# Floristic Composition and Functional Stability of Black Spruce-*Kalmia* Shrub Savannah

A thesis presented to

The Faculty of Graduate
Studies

of

Lakehead University

by

Colin St. James

In partial fulfillment of
requirements for the degree of
Master of Science in Biology

December 24, 2022

## Abstract

*Scope*: In eastern Canada, black spruce (*Picea mariana*)-*Kalmia angustifolia* forest revert into forest, or become *Kalmia* heath, or *Kalmia*-spruce shrub savannah (SS) depending on fire severity. My main research objective was to identify the mechanisms that maintain SS vegetation structure and function. I hypothesized that microhabitat conditions and function of dominant plants of island and heath confer SS stability.

*Methodology*: I used a multivariate approach to quantify the difference in habitat condition, floristic structure and composition between island and heath of SS. I compared soil nutrient availability and litter decomposition between island and heath to assess growth limitations and nutrient cycling. This was followed by determining functional hypervolumes of the four most abundant species in island and heath considering four functional traits representing resource acquisition and use. I used a dendrochronological approach to determine island expansion rate to predict future island cover.

*Results*: Shrub cover, light availability, and soil moisture were positively related to heath, and cryptogamic species and tree cover and organic matter depth were positively related to island. Heath soil had higher total N, but lower total C, and K than island. All other measured nutrients were similar. Black spruce litter decomposed faster than *Kalmia*. Litter mass, foliar N, and foliar C did not differ when decomposed in heath or island. Functional niche overlap was high in both island and heath. In island, *Kalmia* hypervolume was reduced compared to heath but other ericaceous species' hypervolume was greater in island than heath. Ericaceous species showed a tradeoff between resource investment to resource acquisition traits in island and heath. Island expansion rates were negatively related to island size. At current expansion rates, it will take ~340 years to achieve canopy closure.

*Conclusions*: Distinct microhabitat conditions, functional niche utilization, and slow island expansion rate appear to be stabilizing mechanisms that maintain SS vegetation structure. Soil nutrient availability and cycling play a minimal role in maintaining structure. The long time to canopy closure exceeds the region's natural fire cycle. Therefore, canopy closure may not occur under the natural fire regime and black spruce-*Kalmia* SS will likely continue as an alternate vegetation state.

# Lay summary

Faculty and students in the Department of Biology are bound together by a common interest in explaining the diversity of life, the fit between form and function, and the distribution and abundance of organisms. My study observed how plant species abundance and distribution are constrained to two distinct vegetation assemblages throughout a vegetation mosaic. Furthermore, I examined how plant function shifts between varying microhabitats in response to stress via microhabitat characteristics and competition with other species. The results of this study broadly show a limited potential for state shift to occur and concludes that the *Kalmia*-black spruce shrub savannah is not a successional state leading to forest or heath. Hence, my thesis advances understanding on the fit between form and function, the distribution and abundance of organisms, and outlines processes driving biodiversity.

# Acknowledgments

I would like to express my appreciation to my supervisor Dr. Azim Mallik for his countless hours of inspiring conversation throughout the duration of my undergraduate, and post graduate research. His persistent patience and willingness to challenge me was critical to my development as a researcher and it provided me with an alternative view on the natural world. I would also like to thank my committee members. Drs. Mike Rennie, Adam Algar, and Brian McLaren for their valuable insights into the development and revision of these thesis. I was fortunate to have supervisory committee members of such diverse research backgrounds and each brought unique, but necessary viewpoints on the ecological world. I also express my thanks to Dr. Laura Siegwart of Terra Nova National Park for her generous accommodations and seemingly unlimited willingness to help whenever needed. I would like to personally thank my friend David for his support through conversations over coffee and sustaining me with free hamburgers during my research. Lastly, I thank my family for their constant support and aid throughout my education.

## Table of Contents

## List of Tables

## List of Figures

## 1. Introduction

In eastern Canada, three distinct vegetation communities dominate the upland landscape, forest, heath, and shrub savannah (SS A.K.A. lichen woodland). Forests in this region are characterized by trees often dominated by black spruce (*Picea mariana*) with ericaceous understory, ericaceous heath often dominated by *Kalmia angustifolia* (hereafter referred to as *Kalmia*), and SS with discontinuous vegetation pattern consisting of a mosaic of vegetatively reproducing black spruce island (hereafter referred to as island) dispersed throughout ericaceous heath (hereafter referred to as heath). Functional and taxonomic diversity is generally highest in forest and lowest in heath and SS, with functional and taxonomic diversity of SS being intermediate between forest and heath (St. James & Mallik, 2021). These three systems originate from varying post-fire conditions (Mallik, 2021); thick residual organic matter after low-severity fires promotes vegetatively regenerating plants which primarily favours ericaceous heath, thin residual organic matter following high-severity fires favours seed regeneration leading to spruce establishment and patchy fire severity leads to discontinuous vegetation patterns with black spruce island among *Kalmia* heath (Siegwart Collier & Mallik, 2010). It appears that heath and SS exist as an alternative vegetation state to the pre-existing forest community.

### *1.1 Alternate stable states*

Alternate stable states occur as an abrupt response to one or several environmental parameters beyond a threshold limit (Lewontin, 1969), and result in structural and functional characteristics that differ from the pre-existing community persisting under the same climatic conditions (Holling, 1973). The ecological impacts of state shifts from forest are considered catastrophic (Reitkerk *et al*., 1996; Beisner *et al*., 2003). Environmental impacts of alternate stable states include altered species composition, microhabitat properties and ecosystem services.

The origin of ASS is governed by the dependance of the biota on the history of its environment (Hysteresis). Hysteresis induced ASS can be facilitated by alterations to landscape conditions (i.e. parameter shift), through biotic pressures that overcome the resilience of a community and alter the niche availability (i.e. state shift), or a combination of both (Beisner et al., 2003). Parameter shift occurs when landscape conditions are altered to permit the formation of an alternative state but an equal, reverse perturbation will not revert the system. Parameter shift is driven by changes to processes that alter environmental abiotic conditions, such as fire severity & frequency, that have long term effects on the forest regeneration dynamics (Miller et al., 2019). In contrast, state shifts occur when the landscape remains relatively static but biotic pressures within a community alter community dynamics. These pressures are primarily driven by the priority effects of the assembly history even when all species in the regional species pool have the potential to establish (Chase, 2003).

The transition between alternate stable states can be triggered by herbivory, logging, pests, or a change in fire severity, and are often comprised of compounding effects from several disturbances (Stromayer, 1997; Jasinski & Payette, 2005; Siegwart Collier & Mallik, 2010). The mechanisms that promote state shifts include environmental conditions (termed environmental drivers) that favour alternate life histories and traits (i.e., response traits) of dominant plants. Such “response traits” confer subdominant or transient species with the ability to cope with changes and become dominant in the new community (Sánchez-Pinillos *et al*., 2016). Identification of both environmental divers and associated response traits are necessary to define what drives the transition between alternate states, but they cannot be used to comment on their persistence or stability. Stability is dictated by processes of community assembly and coexisting. Hence, defining stability requires metrics that reflect these processes.

Selecting suitable metrics and approaches to represent stability has received increasing interest in ecology for the past 70 years. Historically, stability was viewed as being positively correlated with biodiversity (MacArthur, 1955; Odum, 1953, Elton, 1958). Essentially, this view attributes stability to having a high level of redundancy in a given system. However, later work showed more refined definitions of stability suggests that high diversity makes systems more complex and thus less likely to return to the original state following disturbance (May, 1973; Pimm, 1980). For instance, Lyapunov stability: The probability that the population size of all species returns to equilibrium following small perturbations, and Species-deletion stability: The probability that removal of one species will not lead to further local extinctions). More recently, the effect of diversity on stability was recognized as scale-dependent; in that increasing species diversity may decrease population stability but simultaneously increase the stability of community-level processes and function (Tilman & Downing, 1994; Tilman *et al*., 1996). Ultimately, this discussion led to novel metrics of both stability, and diversity with a consensus that research should take a broader approach to investigate relationships between ecosystem functions and processes that confer stability.

Upland ecosystems in boreal latitudes exhibit three alternate stable states defined by tree cover including a treeless state (heath), an open woodland state (shrub savannah), and a forest state (Abis & Brovkin, 2017). Treeless states may perpetuate by low-severity fires which create inhospitable seedbeds for seed-regenerating tree species but promote vegetatively regenerating shrubs (Mallik, 2003). Palaeoecological studies have identified alternative stable states persist for millennia in the presence of multiple disturbances (Jasinski & Payette, 2005). The treeless vegetation (heath) and forest have been thoroughly studied to identify the mechanisms that maintain their structure. However, mechanisms driving the apparent stability of the SS alternative state have received little attention (Girard *et al*., 2011).

### *1.2 Black spruce-*Kalmia *SS alternate stable state*

The SS alternate state is expanding beyond its natural range into closed crown conifer forests (CCCF) across Canada; based on SS distribution and expansion rates over the past 70 years, Girard *et al*. (2008) suggested that closed crown conifer forests will cease to exist in 550 years. A combination of direct and indirect anthropogenic disturbances favour the transition from CCCF to SS. These disturbances are increased drought frequency, logging, insect outbreaks, and temperature-related fire frequency which directly alter the natural disturbance regime (Bergeron *et al*., 2004; Girard *et al.,* 2009). Compound effects from such disturbances above can interact to decrease disturbance severity and fire return interval which creates conditions that limit the re-establishment of the pre-disturbance community (i.e., CCCF) (Enright *et al*., 2015).

The long residency times of SS suggest they are a persistent community. Palaeoecological records of plant macrofossils, charcoal, defoliating insects, and pollen have defined SS systems as "stable" based on their inception date of >1000 yr. before present (Jasinski & Payette, 2005). Given that these systems have undergone multiple perturbations without a state shift, these systems are considered "ecologically resilient" (Sensu Peterson *et al*., 1998). In other words, SS has been capable of persisting through historical disturbances, but can also modify the characteristics of future disturbances. Previous research on black spruce *Kalmia*-lichen SS (also called lichen woodland, Girard *et al*. 2008) suggested its long-term persistence (i.e., stability based on lack of tree regeneration) but little is known as to how the community dynamics and plant-soil feedback help to maintain this SS alternate state.

### *1.3 Identifying ecological mechanisms of stability*

Contrary to the classical belief that spatial heterogeneity maintains high species richness (Ricklefs, 1997), interspecific resource use drives coexistence (Kraft *et al*., 2015; Tilman, 1987). At the local scale, resource limitation controls species diversity and inhibit competitors with different plant strategies from being dominant in the community (Stevens & Carson, 2002). A plant strategy is the fixed or plastic characteristics (A.K.A. traits) shared among individuals or populations which share ecological niches (Grime, 2006). While plant strategies can represent adaptations to neighbours, they are broadly thought to be density-dependent responses to environmental conditions and thus primarily responding to microhabitat availability (Nickle & Dybzinski, 2013). Therefore, while resource availability has strong effects on community assembly, community stability is maintained through competitive exclusion from groups of specific plant strategies that confer success in the present environmental conditions.

Environmental conditions and resource availability control the establishment and persistence of populations coexisting in a community. Ecological factors change the number of coexisting species when conditions change and permit species pool replacement (Zobel, 1992). This species pool replacement can be biologically modified through soil modification, light availability, allelopathy, etc. (Bever, 2003; Mallik, 2003). Alternatively, species pool replacement can be abiotically induced through disturbance (Siegwart Collier & Mallik, 2010). Understanding how the species pool responds to the current range of environmental conditions helps understand how susceptible the system is to species replacement.

The success of species along environmental gradients is dictated by their adaptations and tolerance to environmental variables. As per community assembly theory, a species pool is broadly controlled by dispersal, evolutionary history, and complimentary niche-based processes of establishing species (Weiher *et al.*, 2011; Ricklefs, 2008). Community persistence follows these rules but includes the tenet that dominant species in the community have more influence on ecosystem processes than subdominant species which alter environmental conditions (Grime, 1998). Such changes can mitigate environmental stress and permit the establishment of neighbouring species (Klanderud & Totland, 2005). On the other hand, plants are capable of creating unsuitable conditions for neighbouring species. For example, highly competitive species alter the microbial soil community to a degree that negatively impacts the rhizosphere of allospecifics (Kourtev *et al.*, 2002). Therefore, while the priority effects and inherent post-disturbance site conditions dictate the initial species assemblage, interactions between species and environmental filters can help to maintain community structure and composition.

### *1.4 Defining stability in black spruce-*Kalmia *SS*

Since the black spruce-*Kalmia* SS is composed of two distinct vegetation assemblages (island and heath), the stability of this community structure must be maintained to prevent state shifts between disturbance events. Community structure can be maintained through a plethora of processes including microhabitat modification, soil nutrient availability, and niche conservation. In this study, I considered four broad factors: namely, microhabitat conditions, soil nutrient cycling, niche differentiation of dominant plants, and spruce island expansion rates, to identify key characteristics separating island from heath and the underlying mechanisms driving stability.

Species persistence and abundance are directly linked to the local microhabitat conditions in a system. Differences in vegetation types are dependent on several microhabitat conditions such as soil moisture, light availability, and substrate which confers dominance of respective taxa (Lundholm & Marlin, 2006). Soil nutrient availability and cycling are a direct consequence of such factors and have strong implications for community assembly (Dantas de Paila *et* al., 2021). At a broader scale, the level of microhabitat variability in a system governs spatial distribution of the community (Vimos-Lojano *et al*., 2017). Therefore, identifying key differences in microhabitat conditions between vegetation states reveal environmental drivers of community structure and composition.

The functional niche (A.K.A Elthonian niche), while also heavily influenced by soil nutrient availability in plants, has strong selective effects on coexistence and competition. The functional niche of an individual is the combined effect of functional traits on resource acquisition and use. Habitat filtering constrains the total niche volume and limiting similarity restricts the degree of overlap (Li *et al*., 2017) Poor nutrient availability causes stochastic effects which reduce the strength of these processes in the community (Conradi *et al*., 2017). These effects have a stronger influence on community assembly than persistence but are necessary to explore when identifying habitat filters leading to stability (Chang & HilleRisLambers, 2019). In nutrient-poor conditions, the contribution of functional niche to community-level processes has greater stochastic effects. Under favourable soil nutrient availability, larger niche volumes of species indicate relatively low stress, and overlap results in functional redundancy.

Soil nutrient availability relates strongly to habitat filtering and indirectly to functional niche complementarity. Soil nutrient availability is primarily driven by i) plant-soil feedback, and ii) nutrient cycling. Plant-soil feedback modifies nutrient availability by influencing soil microbiota and through the formation of unique nutrient complexes unavailable to competitors (Ehrenfeld *et al*., 2005; Read & Perez-Moreno, 2003). Leaf litter accounts for ~90% of litterfall and its quality remains the most important aspect of geochemical cycling, and hummus formation until the late stages of decomposition (Couteaux *et al.,* 1995; Krishna & Mohan, 2017). Exploring litter decomposition in SS systems may aid in explaining changes in soil nutrient availability and permit insights into the expected changes in the long-term absence of disturbance.

Previous research (Girard *et al*., 2008; Siegwart Collier & Mallik, 2003) has described the creation and longevity of these SS systems. Yet no study has explored dynamic vegetation interactions or identified key characteristics that maintain the SS structure. My study was designed to (1) identify key microhabitat characteristics that maintain the SS structure, (2) determine how functional traits of the dominant species coexist with each other and respond to diverse conditions within island and heath microhabitats in the SS state, and (3) determine the potential for vegetatively regenerating black spruce island to expand into *Kalmia-dominated* heath, thereby transforming the SS state to high tree cover. The main objective of this study was to determine the stability of this SS community by identifying the primary mechanisms that maintain this vegetation structure and composition. To this end, I asked three questions: 1) How do the island and heath components of the SS system differ with respect to microhabitat (soil nutrient availability, moisture, light availability, organic matter depth) and floral composition? 2) Do ericaceous shrubs exhibit distinct changes in resource use, and functional niche, in island compared to heath? 3) What is the projected tree cover of black spruce island based on the current expansion rates of layering stems expanding the island periphery?

I hypothesized that: 1) Microhabitat differentiation between island and heath will reduce the potential for establishment of heath vegetation into island and vice versa which will maintaining SS structure; Microhabitats will differ greatly between islands and heath in favour of the dominant vegetation types in the respective components, 2) Island and heath will both show high degree of functional overlap within them but island will have greater niche convergence caused by more stressful conditions (e.g., resource limitation, competition, environmental filtering) for the ericaceous species and result in relatively poor competitive ability and 3) black spruce island expansion rate will decrease toward the island periphery as layered stems establish in heath soil which is known to induce stunted growth in spruce; decreased expansion rate over time will prevent canopy closure in the absence of disturbance.

## 2 Methods

### *2.1 Study Area*

This study was conducted in Terra Nova National Park, Newfoundland, Canada (48◦3103300 N, 53◦57058.400 W) (Figure 1). This area is in the boreal region but oceanic influence causes unique vegetation patterns compared to inner-continental Canada (South, 1983). The region receives 1801–1200 mm precipitation (~30% as snow) and has mean summer and winter temperatures of 13 and −5 ◦C, respectively (Environment Canada, 2017). In Terra Nova National Park, there are three well developed, mature SS communities: Terra Nova Road, Ochre Hill, Rocky Pond. These communities are similarly aged (~80 years). Vegetation is relatively most vigorous in Terra Nova Road and lowest in Rocky Pond but all sites share the island-heath structure characteristic to SS.

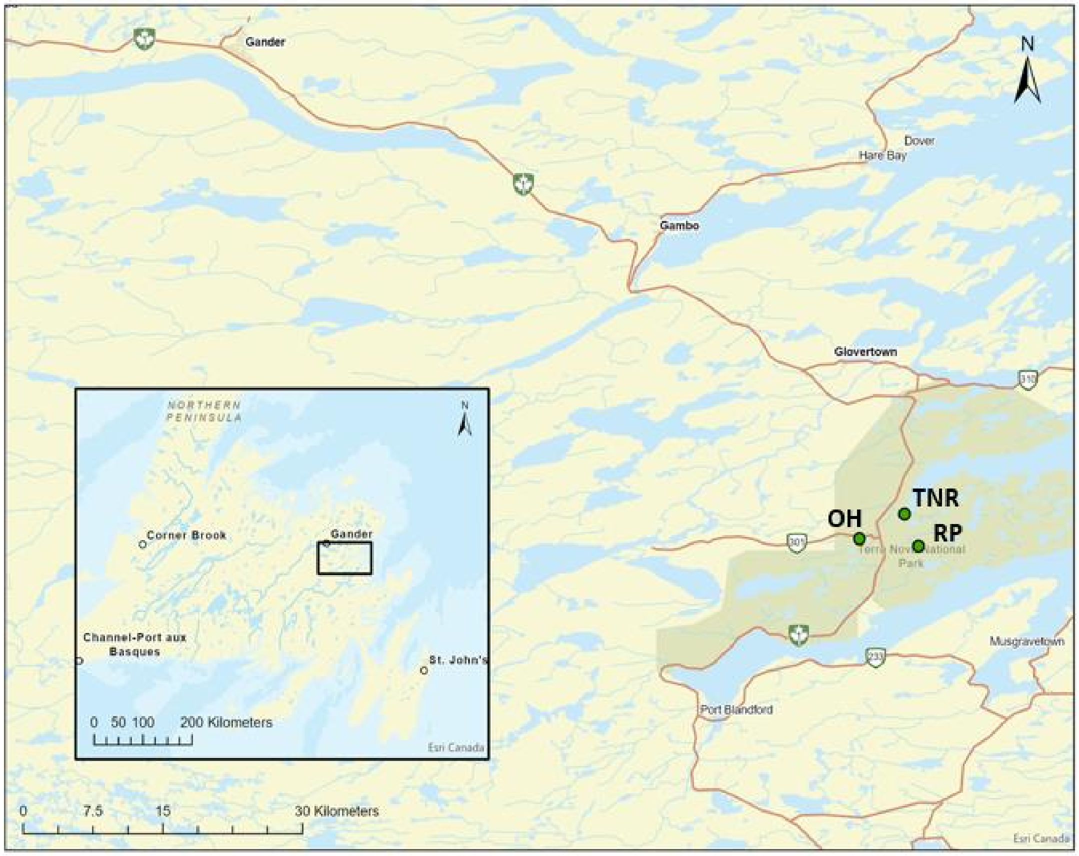

Figure 1. Location of Terra Nova Road (TNR), Ochre Hill (OH), and Rocky Pond (RP) SS communities in Newfoundland, Canada (Esri, 2020).

Black sprue-*Kalmia* SS is one of three vegetation states in this region, along with forest and heath. A SS is composed of a mosaic of two distinct vegetation structures, treed island distributed throughout *Kalmia* heath. The heath component is more prominent throughout the system and is dominated by ericaceous shrubs (*Kalmia angustifolia*, *Vaccinium angustifolium*, *Rhododendron groenlandicum*, *Rhododendron canadense*) overtop a dense lichen cover dominated by *Cladonia stellaris.* The island component is composed of vegetatively regenerating (layered) black spruce (*Picea mariana*) which forms a dense canopy overtop a pleurocarpous moss mat. Black spruce island understory is dominated by ericaceous shrubs (*Kalmia angustofolia*, *Vaccinium angustofolium*, *Rhododendron canadense*) but in lower abundance than in the heath. Herbaceous species (*Cornus canadensis, Maianthemum canadense, Trientalis borealis*) are common in island but in low abundance (Figure 2).

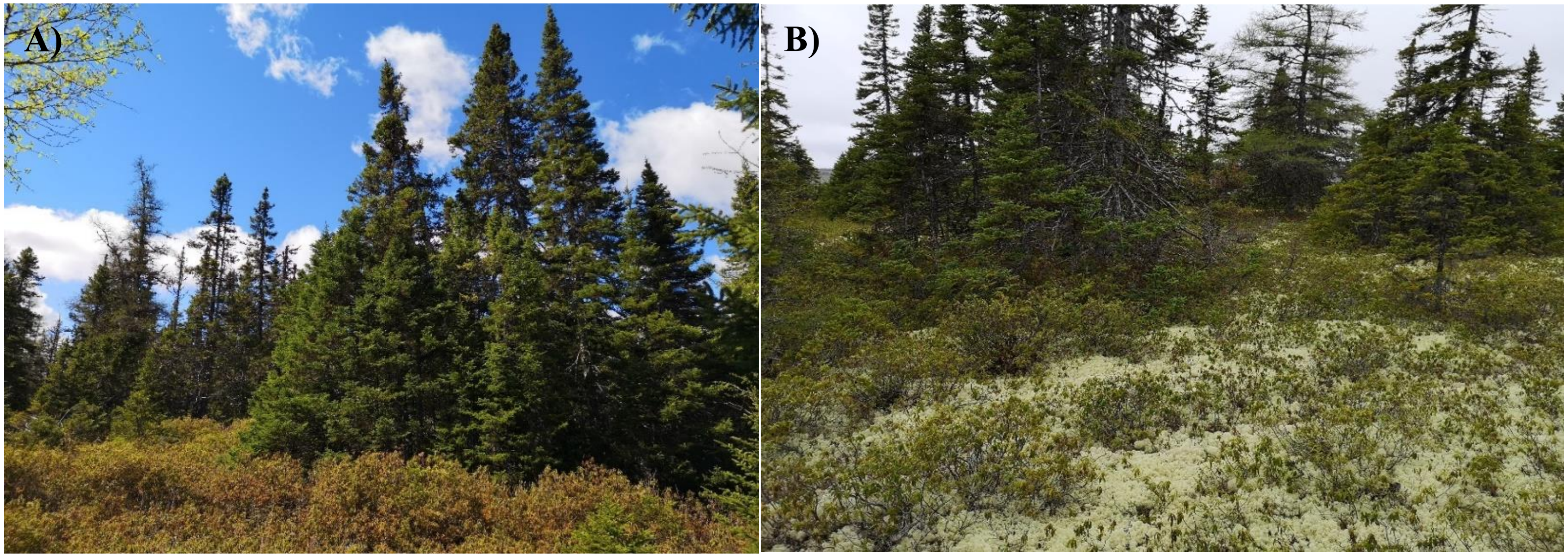

Figure 2. Back spruce-*Kalmia* shrub savannah communities showing A) island and B) heath vegetation structure in the foreground. Island are dominated by clonal *Picea mariana* and the heath is dominated by ericaceous shrubs, particularly *Kalmia*.

### *2.2 Floristic composition and microhabitat conditions in SS heath and island (Question 1)*

In each of the three sites, I randomly selected 10 island and heath pairs. Island and heath pairs were a minimum of 50 m apart. Sufficient distance between island and heath locations was necessary to reduce the effects of the island periphery on the heath data. Three quadrats were placed between 1-3 meters apart in each island and heath sampled (n=180). Additionally, the first 10 island and heath location pairs were marked for soil collection used for another part of the study (Figure 3).

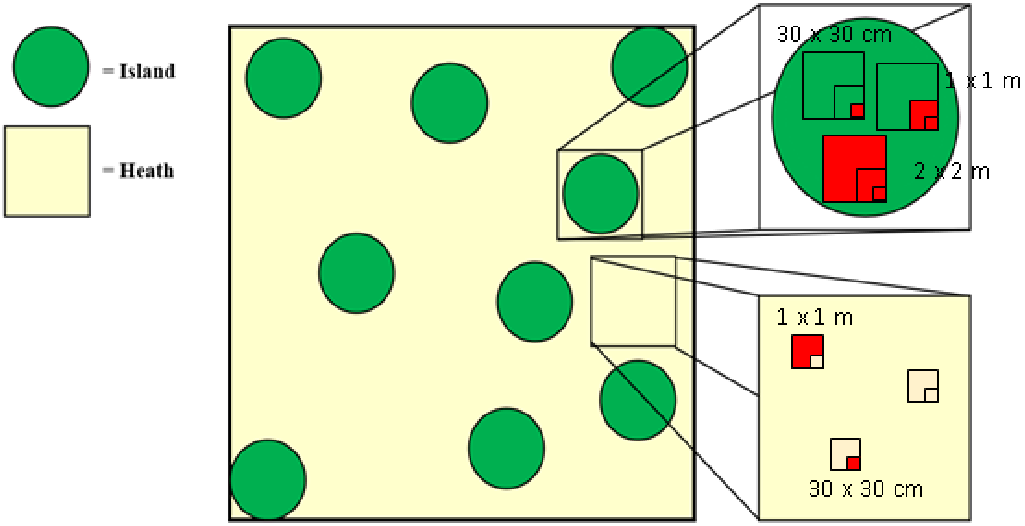

Figure 3. Sampling design for floristic composition and microhabitat conditions in SS. Magnified areas of the figure indicate one replicate of an island and heath pair. Within each island and heath, three quadrats were placed in each location. Tree abundance was assessed in 2 x 2 m quadrats. Herb and shrubs were assessed in 1 x 1 m nested quadrats. Mosses and lichens were assessed in 30 x 30 cm nested quadrats. Quadrat colours correspond to the related quadrat size. All plant groups were measured in all three plots. Island size, distance between heath and island locations, and relative cover are not to scale.

I selected organic matter depth, light penetration to the ground level, canopy cover, and moisture as environmental variables. Organic matter depth impacts the vegetative regeneration of *Kalmia* and layering of black spruce (Bloom & Mallik, 2006; Stanek, 1961). Light penetration to the ground is related to tree and ericaceous canopy but provides additional information on how light is utilized below the canopy. Soil moisture is an important factor in the production of advantageous root growth of layered stems and seed germination.

Within each island and gap pair, species abundance and composition, light penetration, organic matter depth, canopy cover, and moisture were measured. Species abundance and composition were measured with 2 x 2 m quadrats for tree species in island habitats only, and in both island and heath habitats with, 1 x 1 m quadrats for herb and shrub species, and 30 x 30 cm quadrats for lichen and moss cover. Light penetration, organic matter depth, soil moisture, and canopy cover were measured within the 1 x 1 m quadrat. Light penetration was measured with an LP-80 Accupar PAR/LAI light meter (Decagon Devices Inc. Pullman, Washington, United states) and was represented as the proportion of light at the ground level. The proportion of light penetration was determined by the photosynthetically active radiation (PAR) at ground level divided by a control PAR reading. Control PAR readings were simultaneously taken to ground level PAR readings in the absence of light obstructions (i.e., no canopy). Organic matter depth was measured by taking the average of four measurements of organic matter depth from the soil surface to mineral soil from each side of two 30 x 30 cm soil cores in each 1 x 1 m quadrat. The canopy cover was measured with a spherical densiometer. Soil moisture content was measured with an HH2 moisture meter and a Theta probe-type MLX2 (Delta-T devices, Cambridge, United Kingdom).

To determine the relationship between vegetation and environmental variables measured in each quadrat, I performed a canonical correspondence analysis (CCA). CCA is a multivariate constrained ordination analysis modified from correspondence analysis which extracts principal axes to explain the relationship between objects and variables (inertia) while maximizing their correlation with additional variables (Quinn & Keough, 2002; Ter braak, 1986). CCA uses an eigen analysis approach to provide numerical descriptions such as eigenvalues, eigenvectors, r-values, and $R^2$-values, to describe relationships between species and their environment. Eigenvalues represent the degree of characterization, eigenvectors represent linear association scaled by the eigenvalue, r-value (Pearson correlation coefficient) is the correlation a species has to axes, and $R^2$ (coefficient of determination) is derived by eigenvalues and represents how well data summarizes or explains patterns (Legendre & Legendre, 2012). Coefficients of determination were calculated using chi-squared analysis. CCA ordination was performed with the PC-ORD program (McCune & Mefford, 1998).

These data were transformed in two ways for the CCA. First, the actual species richness (41) of the pooled SS communities was reduced to 14. This was done to satisfy the requirements of the ‘one in ten’ rule which states that at least 10 observations are needed per variable to evaluate a relationship between them. Selected species were chosen based on the criteria that species must account for a minimum average cover of 1% across pooled plots. This approach permitted sufficient observations as the necessary minimum number of observations was reduced to 140 where I had 180 observations. One species (*Bryoria fremontii*) was removed in order to improve the axes scaling on the CCA figure. Environmental variables (canopy cover, light penetration, organic matter depth, and moisture) produced a wide range of values because of the use of different units. This created a bias as measures with higher values overall (e.g., light penetration) appeared to have a greater effect on species distribution regardless of real effects in preliminary analysis. Thus, environmental variables were z-scored to normalize the data and better represent comparative effects.

Although CCA describes community-wide relationships, it does not identify small-scale differences between individual factors in SS components quantitively. To better quantify how individual environmental variables differ between island and heath, I employed a linear discriminant function analysis (LDA). Linear discriminant function analysis tests for differences in predictor variables among groups using Wilks lambda then LDA identifies linear combinations to determine which predictor variables best discriminate groups (Legendre & Legendre, 2012). In this case, the predictor variables were environmental variables, and the groups were component types (island or heath). LDA was performed using the “lda” function of the “MASS” package (Venables & Ripley, 2002), and corresponding figures were generated with the “ggord” function of the “ggplot2” package (Wickam, 2016) on R version RStudio 2022.07.1+554 (R-core team, 2020).

### *2.3 Soil nutrient availability in heath and black spruce island (Question 1)*

Three soil samples were collected from the organic layer of ten island and heath locations in each of the three sites. The three soil samples from each island and heath location and then homogenized (total = 30). Samples were kept frozen until laboratory analysis where extractable nitrate, extractable ammonia, extractable phosphate, total potassium, total carbon, and total nitrogen were measured. These parameters were selected to represent soil NPK and CN ratio.

In total, five separate analyses were used to detect nitrate, ammonia, phosphate, and total recoverable metals from dried soil samples. Nitrate was extracted with 1.0 M KCl then the extract was determined by the Griess reaction after reduction of the nitrate to nitrite by a cadmium copper reactor and the colour was measured at 540 nm using a SKALAR autoanalyzer (Kalra & Maynard, 1991). Ammonia was also measured using a 1.0 M KCl extraction in the SKALAR autoanalyzer but the colour developed from the Berthelot reaction was measured at 600 nm (Kalra & Maynard, 1991). Phosphate was analyzed using the BRAY P2 method where the phosphates in the extract was determined by inductively coupled plasma (ICP) analysis (Kalra & Maynard, 1991). Total recoverable metals were measured by digesting homogenized samples in a CEM Mars xpress microwave oven using XPRESS Teflon closed vessels with nitric and hydrochloric acids. After digestion, samples were diluted with Type 1 DDW and analyzed by ICP-AES Varian (Element, 2007). Total nitrogen was determined via combustion into gaseous $CO_2$, $N_2$, and $NO_x$, into $WO_3$ granulated tubes which delivers oxygen as a catalyst and to prevent non-volotile sulphate formation. Then, $NO_x$ and $SO_3$ were reduced to $N_2$ and $SO_2$, respectively, and adsorbed into columns where they were transported into a measuring cell of the thermal conductivity detector.

I pooled all heath, and island soil replicates together to analyze soil nutrient availability to reflect general trends in SS, reduce environmental noise, and permit more powerful analyses (number of heath soil samples = 30, number of island soil samples = 30). By pooling sites together, the number of comparisons was reduced, and this increased statistical power. Hence, I focused on identifying differences between island and heath under the assumption that significant trends will better reflect SS function rather than site-level differences.

To identify and characterize differences between SS island and heath, I performed one-way ANOVA and Kruskal-Wallis tests where applicable ($\alpha = 0.05$). Only C:N met the parametric assumptions of normality and homogeneity of variance necessary to perform a one-way ANOVA without data transformation. Other parameters such as K, $NH_3N$, P, and $PO_4P$ met the parametric assumptions when log-transformed and were therefore analyzed in that fashion. The remaining three parameters (total C, total N, nitrate N) failed to meet parametric assumptions when data transformation was applied. For these parameters, I took a non-parametric approach and tested differences between treatments with a Kruskal-Wallis test. The Kruskal-Wallis test is a non-parametric approach that is governed under the assumption that 1) samples are random, 2) treatments are mutually independent, and 3) the measurement scale is at least ordinal and the variable is continuous. Soil nutrients analyzed with the Kruskal-Wallis test met these assumptions. One-way AVOVA and Kruskal-Wallis tests were analyzed using the base ‘stats’ package of R Version 1.3.5 (R Core team, 2022).

### *2.4* Kalmia *and* black spruce *litter decomposition in island and heath (Question 1)*

Litter decomposition in SS island and heath was examined in three sites (Terra Nova Road, Rocky Pond, Ochre Hill) with autochthonous litter. Black spruce and *Kalmia* litter were collected from each site and dried at room temperature (~20°C) for 72 hours to remove water content. Approximately one gram of either black spruce or *Kalmia* leaves from each site was placed in 10 cm x 10 cm polyester litter bags with <0.5 mm mesh size. Exact masses were recorded and compared with decomposed litter mass. Additionally, black spruce and *Kalia* litter from each of the three sites were kept frozen to be used as undecomposed control samples. After field decomposition (68 days), the samples were dried at room temperature for 72 hours. The litter bags were identified by species and site to ensure that local litter was retained within sites. Litter from each site was set aside and frozen to serve as a control for C and N content.

Within each site, 10 island and 10 heath locations in were selected for litter decomposition. Three litter bags of each species (black spruce and *Kalmia*) were placed in each island and heath location for a total of 6 litter bags in each island and heath. Litter bags were placed on top of pleurocarpous moss mats in island and inserted into *Cladonia stellaris* in heath. The orientation of litter was based on observations made on natural litter found in these systems. In island, litter naturally remains overtop *Pleurozium schreberi* whereas, in the heath, litter primarily resides throughout the vertical *Cladonia stellaris* skeletal structure. Hence, litter bags were placed horizontally on top of *Pleurozium schreberi* in island and vertically in the *Cladonia stellaris* column in heath. In total, 180 litter bags were placed in the sites and were allowed to decompose for three months before retrieval. Retrieved samples were kept frozen until further analysis.

Air dried decomposed litter mass was recorded then samples were homogenized using mortar and pestle. The Homogenized samples were used for total carbon and total nitrogen contents described above.

Litter decomposition, represented by 1) mass loss, 2) total C loss, 3) total N loss, 4) C:N change, in island and heath were compared separately with *Picea mariana* and *Kalmia*. Although litter was retained within the site of origin, differences between sites were not explored. Rather, differences between island and heath were examined to allow broader generalization about the SS community as a whole as opposed to fine-scale differences between the three selected sites. Initial analyses revealed that none of the measured parameters met the assumptions of normality or homogeneity of variance needed to permit parametric analyses. Hence, Kruskal-Wallis tests were applied to identify differences between factors and were complimented by a Dunn test of multiple comparisons using the Bonferroni approach when significant differences were identified ($\alpha = 0.05$). The Bonferroni approach adjusts $\alpha$ based on the number of comparisons being made to mitigate the risk of type 1 errors. Kruskal-Wallis tests were performed with the base ‘stats’ package and Dunn tests were performed with the ‘dunn.test’ function in the “dunn.test” package (Alexis & Dinno, 2017) on R version 1.3.5 (R Core team, 2022).

### *2.5 Functional niche utilization of dominant species in SS heath and island (Question 2)*

I took a functional trait-based approach to quantify niche utilization and occupancy in heath and island. I examined four functional traits of the four most dominant species in island and heath. The four most dominant species in island were *Picea mariana*, *Kalmia angustifolia*, *Vaccinium angustifolium*, and *Rhododendron canadense* and those in heath were *Rhododendron groenlandicum*, *Kalmia angustifolia*, *Vaccinium angustifolium*, and *Rhododendron canadense*. Thus, heath and island have three common species among their four most abundant species. The average abundance of species in island was 78, 17, 1.5, and 0.56 % for *Picea mariana*, *Kalmia angustifolia*, *Rhododendron canadense*, and *Vaccinium angustifolium*, respectively. In heath plots, *Kalmia angustifolia*, *Rhododendron canadense*, *Rhododendron groenlandicum*, and *Vaccinium angustifolium* averaged 49, 9.9, 3.2, and 4.6 % respectively. Thus, although *Kalmia angustifolia*, *Rhododendron canadense*, and *Vaccinium angustifolium* dominate in both island and heath, they were relatively more abundant in heath.

I selected four functional traits to represent the niche utilization of each of the four dominant species in island and heath. These were specific root length (SRL), specific leaf area (SLA), leaf dry matter content (LDMC), and height. SRL is the ratio of root length to dry mass of fine roots which represents resource acquisition to resource investment. SLA (leaf area:leaf mass) is an aboveground analogue to SRL where leaf area is a proxy for resource acquisition and leaf mass is a proxy for resource investment. LDMC is the oven-dry mass of the leaf divided by its water-saturated fresh mass. LDMC tends to inversely relate to SLA but provides additional information, where higher LDMC typically relates to lower relative growth rates, longer leaf life span, and slower rates of decomposition (Perez-Harguindeguy *et al.*, 2013). Conversly, species with low LDMC are typically associated with more productive environments. Plant height (the distance between the ground level and the uppermost photosynthetic tissue) represents several plant functions including growth form, the vertical position of the species, vigour, reproductive size, lifespan, and resistance to disturbance (Perez-Harguindeguy *et al.*, 2013).

Functional trait and niche utilization analysis was conducted at the Terra Nova Road site only, vegetation was more vigorous (relatively greater plant height, stem density, and cover) than either Ochre Hill and Rocky Pond (personal observation). In relatively saturated and vigorous communities, plants establish in environments to which they are well adapted which reflect spatially and temporally optimal environmental conditions for their distribution and functional traits (Ackerly, 2003). Since trait values more accurately relate to habitat occupancy, they better reflect stabilizing selection over stochastic effects.

Ten species sets were collected from each island and heath location. For this analysis all species were required to occur within a single 1 x 1 m quadrat. This was done to ensure that interspecific competition was occurring within all quadrats examined. The island and heath species sets were sampled a minimum of 1 m from the island periphery. For shrubs, I performed whole-plant extractions of individuals. This included extracting sufficient volumes of the soil to include fine roots in the rhizosphere. The soil column was then placed in water for 24 hours to ensure complete hydration of all plant tissues. For *Picea mariana*, whole-plant extraction was not possible. Therefore, twigs containing an abundance of healthy leaves were cut and stored in sealed plastic bags. Humid air produced from the lungs was blown into the bag to avoid rapid desiccation of these samples before the twig base could be fully submerged in water for complete rehydration. Root samples were extracted from the soil and fine roots were taken from the extracted roots. Height was measured using the “arm and stick” method as follows. A marker was placed at eye level around the tree and a meter stick was held perpendicular to the ground in a matter that the uppermost length was equal to arm length. I distanced myself from the tree so the top of the meter stick was sighted with the tree top and measured the distance to the base of the tree. The distance to the tree base was added to the height of the marker to determine tree height. Initially, we had planned to measure height with a digital clinometer but the equipment did not work. Although the “arm and stick” method results in less precise measurements, it remains a valid field method in ecology (Brower *et al.*, 1998).

After samples were rehydrated for 24 hours, 3-6 leaves, and fine roots were collected from the individual. Leaf fresh weight was immediately measured with a Mettler Toledo XS4035 balance. Then, leaves and roots from each individual were scanned at a resolution of 1200 DPI using an HP Envy 4520 scanner. before the area of each was determined with Winfolia Pro (Regent Instruments, 2007) and Winrhizo Pro software, respectively. Scanned leaves were dried at 35°C for 72 hours and weighed to determine dry mass.

Functional niche, also termed niche hypervolume, uses species traits to represent resource use, competition, and complementarity. In this analysis, functional niche was used to determine shifts in resource investment for three ericaceous species (*Kalmia angustifolia*, *Vaccinium angustifolium*, and *Rhododendron groenlandicum*) when co-dominant with *Picea mariana* in island or *Rhododendron groenlandicum* in heath. In total, three metrics were used to define he functional niche and represent dominant species hypervolume changes between island and heath. These metrics were 1) probabilistic hypervolume: the total niche space occupied by a species, 2) hypervolume centroids: the mean trait values within the hypervolume for each species traits, and 3) hypervolume overlap: the degree to which pairwise overlap of species traits occur in the functional space.

Functional hypervolume was represented by Huchinson’s n-n-dimensional hypervolume concept. This concept assumes that systems can be characterized by a suite of independent axes (e.g., functional traits, resource requirements, abiotic tolerances). In this analysis, I took a functional trait approach. To construct hypervolumes, species traits were first log-transformed to rescale axes then hypervolumes were produced using the Gaussian method of kernel density estimation. The Gaussian kernel density estimate is built on an adaptive grid of random points surrounding the original data points. Random points were based on the standard deviation of the original data. This method ensured that 95% of the simulated probability density is within the hypervolume boundary (Blonder *et al*., 2022). Then, the total hypervolume space for each species and centroid trait values were derived from the constructed hypervolumes. Hypervolumes were generated using the ‘hypervolume_gaussian’ function of the “Hypervolume” (Blonder *et al*, 2022) R package and figures were generated with the base ‘plot’ function on R version 3.0.2 (R core team, 2022).

Hypervolume overlap was calculated to quantify the degree to which species occupy the same niche space and to aid in explaining how the realized niche of species differs in island versus heath. Pairwise comparison between all combinations of species in island and heath were conducted using all functional traits measured (SLA, LDMC, SRL, height). Hypervolumes for each species were individually recalculated then the overlap was represented with the Sorensen dissimilarity index. Differences in hypervolume overlap could not be assessed therefore differences between species in island and heath were interpreted qualitatively. Hypervolume overlap was calculated using the ‘hypervolume_overlap_statistics’ function of the “hypervolume” package (Blonder *et* al., 2022) on R version 3.0.2 (R core team, 2022).

### *2.6 Black spruce island distribution and expansion rate (Question 3)*

Black spruce island distribution within each site was sampled along 50 x 10 m belt transects. Three belt transects were placed at randomly selected coordinates in each of the three sites (Terra Nova Road, Ochre Hill, and Rocky Pond). Each belt transect was systematically mapped placing 1 x 1 m quadrats consecutively along the transects to determine island size.

Ten black spruce islands were selected from each of the three sites. These islands were selected based on a minimum of tertiary layering occurring. Islands were sampled radially from the parent tree at the centre. I sampled 30 cm wide radial quadrats from the living parent tree to the island periphery. All radii were further divided into two subsections, determined by either northward or southward facing. Up to three individual stems were sampled randomly per radii subsection (Figure 4). The sampling of individuals was done within 30 cm of the tree base. Tree core samples were collected with an increment borer but some layers were sampled with stem cookies when necessary. Tree age (number of annual rings), and stem diameter growth per year were analyzed using WinDendro software.

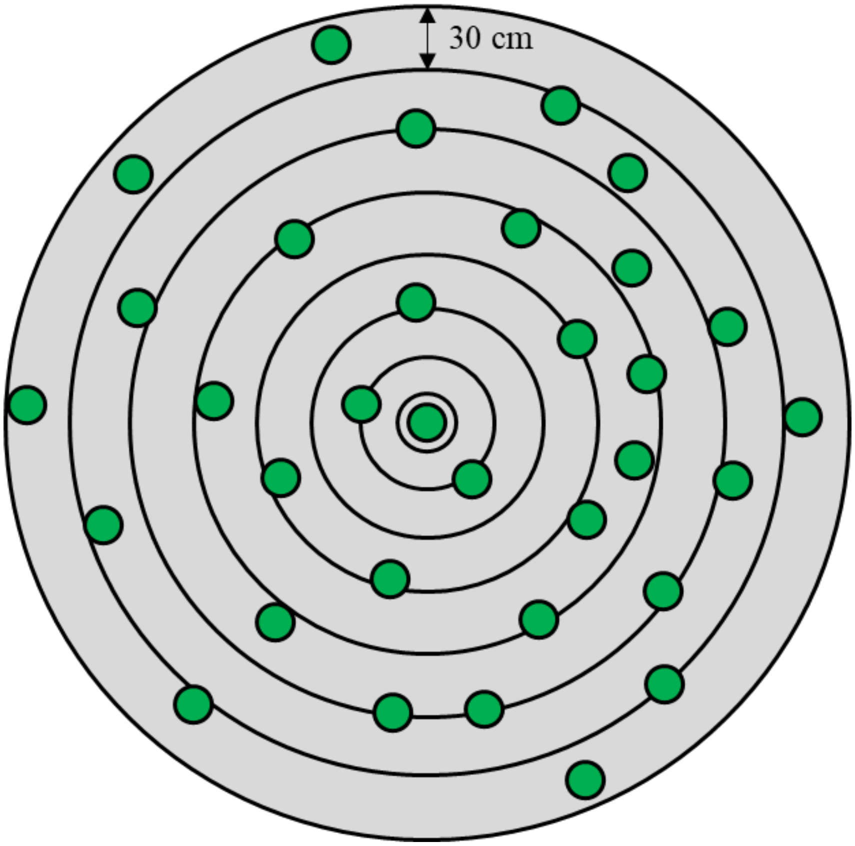

Figure 4. Schematic diagram of black spruce stem sampling in spruce island. Circles represent 30 cm wide concentric plots. Green dots represent black spruce stems. When possible, a total of 6 black spruce layers were sampled within each concentric plot at 30 cm interval. Tree basal area, distribution, and cover is not to scale.

I pooled the site data and created subsets based on island size. These subset data permitted reduced variance introduced via time since the parent tree was established and reduced fine-scale environmental differences between island which would be expressed by different growth patterns. Island sizes varied; therefore, they were separated into four different size classes. The first subset contained island that had a 0-150 cm radius then each subsequent subset radius increased by 60 cm increments to a maximum of 360 cm radius for the largest island. Relationships between tree age with distance from the parent tree were analyzed with model 1 regression for each subset. Model 1 regression was conducted using the “stats” base package of R 4.0.2 (R Core team, 2022).

I used the expansion rates of island size subsets to determine multiple expansion rates. Although four island subsets were determined (150 cm, 200 cm, 260 cm, and 360 cm radius), three expansion rates were selected for future canopy cover. Three expansion rates were used because the radial expansion rates in the 200 and 260 cm subsets were similar. Representing these two subsets as one expansion rate increased the sample size and provides presumably similar information because expansion rates of these two subsets were similar. In order to determine the expansion rates of island, I made the assumption that black spruce island are circular (for simplicity) and have symmetrical growth patterns from the parent tree to the island periphery. These assumptions permitted converting radial growth to growth of the island circumference using $C = 2\pi r$. Hence, expansion rates of island circumference were derived from identified differences in radial expansion.

To determine future cover of black spruce island, I used two approaches. First, sites were pooled, and the average cover of all sites was used to determine how changes in expansion rates, determined from island size, influence future island cover. Second, the mean value of the three expansion rates was used to identify differences between the three sites. In each case, future canopy cover after 50 and 100 years (Eq. 1) and time to 100 % island cover (Eq. 2) was calculated. Initial cover was determined from the above mentioned island distribution throughout heath in SS. Future cover, and time to 100 % cover between sites was compared using one-way ANOVA.

$$Eq. 1: Future\ cover = Number\ of\ islands * Expansion\ rate * Time + Initial\ Cover$$

$$Eq. 2: Time\ to\ 100\%\ Cover = \frac{(100\%\ \ Cover - Initial\ Cover)}{(Number\ of\ islands)} \div Expansion\ rate$$

## 3 Results

### *3.1 Floristic composition and microhabitat conditions in heath and island (Question 1)*

CCA ordination yielded two significant axes with clear distinctions between island and heath locations within SS. Eigenvalues for axes 1 and 2 were 0.601 and 0.030, respectively. Axis 1 explained 38.0% of species variation with an $R^2$ of 0.002, and axis 2 explained 1.9% of the variation with an $R^2$ of 0.324. Although axis 2 had an eigenvalue < 0.4, the occurrence of an $R^2 > 0.2$ warranted consideration. Likewise, axis 1 had an acceptable eigenvalue but not an acceptable $R^2$. All environmental variables showed a strong correlation to at least one axis. Organic matter depth had a weak positive correlation (r = 0.379) and canopy cover showed a strong positive correlation (r = 0.964). with axis 1, whereas soil moisture (r = -0.777), and light penetration (-0.821) both had strong negative correlations with axis 1. With axis 2, Organic matter depth strongly positively correlated (r = 0.544) with axis 2 and light penetration negatively correlated (-

0.520) to axis 2. soil moisture (0.055) and canopy cover (-0.189) were strongly correlated with axis 2 (Table 1).

Table 1. Eigenvalues, percent of species variation explained by each axis, and $R^2$s for two axes determined by a CCA. Pearson correlation coefficients (r) between environmental variables and axes are also shown. Acceptable values are indicated by a "*".

| | CCA Axis 1 | CCA Axis 2 |
|---|---|---|
| Eigenvalue | 0.601* | 0.030* |
| % Variance explained | 38.0 | 1.9 |
| $R^2$ | 0.002 | 0.324* |

| Variables | r | r |
|---|---|---|
| Organic matter | 0.379* | 0.544* |
| Canopy cover | 0.964* | -0.189* |
| Moisture | -0.777* | 0.055* |
| Light penetration | -0.821* | -0.520* |

These data showed minimal overlap with respect to environmental variables in island and heath. Light penetration and soil moisture were greater in heath than in island locations. Conversely, organic matter depth and canopy cover were greater in island than in heath. Although ericaceous species were common in each island and heath location, the CCA showed that their abundance in either location were dictated by strong gradients (Figure 5).

A total of 180 plots were sampled between island and heath containing a total of 41 plant and lichen taxa. Of the 41 species, 13 species were used in the analysis. These species included *Picea mariana, Kalmia angustifolia, Rhododendron groenlandicum, Rhododendron canadense, Vaccinium angustifolium, Ilex mucronata, Camedaphne calcuta, Cladonia stellaris, Cladonia rangiferina, Pleurozium schreberi, Usnea longissimi, Parmelia sulcata*, *Hypogymnia physodes* (Table 2). Generally, ericaceous species (top right) were strongly separated from tree species and epiphytic lichen species (bottom left) in the ordination space (Figure 5).

Table 2. Pearson correlation coefficients (r) between species and axes derived from a canonical correspondence analysis (CCA). Indicator species (r > |0.2|) are selected in green (positive correlation) and red (negative correlation) with respect to each axis.

| Species | Axis 1 | Axis 2 |
|---|---|---|
| | r | r |
| *Picea mariana* | -0.057 | -0.833 |
| *Kalmia angustifolia* | 0.330 | 0.348 |
| *Rhododendron groenlandicum* | 0.162 | 0.316 |
| *Rhododendron canadense* | -0.299 | 0.239 |
| *Vaccinium angustifolium* | -0.214 | 0.240 |
| *Ilex mucronata* | 0.113 | -0.028 |
| *Camedaphne calcuta* | 0.035 | 0.156 |
| *Cladonia stellaris* | -0.089 | 0.877 |
| *Cladonia rangiferina* | 0.081 | -0.018 |
| *Pleurozium schreberi* | 0.129 | -0.625 |
| *Usnea longissimi* | -0.049 | -0.305 |
| *Parmelia sulcata* | -0.026 | -0.447 |
| *Hypogymnia physodes* | -0.064 | -0.486 |

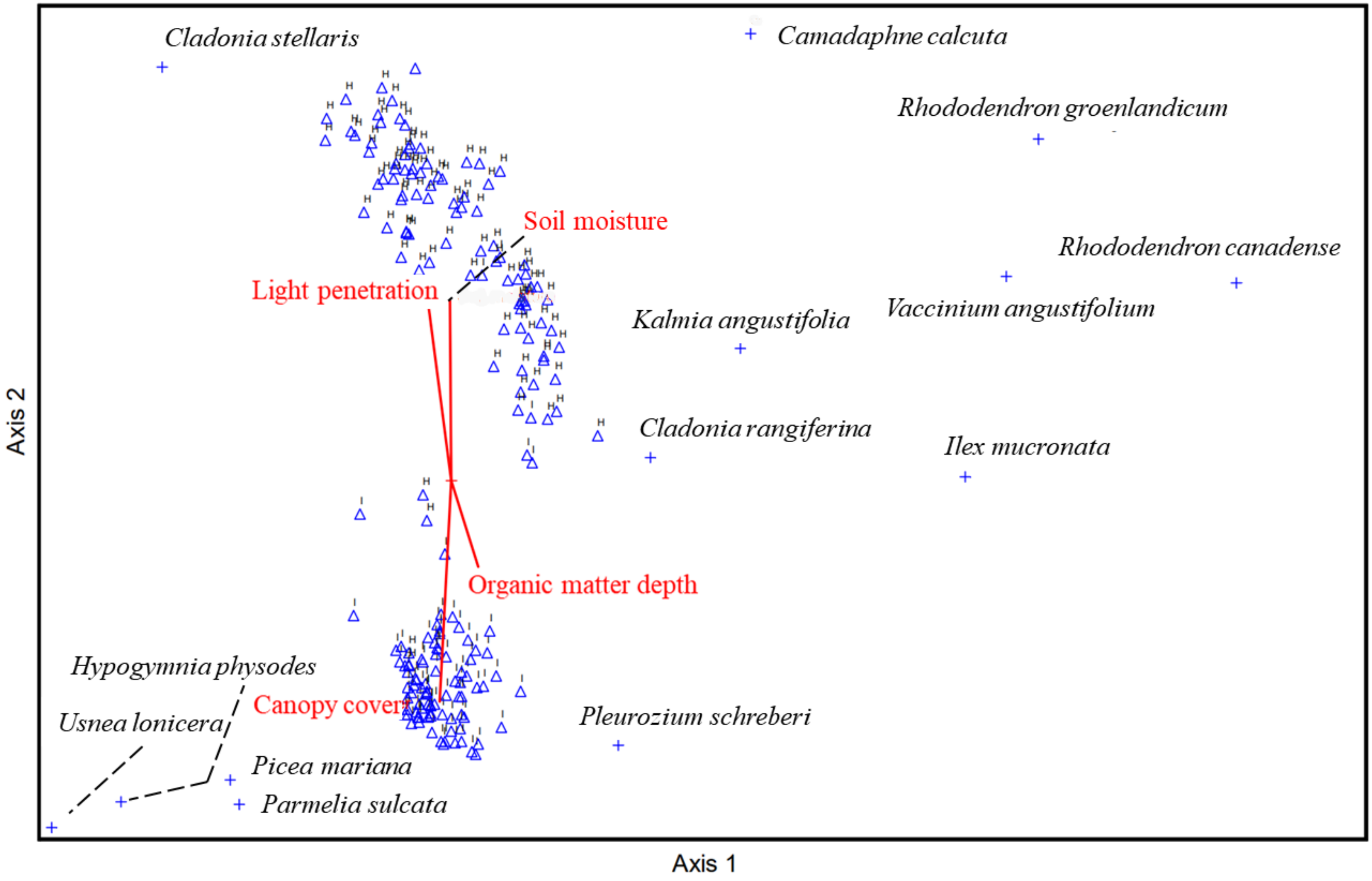

Figure 5. CCA ordination biplot depicting species abundances and eigenvectors of light penetration, soil moisture, canopy cover, organic matter depth, and plot position (H = heath, I = island). All environmental variables are more strongly correlated to axis 1 with the exception of organic matter which is strongly positively correlated with axis 2.

Linear discriminant analysis identified strong separations between the environmental variables observed  in island and heath. Microhabitat variables had little overlap between island and heath which indicated distinct environmental conditions. Light penetration to the ground was 31.6 % greater in heath than in island. Canopy cover was 75.8 % lower in heath than in island. soil moisture is 33.2 % higher in the heath than in the island. Organic matter depth is 33.1 % lower in heath than in island. Coefficients of linear discriminants for light penetration, canopy cover, soil moisture, and organic matter depth were -1.286, 0.116, -0.013, and 0.007, respectively. Hence, heath and island components had minimal overlap in microhabitat conditions (Figure 6).

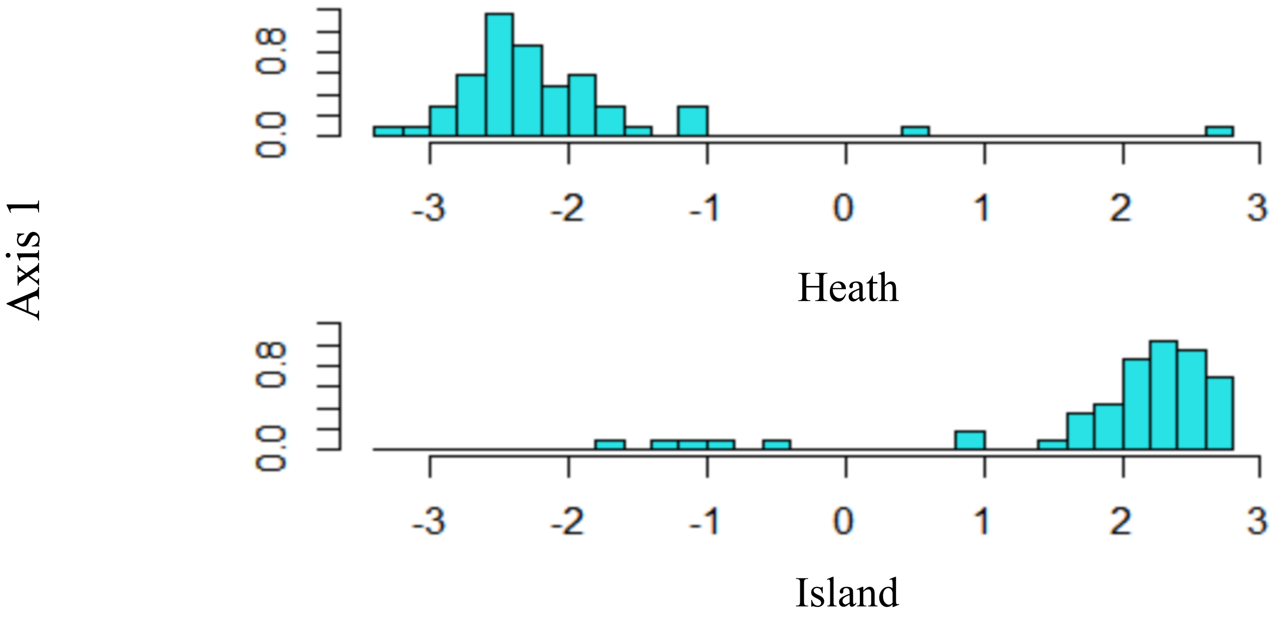

Figure 6. Linear discriminant analysis histogram showing strong separation of environmental variables in island, and heath. Separation is determined by light penetration (coefficient of linear discriminant = -1.286), canopy cover (coefficient of linear discriminant = 0.116), soil moisture (coefficient of linear discriminant = -0.013), and organic matter depth (coefficient of linear discriminant = 0.007).

### *3.2 Soil nutrient status in SS (Question 1)*

Across all soil organic matter nutrients measured (C:N, total C, total N, $NH_3$-N, Nitrate N, total K, total P, and $PO_4$-P), and unlike soil moisture and organic matter depth metrics, I found little evidence of nutrient differences between island and heath locations. Some metrics, such as C:N, total carbon, total nitrogen, and potassium differed between island and heath while nitrate-N, NH3-N, phosphorus, and PO4-P did not. C:N in island was 20.8 % higher than in heath C:N (F = 26.11, $p < 0.001$; Figure 7A). Total carbon was 2.61 % greater in island than in heath (KW, $x^2 = 4.253$, p = 0.039; Figure 7B). Total nitrogen was 18.4 % lower in island than heath (H = 12.86, $p < 0.001$; Figure 7C). Potassium was significantly higher in island ($\bar{x}$ = 785.58 g/kg) than heath ($\bar{x}$ = 517.08 g/kg) (F = 40.16, $p < 0.001$; Figure 7D). Nitrate-N ($x^2$ = 1.683, p = 0.195), NH3-N (F = 1.353, p = 0.250), and PO4-P (F = 3.682, p = 0.060) did not differ between island and heath (Figure 7E-G). Total phosphorus in island and in heath did not differ significantly (F = 2.251, p = 0.139; Figure 7H).

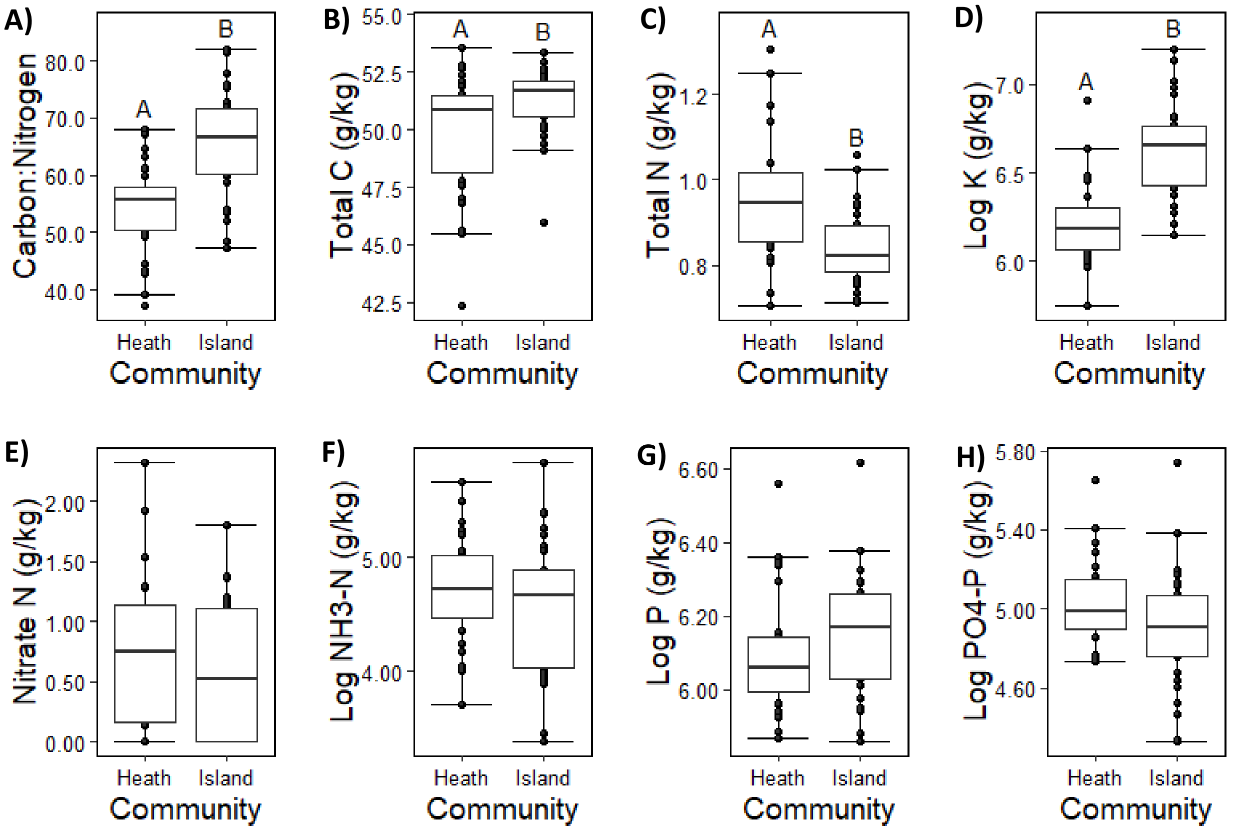

Figure 7. The soil nutrient contents black spruce island and *Kalmia* heath. A) The ratio of carbon to nitrogen (C/N), B) Total soil C, C) Total soil N, D) Total soil K, E) Soil Nitrate-N, F) Total soil ammonia, G) Total phosphorus, H) Soil phosphate. Different letters represent significant differences at α = 0.05.

### *3.3 Black spruce and* Kalmia *litter decomposition in island and heath (Question 1)*

Foliar total nitrogen and carbon content showed similar decomposition rates in island and heath for *Kalmia* and black spruce litter for all metrics (C:N, total N, total C). *Kalmia* foliar C:N ratio was significantly lower in island ($z = 4.801$, $p < 0.001$) than in heath ($z = 3.975$, $p = 0.001$) compared to the control samples but litter decomposition did not differ between island and heath ( $z = 1.384$, $p = 0.250$; Figure 8A). Black spruce C:N ratio did not differ between litter locations or control samples ($x^2 = 5.948$, $p = 0.051$; Figure 8B). Decomposed *Kalmia* litter had higher foliar N content than controls in both island ($z = -3.870$, $p < 0.001$) and heath ($z = - 4.811$, $p < 0.001$; Figure 8C). *Kalmia* foliar N content did not differ between island and heath ($z = -1.561$, $p = 0.177$; Figure 8D). Conversely, *Kalmia* foliar C content was significantly lower in island ($z = 3.535$, $p < 0.001$) and heath ($z = 3.961$, $p < 0.001$) than control but did not differ between heath and island ($z = -0.573$, $p = 0.850$; Figure 8E). In contrast, decomposed black spruce litter had higher N and C content in island (N: $z = -2.765$, $p = 0.009$; C: $z = -2.526$, $p = 0.017$) and in heath (N: $z = -2.778$, $p = 0.008$; C: $z = -2.888$, $p = 0.006$) than in control samples (Figure 8 E-F). Black spruce litter decomposition did not differ between island and heath for N content ($z = -0.018$, $p > 0.999$) or C content ($z = 0.531$, $p = 0.892$; Figure 8F).

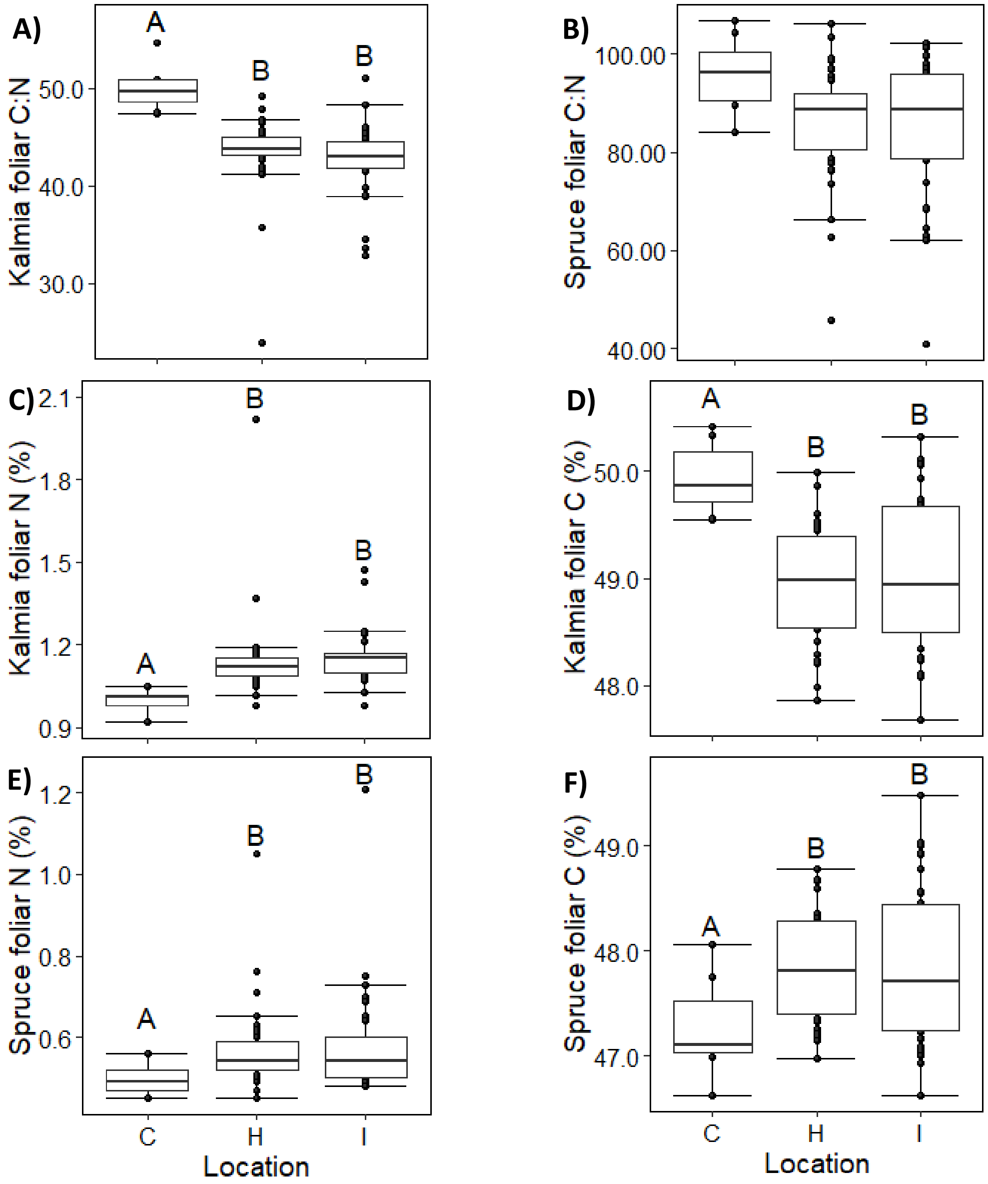

Figure 8. Changes in foliar nutrient contents island (I), heath (H), and frozen control (C) samples for *Kalmia angustifolia* (Kalmia) and *Picea mariana* (Black spruce). A) *Kalmia* foliar C:N, B) Spruce foliar C:N, C) *Kalmia* foliar N, D) *Kalmia* foliar C, E) Spruce foliar N, and F) Spruce foliar C. Black spruce broadly exhibited higher rates of change compared to *Kalmia*. Different letters above each treatment indicate significant differences at α = 0.05. Letter notations between figures are significantly different from each other.

The total mass loss of black spruce litter was greater than *Kalmia* litter in island and heath. In heath, black spruce litter mass loss was 35.8 % higher than *Kalmia* litter mass loss ($z = -5.179$, $p < 0.001$). Likewise, spruce litter mass loss was 27.7 % higher than *Kalmia* litter mass loss in island ($z = -3.046$, $p = 0.007$). Black spruce mass loss ($z = 0.3798$, $p > 0.999$) and *Kalmia* mass loss ($z = -1.178$, $p = 0.718$) were not significantly different between island and heath (Figure 9).

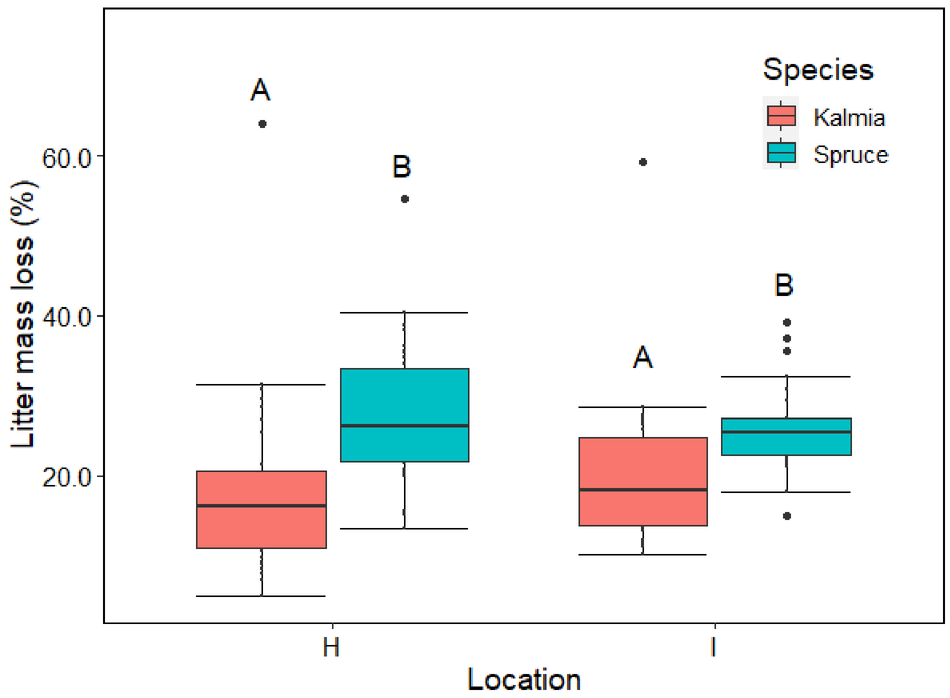

Figure 9. Litter mass loss of black spruce (*Picea mariana*) and *Kalmia angustifolia* (Kalmia) in SS heath (H) and spruce island (I) after three months of *in situ* decomposition. Black spruce showed higher rates of decomposition than *Kalmia* but neither differed between heath and island. Different letters indicate significant differences at α= 0.05)

### *3.4 Functional hypervolumes of dominant species in island and heath (Question 2)*

Overall, the functional hypervolume utilized by the four most dominant species in island (HV = 0.953) was far greater than that of heath (heath HV = 0.415). Black spruce hypervolume (HV = 0.395) in island was greater than *Rhododendron groenlandicum* (HV = 0.086) in heath. Surprisingly, *Vaccinium angustifolium* and *Rhododendron canadense* utilize more niche space in island (*Vaccinium angustifolium*: HV = 0.344. *Rhododendron canadense*: HV = 0.452) than in heath (*Vaccinium angustifolium*: HV = 0.052. *Rhododendron canadense*: HV = 0.051). This indicates a 6.57X and 8.94X increase for *Vaccinium angustifolium* and *Rhododendron canadense* hypervolumes in island respectively. *Kalmia* exhibited an 0.47X reduction of total hypervolume in island (HV = 0.107) compared to heath (HV = 0.226; Figure 10).

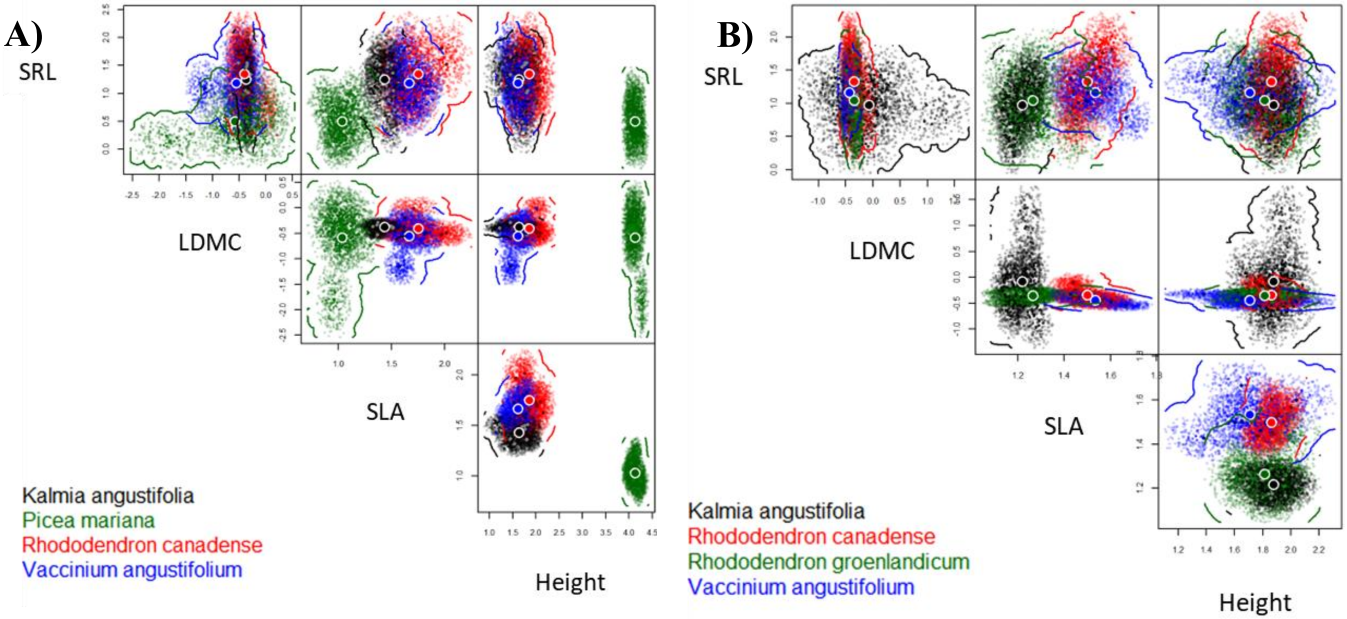

Figure 10. Funcitonal trait space of the four most dominant species in A) island and B) heath. Trait space is represented as functional hypervolumes with respect to four functional traits: specific root length (SRL), leaf dry matter content (LDMC), specific leaf area (SLA), and height. Overall, functional overlap was greater in heath and total functional space utilization was greater in island.

There was a general trend indicating niche conservation in island compared to heath. Functional trait space occupancy of *Kalmia angustifolia*, *Rhododendron groenlandicum*, and *Vaccinium angustifolium* was less constrained in island than in heath assemblages. Trait values for SRL, LDMC, and SLA were more extreme in island apart from *Vaccinium angustifolium* LDMC, which were more extreme in heath assemblages. Height was greater among shared species in heath. This showed a trend whereby more resources were allocated to resource acquisition, ultimately at the detriment of height in island (Table 3).

Table 3. Hypervolume centroids of four functional traits (specific root length (SRL), leaf dry matter content (LDMC), specific leaf area (SLA), and height) for the four most dominant species in heath and island. Values that deviate further than zero (indicating greater niche divergence) within each heath–island pair are highlighted in green. Common ericaceous species generally exhibited higher degrees of niche divergence in island compared to heath.

| Species | SRL | | LDMC | | SLA | | Height | |
|---|---|---|---|---|---|---|---|---|
| | Heath | Island | Heath | Island | Heath | Island | Heath | Island |
| *Kalmia angustifolia* | 0.989 | 1.233 | -0.064 | -0.379 | 1.220 | 1.431 | 1.878 | 1.635 |
| *Rhododendron canadense* | 1.331 | 1.344 | -0.345 | -0.400 | 1.498 | 1.848 | 1.861 | 1.856 |
| *Vaccinium angustifolium* | 1.172 | 1.185 | -0.434 | -0.057 | 1.533 | 1.662 | 1.705 | 1.612 |
| *Rhododendron groenlandicum* | 1.025 | - | -0.353 | - | 1.266 | - | 1.827 | - |
| *Picea mariana* | - | 0.496 | - | -0.583 | - | 1.029 | - | 4.126 |

Functional trait overlap between species pairs was generally greater in heath than island. Little overlap occurred between *Kalmia* (Sorensen = 0.060)*, Vaccinium angustifolium* (Sorensen = 0.098), and *Rhododendron canadense* (Sorensen = 0.098) with *Rhododendron groenlandicum*, no overlap was found between these species and *Picea mariana* (Sorensen < 0.0001). Hypervolume overlap between *Kalmia* and *Rhododendron canadense* (island: Sorensen = 0.043, heath: 0.027), and *Vaccinium angustifolium* (island: Sorensen = 0.151, heath: Sorensen = 0.048) were greater in island vs. heath locations. In contrast, functional overlap between *Rhododendron canadense* and *Vaccinium angustifolium* was greater in heath (Sorensen = 0.112) than island (Sorensen = 0.081). Thus, these species exhibited lower degrees of niche partitioning in island locations than in heath.

### *3.5 Black spruce island expansion and growth (Question 3)*

Distribution and percent cover of black spruce island varied across sites. These data showed a wide range of black spruce island canopy cover from 19.1 ± 3.83, 21.4 ± 4.52, and 35.1 ± 3.72% for Ochre Hill, Terra Nova Road, and Rocky Pond sites respectively. Black spruce island cover was significantly higher in Rocky Pond than Ochre Hill ($p = 0.007$), and Terra Nova Road ($p = 0.014$). Terra Nova Road black spruce island cover and Ochre Hill island cover did not differ ($p = 0.778$; Figure 11). The average % canopy cover was 21.4 ± 4.52, 35.1 ± 3.72, and 19.1 ± 3.83 respectively for, Terra Nova Road, Rocky Pond, and Ochre Hill sites, respectively

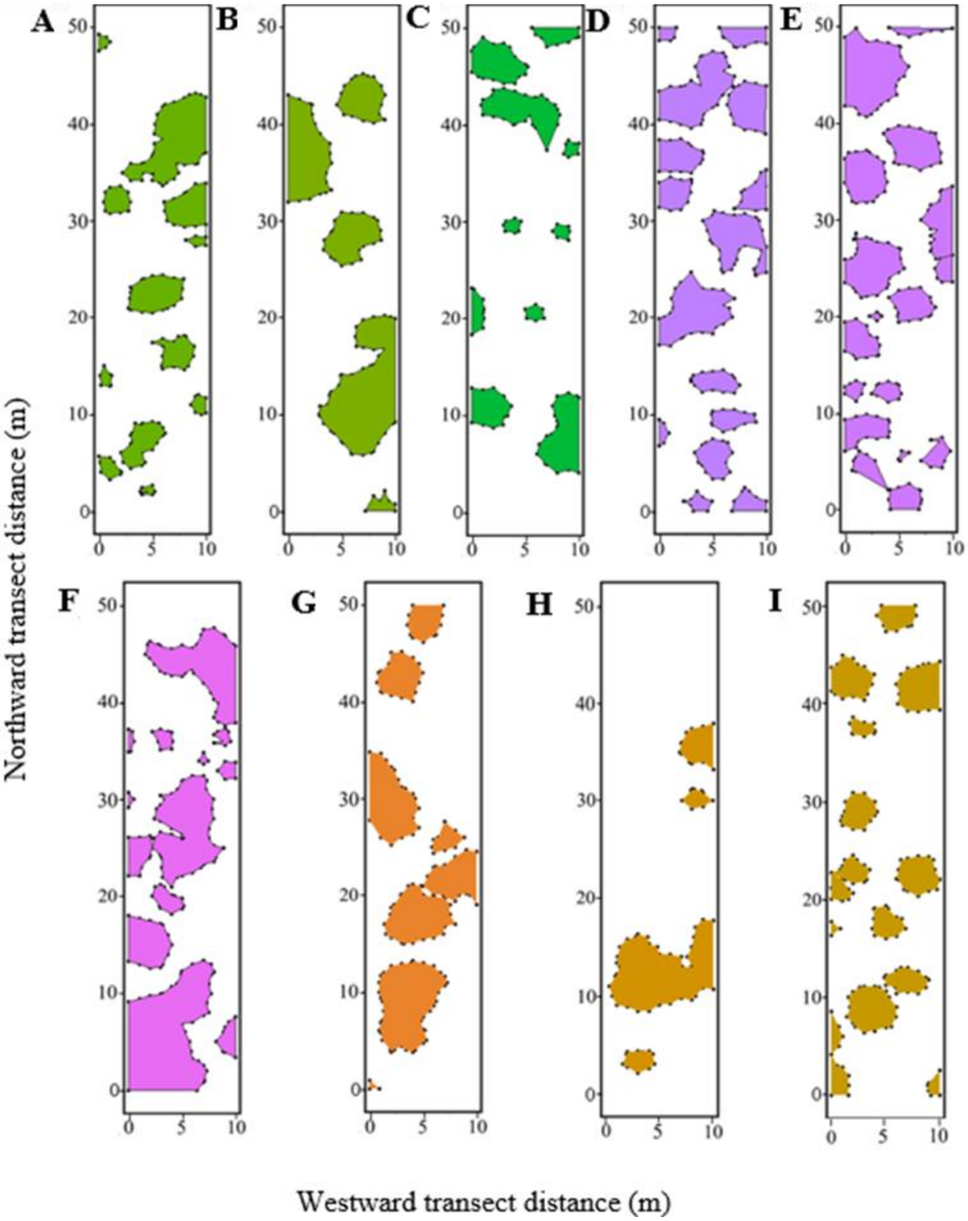

Figure 11. Distribution of black spruce (*Picea mariana*) island in three 50 m x 10 m belt transects in three shrub savanna sites: Terra Nova Road (green), Rocky Pond (Purple), and Ochre Hill (Orange).

I found negative correlations between tree age and distance from the parent tree in all subsets of island size including 120 – 150 cm radius (Pearson correlation = - 0.341), 151 – 210 cm radius (Pearson correlation = -0.383), 211 – 270 cm radius (Pearson correlation = -0.242), and 271 – 360 cm radius (Pearson correlation = -0.4897). I found that distance from the parent tree poorly explained variation in tree age but remained significant nonetheless in 120 – 150 cm radius (coefficient of determination = 0.116; $P = 0.015$), 151 – 210 cm radius (coefficient of determination = 0.147; $P < 0.001$), 211 – 270 cm radius (coefficient of determination = 0.058; $P < 0.001$), and 271 – 360 cm radius (coefficient of determination = 0.240; $P < 0.001$) spruce island.

Overall, the expansion rates of island by layered black spruce stems encroachment into heath decreased over time and with island size. Regression showed in all cases, tree age declining with distance from the parent tree. However, this relationship becomes weaker with increasing island size. Thus, 120 – 150 cm radius island expanded at a rate of 2.5 cm/year (Model 1 regression, $y = -0.160x + 54.56$) (Figure 12A), whereas island expansion rate was reduced to 2.1 cm/year, 2.1 cm/year, and 1.9 cm/year for island with a radius of 151- 210 cm (Model 1 regression, $y = -0.138x + 61.52$), 211 – 270 cm (Model 1 regression, $y = -0.060x + 54.27$), and 271 – 360 cm (Model 1 regression, $y = -0.074x + 60.17$), respectively (Figure 12B-D). In other words, a 120 – 150 cm radius island expanded 1 m in 38.6 years and 151- 210 cm, 211 – 270 cm, and 271 – 360 cm radius island expanded 1 m in 47.7 years, 48.3 years, and 52.6 years, respectively

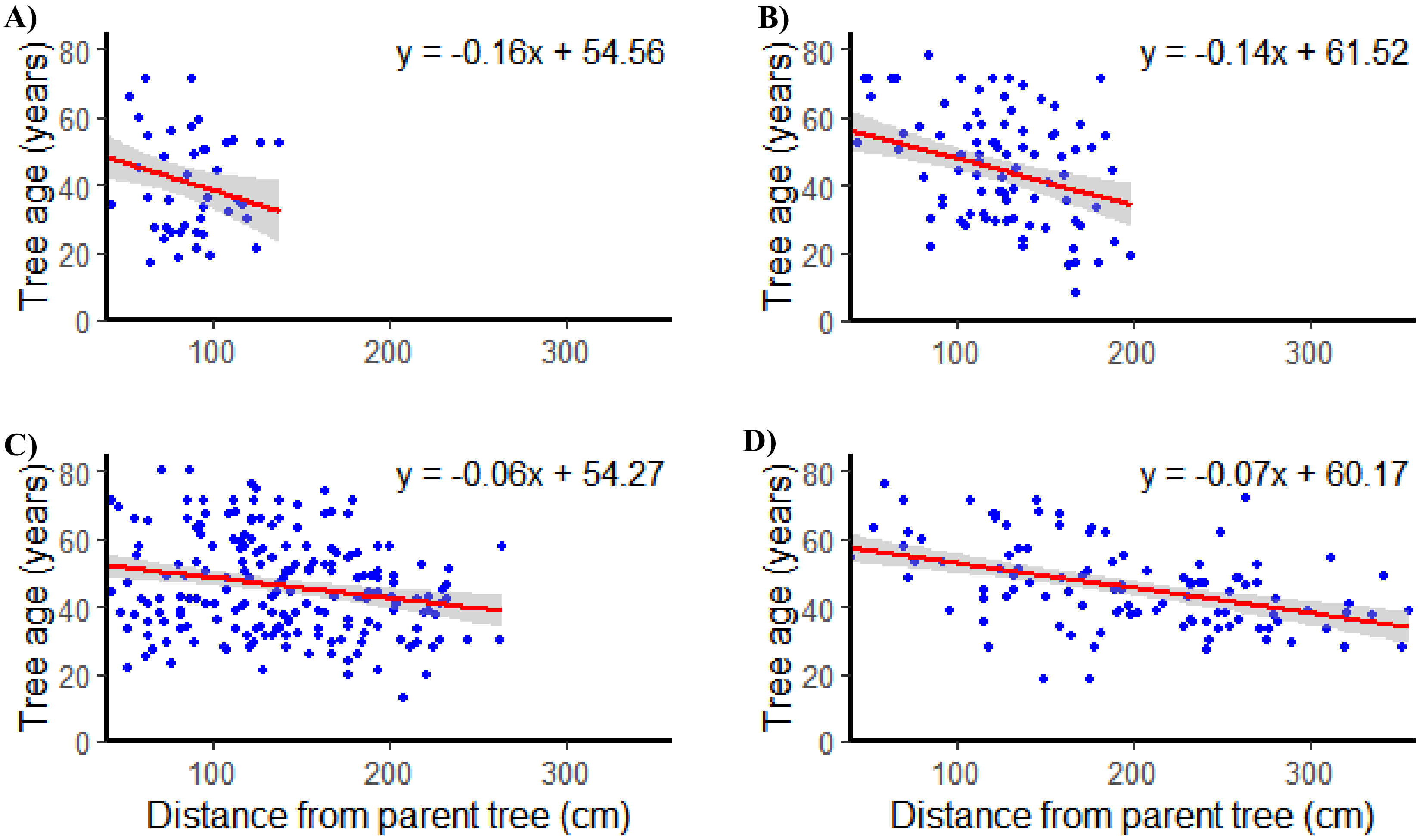

Figure 12. Radial expansion rates of black spruce (*Picea mariana*) island represented by four subsets based on island size. A) 140 cm, B) 200 cm, C) 260 cm, and D) 350 cm radius length of island. The rate of radial expansion decreased as island size increases. These radial expansion rates were 5.3, 2.1 , 2.1, and 1.9 cm/year for A, B, C, and D, respectively.

Combined site data on cover revealed an average island cover of 25.2 ± 8.27 %. This baseline cover increased to 37.9 ± 12.3 % with low expansion rates (0.119 m/year) from the largest island size subset, 39.2 ± 12.7 % with moderate expansion rates (0.130 m/year) from the intermediate island size subsets, and 42.6 ± 13.9 % with high expansion rates (0.119 m/year) from the smallest island size subset in 50 years. Furthermore, when the model was adjusted to predict cover in 100 years, low, moderate, and high expansion rates were 50.7 ± 17.0, 53.1 ± 18.0, and 59.9 ± 20.6 %, respectively. Hence, while differences in future canopy cover were found within expansion rates of between 50 and 100 years ($p = 0.033$), the treatments that differed could not be identified through multiple comparisons ($\alpha = 0.05$) (Figure 13A). Additionally, I found no significant differences between expansion rates and time to 100% canopy cover ($p = 0.606$). Low expansion rates reached 100% island cover in 376 ± 241 years, moderate and high expansion rates reached 100% cover in 343 ± 220 years, and 276 ± 177 years, respectively (Figure 13B).

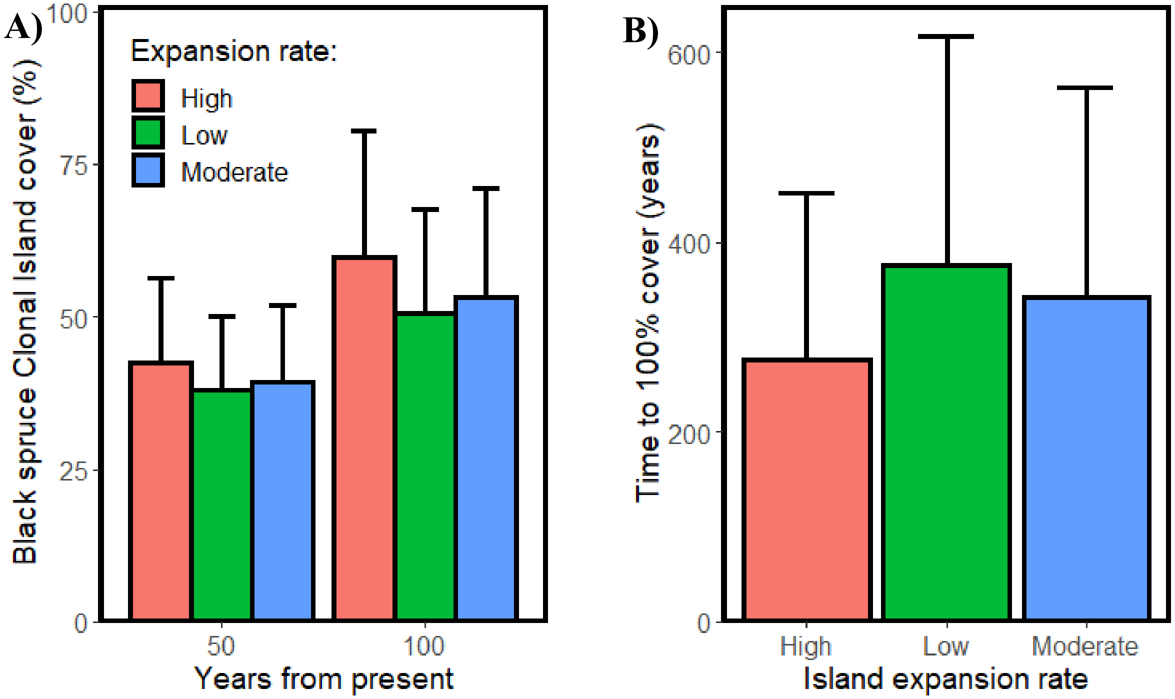

Figure 13. Predicted cover of Black spruce (*Picea mariana*) island A) canopy percent cover in 50 and 100 years, and B) time to 100% canopy cover based on high (0.163 m/year), moderate (0.130 m/year), and low (0.119 m/year) circumference expansion rates. Error bars represent one standard deviation. Relative expansion rates of black spruce island did not significantly affect future canopy cover (α = 0.05).

The average expansion rate of all island sizes was 0.137 ± 0.022 m/year. When this rate was applied to the three SS sites, Ochre Hill reached 100% island canopy cover in 461 ± 314 years, Rocky Pond in 169 ± 9.49 years, and Terra Nova Road in 394 ± 147 years. No significant differences were found between time to 100% island cover and site ($p = 0.251$; Figure 14A). However, differences in projected cover exist between sites over shorter time scales. Rocky pond island cover in 100 years (73.7 ± 1.64 %) was significantly higher than Ochre Hill in 50 years (31.0 ± 10.9) ($p < 0.001$), Ochre Hill in 100 years (42.8 ± 18.2 %) ($p = 0.001$), Terra Nova Road in 50 years (32.4 ± 2.66 %) ($p = 0.012$), and Terra Nova Road in 100 years (43.3 ± 5.10 %) ($p = 0.014$). However, island cover of Rocky Pond did not differ between 50 (54.4 ± 2.1 %) and 100 years (Tukey's HSD, $p = 0.165$). Thus, no differences were found between 50 and 100 years within individual sites ($\alpha = 0.05$; Figure 14B).

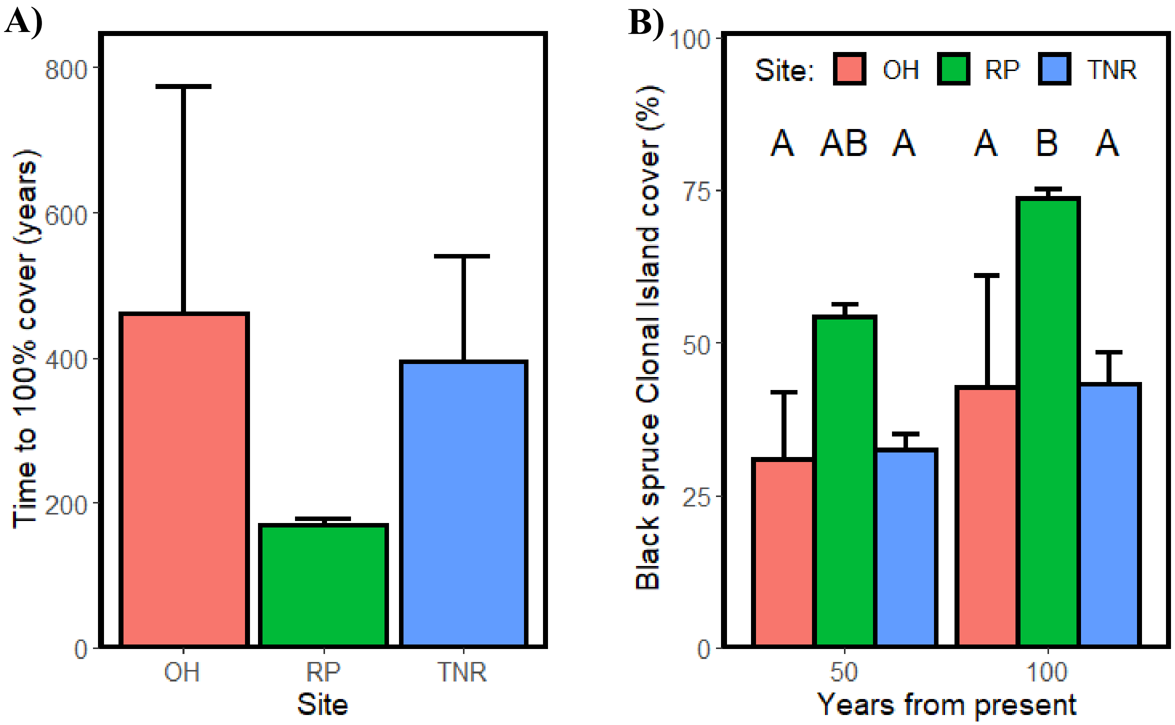

Figure 14. Predicted cover of black spruce (*Picea mariana*) island in Ochre Hill (OH), Rocky Pond (RP), Terra Nova Road (TNR) indicated by A) time to 100% island cover, and B) Canopy cover in 50 and 100 years based on average circumference expansion rate (0.137 m/year) of all island sizes. Significant differences are indicated by different letters (α = 0.05).

## 4 Discussion

Overall my results provide strong evidence of microhabitat and niche differentiation between island and heath in black spruce-*Kalmia* SS. The data identified a strong relationship between microhabitat (environmental) characteristics, resource use, and interspecific competition maintaining the heath–island structure of SS. There is little evidence that black spruce island will expand to the point of a closed canopy forest in this community in between the fire return interval predicted for this region (~150 years; Walker, 2021). Therefore, the long-term stability of this SS community between disturbances is presumably maintained through community dynamics.

### *4.1 Floristic composition and microhabitat conditions are distinct between island and heath (Question 1)*

The inclusion of environmental variables improves conclusions regarding vegetation and community structure more than vegetation analysis alone (Row, 1986). The CCA results indicate strong gradients reflecting abiotic factors and species composition between island and heath. Axis 1 showed greater influence over assemblage where light availability (canopy and ground level light) and soil moisture were the primary drivers. Organic matter depth also differed along this axis though to a lesser extent. Alternatively, axis 2 indicates a gradient in which organic matter depth and light penetration varied with community assembly with minimal influence by soil moisture. Overall, heath and island exhibited significant differences with respect to all measured environmental factors.

Microsite light availability (represented by canopy cover and light penetration) is a direct consequence of community structure, namely floristic composition, and plant height. In this study, microsite light availability appears to stabilize vegetation composition in island and heath through positive plant-soil feedback by fostering optimal condiiotns for eicacious species in heath and nitrogen-fixing understory species in island locations. The trend showing an inverse relationship between light penetration and canopy cover is coherent given the obvious effects that a high canopy has on light at the ground level. However, including both of these factors is necessary to assess the degree to which microsite variation can provide safe sites for competitive shade-tolerant species, such as ericaceous shrubs (Montgommery & Chazdon, 2002). Under a reduced canopy, the growth and reproduction of ericaceous shrub increase, which indirectly reduces nitrogen mineralization and imposes long-term negative effects on conifer seedling recruitment and growth (Reicis *et al*., 2020). Conversly, in island locations, nitrogen fixation is perfomed by feathermoss (*Pleurozium shreberi)* ground layer. Feathermoss is a major contributor to forest N input (Rousk *et al*., 2014). Increased nitrogen availability likely affords black spruce with a competitive advantage through indirect effects driven by optimizing conditions for increased growth and canopy cover. Thus, as found in my study, light availability particular to each location (island and heath) may reinforce the system through direct and indirect effects and contribute to feedback between shade tolerance and nutrient availability. The direct relationship between species niche utilization and nutrient availability is further explored in section 4.4 of this thesis.

Soil moisture differs greatly between island and heath and is a significant indicator of vegetation composition along both axes. Here, the dominant species in heath are favoured by increased soil moisture. Soil moisture in island was lower than in heath. Typically, plant-soil feedbacks reduce evaporative stress via the canopy of woody species. However, there is evidence to suggest that the strength and importance of this feedback are less influential under mesic and hydric soil conditions such as SS (D'Odorico *et al*., 2007). Alternatively, the higher moisture levels reported in heath may be driven by two processes. First, *Cladonia stellaris* correlates with axes proportionately to soil moisture. *Cladonia stellaris* is known to increase soil moisture content due to a thick, dense growth form that captures and retains water while reducing evaporative stress with a high albedo (Kytöviita & Stark, 2009). In contrast, changes in soil moisture may not be driven by water loss to evaporative stress but by water use by dominant species. Although this study does not measure water use among plants, tree species typically have a higher average water uptake than shrub species during the growing season (Flanagan *et al*., 1992). Therefore, soil moisture in heath and island may be regulated by two alternative processes. In conclusion, soil moisture is an important driver of nutrient cycling and will favour the moister heath component irrespective of other factors influencing nutrient cycling such as microbial activity and nutrient availability (Walse *et al*., 1998).

Organic matter depth is correlated with both ordination axes but is more strongly correlated to axis 2 (Figure 5). Post-disturbance establishment of species in heath and island is driven by organic matter which limits black spruce germination (Siegwart Collier & Mallik, 2010). Germination and seedling recruitment in post-fire black spruce-*Kalmia* community is dictated by residual organic matter (ROM) thickness (Siegwart Collier & Mallik, 2010). Under thin ROM (< 2 cm), island are established from black spruce seeds, and thick ROM (> 2 cm) favours the reestablishment of remaining reproductive propagules of *Kalmia* and other vegetatively reproductive species within the soil. Thicker organic matter in islands shown in this study suggests that organic matter accumulates faster in spruce islands. This is done by either an increased deposition or decreased decomposition of organic matter. Decreased decomposition in islands is unlikely because, once established, *Kalmia* modifies soil conditions by releasing allelopathic chemicals that have a range of effects including reduced decomposition compared to black spruce forests (Mallik 1987; Mallik, 1999). Therefore, thicker organic matter depth in islands must be driven by increased litter deposition. Although there is currently no literature on wind dynamics in SS communities, allochthonous debris may be deposited in island that are more sheltered than heath. Allochthonous litter deposition is a significant source of organic matter which affects nutrient cycling and soil respiration in open areas (Fahnstock *et al*., 2000). Consequently, *Kalmia* litter deposited into black spruce island will inhibit soil enzyme activity and restrict organic matter decomposition (Joanisse *et al*., 2007). Therefore, organic matter depth appears to be related to species distribution in a counter-intuitive way but windblown *Kalmia* litter into island likely increases litter deposition rates while inhibiting decomposition.

### *4.2 Community dynamics of the dominant species in SS (Question 1)*

Although the abovementioned effects of environmental variables impose strong selections for specific species, examining species assemblages with respect to environmental gradients permits a further understanding of coexistence and persistence in SS. Here, axis 1 of the CCA recognized few significant correlations. All negatively correlated species (*Rhododendron canadense*, *Vaccinium angustifolium*) and positively correlated species (*Kalmia* angustifolia) were more abundant in heath than island. However, *Kalmia* was far more abundant in island than the other ericaceous species.

The separation of ericaceous species along axis 1 is poorly explained by environmental parameters included in this CCA. Indeed, these data show that *Kalmia* corresponds with increasing shade, and decreased moisture, whereas *V. angustifolium* and *R. canadense* correspond with decreased abundance under these parameters. However, overstory growth providing partial shade has been shown to increase *Kalmia* vigor, *V. angustifolium* growth, and aboveground growth of related *Rhododendron* sp. (Bloom & Mallik, 2004; Hoefs & Shay, 1981; Baldwin & Oberbauer, 2022; Mallik, 2021). Additionally, differentiation of these species through soil moisture seems unlikely as all are well adapted to moist environments but persist under limited water availability (Lattier *et al*., 2013; Mallik *et al*., 2012; Glass *et al*., 2005). Therefore, the correspondence that environmental variables have with indicator species are constructed under poor relationships which suggests that factors other than the ones measured might be responsible for this separation.

Previous research in Terra Nova National Park has identified the separation of common ericaceous species, including *Kalmia* and *V. angustifolium*, to be driven by pH and conductivity (Karim & Mallik, 2008). The plots sampled in my study were much closer than in this other previous work. The close proximity of plots combined with mesic site conditions permits nutrient mobility between island and heath which directly affects soil properties (Thomas, 1970). Therefore, differences between these soil parameters have limited potential to create significant gradients at a small scale.

Differences in trait plasticity between *Kalmia*, *V. angustifolium*, and *R. canadense* may lead to exclusion of functional space use under strong competitive stress. While related species are known to coexist through functional trait partitioning (He & Lamont, 2014), stress reduces this level of variation (Jung *et al*., 2010). In such situations, the more stress-tolerant species (in this case, *Kalmia*), will fail to partition its niche under kin recognition (File *et al*., 2012). While the precise stress causing this response cannot be identified, I theorize that the presence of low resource availability may be sufficient to reduce *Kalmia* coexistence with other ericads.

Axis two identified five positively correlated indicator species (*Kalmia angustifolia, Rhododendron groenlandicum, Rhododendron canadense, Vaccinium angustifolium, Cladonia stellaris*) and five negatively correlated indicator species (*Picea mariana*, *Pleurozium schreberi*, *Usnea longissimi*, *Parmelia sulcata*, *Hypogymnia physodes*). Positively correlated species position on the CCA corresponds to heath plot location and negatively correlated species correspond to island plot location (Figure 5).

Plant associations in island and heath showed similarities with *Kalmia* heath and closed-crown black spruce forest in regard to composition, resource use, competition, and microhabitat availability. Island plots showed high aboveground competition while the heath plots showed high below-ground competition. Black spruce provides the substrate for epiphytic lichens while permitting a bed of *Pleurozium schreberi* similar to closed-crown black spruce forests (Foster, 1985). Conversely, SS heath, much like typical *Kalmia* heath, is dominated by ericaceous shrubs which select for belowground resource acquisition under limited resource availability (St. Martin & Mallik, 2021). Notably, open shrubland shares more similarities with *Kalmia* heath than island share with closed-crown black spruce forest. In contrast to black spruce island, closed-crown black spruce forest has far greater productivity driven by high taxonomic and functional diversity (St. James & Mallik, 2021).

### *4.3 Soil nutrient availability has little stabilizing effects in SS (Question 1)*

Contrary to my hypothesis, soil nutrients did not appear to have a direct influence on the belowground restriction of cross colonization between island and heath. Boreal ecosystems are N limited and nearly all mineralized N is taken up by roots (Tamm, 1991). Given the higher C:N identified in island was driven by more carbon and less nitrogen than what was found in heath soil, N input is playing a pivotal role in black spruce growth limitation overall. Total N in island

and heath are far lower than those reported in nearby, productive, natural forest communities (St. Martin & Mallik, 2021). Total C suggests that SS island have poor capacity to support the level of ecosystem function and productivity found in forest ecosystems under typical successional and soil processes.

Although differences in total C and N exist between island and heath, available nitrogen was similar between the two. These data suggest that N mineralization inhibition was greater in heath than island. *Kalmia* is a dominant species in both island and heath. *Kalmia* is known to inhibit N mineralization, lower phosphorus, and lower potassium content in soils (LeBel *et al*., 2008). However, the mechanisms that drive these changes (namely through ericoid mycorrhizae exploitation of taxa-specific nutrient complexes) have a relatively low capacity to do so under stressed conditions found in island (Read & Peres-Moreno, 2003). Although this study does not directly explore mycorrhizae productivity, the similar nitrate and ammonia availability combined with overall lower total N content in island suggests that litt N mineralization occured in heath.

Potassium and phosphorus/phosphates did not indicate growth inhibition in island. In fact, higher potassium availability in island locations suggests less inhibition, as K is positively related to higher rates of photosynthesis and cellular respiration, but that black spruce faces these challenges when establishing in heath (Steven, 1985). From the perspective of future island expansion, lower K in heath is the only identified nutrient that has the capacity to stress black spruce layers at the island periphery. In contrast, total P and phosphates were similar between island and heath which does not suggest that it acts as a geochemical barrier limiting cross-establishment of island and heath flora. Nonetheless, these data provide support for the hypothesis that soil processes differ between locations.

Litter decomposition was similar in island and heath regardless of the litter source. Litter decomposition is the mechanism by which organic nutrient complexes are returned to the geochemical cycle. In undecomposed control litter samples, foliar N was greater, foliar C was lower, and C:N was greater in spruce litter relative to *Kalmia* litter. While the relative decomposition rates of these species' litter C, N, and mass loss did not differ between island and heath locations, spruce litter decomposes at faster rates than *Kalmia* litter. Although litter decomposition is driven by climate, soil microbiota productivity, and litter quality, the latter has less regulatory effects in unfavourable conditions (Couteaux *et al*., 2005). Hence, while we expected spruce litter to have greater rates of decomposition, and consequently result in more efficient nutrient cycling and availability, the combined effects of poor soil nutrient availability, and allelochemicals reduce the influence of litter quality on nutrient cycling. *Kalmia* litter decomposition has previously been shown to improve via altered soil conditions which improve soil respiration (Walker *et al*., 2009). From this study, I conclude that litter decomposition is limited by soil conditions with minimal influence from the source species. By extension, the dominant species then possess limited capacity to alter soil nutrient availability through litter decomposition.

### *4.4 Functional differentiation and processes of the dominant species in SS island and heath (Question 2)*

Functional differentiation, represented by functional niche volume and overlap, supports my hypothesis that island and heath locations operate with distinct mechanisms and ericaceous shrubs experience more competitive stress in black spruce island locations. Under favorable conditions, species generally exhibit larger hypervolumes and higher degrees of overlap (de la Riva *et al*., 2018). However, these trends are not observed for all ericaceous species in SS island

and heath. Hypervolume size and overlap for *Rhododendron canadense* and *Vaccinium angustifolium* suggest that island conditions are more favorable for growth for these species, whereas *Kalmia* performs relatively poorly in island locations compared to heath. *Kalmia* niche size and functional niche overlap of closely related taxa were greater in heath. This observation suggests that *Kalmia* constrains the niche of *Rhododendron canadense*, and *Vaccinium angustifolium* in heath locaitons but its capacity to do so diminishes under stressful conditions (i.e, island locations). The effects of competitive exclusion are relative to environmental stress whereby the more well-adapted species dictate niche utilization from competing species (Mao *et al*., 2018).

*Kalmia* was relatively poorly suited for colonization in islands compared to *Rhododendron canadense*, and *Vaccinium angustifolium.* Generally, these species invest more resources in above and below-ground resource acquisition in island locations. The exception to this statement is height which was greater in heath for all ericaceous species. Hence, we see that species are investing in competitive strategies at the detriment of vigor. In other words, competitive stress is driving niche convergence and weaker co-dominance. Species with similar functional traits (i.e., high functional overlap) are known to respond to environmental stress by competitive exclusion and result in higher beta-functional diversity (Pierce *et al*., 2007). Although I could not directly measure beta-functional diversity due to mathematical limitations (number of species < traits, in brief), I expect this to be a driving factor in the sparse ericaceous cover in island.

Overall, functional niche utilization and overlap support my hypothesis that island have higher degrees of niche convergence from environmental stress. Functional overlap is representative of functional redundancy and is commonly used as a metric of stability. In SS, overall hypervolume overlap in each community was high but the species-specific overlap differs between island and heath. Lack of overlap suggest species traits are using alternative strategies to confer dominance relative to competitive stress.

### *4.5 Black spruce island distribution and regeneration in SS (Question 3)*

Black spruce island distribution and cover throughout SS in this study are similar to tree cover in other savannah systems across Canada. The other ecosystems vary in the dominant tree, and ground cover species including Jack pine (*Pinus banksiana*) – *Cladonia stellaris* lichen woodland (LW) in Northern Quebec, Tamarack (*Larix laricina*) LW in the arctic tree line, White spruce (*Picea glauca*) – *Stereocaulon paschale* LW in Northern Ontario, and other black spruce-ericad SS systems in their native range along the arctic tree line (Payette & Delwaide, 2018). Additionally, the mean cover of black spruce island measured in this study (~25%) falls within the defined tree cover of 10-40% tree cover reported in the abovementioned communities (King, 1993). Threshold transitions in the boreal biome are defined as high (~75%), intermediate (20-45%), and low (<10%) tree cover (Scheffer *et al*., 2012). Thus, I conclude that the SSs in eastern Canada can be defined as an intermediate tree cover alternative state.

While the SS community used in this study shares similarities with other savannah/woodland systems across Canada, it has unique community composition which has strong implications for stability. Community stability is dictated by asynchronous responses of species to environmental fluctuations and the effects that dominant species have on habitat conditions (De Mazancourt *et al*., 2013). Thus, although stability has been defined based on tree cover for systems with similar structure, it is unsafe to assume the same definition in SS based on tree cover alone.

As island size increases, the total radial expansion rates of these island steadily decrease as a result of competition from dominant species in heath with unfavorable soil conditions. Black spruce layers are favoured by sufficient soil moisture, soil organic matter thickness, light availability and rooting medium (Stanek, 1961). Since soil moisture content and light availability were higher in heath than in island than I deduce that organic matter thickness (lower in heath), favourable rooting medium (lacking in heath, e.g., shallower organic matter), and competition with surrounding vegetation result in less successful layering in black spruce. The periphery of black spruce island suffers from stronger competitive forces from heath vegetation and the layered stems grow in poorer soil conditions than within island locations. *Kalmia* litter sequesters soil nitrogen as tannin-protein complexes which limit black spruce nitrogen uptake and reduces its growth (Jonaisse *et al*., 2009). As the post-fire community develops, these interactions strengthen over time and the soil changes imparted by areas colonized by *Kalmia* become more prominent and detrimental to competing species. However, given the lack of evidence for decreased expansion rates impact future cover, these effects are of little importance.

Although black spruce island expansion rate was inversely proportional to island size, they still possess the capability to encroach into the heath component of the SS. Cumulative expansion rates of all island cover on average was 1.46 $m^2$/year (figure 12). This expansion rate is far greater than the 0.20 $m^2$/yr. canopy closure rate reported by Bloom & Mallik (unpublished data) whose model lacked island size subsets and their expansion rates were derived from trees sampled between the island center and periphery. Hence, the model used in this study provides a better estimate of canopy closure because it accounts for the effect of island size. Given a cover expansion of 1.46 $m^2$/year, it would take ~340 yrs. (i.e., twice the natural fire cycle) to achieve full canopy closure, providing that disturbance does not occur and island continue to maintain themselves (Legere & Payette, 1981).

### *4.6 Limitations and future direction*

The study showed some important limitations of using static measurements to represent long-term community dynamics. As a community develops, succession involves numerous feedback mechanisms between vegetation and habitat conditions. Habitat conditions affect community dynamics by influencing biotic interactions, plant growth, and population dynamics (Holmgren *et al*., 1997). While this study related microhabitat conditions to island and heath vegetation assemblages and discussed potential causal mechanisms for plant distribution, I did not directly measure the strength of these interactions or draw conclusions on their rate of change over time. In successional terms, plant-soil feedback is primarily negative, neutral, then positive for early, mid, and late-successional stages, respectively (Kardol *et al*., 2006). This study identifies late-successional stage dynamics but the processes that form the distinct vegetation structure of SS cannot be directly inferred from these data. Given that positive feedback typically accelerate change in a system (Bever, 1994), a quantitative assessment of feedback strength will strengthen my conclusions on the stability conferred through community dynamics.

Litter decomposition measures the rate of nutrient loss and serves as a proxy for nutrient cycling (Hobbie, 2015). Litter decomposition is directly affected by temperature, moisture, litter quality, and soil microbial productivity (Zhang *et al*., 2008). Although I explored the relationship of litter decomposition between locaiton and litter quality, the effect of soil microbiota and temperature on these rates remain uncertain. I propose that the relative soil microbial productivity in island and heath could account for the lack of leaf nutrient differences found between the decomposed litter despite changes in soil moisture and organic matter depth.

Additionally, longer-term decomposition measured at multiple discrete time intervals would permit linear model analysis to estimate litter decay rate and directly determine nutrient turnover (Manzoni *et al*., 2012). However, this approach was not possible over my study duration.

I estimated island expansion and canopy closure based on two assumptions: i) all islands are circular and ii) island distribution is even throughout SS. Mapping the spatial distribution of several SS revealed that these assumptions falsely represent the community. In light of this finding, I propose that my estimate of canopy closure is conservative and underestimates reality. First, the typical polygonal shape of an island will require more time to fill in than an already circular island. Outward points would need to expand into the island to avoid canopy gaps. Secondly, if two nearby islands connect, then their cumulative radial growth would be lesser than an island that would expand evenly because the peripheral growth would be expanding in more directions. Similarly, uneven island distribution would require greater expansion to reach canopy closure. Therefore, addressing these issues with a more accurate model would result in a longer time to canopy closure but would not alter conclusions regarding stability.

What remains to be determined for shrub savannah stability is empirical evidence on post-disturbance community assembly. My approach to SS persistence is largely based on the assumption that i) processes in SS heath are similar to uniform *Kalmia*-heath and ii) post-disturbance conditions are similar across multiple disturbances. In uniform *Kalmia*-heath, Mallik *et al*. (2010) reported that *Kalmia* cover declines ~40 years after disturbance. Yet, *Kalmia* cover in SS often remained vigourous in sites with trees in island locations aged 70+ years. This discontinuity may be driven by the shaded *Kalmia* phenotype (e.g., grown under a canopy) being more vigorous with relatively benign plant-soil feedbacks (Bloom & Mallik, 2004). Yet, fine-scale measures of *Kalmia* vigour along a shade gradient from heath to island in SS is needed to support this claim. Secondly, post-disturbance conditions could vary over time. Fire severity is directly affected by the dominant species' fire-adaptive traits and their influence on fire regime (Keely *et al*., 2011). The relative fire-severity is dependent on the abundance of highly flammable species. In open black spruce stands, low fire severity results in incomplete burning of black spruce and a thick layer of ROM (Angers *et al.*, 2011; Veilleaux-Nolin & Payette, 2012). These conditions would not be conducive to post-fire seedling regeneration. Understanding how post-disturbance conditions in SS vary and consequently dictate early successional dynamics will further shed light on the stability and persistence variability in the black spruce-*Kalmia* SS of eastern Canada.

## 5 Summary

Black spruce-*Kalmia* SS in eastern Canada is composed of two distinct vegetation components: black spruce island locations, surrounded by heath dominated by ericaceous plants. This study aimed to provide supporting evidence on the stability of this system by identifying key elements of community dynamics that maintain vegetation structure and composition in island and heath locations. I found a strong separation between the island and heath communities based on light availability, soil moisture, and soil organic matter depth which are directly influenced by the dominant species in island and heath. However, soil nutrient availability varied little between island and heath which was attributed to N mineralization inhibition in heath,combined with higher total available nitrogen content in heath soil. Additionally, I have identified niche convergence and competitive exclusion to occur among ericaceous species in island despite having minimal direct niche overlap with black spruce. This lack of overlap suggests that ericaceous species are responding to environmental stress by investing resources in resource acquisition at the expense of vigour. While the expansion rates of island varied with island size, this was of little importance regarding future forest canopy cover. Based on average expansion rates of island circumference (0.137 m/yr.), full canopy cover will occur in ~341 years. In conclusion, the evidence presented in this study supports the potential for canopy closure to occur in the absence of disturbance such as wildfire. If canopy closure does happen it would be followed by a shift in abovementioned community processes associated with island. However, canopy closure is unlikely to occur within the natural fire return interval (150 years) of this region (Walker, 2021). Under the influence of natural fire, SS islands will experience more sever burn dule to lower moisture content and higher fuel load than surrounding heath. This variable fire severity will promote future black spruce regeneration in island locations and heath regeneration in heath location thus conferring stability in the black spruce-*Kalmia* shrub savannah alternate state.

## 6 Literature cited

Abis, B., & Brovkin, V. (2017). Environmental conditions for alternative tree-cover states in high latitudes. *Biogeosciences*, *14*(3), 511-527.

Ackerly, D. D. (2003). Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Sciences*, *164*(S3), S165-S184.

Alexis & Dinno (2017). dunn.test: Dunn's Test of Multiple Comparisons Using Rank Sums. R package version 1.3.5.

Angers, V. A., Gauthier, S., Drapeau, P., Jayen, K., & Bergeron, Y. (2011). Tree mortality and snag dynamics in North American boreal tree species after a wildfire: a long-term study. *International Journal of Wildland Fire*, *20*(6), 751-763.

Baldwin, T. A., & Oberbauer, S. F. (2022). Essential oil content of Rhododendron tomentosum responds strongly to manipulation of ecosystem resources in Arctic Alaska. *Arctic Science*, 1-19.

Beisner, B. E., Haydon, D. T., & Cuddington, K. (2003). Alternative stable states in ecology. Frontiers in Ecology and the Environment, 1(7), 376-382.

Bergeron, Y., Flannigan, M., Gauthier, S., Leduc, A., & Lefort, P. (2004). Past, current and future fire frequency in the Canadian boreal forest: implications for sustainable forest management. *AMBIO: A Journal of the Human Environment*, *33*(6), 356-360.

Bever, J. D. (1994). Feeback between plants and their soil communities in an old field community. *Ecology*, *75*(7), 1965-1977.

Bever, J. D. (2003). Soil community feedback and the coexistence of competitors: conceptual frameworks and empirical tests. *New phytologist*, *157*(3), 465-473.

Blonder B., Babich Morrow C., Harris D., Brown S., Butruille G., Laini A., and Chen D. (2022). hypervolume: High Dimensional Geometry, Set Operations, Projection, and Inference Using Kernel Density Estimation, Support Vector Machines, and Convex Hulls. R package version 3.0.2. https://CRAN.R-project.org/package=hypervolume

Bloom, R. G., & Mallik, A. U. (2004). Indirect effects of black spruce (Picea mariana) cover on community structure and function in sheep laurel (Kalmia angustifolia) dominated heath of eastern Canada. *Plant and Soil*, *265*(1), 279-293.

Bloom, R. G., & Mallik, A. U. (2006). Relationships between ericaceous vegetation and soil nutrient status in a post-fire Kalmia angustifolia-black spruce chronosequence. *Plant and soil*, *289*(1), 211-226.

Brower, J. E., Zar, J. H., & Von Ende, C. N. (1998). *Field and laboratory methods for general ecology* (Vol. 4). Boston: WCB McGraw-Hill.

Chang, C. C., & HilleRisLambers, J. (2019). Trait and phylogenetic patterns reveal deterministic community assembly mechanisms on Mount St. Helens. *Plant Ecology*, *220*(7), 675-698.

Chase, J. M. (2003). Community assembly: when should history matter? Oecologia, 136(4), 489-498.

Conradi, T., Temperton, V. M., & Kollmann, J. (2017). Resource availability determines the importance of niche-based versus stochastic community assembly in grasslands. *Oikos*, *126*(8), 1134-1141.

Couteaux, M. M., Bottner, P., & Berg, B. (1995). Litter decomposition, climate and liter quality. *Trends in ecology & evolution*, *10*(2), 63-66.

Crespi, B. J. (2004). Vicious circles: positive feedback in major evolutionary and ecological transitions. *Trends in Ecology & Evolution*, *19*(12), 627-633.

Dantas de Paula, M., Forrest, M., Langan, L., Bendix, J., Homeier, J., Velescu, A. & Hickler, T. (2021). Nutrient cycling drives plant community trait assembly and ecosystem functioning in a tropical mountain biodiversity hotspot. *New Phytologist*, *232*(2), 551-566.

de la Riva, E. G., Violle, C., Pérez-Ramos, I. M., Marañón, T., Navarro-Fernández, C. M., Olmo, M., & Villar, R. (2018). A multidimensional functional trait approach reveals the imprint of environmental stress in Mediterranean woody communities. *Ecosystems*, *21*(2), 248-262.

De Mazancourt, C., Isbell, F., Larocque, A., Berendse, F., De Luca, E., Grace, J. B., ... & Loreau, M. (2013). Predicting ecosystem stability from community composition and biodiversity. *Ecology letters*, *16*(5), 617-625.

Demenocal, P., Ortiz, J., Guilderson, T., Adkins, J., Sarnthein, M., Baker, L., & Yarusinsky, M. (2000). Abrupt onset and termination of the African Humid Period:: rapid climate responses to gradual insolation forcing. *Quaternary science reviews*, *19*(1-5), 347-361.

D'Odorico, P., Caylor, K., Okin, G. S., & Scanlon, T. M. (2007). On soil moisture–vegetation feedbacks and their possible effects on the dynamics of dryland ecosystems. *Journal of Geophysical Research: Biogeosciences*, *112*(G4).

Ehrenfeld, Joan G., Beth Ravit, and Kenneth Elgersma. "Feedback in the plant-soil system." *Annu. Rev. Environ. Resour.* 30 (2005): 75-115.

Element, C. A. S. (2007). Method 3051A microwave assisted acid digestion of sediments, sludges, soils, and oils. *Z. Für Anal. Chem*, *111*, 362-366.

Elton, C. S. (1958). The ecology of invasions by animals and plants. London: Chapman and Hall. 181 P.

Enright, N. J., Fontaine, J. B., Bowman, D. M., Bradstock, R. A., & Williams, R. J. (2015). Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. *Frontiers in Ecology and the Environment*, *13*(5), 265-272.

Environment Canada. Canadian Climate Normals 1981–2010: Gambo, NL. 2017. Available online: http://climate.weather.gc.ca/ (accessed on 5 January 2020).

Esri "World Street Map" [Basemap]. Scale Not Given. 7 January 2020. Available online: https://www.arcgis.com/home/ webmap/viewer.html?useExisting=1 (accessed on 8 January 2020).

Fahnestock, J. T., Povirk, K. L., & Welker, J. M. (2000). Ecological significance of litter redistribution by wind and snow in arctic landscapes. *Ecography*, *23*(5), 623-631.

File, A. L., Murphy, G. P., & Dudley, S. A. (2012). Fitness consequences of plants growing with siblings: reconciling kin selection, niche partitioning and competitive ability. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1727), 209-218.

Flanagan, L. B., Ehleringer, J. R., & Marshall, J. D. (1992). Differential uptake of summer precipitation among co-occurring trees and shrubs in a pinyon-juniper woodland. Plant, Cell & Environment, 15(7), 831-836.

Foster, D. R. (1985). Vegetation development following fire in Picea mariana (black spruce)-Pleurozium forests of south-eastern Labrador, Canada. *The Journal of Ecology*, 517-534.

Girard, F., Payette, S., & Gagnon, R. (2008). Rapid expansion of lichen woodlands within the closed-crown boreal forest zone over the last 50 years caused by stand disturbances in eastern Canada. *Journal of Biogeography*, *35*(3), 529-537.

Girard, F., Payette, S., & Gagnon, R. (2009). Origin of the lichen–spruce woodland in the closed-crown forest zone of eastern Canada. *Global Ecology and Biogeography*, *18*(3), 291-303.

Girard, F., Payette, S., & Gagnon, R. (2011). Dendroecological analysis of black spruce in lichen—spruce woodlands of the closed-crown forest zone in eastern Canada. *Ecoscience*, *18*(3), 279-294.

Glass, V. M., Percival, D. C., & Proctor, J. T. A. (2005). Tolerance of lowbush blueberries (Vaccinium angustifolium Ait.) to drought stress. I. Soil water and yield component analysis. *Canadian journal of plant science*, *85*(4), 911-917.

Grime, J. P. (2006). *Plant strategies, vegetation processes, and ecosystem properties*. John Wiley & Sons.

Grime, J. P. (1998). "Benefits of plant diversity to ecosystems: immediate, filter and founder effects." *Journal of Ecology* 86.6 902-910.

He, T., & Lamont, B. B. (2014). Genetic and ecological consequences of interactions between three banksias in mediterranean-type shrubland. *Journal of vegetation science*, *25*(3), 617-626.

Hobbie, S. E. (2015). Plant species effects on nutrient cycling: revisiting litter feedbacks. *Trends in ecology & evolution*, *30*(6), 357-363.

Hoefs, M. E. G., & Shay, J. M. (1981). The effects of shade on shoot growth of Vaccinium angustifolium Ait. after fire pruning in southeastern Manitoba. *Canadian Journal of Botany*, *59*(2), 166-174.

Holling, C. S. (1973). Resilience and stability of ecological systems. *Annual review of ecology and systematics*, *4*(1), 1-23.

Holmgren, M., Scheffer, M., & Huston, M. A. (1997). The interplay of facilitation and competition in plant communities. *Ecology*, *78*(7), 1966-1975.

Jasinski, J. P., & Payette, S. (2005). The creation of alternative stable states in the southern boreal forest, Quebec, Canada. *Ecological Monographs*, *75*(4), 561-583.

Joanisse, G. D., Bradley, R. L., Preston, C. M., & Munson, A. D. (2007). Soil enzyme inhibition by condensed litter tannins may drive ecosystem structure and processes: the case of Kalmia angustifolia. *New Phytologist*, *175*(3), 535-546.

Joanisse, G. D., Bradley, R. L., Preston, C. M., & Bending, G. D. (2009). Sequestration of soil nitrogen as tannin–protein complexes may improve the competitive ability of sheep laurel (Kalmia angustifolia) relative to black spruce (Picea mariana). *New Phytologist*, *181*(1), 187-198.

Johnstone, J. F., Celis, G., Chapin III, F. S., Hollingsworth, T. N., Jean, M., & Mack, M. C. (2020). Factors shaping alternate successional trajectories in burned black spruce forests of Alaska. *Ecosphere*, *11*(5), e03129.

Jung, V., Violle, C., Mondy, C., Hoffmann, L., & Muller, S. (2010). Intraspecific variability and trait-based community assembly. *Journal of ecology*, *98*(5), 1134-1140.

Kalra, Y. P., & Maynard, D. G. (1991). Methods manual for forest soil and plant analysis, Forestry Canada Information, Report NOR-X-319, Northwest Region, Northern Forestry Centre.

Kardol, P., Martijn Bezemer, T., & Van Der Putten, W. H. (2006). Temporal variation in plant–soil feedback controls succession. *Ecology letters*, *9*(9), 1080-1088.

King, G. A. (1993). Vegetation and pollen relationships in eastern Canada. *Canadian Journal of Botany*, *71*(2), 193-210.

Klanderud, K., & Totland, Ø. (2005). The relative importance of neighbours and abiotic environmental conditions for population dynamic parameters of two alpine plant species. *Journal of Ecology*, 493-501.

Kourtev, P. S., Ehrenfeld, J. G., & Häggblom, M. (2002). Exotic plant species alter the microbial community structure and function in the soil. *Ecology*, *83*(11), 3152-3166.

Kraft, N. J., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional ecology*, *29*(5), 592-599.

Krishna, M. P., & Mohan, M. (2017). Litter decomposition in forest ecosystems: a review. *Energy, Ecology and Environment*, *2*(4), 236-249.

Kytöviita, M. M., & Stark, S. (2009). No allelopathic effect of the dominant forest-floor lichen Cladonia stellaris on pine seedlings. *Functional Ecology*, 435-441.

Lattier, J. D., Ranney, T. G., & Lynch, N. P. (2013). History and cytological reassessment of Rhododendron canadense. *J. Amer. Rhod. Soc*, *67*(2), 92-98.

LeBel, P., Thiffault, N., & Bradley, R. L. (2008). Kalmia removal increases nutrient supply and growth of black spruce seedlings: an effect fertilizer cannot emulate. *Forest Ecology and Management*, *256*(10), 1780-1784.

Legendre, P., & Legendre, L. (2012). *Numerical ecology*. Elsevier.

Légère, A., & Payette, S. (1981). Ecology of a black spruce (Picea mariana) clonal population in the hemiarctic zone, northern Quebec: population dynamics and spatial development. *Arctic and Alpine Research*, *13*(3), 261-276

Lewontin, R. C. (1969). The meaning of stability. In *Brookhaven symposia in biology* (Vol. 22, p. 13).

Li, Y., Shipley, B., Price, J. N., Dantas, V. D. L., Tamme, R., Westoby, M., ... & Batalha, M. A. (2018). Habitat filtering determines the functional niche occupancy of plant communities worldwide. *Journal of Ecology*, *106*(3), 1001-1009.

Lundholm, J. T., & Marlin, A. (2006). Habitat origins and microhabitat preferences of urban plant species. *Urban Ecosystems*, *9*(3), 139-159.MacArthur, R. (1955). Fluctuations of animal populations and a measure of community stability. *ecology*, *36*(3), 533-536.

Mallik, A. U. (1987). Allelopathic potential of Kalmia angustifolia to black spruce (Picea mariana). *Forest Ecology and Management*, *20*(1-2), 43-51.

Mallik, A. U. (1999). Nutrient status of black spruce (Picea mariana [Mill.] BSP) forest soils dominated by Kalmia angustifolia L. *Acta Oecologica*, *20*(2), 87-92.

Mallik, A. U. (2002). Can Kalmia angustifolia interference to black spruce (Picea mariana) be explained by allelopathy?. *Forest Ecology and management*, *160*(1-3), 75-84.

Mallik, A. U. (2003). Conifer regeneration problems in boreal and temperate forests with ericaceous understory: role of disturbance, seedbed limitation, and keytsone species change. *Critical Reviews in Plant Sciences*, *22*(3-4), 341-366.

Mallik, Azim U. "Post-Fire Habitat Heterogeneity Leads to Black Spruce–Kalmia L. Shrub Savannah Alternate State." *Forests* 13.4 (2022): 570.

Mallik, A. U., Bloom, R. G., & Whisenant, S. G. (2010). Seedbed filter controls post-fire succession. *Basic and Applied Ecology*, *11*(2), 170-181.

Mallik, A. U., Wang, J. R., Siegwart-Collier, L. S., & Roberts, B. A. (2012). Morphological and ecophysiological responses of sheep laurel (Kalmia angustifolia L.) to shade. *Forestry: An International Journal of Forest Research*, *85*(4), 513-522.

Manzoni, S., Piñeiro, G., Jackson, R. B., Jobbágy, E. G., Kim, J. H., & Porporato, A. (2012). Analytical models of soil and litter decomposition: solutions for mass loss and time-dependent decay rates. *Soil Biology and Biochemistry*, *50*, 66-76.

Mao, W., Zhao, X., Sun, Z., Felton, A. J., Zhang, T., Li, Y., & Smith, M. D. (2018). Limiting similarity mediates plant community niche hypervolume across a desert-steppe ecotone of Inner Mongolia. *Environmental and experimental botany*, *153*, 320-326.

May, R. M. (1973). Complexity and stability in model ecosystems. *Princeton: Princeton UniversityPress*.

Miller, A. D., Thompson, J. R., Tepley, A. J., & Anderson‐Teixeira, K. J. (2019). Alternative stable equilibria and critical thresholds created by fire regimes and plant responses in a fire‐prone community. Ecography, 42(1), 55-66.

Montgomery, R., & Chazdon, R. J. (2002). Light gradient partitioning by tropical tree seedlings in the absence of canopy gaps. *Oecologia*, *131*(2), 165-174.

Odum, E. P. (1953). Fundamentals of ecology. xii, 387 pp. *W. B. Saunders Co., Philadelphia, Pennsylvania, and London, England*.

Packer, A., & Clay, K. (2000). Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature*, *404*(6775), 278-281.

Perez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., ... & Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. Aust. Bot. 61, 167–234.

Peterson, G., Allen, C. R., & Holling, C. S. (1998). Ecological resilience, biodiversity, and scale. *Ecosystems*, *1*(1), 6-18.

Pierce, S., Luzzaro, A., Caccianiga, M., Ceriani, R. M., & Cerabolini, B. (2007). Disturbance is the principal α-scale filter determining niche differentiation, coexistence and biodiversity in an alpine community. *Journal of Ecology*, *95*(4), 698-706.

Pimm, S. L. (1980). Food web design and the effect of species deletion. *Oikos*, 139-149.

Postel, S., Bawa, K., Kaufman, L., Peterson, C. H., Carpenter, S., Tillman, D., ... & Reichert, J. (2012). *Nature's services: Societal dependence on natural ecosystems*. Island Press.

Quinn, G. P., & Keough, M. J. (2002). *Experimental design and data analysis for biologists*. Cambridge university press.

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rapanoela, R., Raulier, F., & Gauthier, S. (2016). Regional instability in the abundance of open stands in the boreal forest of Eastern Canada. *Forests*, *7*(5), 103.

Read, D. J., & Perez-Moreno, J. (2003). Mycorrhizas and nutrient cycling in ecosystems–a journey towards relevance?. *New phytologist*, *157*(3), 475-492.

Reicis, K., Bradley, R. L., Joanisse, G., Houle, D., Tremblay, S., Barrette, M., & Wotherspoon, A. (2020). Pre-commercial thinning enhances competitive traits of boreal ericaceous shrubs and reduces soil fertility. *Forest Ecology and Management*, *458*, 117801.

Ricklefs, R. E. (2008). Disintegration of the ecological community: American Society of Naturalists Sewall Wright award winner address. *The American Naturalist*, *172*(6), 741-750.

Rousk, K., Jones, D. L., & DeLuca, T. H. (2014). The resilience of nitrogen fixation in feather moss (Pleurozium schreberi)-cyanobacteria associations after a drying and rewetting cycle. *Plant and soil*, *377*(1), 159-167.

Rowe, J. S. (1996). Land classification and ecosystem classification. *Environmental Monitoring and Assessment*, *39*(1), 11-20.

Sánchez-Pinillos, M., Coll, L., De Cáceres, M., & Ameztegui, A. (2016). Assessing the persistence capacity of communities facing natural disturbances on the basis of species response traits. *Ecological indicators*, *66*, 76-85.

Scheffer, M., Hirota, M., Holmgren, M., Van Nes, E. H., & Chapin, F. S. (2012). Thresholds for boreal biome transitions. *Proceedings of the National Academy of Sciences*, *109*(52), 21384-21389.

Scheffer, M., Szabo, S., Gragnani, A., Van Nes, E. H., Rinaldi, S., Kautsky, N., ... & Franken, R. J. (2003). Floating plant dominance as a stable state. *Proceedings of the national academy of sciences*, *100*(7), 4040-4045.

Siegwart Collier, L. C., & Mallik, A. U. (2010). Does post-fire abiotic habitat filtering create divergent plant communities in black spruce forests of eastern Canada?. *Oecologia*, *164*(2), 465-477.

South, R. Biogeography and Ecology of the Island of Newfoundland; Springer Science & Business Media: Berlin/Heidelberg, Germany, 1983; Volume 48. 21.

Stanek, Walter. "Natural layering of black spruce in northern Ontario." *The Forestry Chronicle* 37.3 (1961): 245-258.

Steven, H. C. (1985). Role of potassium in photosynthesis and respiration. *Potassium in agriculture*, 369-396.

St. James, C., & Mallik, A. U. (2021). Functional Ecology of Forest, Heath, and SS Alternate States in Eastern Canada. *Forests*, *12*(1), 93.

St Martin, P., & Mallik, A. U. (2021). Soil chemistry drives below ground traits in an alternate successional pathway from forest to heath. *Oecologia*, *195*(2), 469-478.

Stromayer, K. A., & Warren, R. J. (1997). Are overabundant deer herds in the eastern United States creating alternate stable states in forest plant communities?. *Wildlife Society Bulletin*, 227-234.

Tamm C O 1991 Nitrogen in terrestrial ecosystems: Questions of productivity, vegetational changes, and ecosystem stability. Ecological studies 81, Berlin, Springer. 115 pp

Ter Braak, C. J. (1986). Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, *67*(5), 1167-1179.

Thomas, G. W. (1970). Soil and climatic factors which affect nutrient mobility. *Nutrient mobility in soils: accumulation and losses*, *4*, 1-20.

Tilman, D. (1987). The importance of the mechanisms of interspecific competition. The American Naturalist, 129(5), 769-774.

Tilman, D., & Downing, J. A. (1994). Biodiversity and stability in grasslands. Nature, 367(6461), 363-365.

Tilman, D., Wedin, D., & Knops, J. (1996). Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, *379*(6567), 718-720.

Veilleux-Nolin, M., & Payette, S. (2012). Influence of recent fire season and severity on black spruce regeneration in spruce–moss forests of Quebec, Canada. *Canadian Journal of Forest Research*, *42*(7), 1316-1327.

Venables, W. N. & Ripley, B. D. (2002) Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0-387-95457-0

Vimos-Lojano, D. J., Martínez-Capel, F., & Hampel, H. (2017). Riparian and microhabitat factors determine the structure of the EPT community in Andean headwater rivers of Ecuador. *Ecohydrology*, *10*(8), e1894.

Walker, G. R., & Mallik, A. U. (2009). Black spruce reforestation in Kalmia heath: seedling response to forest floor mixing and mycorrhizal inoculation with Paxillus involutus. *Canadian Journal of Forest Research*, *39*(11), 2007-2020.

Walse C, Berg B, Sverdrup H (1998) Review and synthesis of experimental data on organic matter decomposition with respect to the effect of temperature, moisture, and acidity. Environ Rev 6:25–40

Walker, L. C. (2021). *All fired up: A long-term fire history of the coastal boreal forest of Newfoundland, Canada* (Doctoral dissertation, Memorial University of Newfoundland).

Weiher, E., Freund, D., Bunton, T., Stefanski, A., Lee, T., & Bentivenga, S. (2011). Advances, challenges and a developing synthesis of ecological community assembly theory. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1576), 2403-2413.

Wickham. H. (2016) ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.

WinFolia (2007) Image analysis for plant science. Regent Instruments Inc., Nepean.

Zhang, D., Hui, D., Luo, Y., & Zhou, G. (2008). Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. *Journal of Plant Ecology*, *1*(2), 85-93.

Zobel, M. (1992). Plant species coexistence: the role of historical, evolutionary and ecological factors. *Oikos*, 314-320

**Appendix 1**. Functional trait matrix: mean trait values for four functional traits (specific leaf area (SRL), leaf dry matter content (LDMC), specific root length (SRL), and height) of the four most dominant species in heath and island.

| Species | SRL | | LDMC | | SLA | | Height (cm) | |
|---|---|---|---|---|---|---|---|---|
| | I | H | I | H | I | H | I | H |
| *Kalmia angustifolia* | 21.91 | 12.14 | 0.4299 | 1.780 | 27.58 | 16.49 | 48.60 | 77.40 |
| *Rhododendron canadense* | 31.39 | 28.75 | 0.4064 | 0.4493 | 57.98 | 32.02 | 57.98 | 74.31 |
| *Vaccinium angustifolium* | 18.09 | 16.07 | 0.3291 | 0.3759 | 48.29 | 33.73 | 44.95 | 55.95 |
| *Picea mariana* | 3.811 | X | 0.3805 | X | 10.93 | X | 13250 | X |
| *Rhododendron groenlandicum* | X | 13.16 | X | 0.4575 | X | 18.52 | X | 71.4 |

**Appendix 2.** Mean species abundance in island and heath in Terra Nova Road (TNR), Ochre Hill (OH), and Rocky Pond (RP) sites.

| Species | TNR | | OH | | RP | |
|---|---|---|---|---|---|---|
| | Heath | Island | Heath | Island | Heath | Island |
| *Picea mariana* | 0.40 | 83.80 | 0.00 | 70.07 | 1.00 | 3.67 |
| *Larix laricina* | 2.17 | 0.00 | 0.50 | 0.00 | 0.33 | 0.33 |
| *Kalmia angustifolia* | 62.50 | 17.03 | 42.03 | 22.37 | 37.52 | 36.68 |
| *Rhododendron canadense* | 15.20 | 2.50 | 7.43 | 0.90 | 1.87 | 1.87 |
| *Rhododendron groenlandicum* | 2.37 | 0.00 | 4.43 | 0.37 | 2.47 | 2.47 |
| *Vaccinium angustifolium* | 7.93 | 0.54 | 2.88 | 0.84 | 1.47 | 1.44 |
| *Maianthemum canadense* | 0.00 | 0.00 | 0.03 | 0.00 | 0.00 | 0.00 |
| *Ilex mucronate* | 1.70 | 2.67 | 3.37 | 4.37 | 0.00 | 0.00 |
| *Viburnum cassinoides* | 1.00 | 1.50 | 0.70 | 0.83 | 0.00 | 0.00 |
| *Amelanchier interior* | 0.03 | 0.67 | 1.37 | 0.73 | 0.00 | 0.00 |
| *Cornus canadensis* | 1.90 | 3.01 | 1.14 | 0.83 | 0.00 | 0.00 |
| *Vaccinium uliginosum* | 0.00 | 0.03 | 0.03 | 0.00 | 0.00 | 0.00 |
| *Vaccinium vitis-idaea* | 0.00 | 0.33 | 0.00 | 0.17 | 0.17 | 0.17 |
| *Pteridium aquilinum* | 3.67 | 0.17 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Sorbus americana* | 0.17 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Clintionia borealis* | 0.00 | 0.00 | 0.03 | 0.00 | 0.00 | 0.00 |
| *Gaultheria hispidula* | 0.00 | 0.00 | 0.00 | 0.57 | 0.00 | 0.00 |
| *Myrica gale* | 0.00 | 0.00 | 1.33 | 0.00 | 0.00 | 0.00 |
| *Camadaphne calcuta* | 0.00 | 0.00 | 0.87 | 0.00 | 0.00 | 0.00 |
| *Lucopodium clavatum* | 0.00 | 0.00 | 0.03 | 0.00 | 0.00 | 0.00 |
| *Carex spp* | 0.00 | 0.00 | 0.03 | 0.03 | 0.00 | 0.00 |
| *Cladonia stellaris* | 67.67 | 6.50 | 69.13 | 2.53 | 87.10 | 83.80 |
| *Cladonia rangiferina* | 2.83 | 0.54 | 5.57 | 2.11 | 1.25 | 1.21 |
| *Cladonia mitis* | 0.00 | 0.00 | 0.71 | 0.03 | 0.17 | 0.17 |
| *Cladonia unicialis* | 0.00 | 0.00 | 0.00 | 0.17 | 0.00 | 0.00 |
| *Cladonia cenotea* | 0.00 | 0.20 | 0.00 | 0.03 | 0.00 | 0.00 |
| *alectoria sarmentosa* | 0.00 | 0.00 | 0.00 | 0.04 | 0.00 | 0.03 |
| *polytrichum commune* | 0.00 | 0.00 | 0.67 | 1.07 | 0.01 | 0.01 |
| *cladonia juniperum* | 0.00 | 0.00 | 0.00 | 0.03 | 0.00 | 0.00 |
| *dicranum polysetum* | 1.44 | 1.55 | 0.00 | 0.67 | 0.00 | 0.00 |
| *dicranum scoparium* | 0.67 | 1.00 | 0.17 | 0.07 | 0.00 | 0.00 |
| *dicranum flagare* | 0.33 | 2.67 | 0.17 | 1.33 | 0.00 | 0.17 |
| *pleurozium shreberi* | 13.58 | 49.01 | 8.00 | 75.63 | 0.50 | 1.17 |

| | | | | | | |
|---|---|---|---|---|---|---|
| *vulpicita pinastri* | 0.01 | 0.01 | 0.01 | 0.00 | 0.00 | 0.00 |
| *Usnea longissima* | 2.17 | 9.34 | 0.00 | 0.55 | 0.00 | 0.00 |
| *Parmeliopsis ambigua* | 0.90 | 0.30 | 0.06 | 0.28 | 0.14 | 0.11 |
| *Parmeliopsis hyperoptera* | 0.08 | 0.04 | 0.04 | 0.07 | 0.00 | 0.00 |
| *Cladonia pyxidata* | 0.00 | 0.17 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Hylocomium splendens* | 0.00 | 0.17 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Cladonia deformis* | 0.00 | 0.20 | 0.00 | 0.04 | 0.00 | 0.00 |
| *Cladonia sulpurina* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Sphagnum spp.* | 0.03 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *dicranum undulata* | 0.00 | 0.17 | 0.00 | 0.87 | 0.00 | 0.00 |
| *Cladonia coniocraea* | 0.00 | 0.00 | 0.00 | 0.17 | 0.00 | 0.00 |
| *cladonia chlorophaea* | 0.00 | 0.04 | 0.00 | 0.01 | 0.00 | 0.00 |
| *Rhytidiadelphus triquetus* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Bryoria fremontii* | 0.17 | 3.34 | 0.03 | 0.08 | 0.00 | 0.00 |
| *Parmelia sulcata* | 3.50 | 17.23 | 0.20 | 2.78 | 0.33 | 0.00 |
| *Hypogymnia physodes* | 1.70 | 6.60 | 0.17 | 2.27 | 0.17 | 0.00 |
| *Ptilium crista-castrensis* | 0.04 | 0.20 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Cladonia squamosa* | 0.00 | 0.00 | 0.00 | 0.04 | 0.00 | 0.00 |
| *Hylocomium splendens* | 0.00 | 0.00 | 0.00 | 0.04 | 0.00 | 0.00 |

**Appendix 3.** Mean values of microhabitat characteristics in island and heath in Terra Nova Road (TNR), Ochre Hill (OH), and Rocky Pond (RP) sites.

| Microhabitat characteristic | TNR | | OH | | RP | |
|---|---|---|---|---|---|---|
| | Heath | Island | Heath | Island | Heath | Island |
| Light penetration (%) | 0.28 | 0.13 | 0.43 | 0.09 | 0.60 | 0.58 |
| Organic matter depth (cm) | 17.05 | 20.89 | 15.66 | 23.25 | 3.94 | 4.18 |
| Canopy cover (%) | 7.93 | 32.70 | 0.99 | 29.67 | 3.02 | 4.02 |
| Soil moisture (%) | 33.89 | 5.07 | 31.20 | 8.97 | 40.40 | 40.07 |

**Appendix 4.** Supplementary analysis of site effects on island expansion in shrub savannah.

Factorial analysis of site and island radii on tree age showed that tree age generally declined with increasing radii (r = -0.264) (p <0.001). Among the three sites sampled (Ochre Hill, Rocky Pond, Terra Nova Road), there were differences. Thus, site did not have a significant effect on island expansion rate (p = 0.08). Site and radii did not have a significant interaction (p = 0.45) (Figure 15.

A

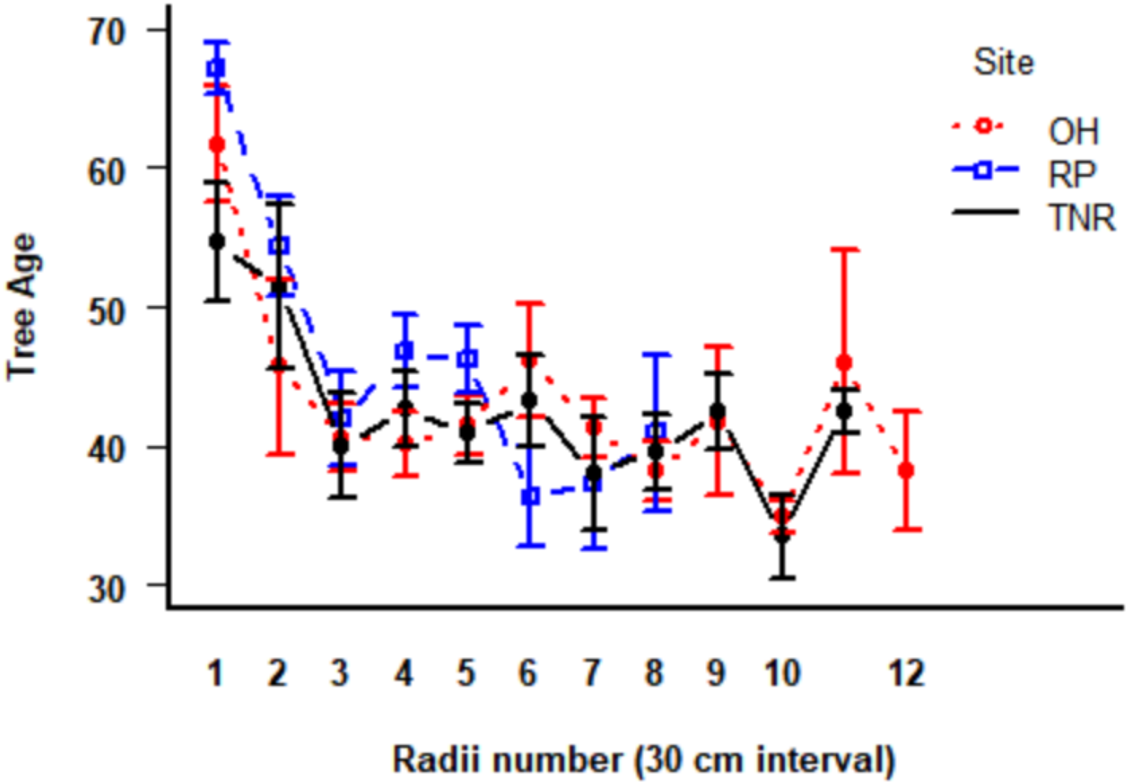

Figure 15. Mean *Picea mariana* age from island center to periphery in Ochre Hill (OH), Rocky Pond (RP), and Terra Nova Road (TNR) SS sites. Distance from island center to periphery is represented by radii sampled in 30 cm intervals. Trends of declining age with increased distance showed no significant differences between sites (α = 0.05).

**Appendix 5.** Age of *Picea mariana* layered individuals and their distance from the parent tree of SS island in Ochre Hill (OH), Rocky Pond (RP), and Terra Nova Road (TNR) sites.

| Site | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| OH | | | RP | | | TNR | | |
| Island ID | Distance | Age | Island ID | Distance | Age | Island ID | Distance | Age |
| C23 | 152 | 71 | A37 | 128 | 35 | A5 | 65 | 17 |
| C23 | 117 | 40 | A37 | 137 | 56 | A5 | 72 | 24 |
| C23 | 66 | 53 | A37 | 32 | 50 | A5 | 91 | 21 |
| C23 | 82 | 36 | A37 | 127 | 37 | A5 | 94 | 25 |
| C23 | 88 | 52 | A37 | 130 | 71 | A5 | 0 | 26 |
| C23 | 88 | 32 | A37 | 166 | 21 | A5 | 114 | 35 |
| C23 | 78 | 37 | A37 | 167 | 29 | A5 | 43 | 34 |
| C23 | 84 | 59 | A37 | 168 | 17 | A5 | 76 | 26 |
| C27 | 136 | 33 | A37 | 63 | 71 | A5 | 81 | 26 |
| C27 | 138 | 33 | A37 | 37 | 71 | A5 | 84 | 28 |
| C27 | 148 | 70 | A37 | 70 | 55 | A5 | 93 | 30 |
| C27 | 157 | 53 | A37 | 132 | 39 | A5 | 94 | 33 |
| C27 | 202 | 49 | A37 | 51 | 71 | B32 | 56 | 66 |
| C27 | 0 | 42 | A8 | 121 | 71 | B32 | 127 | 52 |
| C27 | 103 | 36 | A8 | 133 | 45 | B32 | 163 | 67 |
| C27 | 58 | 58 | A8 | 144 | 49 | B32 | 142 | 58 |
| C27 | 154 | 50 | A8 | 159 | 48 | B32 | 32 | 59 |
| C27 | 159 | 39 | A8 | 164 | 16 | B32 | 147 | 52 |
| C27 | 194 | 50 | A8 | 170 | 28 | B32 | 177 | 54 |
| C27 | 228 | 41 | A8 | 179 | 33 | B32 | 184 | 43 |
| C27 | 234 | 51 | A8 | 181 | 17 | B32 | 47 | 69 |
| C27 | 264 | 58 | A8 | 66 | 71 | B32 | 91 | 63 |
| C27 | 122 | 66 | A8 | 81 | 42 | B32 | 0 | 71 |
| C27 | 153 | 58 | A8 | 122 | 52 | B32 | 112 | 60 |
| C27 | 179 | 71 | A8 | 137 | 69 | B32 | 118 | 58 |
| C7 | 101 | 41 | A8 | 144 | 36 | B32 | 167 | 68 |
| C7 | 108 | 45 | A8 | 151 | 27 | B32 | 218 | 52 |
| C7 | 115 | 57 | A8 | 38 | 57 | B32 | 87 | 80 |
| C7 | 128 | 40 | A8 | 44 | 52 | B32 | 70 | 38 |
| C7 | 134 | 43 | A8 | 48 | 71 | B32 | 72 | 35 |
| C7 | 148 | 32 | B43 | 108 | 48 | B32 | 82 | 33 |
| C7 | 182 | 48 | B43 | 109 | 67 | B32 | 74 | 29 |
| C7 | 63 | 31 | B43 | 136 | 44 | B32 | 82 | 37 |
| C7 | 64 | 35 | B43 | 167 | 29 | D35 | 123 | 71 |
| C7 | 70 | 42 | B43 | 215 | 33 | D35 | 125 | 56 |
| C7 | 106 | 28 | B43 | 62 | 25 | D35 | 125 | 33 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| C7 | 134 | 31 | B43 | 86 | 34 | D35 | 137 | 71 |
| C7 | 142 | 31 | B43 | 0 | 71 | D35 | 164 | 74 |
| C7 | 144 | 44 | B43 | 64 | 65 | D35 | 185 | 49 |
| C7 | 154 | 51 | B43 | 81 | 39 | D35 | 190 | 49 |
| C7 | 164 | 38 | B43 | 93 | 61 | D35 | 200 | 58 |
| C7 | 167 | 52 | B8 | 122 | 67 | D35 | 230 | 45 |
| C7 | 182 | 43 | B8 | 176 | 63 | D35 | 233 | 46 |
| C7 | 194 | 21 | B8 | 182 | 32 | D35 | 52 | 33 |
| C7 | 219 | 38 | B8 | 194 | 46 | D35 | 80 | 52 |
| C7 | 34 | 22 | B8 | 197 | 40 | D35 | 100 | 58 |
| C7 | 52 | 22 | B8 | 232 | 36 | D35 | 113 | 33 |
| C7 | 76 | 23 | B8 | 249 | 62 | D35 | 117 | 40 |
| C7 | 93 | 64 | B8 | 298 | 39 | D35 | 118 | 41 |
| C7 | 0 | 63 | B8 | 309 | 33 | D35 | 122 | 76 |
| C7 | 111 | 71 | B8 | 319 | 28 | D35 | 122 | 65 |
| D12 | 132 | 45 | B8 | 0 | 70 | D35 | 133 | 64 |
| D12 | 234 | 35 | B8 | 108 | 71 | D35 | 233 | 58 |
| D12 | 279 | 37 | B8 | 118 | 28 | D6 | 121 | 28 |
| D12 | 192 | 39 | B8 | 122 | 66 | D6 | 129 | 21 |
| D12 | 276 | 33 | B8 | 128 | 64 | D6 | 143 | 35 |
| D12 | 142 | 47 | B8 | 171 | 40 | D6 | 155 | 26 |
| D12 | 164 | 44 | B8 | 149 | 18 | D6 | 176 | 20 |
| D12 | 188 | 53 | B8 | 124 | 51 | D6 | 176 | 24 |
| D12 | 198 | 37 | B8 | 76 | 53 | D6 | 221 | 20 |
| D12 | 228 | 34 | D22 | 176 | 67 | D6 | 0 | 37 |
| D12 | 243 | 30 | D22 | 222 | 43 | D6 | 89 | 29 |
| D12 | 248 | 33 | D22 | 42 | 44 | G23 | 62 | 58 |
| D12 | 252 | 38 | D22 | 84 | 49 | G29 | 188 | 35 |
| D12 | 282 | 35 | D22 | 86 | 66 | G29 | 141 | 50 |
| D12 | 335 | 37 | D22 | 91 | 42 | G29 | 118 | 50 |
| D12 | 92 | 53 | D22 | 0 | 59 | G29 | 130 | 31 |
| D12 | 178 | 28 | D22 | 122 | 60 | G29 | 134 | 54 |
| D12 | 189 | 45 | D22 | 127 | 34 | G29 | 169 | 43 |
| D12 | 191 | 38 | D22 | 140 | 37 | G29 | 170 | 56 |
| D12 | 194 | 45 | D22 | 144 | 50 | G29 | 194 | 48 |
| D12 | 208 | 50 | D22 | 176 | 36 | G29 | 208 | 13 |
| D12 | 229 | 34 | D22 | 203 | 47 | G29 | 233 | 42 |
| D12 | 233 | 46 | D22 | 43 | 71 | G29 | 140 | 48 |
| D12 | 312 | 54 | D22 | 52 | 47 | G29 | 164 | 52 |
| D12 | 96 | 39 | D22 | 56 | 37 | G29 | 91 | 53 |
| D12 | 242 | 35 | D22 | 63 | 41 | G43 | 92 | 42 |
| D12 | 321 | 38 | D22 | 8 | 54 | G43 | 132 | 24 |
| D12 | 342 | 49 | D22 | 86 | 71 | G43 | 96 | 39 |
| D12 | 352 | 28 | D22 | 92 | 64 | G43 | 95 | 41 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| D12 | 264 | 72 | D22 | 121 | 48 | G43 | 0 | 71 |
| D12 | 356 | 39 | E44 | 102 | 44 | G43 | 112 | 52 |
| D12 | 248 | 38 | E44 | 109 | 32 | G43 | 122 | 54 |
| D43 | 113 | 47 | E44 | 58 | 45 | G43 | 146 | 38 |
| D43 | 117 | 30 | E44 | 63 | 54 | G43 | 152 | 45 |
| D43 | 107 | 31 | E44 | 80 | 18 | G43 | 96 | 58 |
| D43 | 121 | 52 | E44 | 86 | 43 | H12 | 73 | 62 |
| D43 | 123 | 51 | E44 | 0 | 70 | H12 | 146 | 68 |
| D43 | 132 | 30 | E44 | 0 | 47 | H12 | 0 | 66 |
| D43 | 156 | 55 | E44 | 67 | 27 | H12 | 17 | 58 |
| D43 | 189 | 23 | E44 | 76 | 56 | H12 | 171 | 49 |
| D43 | 0 | 71 | E44 | 96 | 50 | H12 | 264 | 46 |
| E11 | 105 | 28 | F46 | 222 | 39 | H12 | 322 | 41 |
| E11 | 111 | 61 | F46 | 119 | 31 | H12 | 70 | 58 |
| E11 | 114 | 38 | F46 | 59 | 42 | H17 | 103 | 29 |
| E11 | 127 | 58 | F46 | 91 | 53 | H17 | 116 | 31 |
| E11 | 148 | 65 | F46 | 0 | 69 | H17 | 129 | 29 |
| E11 | 167 | 8 | F46 | 138 | 47 | H17 | 129 | 29 |
| E11 | 38 | 46 | F46 | 146 | 38 | H17 | 0 | 53 |
| E11 | 101 | 44 | F46 | 160 | 31 | H17 | 122 | 29 |
| E11 | 138 | 24 | F46 | 167 | 26 | H17 | 138 | 22 |
| E11 | 154 | 54 | F46 | 96 | 67 | H17 | 161 | 43 |
| E11 | 32 | 28 | F46 | 96 | 50 | H17 | 113 | 49 |
| E11 | 33 | 25 | F6 | 138 | 52 | H17 | 176 | 51 |
| E11 | 91 | 54 | F6 | 92 | 59 | H23 | 143 | 36 |
| E11 | 92 | 34 | F6 | 97 | 36 | H23 | 160 | 33 |
| E11 | 0 | 53 | F6 | 0 | 69 | H23 | 184 | 29 |
| E9 | 111 | 43 | F6 | 117 | 34 | H23 | 206 | 30 |
| E9 | 126 | 38 | F6 | 53 | 66 | H23 | 48 | 38 |
| E9 | 138 | 51 | F6 | 89 | 49 | H23 | 66 | 27 |
| E9 | 152 | 41 | F6 | 94 | 50 | H23 | 74 | 49 |
| E9 | 162 | 35 | F6 | 111 | 53 | H23 | 13 | 42 |
| E9 | 182 | 71 | H28 | 106 | 57 | H23 | 113 | 39 |
| E9 | 84 | 78 | H28 | 124 | 38 | H23 | 123 | 29 |
| E9 | 92 | 36 | H28 | 128 | 49 | H23 | 133 | 38 |
| E9 | 111 | 52 | H28 | 170 | 58 | H23 | 137 | 34 |
| E9 | 114 | 58 | H28 | 79 | 57 | H23 | 173 | 30 |
| E9 | 124 | 38 | H28 | 93 | 64 | H23 | 176 | 34 |
| E9 | 126 | 42 | H28 | 102 | 71 | H23 | 185 | 32 |
| E9 | 67 | 50 | H28 | 102 | 49 | H23 | 194 | 34 |
| E9 | 86 | 30 | H28 | 131 | 62 | H23 | 216 | 29 |
| E9 | 52 | 66 | H28 | 156 | 63 | H23 | 226 | 37 |
| G12 | 119 | 30 | H28 | 167 | 8 | H23 | 57 | 55 |
| G12 | 124 | 21 | H28 | 184 | 54 | H23 | 82 | 43 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| G12 | 38 | 65 | H28 | 199 | 19 | H23 | 87 | 42 |
| G12 | 73 | 48 | H28 | 86 | 22 | H23 | 96 | 41 |
| G12 | 74 | 27 | H28 | 0 | 69 | H29 | 214 | 23 |
| G12 | 75 | 35 | J23 | 113 | 68 | I23 | 237 | 47 |
| G12 | 91 | 26 | J23 | 127 | 66 | I23 | 259 | 48 |
| G12 | 94 | 25 | J23 | 142 | 28 | I32 | 20 | 46 |
| G12 | 0 | 71 | J23 | 168 | 50 | I32 | 132 | 49 |
| G12 | 108 | 52 | J23 | 188 | 44 | I32 | 158 | 64 |
| G12 | 127 | 52 | J23 | 211 | 28 | I32 | 228 | 34 |
| G12 | 58 | 60 | J23 | 71 | 80 | I32 | 24 | 33 |
| G12 | 88 | 71 | J34 | 108 | 27 | I32 | 254 | 34 |
| G12 | 88 | 57 | J34 | 108 | 48 | I32 | 271 | 33 |
| G12 | 99 | 19 | J34 | 115 | 59 | I32 | 33 | 64 |
| G12 | 64 | 36 | J34 | 128 | 57 | I32 | 53 | 63 |
| G12 | 62 | 71 | J34 | 138 | 71 | I32 | 129 | 43 |
| G12 | 39 | 52 | J34 | 14 | 56 | I32 | 158 | 34 |
| G23 | 77 | 71 | J34 | 167 | 57 | I32 | 184 | 62 |
| G12 | 94 | 61 | N22 | 151 | 47 | I32 | 203 | 38 |
| H22 | 63 | 23 | - | - | - | I32 | 213 | 39 |
| H23 | 124 | 40 | - | - | - | I32 | 217 | 41 |
| H23 | 121 | 53 | - | - | - | I32 | 231 | 43 |
| H23 | 127 | 39 | - | - | - | I32 | 237 | 52 |
| H23 | 76 | 44 | - | - | - | I32 | 242 | 27 |
| H23 | 88 | 44 | - | - | - | I32 | 255 | 44 |
| H23 | 88 | 59 | - | - | - | I32 | 270 | 52 |
| H23 | 0 | 61 | - | - | - | I32 | 280 | 42 |
| I42 | 132 | 26 | - | - | - | I32 | 290 | 29 |
| I42 | 118 | 61 | - | - | - | I32 | 40 | 54 |
| I42 | 148 | 63 | - | - | - | I32 | 73 | 48 |
| I42 | 182 | 56 | - | - | - | I32 | 80 | 60 |
| I42 | 194 | 44 | - | - | - | I32 | 158 | 67 |
| I42 | 202 | 39 | - | - | - | I32 | 174 | 50 |
| I42 | 204 | 41 | - | - | - | I37 | 118 | 30 |
| I42 | 215 | 42 | - | - | - | I37 | 123 | 24 |
| I42 | 228 | 30 | - | - | - | I37 | 130 | 29 |
| I42 | 244 | 30 | - | - | - | I37 | 150 | 34 |
| I42 | 262 | 30 | - | - | - | I37 | 0 | 69 |
| I42 | 124 | 75 | - | - | - | I40 | 135 | 57 |
| I42 | 137 | 66 | - | - | - | I40 | 140 | 57 |
| I42 | 153 | 41 | - | - | - | I40 | 150 | 43 |
| I42 | 178 | 55 | - | - | - | I40 | 160 | 48 |
| I42 | 187 | 42 | - | - | - | I40 | 165 | 31 |
| I42 | 194 | 58 | - | - | - | I40 | 175 | 18 |
| I42 | 201 | 43 | - | - | - | I40 | 23 | 39 |

|  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|
| I42 | 229 | 41 | - | - | - | I40 | 60 | 76 |
| I42 | 27 | 71 | - | - | - | I40 | 70 | 71 |
| I42 | 94 | 71 | - | - | - | I40 | 0 | 71 |
| I42 | 117 | 53 | - | - | - | I40 | 115 | 45 |
| I42 | 182 | 26 | - | - | - | I40 | 115 | 35 |
| I42 | 224 | 28 | - | - | - | I40 | 115 | 42 |
| - | - | - | - | - | - | I40 | 120 | 67 |
| - | - | - | - | - | - | I40 | 130 | 55 |
| - | - | - | - | - | - | I40 | 135 | 57 |
| - | - | - | - | - | - | I40 | 135 | 51 |
| - | - | - | - | - | - | I40 | 145 | 71 |
| - | - | - | - | - | - | I40 | 175 | 62 |
| - | - | - | - | - | - | I40 | 195 | 55 |
| - | - | - | - | - | - | I40 | 228 | 48 |
| - | - | - | - | - | - | I40 | 232 | 47 |
| - | - | - | - | - | - | I40 | 240 | 47 |
| - | - | - | - | - | - | I40 | 260 | 36 |
| - | - | - | - | - | - | I40 | 260 | 48 |
| - | - | - | - | - | - | I40 | 270 | 47 |
| - | - | - | - | - | - | I40 | 275 | 30 |