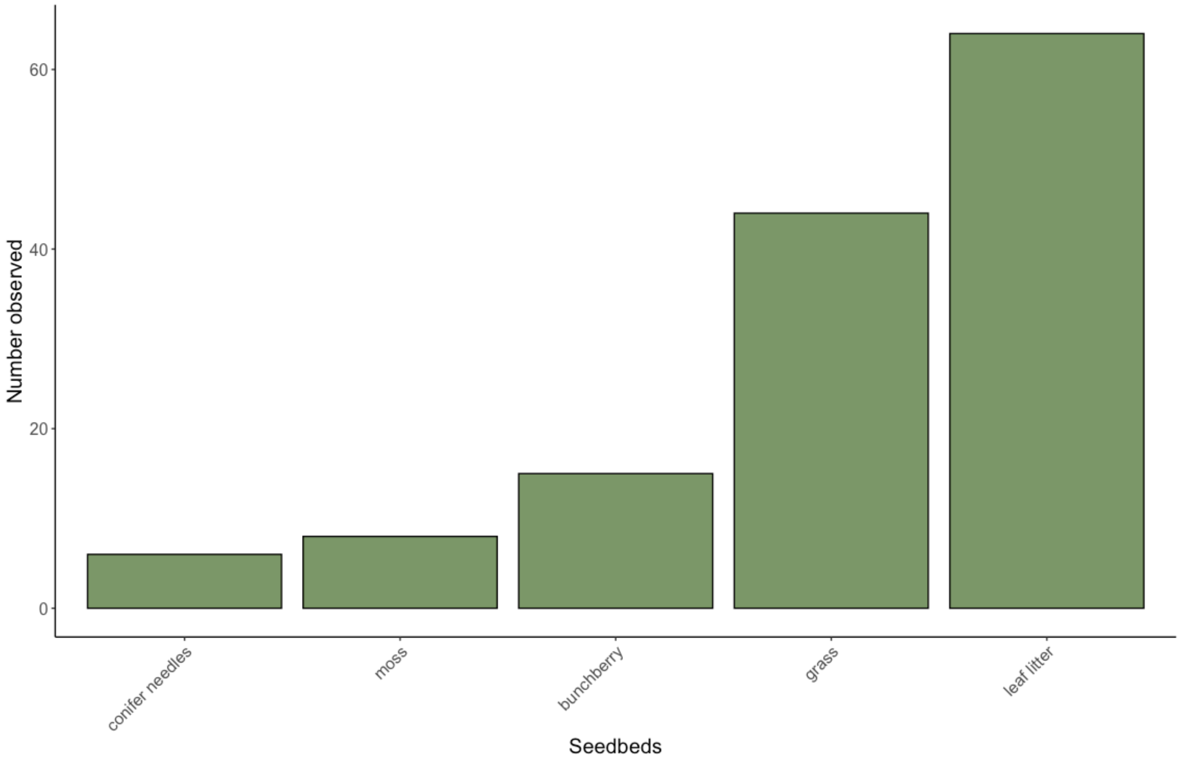

Figure 2.15. Most common seedbeds observed at seedling microsites in CBHNP.

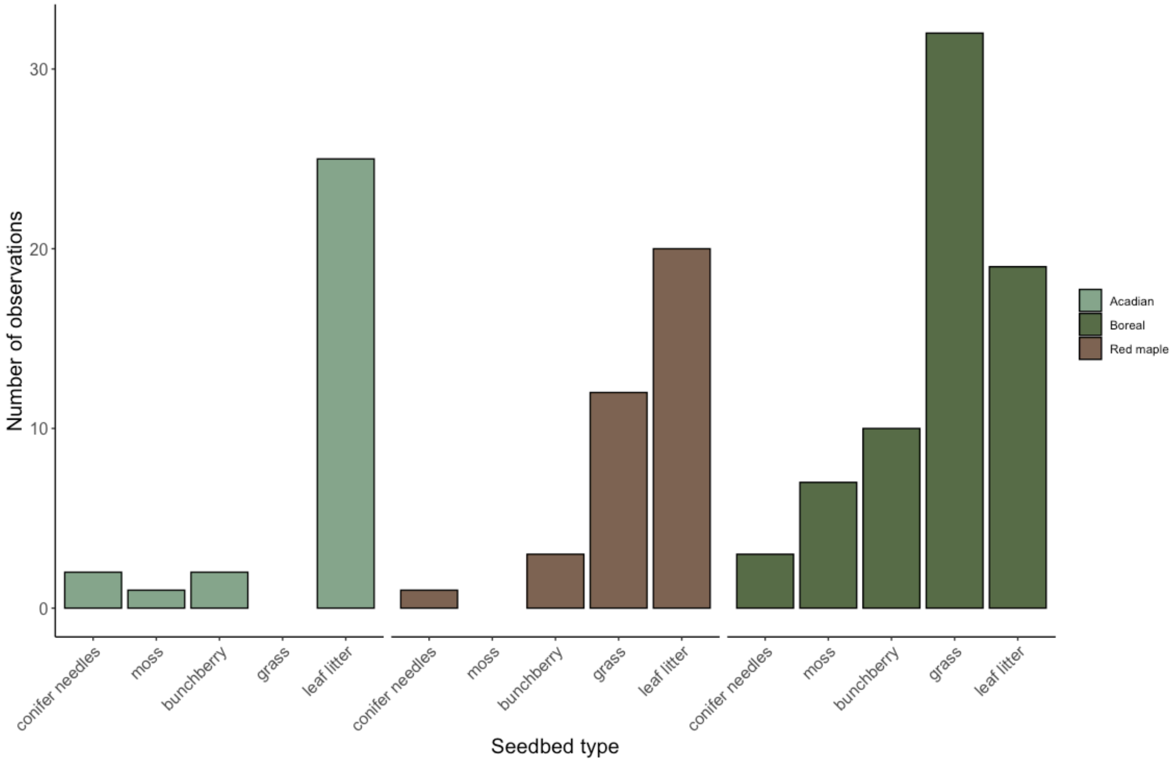

Figure 2.16. Most common seedbeds observed at seedling microsites within three species groups: Acadian, red maple, and boreal.

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Chapter 3 : Summary and conclusions

3.1 Summary of findings

Understanding how forests respond to regional mechanisms of change is critical if we want to limit the adverse effects of climate change on forests and enhance how forests affect climate change mitigation. Current scholarship calls for an increase in our understanding of forest refugia (Stralberg et al., 2020), forest range shifts (Brown & Vellend, 2014), and the biotic and abiotic drivers that influence tree species distributions (Evans et al., 2020). Temperate and boreal forests are particularly integral to this discussion. Temperate forests are exposed to high quantities of anthropogenic activity (Gilliam, 2016), and boreal forests occur in latitudinal ranges particularly affected by climate change (Collier et al., 2022; Gauthier et al., 2015). Although studies on temperate-boreal forest transitions have occurred in northeastern North America (e.g., Brice et al., 2020; Evans & Brown, 2017; Frei et al., 2018), our understanding of temperate-boreal refugia needs improvement. Our research contributes to this field of study by exploring forest dynamics within Acadian-boreal forest refugia, providing critical insight into how species distributions respond to changes at their geographic extremes.

Our study characterized Acadian and boreal forests, biotic and abiotic mechanisms that influence their distributions, and investigated how forest refugia may be particularly affected by species range shifts. We looked at altitudinal range shifts in western Cape Breton Highlands National Park (CBHNP) to assess whether Acadian forests encroached on high-elevation boreal forest stands. Generally, we found that Acadian species were more common at lower altitudes, boreal species at higher altitudes, and red maple (*Acer rubrum*) across altitudinal gradients. Although we frequently observed boreal seedlings at lower elevations, we did not observe Acadian seedlings above 300m, except for yellow birch, a common ecotone species in this region. Ultimately, we did not find evidence of Acadian forest range expansions, and our findings suggest multiple constraints on temperate forest range shifts, including altitude, moose herbivory, and limited seedbed availability. These constraints may be characteristic of southern boreal forest refugia, indicating that temperate forest advancement might be limited under similar conditions elsewhere in Canada. Presently, transitional stages at moose meadow sites persist due to red maple's success, inhibiting natural boreal forest succession. Eventually, the establishment of this deciduous species could facilitate Acadian forest range expansions if moose pressures are reduced.

Our herbivory analysis indicated that moose herbivory was most common on their preferred forage (i.e., deciduous species) regardless of location and elevation. It is possible that moose may demonstrate a preference towards more desirable boreal forage over red maple, increasing the chance of red maple success at moose meadow sites. Although moose browsing has significantly impacted the boreal forest in Cape Breton (Basquill & Thompson, 1997; D'Orsay & Howey, 2020), we expect climate-linked abiotic mechanisms to become more influential on tree species distributions as regional warming continues. Our findings also demonstrated that seedbed type significantly influenced the number of seedlings we observed within species groups. We did not observe any Acadian seedlings on grass seedbeds (i.e., moose meadow habitat) and rarely on boreal seedbeds, meaning seedbed availability also limited Acadian forest range expansion. In summary, altitude, herbivory, and seedbed availability significantly contribute to the presence or absence of species across altitudinal gradients in CBHNP.

3.2 Study considerations and next steps

Our study is one of the first examples of Acadian-boreal ecotone research in CBHNP, examining different forests and ecosystems across altitudinal gradients. We approached this study from an observational perspective to gain a broad understanding of temperate-boreal forest dynamics. Our work has presented three mechanisms that inhibit forest range shifts: altitude, herbivory, and seedbed availability. Future studies on this refugia should build on this empirical analysis to quantify Acadian and boreal species' responses to climate change.

Selecting and accessing study sites for this project was challenging. Most established field sites were over a kilometre hike through steep and dense forest terrain. While this provided great field site diversity for our project, time constraints meant we could only visit 28 sites instead of our initially proposed 40. This smaller sample size meant that we had disproportionate data on our study species, which allowed us to go more in-depth on some species' response to biotic and abiotic mechanisms than others.

To examine different site types, we selected sites from three different datasets provided to us by Parks Canada with varying characteristics, disparate variables, distinct study goals, and inconsistent monitoring across datasets. Initially, we wanted to analyze our data with previous data to assess any long-term trends in forest transitions; however, these divergent datasets did not provide a complete, temporal picture of the Acadian-boreal ecotone within CBHNP, so we could not assess long-term trends. Our data sets the stage for long-term monitoring within this ecotone, with an opportunity to build upon pre-existing, accessible field sites.

Establishing multi-year monitoring of Acadian-boreal forest transitions within CBHNP was beyond the range of a two-year Master's thesis. Nevertheless, this research can create a solid foundation for future monitoring of this ecotone. Future research should continue to take advantage of the natural elevational delineation between forests present in CBHNP. Visiting field sites for annual assessment would allow us to evaluate seedling recruitment, growth, and mortality, providing much-needed insight into temporal forest patterns. We recommend that future studies explore climate-linked abiotic mechanisms in this region over time, such as soil characteristics, temperature, and precipitation. Further, we cannot ignore the influence of 'les suêtes' (regional winds from the Gulf of St. Lawrence) on the ecology of the Western side of the National Park. Future research should explore Acadian-boreal forest dynamics on the Eastern side of the island (i.e., Ingonish area) and in other regions affected by 'les suêtes' (i.e., Gaspé peninsula) to explore climate-linked differences at the local and regional scales.

We found that red maple is remarkably resilient to the biotic and abiotic mechanisms we examined. As red maple establishment can provide corridors for Acadian seedling recruitment at higher altitudes, future studies should closely examine red maple recruitment across altitudinal gradients in concert with the climate-linked abiotic mechanisms mentioned previously. Annual visits to sites with red maple seedlings would allow us to identify if they are growing, affecting seedbed and light conditions, and contributing to the establishment or mortality of Acadian and boreal seedlings.

Lastly, it is important to address that we could only observe the presence of a variable at a field site. The absence of a variable, such as seedlings, species, herbivory, or seedbed, is challenging to quantify. For example, Acadian seedlings could have germinated at higher altitudes; however, we might not have observed them due to moose herbivory. Since we did not explicitly observe Acadian seedlings at higher altitudes, we can only say that moose herbivory is likely limiting Acadian forest range expansion, not definitively; however, the absence of that evidence does not mean the data does not exist. Our observations of moose herbivory identified regional moose foraging preferences, but our broad-scale analysis limited our capacity to produce quantitative data. Previous research by Parks Canada (D'Orsay & Howey, 2020) has looked at browse intensity at moose meadow sites over time, and we suggest that future research builds on this by quantifying species-specific browsing patterns at different site types. Using pre-existing moose exclosures and establishing smaller exclosures would allow a more controlled assessment of moose foraging patterns across altitudinal gradients.

3.3 Management recommendations

CBHNP contains rare patches of boreal and old-growth Acadian forests in Nova Scotia, making it a refugium and climate buffer for species. The boreal forest of Cape Breton has been slowly receding over the last few centuries, with the extirpation of caribou, native moose, wolves, and other keystone species as an indication of these changes (Dauphiné, 1974; D'Orsay & Howey, 2020; Smith et al., 2010). Parks Canada has been invested in researching boreal forest health in CBHNP in the last decade (Charron et al., 2020; C. Franklin et al., 2015), and in 2014, they launched their five-year forest restoration project called Bring Back the Boreal (D'Orsay & Howey, 2020). Today, the boreal forest remains patchy and vulnerable to Acadian forest range expansion, yet temperate range shifts have yet to occur, and post-disturbance transitional stages persist. Despite a recent increase in forest research, these ecosystems lack consistent long-term monitoring data, making the future of these forests challenging to predict. Conducting large-scale forest monitoring requires extensive time and resources. Considering this, we've identified three areas of improvement for management: plan for success, share the load, and prioritize and maximize conservation.

3.3.1 Plan for success

Research of this scale should maximize on site accessibility so that consistent, annual monitoring is achievable and low maintenance for researchers. Establishing a framework of field sites from new and pre-existing sites near access roads, across altitudinal gradients, and covering a range of habitats would facilitate data collection by increasing the quantity and quality of data collected within the Acadian-boreal ecotone of this region. Currently, many field sites in western CBHNP are several hundred metres off the nearest access road. Future sites should be less than 300m from primary roads (e.g., The Cabot Trail) or be located less than 100m off a Park hiking trail for easy access.

Further consideration should be made so that it is easy for researchers to access three to four field sites in a day to maximize research outputs and facilitate management. For many of our field days, the distance and difficulty of access meant we could only visit two field sites daily. Even though our data collection methods were straightforward and took little time, most of our time was spent driving and hiking to our sites. Field researchers should be permitted to remain overnight near sites or overnight accommodations should be made available to researchers as close to field sites as possible to reduce commute times. The current layout of moose browse plots is an excellent example of site selection and layout, as it is easy to sample multiple field sites consecutively. If a similar strategy were utilized to select field sites across an altitudinal gradient, it would facilitate data collection and ensure field sites encompass the diversity of habitat within the Acadian-boreal ecotone, which would help guide future CBHNP management decisions.

In addition to site selection, future management plans should include specific goals and itemized tasks to ensure success. By creating a long-term data collection plan that reflects research priorities, we can actualize research by ensuring our success in the field. Research actualization starts with establishing field method protocols that cover a range of biotic and abiotic mechanisms to ensure that various research questions can be explored from a singular dataset (Table 3.1). Collecting this information would ensure we are prepared for future research needs and allow organized data to be seamlessly shared with external collaborators.

3.3.2 Share the load

Collaborations with other National Parks with similar ecology and research interests (e.g., Terra Nova National Park, Forillion National Park, Fundy National Park) will help increase our understanding of changing temperate and boreal forest ecosystems while relieving research pressures from Parks Canada researchers. We can ask questions that benefit all parties by identifying joint research priorities. For example, future collaborative research could explore how the temperate-boreal ecotone in different National Parks across Atlantic Canada have responded to disturbances (e.g., spruce budworm outbreaks, increase in moose browse intensity) and how succession has differed.

In addition to collaborating with other National Parks, future research could be conducted alongside academic institutions, specifically by working with undergraduate, graduate, and college student researchers to explore specific research questions within the broader scope of the temperate-boreal ecotone. Further, these collaborations would also increase our capacity to conduct management. This project has demonstrated that collaborating with students is a great way to engage with early career researchers, provide them with invaluable fieldwork experience and networking opportunities, and receive high-quality research outputs. Undergraduate honours students can actively participate in one season of data collection and produce data within a short timeline. Master's students have a longer timeline (approx. two years), meaning they can collect data for one or two field seasons, allowing them to conduct a more thorough analysis. Doctoral students require a more significant time commitment (approx. four years); however, this allows for extensive spatial and temporal analysis by exploring multiple research questions. Establishing relationships with university research labs will ensure ongoing collaborations with researchers, benefiting both parties.

3.3.3 Prioritize and maximize conservation

Climate change has led us to expect species range shifts and ecosystem changes, resulting in "ecosystem transformations" as communities diverge from their historic forest states (Brice et al., 2020; Lynch et al., 2021). Although exacerbated by climate change, these changes in ecosystem composition are natural, yet, most management practices still focus on resisting change, pouring resources into maintaining historic ecosystem structures (Lynch et al., 2021). In some cases, however, conservation may not be feasible or desirable due to time, financial, and resource constraints. In these situations, we recommend utilizing the *resist, accept, or direct* (RAD) framework outlined by Lynch et al. (2021). Following the RAD framework gives resource managers three options: *resist* ecosystem change by employing conservation strategies, *accept* inevitable ecosystem transformations where conservation is not feasible, or *direct* change towards a new ecosystem (i.e., encourage range shifts) (Lynch et al., 2021).

The most recent boreal forest research conducted in CBHNP has primarily focused on *resisting* ecosystem transformation; however, continued resistance is not financially viable and may negatively affect ecosystem services and inherent functioning long-term (Lynch et al., 2021). Future management should employ RAD strategies that are site specific to optimize *resist* and *direct* capacity. For example, it is possible to *resist* change in some regions of the Park where boreal forests persist, or re-borealization is possible. In this situation, management responses could include planting seedlings, installing moose exclosures, ameliorating seedbeds, or a combination of all three. When resistance is futile, we can *direct* Acadian forest range expansion at the ecotone and encourage temperate trajectories of change. Directing change should be considered extensively before implementation. Monitoring and learning from these ecosystems should always be our primary objective, as meddling with ecosystem succession can have severe implications if executed on impulse or intuition. In some remote areas of the Park, resisting or directing change might be too costly or time-consuming. In these cases, we can *accept* changes by allowing natural succession to occur without interference.

In summary, the changes occurring in the refugia of CBHNP are an indication what might occur in other temperate-boreal ecotones. Although Acadian forest range expansions have yet to occur in CBHNP, that does not mean this shift is not possible. By collaborating with other National Parks and academic institutions, we can develop efficient forest monitoring procedures that cover a range of biotic and abiotic mechanisms across the Acadian-boreal ecotone of CBHNP. Learning about Acadian and boreal forest dynamics will help us anticipate future changes to these ecosystems at the regional and global scales so that we can respond with site-specific management strategies. Using methodologies such as the RAD framework, we can resist change in areas of the Park where boreal forests remain, accept changes to regions where conservation is not feasible, and cautiously direct ecosystem transformations towards Acadian forests where appropriate. Instead of viewing the forest as something we should manage, we need to shift towards seeing the forest for what it is: a teacher. Learning from the Acadian and boreal forests will help us become better environmental stewards and members of the ecological community, better equipped to support the forest as it grows and changes in the coming years.

3.4 Tables

Table 3.1. Biotic and abiotic mechanisms recommended to be included in regular site monitoring.

Biotic mechanisms	Abiotic mechanisms
Seedling count (by species)	Canopy cover (light)
Tree count (by species)	Altitude
Tree DBH	Temperature
Tree age	Precipitation
Herbivory	Seedbed type
Canopy type	Soil type

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Appendix I: Tree species identification guide

Table AI.I Boreal and Acadian species identification characteristics in CBHNP used for data collection. Mi'kmaw names sourced from AMEC Environment and Infrastructure (2013) although the exact names and spelling of these species can differ in Mi'kmaw based on the region.

Species	Scientific name	Mi'kmaw name	Identification characteristics
Boreal			
balsam fir	*Abies balsamea*	Stoqn	Flat, opposite needles that are darker on the top with two, thin white lines on the underside. Grey bark, often covered in sap blisters. Barrel-shaped cones sit upright. Aromatic foliage.
white birch	*Betula papyrifera*	Maskwi	Distinctive, white, paper-like bark. Alternate, ovular, leaves have serrated edges. Long catkins hang from branches.
			Reddish brown twig colouring
white spruce	*Picea glauca*	Kawatkw	Large trees, full, conical-shaped trees with four-sided needles that you can eaily roll between your fingers. Needles have a slight bluish tint. Narrow, cylindrical cones hang beneath branches.
black spruce	*Picea mariana*	Kawatkw	Narrow tree with drooping branches. Grey/brackish scaly bark. Four-sided needles are green. Small, egg-shaped cones hang beneath branches
American mountain ash	*Sorbus americana*	E'psemusi	Compound leaves with leaf stalks, thin and smooth bark, fleshy, clumped, bright red fruit
pin cherry	*Prunus pensylvanica*	Maskwe'smanaqsi	Small tree or shrub with horizontal branches broad, lance shaped leaves that are long pointed, finely and sharply saw toothed bark is reddish grey, smooth, and thin, distinguishable "pin pricks" on the bark

Acadian			
sugar maple	*Acer saccharum*	Snawey	Simple, lobed, leaves with "u" shape in between lobes. Ridged/plated bark and golden brown wood
yellow birch	*Betula alleghaniensis*	Nimnoqn	Simple teethed leaves with stalks. Bark is smooth and is golden in colour….more shaggy than white birch fall leaves are yellow
American beech	*Fagus grandifolia*	Su'omusi	Large tree with rounded crown of many long, spreading horizontal branches. Elliptical/ovate leaves, long pointed tip with many straight, parallel slightly sunken side veins with coarsely saw toothed edges
Eastern hemlock	*Tsuga canadensis*	Ksu'skw	Evergreen needles slightly shorter than balsam fir needles are flat and rounded at the tip. Needles are shiny dark green above and have two white bands underneath. Twigs are yellow/brown, finely hairy, and are rough with peglike bases
Northern red oak	*Quercus rubra*	Mimqwanmusi	Leaves are elliptical, shallow, wavy, lobes with irregular teeth dull green turning to dark brown/red in fall
white ash	*Fraxinus americana*	Aqamoq	Compound leaf blade usually 7-9 leaflets, two leaves per node along the stem, edge of the leaf blade has teeth, leaves have leaf stalks
red maple	*Acer rubrum*	Malsnawey	Simple leaves with ridged lobes, plated bark, leaves red colour in fall. Leaves are characteristically teethed and divided into lobes unlike sugar maple which has lobes that form a "u" shape

Appendix II: Field sites

Table AII.I Data collection sites (n=28) at varying altitudes throughout CBHNP. Site types include: boreal, moose meadow, ecotone, and Acadian.

Site	Site (Parks Canada ID)	Altitude (m)	Seedling density			Seedling proportion			Acadian canopy	Boreal canopy
			Acadian	*A. rubrum*	Boreal	Acadian	*A. rubrum*	Boreal		
Boreal										
B1	mbr 69	405	N/A	0.031	0.437	N/A	0.066	0.933	0.000	0.040
B2	E5	440	N/A	N/A	1.000	N/A	N/A	1.000	0.000	0.780
B3	L3	436	N/A	0.094	0.406	N/A	0.187	0.812	0.000	0.040
B4	C6	445	N/A	0.156	0.5	N/A	0.238	0.762	0.000	0.380
B5	I4	430	N/A	N/A	0.844	N/A	N/A	1.000	0.000	0.040
Moose Meadow										
M1	L6	423	N/A	0.094	0.813	N/A	0.103	0.897	0.000	0.040
M2	B3	461	N/A	0.031	0.156	N/A	0.167	0.833	0.000	0.040
M3	Acadian 2	410	N/A	N/A	0.156	N/A	N/A	1.000	0.000	0.040
M4	H2	430	N/A	0.188	0.500	N/A	0.273	0.727	0.000	0.040
M5	I2	445	N/A	1.000	N/A	N/A	0.094	N/A	0.000	0.040
M6	J3	456	N/A	0.188	0.094	N/A	0.667	0.333	0.000	0.040
M7	D5	445	N/A	0.031	0.312	N/A	0.091	0.909	0.000	0.040
M8	F2	427	N/A	0.219	0.563	N/A	0.280	0.720	0.000	0.040
M9	C5	440	N/A	0.250	0.250	N/A	0.500	0.500	0.000	0.060
Ecotone										
E1	11003002	301	0.125	N/A	1.656	0.070	N/A	0.930	0.000	0.210
E2	HKEP1	324	0.063	0.870	N/A	0.067	0.933	N/A	0.000	0.960
E3	EMAN FC	264	0.031	0.219	0.188	0.071	0.500	0.429	0.000	0.930
E4	GA3	151	0.406	0.656	0.250	0.302	0.512	0.186	0.910	0.000

E5	13003001	58	0.313	N/A	N/A	1.000	N/A	N/A	0.950	0.000
Acadian										
A1	21004001	102	0.375	0.125	0.031	0.705	0.235	0.059	0.930	0.000
A2	NA2	89	0.156	0.031	0.031	0.714	0.143	0.143	0.910	0.000
A3	GA2	58	0.687	N/A	N/A	1.000	N/A	N/A	0.920	0.000
A4	14003002	40	0.188	0.156	1.000	0.136	0.114	0.750	0.910	0.000
A5	14001005	27	0.344	0.031	N/A	0.923	0.077	N/A	0.780	0.000
A6	14002009	34	N/A	0.406	0.375	N/A	0.52	0.480	0.790	0.000
A7	EMAN CB	59	0.281	0.219	0.219	0.391	0.304	0.304	0.940	0.000
A8	10002003	240	1.188	0.406	0.063	0.717	0.245	0.038	0.900	0.000
A9	GA1	66	0.375	0.031	N/A	0.923	0.077	N/A	0.910	0.000

Appendix III: Generalized linear model outputs

AIII.I A generalized linear model showing the proportion of Acadian seedlings present at different altitudes(m) across 28 field sites (Figure 2.10).

```
Call:
glm(formula = proportion ~ altitude, family = gaussian(link = "identity"),
   data = proportion_density_A)

Deviance Residuals:

   Min       1Q      Median    3Q        Max
-0.6261  -0.1767   0.0643   0.2203   0.4137


Coefficients:
                    Estimate Std. Error t value Pr(>|t|)
(Intercept)  0.854357   0.138306   6.177 6.93e-05 ***
altitude    -0.002296   0.000808  -2.842    0.016 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for gaussian family taken to be 0.08973143)

   Null deviance: 1.71177  on 12  degrees of freedom
Residual deviance: 0.98705  on 11  degrees of freedom
AIC: 9.3786

Number of Fisher Scoring iterations: 2
```

AIII.II A generalized linear model showing the proportion of boreal seedlings present at different altitudes(m) across 28 field sites (Figure 2.10)

```
Call:
glm(formula = proportion ~ altitude, family = gaussian(link = "identity"),
   data = proportion_density_B)

Deviance Residuals:
    Min        1Q        Median      3Q         Max
-0.49061  -0.17597   0.01474   0.20874   0.47916
```

```
Coefficients:
              Estimate   Std. ErroR  t value Pr(>|t|)
(Intercept) 0.2193385  0.1245018   1.762  0.09340 .
altitude    0.0012875  0.0003539   3.638  0.00164 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 0.06771537)

    Null deviance: 2.2504  on 21  degrees of freedom
Residual deviance: 1.3543  on 20  degrees of freedom
AIC: 7.1027

Number of Fisher Scoring iterations: 2
```

AIII.III A generalized linear model showing the proportion of red maple seedlings present at different altitudes(m) across 28 field sites (Figure 2.10)

```
Call:
glm(formula = proportion ~ altitude, family = gaussian(link = "identity"),
    data = proportion_density_RM)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-0.29943  -0.18314  -0.09688   0.16340   0.62174

Coefficients:
              Estimate  Std. Error  t value  Pr(>|t|)
(Intercept) 0.2429562  0.1113080   2.183   0.0411 *
altitude    0.0003041  0.0003375   0.901   0.3783
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 0.07298262)

    Null deviance: 1.5189  on 21  degrees of freedom
Residual deviance: 1.4597  on 20  degrees of freedom
AIC: 8.7507

Number of Fisher Scoring iterations: 2
```

AIII.IV A generalized linear model showing the population density of Acadian seedlings present at different altitudes(m) across 28 field sites (Figure 2.10).

```
Call:
glm(formula = density ~ altitude, family = gaussian(link = "identity"),
    data = proportion_density_A)

Deviance Residuals:
     Min        1Q      Median      3Q        Max
-0.28092  -0.18877  -0.05862   0.01647   0.86846

Coefficients:
                  Estimate    Std. Error  t value   Pr(>|t|)
(Intercept)  0.3877208  0.1468943   2.639    0.023 *
altitude    -0.0002862  0.0008582  -0.333    0.745
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for gaussian family taken to be 0.1012221)

    Null deviance: 1.1247  on 12  degrees of freedom
Residual deviance: 1.1134  on 11  degrees of freedom
AIC: 10.945

Number of Fisher Scoring iterations: 2
```

AIII.V A generalized linear model showing the population density of boreal seedlings present at different altitudes(m) across 28 field sites (Figure 2.10).

```
Call:
glm(formula = density ~ altitude, family = gaussian(link = "identity"),
    data = proportion_density_B)

Deviance Residuals:
    Min       1Q      Median     3Q       Max
-0.4004  -0.3028  -0.1122   0.0636   1.2134

Coefficients:
                Estimate     Std. Error   t value  Pr(>|t|)
(Intercept) 0.3432070  0.1953471   1.757   0.0942 .
altitude    0.0003310  0.0005553   0.596   0.5578
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
(Dispersion parameter for gaussian family taken to be 0.1667054)

    Null deviance: 3.3933  on 21  degrees of freedom
Residual deviance: 3.3341  on 20  degrees of freedom
AIC: 26.923

Number of Fisher Scoring iterations: 2
```

AIII.VI A generalized linear model showing the population density of red maple seedlings present at different altitudes(m) across 28 field sites (Figure 2.10).

```
Call:
glm(formula = density ~ altitude, family = gaussian(link = "identity"),
    data = proportion_density_RM)

Deviance Residuals:
     Min        1Q      Median       3Q        Max
-0.20949  -0.13915  -0.05513   0.02696   0.67473

Coefficients:
              Estimate   Std. Error   t value  Pr(>|t|)
(Intercept)  0.2444214  0.0899973   2.716   0.0133 *
altitude    -0.0001363  0.0002729  -0.499   0.6230
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 0.04771171)

    Null deviance: 0.96613  on 21  degrees of freedom
Residual deviance: 0.95423  on 20  degrees of freedom
AIC: -0.60025

Number of Fisher Scoring iterations: 2
```

AIII.VII A two-way ANOVA showing seedling proportion of seedlings present at different site types within species groups across 28 field sites (Figure 2.11).

```
> anova_11 <- aov(proportion ~ site_type*taxon, data=proportion)
> summary(anova_11)
                Df Sum Sq Mean Sq F value   Pr(>F)
site_type        3  0.388  0.1292   1.825 0.155498
taxon            2  1.095  0.5477   7.736 0.001247 **
site_type:taxon  4  1.674  0.4186   5.912 0.000614 ***
Residuals       47  3.328  0.0708
```

AIII.VIII A generalized linear model showing seedling proportion of Acadian seedlings present with Acadian canopy coverage across 28 field sites (Figure 2.12).

```
Call:
glm(formula = proportion ~ acadian.canopy, family = gaussian(link = "identity"),
    data = proportion_density_A)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-0.51510  -0.21376   0.04626   0.27161   0.64266

Coefficients:
               Estimate Std. Error t value Pr(>|t|)
(Intercept)    0.280422   0.173262   1.618    0.134
acadian.canopy 0.004077   0.002263   1.802    0.099 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 0.1201574)

    Null deviance: 1.7118  on 12  degrees of freedom
Residual deviance: 1.3217  on 11  degrees of freedom
AIC: 13.174

Number of Fisher Scoring iterations: 2
```

AIII.IX A generalized linear model showing seedling proportion of boreal seedlings present with Acadian canopy coverage across 28 field sites (Figure 2.12).

```
Call:
glm(formula = proportion ~ acadian.canopy, family = gaussian(link = "identity"),
    data = proportion_density_B)

Deviance Residuals:
     Min        1Q     Median       3Q       Max
-0.45363  -0.11716   0.03595   0.14243   0.47918

Coefficients:
                Estimate  Std. Error  t value  Pr(>|t|)
(Intercept)     0.786963   0.057869   13.599 1.45e-11 ***
acadian.canopy -0.005672   0.001140   -4.975 7.29e-05 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 0.05029357)

    Null deviance: 2.2504  on 21  degrees of freedom
Residual deviance: 1.0059  on 20  degrees of freedom
AIC: 0.55916

Number of Fisher Scoring iterations: 2
```

AIII.X A generalized linear model showing seedling proportion of red maple seedlings present with Acadian canopy coverage across 28 field sites (Figure 2.12).

```
Call:
glm(formula = proportion ~ acadian.canopy, family = gaussian(link = "identity"),
    data = proportion_density_RM)

Deviance Residuals:
     Min        1Q     Median       3Q       Max
-0.29861  -0.18457  -0.08891   0.13472   0.63472

Coefficients:
               Estimate Std. Error t value Pr(>|t|)
(Intercept)     0.365277   0.072345   5.049 6.14e-05 ***
acadian.canopy -0.001116   0.001331  -0.838    0.412
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

```
(Dispersion parameter for gaussian family taken to be 0.07336952)

    Null deviance: 1.5189  on 21  degrees of freedom
Residual deviance: 1.4674  on 20  degrees of freedom
AIC: 8.867

Number of Fisher Scoring iterations: 2
```

AIII.XI A generalized linear model showing seedling proportion of Acadian seedlings present with boreal canopy coverage across 28 field sites (Figure 2.12).

```
Call:
glm(formula = proportion ~ boreal.canopy, family = gaussian(link = "identity"),
    data = proportion_density_A)

Deviance Residuals:
     Min        1Q     Median       3Q       Max
-0.48868  -0.23374   0.08084   0.29803   0.59704

Coefficients:
               Estimate   Std. Error  t value  Pr(>|t|)
(Intercept)    0.625045   0.117068   5.339 0.000238 ***
boreal.canopy -0.003833   0.002703  -1.418 0.183796
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 0.1315564)

    Null deviance: 1.7118  on 12  degrees of freedom
Residual deviance: 1.4471  on 11  degrees of freedom
AIC: 14.353

Number of Fisher Scoring iterations: 2
```

AIII.XII A generalized linear model showing seedling proportion of boreal seedlings present with boreal canopy coverage across 28 field sites (Figure 2.12).

```
Call:
glm(formula = proportion ~ boreal.canopy, family = gaussian(link = "identity"),
    data = proportion_density_B)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-0.5593  -0.2877   0.1178   0.2723   0.3941

Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   0.597027   0.079081   7.550 2.82e-07 ***
boreal.canopy 0.002214   0.002861   0.774    0.448
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 0.1092501)

    Null deviance: 2.2504  on 21  degrees of freedom
Residual deviance: 2.1850  on 20  degrees of freedom
AIC: 17.626

Number of Fisher Scoring iterations: 2
```

AIII.XIII A generalized linear model showing seedling proportion of red maple seedlings present with boreal canopy coverage across 28 field sites (Figure 2.12).

```
Call:
glm(formula = proportion ~ boreal.canopy, family = gaussian(link = "identity"),
    data = proportion_density_RM)

Deviance Residuals:
     Min        1Q      Median       3Q         Max
-0.41099  -0.16798  -0.04814   0.15115   0.70134

Coefficients:
               Estimate     Std. Error   t value   Pr(>|t|)
(Intercept)   0.288431   0.063339   4.554 0.000193 ***
boreal.canopy 0.002557   0.001858   1.377 0.183857
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

```
(Dispersion parameter for gaussian family taken to be 0.06937166)

    Null deviance: 1.5189  on 21  degrees of freedom
Residual deviance: 1.3874  on 20  degrees of freedom
AIC: 7.6344

Number of Fisher Scoring iterations: 2
```

AIII.XIV A generalized linear model showing the proportion of herbivory on different species across 28 field sites (Figure 2.13).

```
Call:
glm(formula = proportion ~ species, family = gaussian(link = "identity"),
    data = species_site_herbiv)

Deviance Residuals:
    Min       1Q    Median     3Q       Max
-0.6944  -0.1548   0.0000   0.2203   0.5047

Coefficients:
                          Estimate  Std. Error t value Pr(>|t|)
(Intercept)                0.66667    0.18770   3.552 0.000641 ***
speciesEastern hemlock        0.33333    0.37540   0.888 0.377200
speciesRed oak              0.02778    0.22988   0.121 0.904122
speciesSugar maple          -0.16096    0.22010  -0.731 0.466688
speciesWhite ash            0.01852    0.26545   0.070 0.944554
speciesYellow birch          0.20833    0.29678   0.702 0.484703
speciesRed maple            -0.13303    0.20009  -0.665 0.508025
speciesBalsam fir           -0.17141    0.20129  -0.852 0.396956
speciesWhite birch           0.33333    0.21401   1.558 0.123237
speciesBlack spruce         -0.66667    0.26545  -2.511 0.014010 *
speciesAmerican mountain ash  0.25000    0.24830   1.007 0.317013
speciesPin cherry            0.08333    0.29678   0.281 0.779585
speciesWhite spruce         -0.60952    0.21401  -2.848 0.005573 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 0.1056932)

    Null deviance: 15.2514  on 93  degrees of freedom
Residual deviance:  8.5612  on 81  degrees of freedom
AIC: 69.531
```

```
Number of Fisher Scoring iterations: 2
```

AIII.XV A two-way ANOVA showing the proportion of herbivory at different site types within species groups across 28 field sites (Figure 2.14).

```
> anova_14 <- aov(proportion ~ site_type*taxon, data=species_site_herbiv)
> summary(anova_14)
                Df Sum Sq Mean Sq F value Pr(>F)
site_type        3  0.576  0.1919   1.225 0.3057
taxon            2  1.205  0.6023   3.847 0.0252 *
site_type:taxon  4  0.318  0.0795   0.508 0.7302
Residuals       84 13.153  0.1566
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

AIII.XVI A Fisher’s Exact Test for Count Data showing the interaction between the seedbed type and species group on the number of species observations across 28 field sites.

```
> table_16

          conifer needles moss bunchberry grass leaf litter
Acadian          2           1          2     0          25
Boreal           3           7         10    32          19
Red maple        1           0          3    12          20
> test_16

        Fisher's Exact Test for Count Data with simulated p-value (based on 2000 replicates)

data:  table_16
p-value = 0.0004998
alternative hypothesis: two.sided
```