Can dominant species traits and soil chemistry explain stability in *Kalmia* heath?

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Abstract

In eastern Canada, black spruce (*Picea mariana*)-*Kalmia angustifolia* forests exist in one of three states: *Kalmia* heath, shrub savanna (SS), and black spruce forest. My main objective was to determine whether the strength of a plant-soil feedback (PSF) implicating abiotic soil properties distinguishes these three states. It is thought that traits of ericaceous shrubs (recalcitrant litter, low foliar nutrients, and high production of phenolic compounds) create nutrient-poor conditions in *Kalmia* heath and that this PSF explains long-term black spruce regeneration failure in heath. To test the importance of this PSF, I measured four above-ground *Kalmia* traits related to litter quality (leaf dry matter content, specific leaf area, foliar C:N, and foliar total phenolics) and six indicators of soil nutrient availability (soil respiration, pH, total N, inorganic N, organic N to inorganic N ratio, and total phenolics) at eight sites in and around Terra Nova National Park, Newfoundland, Canada. The eight sites consisted of four vegetation types, which were, in order of least to most spruce dominance and post-fire spruce canopy expansion, *Kalmia* heath, early-stage SS (eSS), mature SS (mSS), and black spruce forest. I found that the four vegetation types differed based on *Kalmia* traits, and that *Kalmia* litter quality increased from heath to eSS, to mSS, to forest. I also found that forest had higher soil nutrient availability than heath, eSS, and mSS. This means that the strength of a PSF creating nutrient-poor soil was weaker in the forest than in the other vegetation types. Contrary to expectation, the heath, eSS, and mSS vegetation types were not different based on the soil nutrient availability indicators measured. Therefore, a PSF involving the abiotic soil properties measured here did not explain the improved black spruce colonisation success in SS compared to *Kalmia* heath.

Land Acknowledgement

I acknowledge that Terra Nova National Park and eastern Newfoundland, the area in which I collected all the data for my thesis, is the traditional homeland of the Beothuk and Mi’kmaq peoples. I also acknowledge that the Lakehead University Thunder Bay campus is located on the traditional lands of the Fort William First Nation, signatory to the Robinson Superior Treaty of 1850.

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1. Introduction

1.1 Alternative stable states in the *Kalmia*-black spruce system of eastern Newfoundland

In ecology, alternative stable states describe a situation where an ecosystem can exist in two or more distinct states within the same area and under similar climatic conditions (Beisner et al., 2003). An ecosystem state is characterized by a chosen set of dynamic state variables that describe the community, such as species abundances and/or functional traits (Beisner et al., 2003). In the boreal forest of Newfoundland, three alternative stable states are recognized, each defined by its species composition. The three ecosystem states are *Kalmia angustifolia* (hereafter referred to as *Kalmia*) heath, shrub savanna (SS), and black spruce forest (Mallik, 2022). *Kalmia* heath is an ecosystem characterized by low black spruce (*Picea mariana*) cover and ericaceous shrub dominance, especially *Kalmia angustifolia*, *Rhododendron groenlandicum*, *R. canadense*, and *Vaccinium angustifolium* (Appendix 1). SS is an ecosystem containing areas of *Kalmia* heath and islands of black spruce that expand via layering (St. James, 2023). Black spruce forest is an ecosystem where black spruce is dominant and forms a closed canopy.

In alternative stable state theory, a shift in ecosystem state can occur either by directly manipulating state variables (e.g., species abundances) or by changing internal ecosystem parameters that influence the state variables (e.g., soil properties; Beisner et al., 2003). To understand how the *Kalmia* heath/SS/black spruce forest alternative stable states could potentially shift from one state to another, it is important to consider two distinct ways this could happen: (i) disturbances such as forest fire, and (ii) weakening of internal dynamics (e.g., plant-soil feedback) that maintain the current vegetation state. Forest fire severity is an abiotic filter that determines post-fire species composition (Siegwart Collier & Mallik, 2010). This represents a direct modification of the state variables (e.g., species composition) that define the alternative stable states. Low-severity fires lead to *Kalmia* heath, high-severity fires lead to black spruce forest, and patchy low/high-severity fires lead to SS (Mallik, 2022). Low-severity fires lead to heathland because low-severity fires fail to consume the underground rhizomes of *Kalmia* and other ericaceous plants (Siegwart Collier & Mallik, 2010; Whittle et al., 1997). *Kalmia* then resprouts more quickly than seed-regenerating black spruce trees, thus gaining a competitive advantage over black spruce (Siegwart Collier & Mallik, 2010). Furthermore, organic matter depth remains high following a low-severity fire, which is known to reduce black spruce seed germination and seedling regeneration (Mallik & Kayes, 2018; Mallik & Kravchenko, 2018).

The role of fire severity in determining the assembly of *Kalmia* heath or black spruce forest ecosystem states is well known and is not the focus of this study. This study focuses on the stability of *Kalmia* heath in the absence of disturbance. Several definitions of ecosystem stability exist, depending on the context (Kéfi et al., 2019; Van Meerbeek, 2021). Stability sometimes refers to the resistance or resilience of an ecosystem to disturbance (de Bello et al., 2021; Ingrisch & Bahn, 2018; Kéfi et al., 2019; Van Meerbeek, 2021). Resistance refers to the extent to which ecosystem properties change after a disturbance, and resilience is the speed at which an ecosystem returns to its pre-disturbance state (de Bello et al., 2021). From this perspective, a stable ecosystem returns quickly to the same state after disturbance. Stability can also refer to the temporal variability in ecosystem properties in the absence of major disturbances (de Bello et al., 2021; Fernández-Martínez et al., 2018; Kéfi et al., 2019; Van Meerbeek, 2021). The present study examines the stability of *Kalmia* heath in the absence of fire, so the latter definition of ecosystem stability applies. More specifically, ecosystem stability will be defined as low temporal variability in species composition, since *Kalmia* heath remains stable as long as black spruce cover remains low and ericaceous shrubs remain dominant.

This study focuses on the role of plant-soil feedback (PSF), specifically the feedback of dominant species traits on abiotic soil properties, in explaining the long-term persistence of *Kalmia* heath in the absence of disturbance. PSF is defined as changes to soil properties (chemical, physical, and/or biological properties) caused by plants that influence the performance of themselves and/or other plants (van der Putten et al., 2013). A positive PSF describes a situation where soil properties are altered such that the performances of current dominant species are improved relative to others. Positive PSFs may contribute to stability in certain systems. For example, PSFs have been shown to shift from negative to positive when transitioning from early to later stages of succession (De Deyn et al., 2003; Kardol et al., 2006; Kardol et al., 2007; Qu et al., 2022). Therefore, negative PSFs are associated with changing species composition, whereas positive PSFs are associated with static species composition. There are examples where negative PSFs are associated with stability (Chung et al., 2019). However, this is most applicable to high-diversity systems where negative PSFs prevent the competitive exclusion of rare species by dominant species. Examples of positive PSFs stabilizing a non-forested alternative stable state include (i) low transpiration rates in shrubs of Tasmanian moorlands causing waterlogging, which prevents tree colonisation (Fletcher et al., 2014; Wood & Bowman, 2011) and (ii) persistence of unmanaged heathlands due to dominant shrub species maintaining nutrient-poor soil conditions that prevent tree colonisation (Mallik, 2022; Ransijn et al., 2014).

Kalmia heath of eastern Canada provides an excellent opportunity to test if dominant species traits and their impact on abiotic soil properties can explain stability in a non-forested alternative stable state. This is because *Kalmia* heaths differ in their post-fire black spruce colonisation rate (Mallik, 2022; Mallik & Kravchenko, 2018). The most stable sites are the heath sites where spruce cover has remained low for decades after fire. Less stable sites are heath sites transitioning to SS and SS sites. SS is less stable than heath because there is black spruce canopy expansion via layering. Black spruce canopy expansion is slow in SS, and the time to full canopy closure is about 3-4 times longer than the fire return interval in Terra Nova National Park (St. James, 2023; Walker, 2021). Since the stability of ecosystems in the absence of disturbance is important when examining PSFs and since there is canopy expansion in SS between fires, the PSFs maintaining the *Kalmia* heath vegetation state are expected to be stronger in heath than in SS. However, the differences may be subtle, versus when the forest state is compared to heath and SS. By measuring the traits of dominant species (*Kalmia*) and soil properties in sites that differ in heath stability, the hypothesized positive PSFs that maintain the *Kalmia* heath state can be tested under field conditions.

1.2 *Kalmia*-black spruce interaction

Kalmia heath is stable as long as black spruce density and cover remain low (Mallik, 2022). This is because ecosystem properties of *Kalmia* heath, such as species composition, community biomass, and primary productivity, will have low variability as long as the site resists black spruce colonisation (Bloom & Mallik, 2004). In the boreal forest of eastern Canada, particularly in Newfoundland, there are decades-old heath sites where black spruce cover and density increase very slowly (Mallik & Kravchenko, 2018). This implies that *Kalmia* heath is a stable ecosystem for at least the first few decades after fire. Previous work has identified high organic matter depth (Mallik & Kravchenko, 2018), allelopathy (Inderjit & Mallik, 2002; Mallik, 1987; Yamasaki et al., 2002; Zhu & Mallik, 1994), PSFs (Bloom & Mallik, 2006; Joanisse et al., 2008a; Joanisse et al., 2018; St. Martin & Mallik, 2021; Yamasaki et al., 2002), and the limitations of black spruce ectomycorrhizal fungi in nutrient-poor soils (Read et al., 2004; Joanisse et al., 2008b; St. Martin & Mallik, 2016) as probable mechanisms explaining the long-term regeneration failure of black spruce in heath.

PSF is likely an important mechanism driving *Kalmia* heath stability (Bloom & Mallik, 2006; Joanisse et al., 2008a; St. Martin & Mallik, 2021; Wurzburger & Hendrick, 2009). The positive PSF that is hypothesized to maintain *Kalmia* heath stability has the following components: (i) *Kalmia* exhibits intraspecific variation in above-ground traits based on black spruce cover, (ii) *Kalmia* is most effective at creating nutrient-poor soils in heath due to its above-ground traits under low canopy cover, and (iii) *Kalmia* has a competitive advantage over black spruce in the nutrient-poor soil created by its own litter. Firstly, *Kalmia* is known to have lower litter quality (high carbon to nitrogen ratio and high recalcitrant leaf structural compounds, such as lignin, fibres, and condensed tannins) and produce more phenolic compounds under low canopy cover than under high canopy cover (Bloom & Mallik, 2004; Joanisse et al., 2018). The properties of *Kalmia* litter under low canopy cover can promote nutrient-poor soils that create a competitive advantage for *Kalmia* over black spruce for the following reasons: (i) *Kalmia* phenolic compounds sequester nitrogen (N) in protein-tannin complexes that are much more accessible to the ericoid mycorrhizae of *Kalmia* than to the ectomycorrhiza of black spruce (Inderjit & Mallik, 2002; Joanisse et al., 2008b; St. Martin & Mallik, 2016), (ii) *Kalmia* phenolic compounds reduce the activity of N mineralisation enzymes (Chomel et al., 2016; Joanisse et al., 2007; Joanisse et al., 2018), (iii) high carbon to nitrogen (C:N) ratio in *Kalmia* litter means a low input of N into the soil (Bloom & Mallik, 2004), and (iv) high amount of recalcitrant leaf structural compounds in *Kalmia* litter reduces organic matter decomposition rate and N mineralisation (Chomel et al., 2016; Hobbie, 2015). These influences of *Kalmia* litter on N availability are important since the boreal forest is an N-limited system (Näsholm et al., 2013). Consistent with this PSF, *Kalmia* heath is known to have lower plant-available inorganic N (NH_4^+ and NO_3^-), lower total soil N, lower soil pH, and a lower soil respiration rate than black spruce forest (Bloom & Mallik, 2004; Bloom & Mallik, 2006; Joanisse et al., 2008a; Joanisse et al., 2018; St. Martin & Mallik, 2021).

The hypothesized PSF implies that *Kalmia* and community-weighted mean (CWM) functional traits should correlate with indicators of soil nutrient availability along a gradient of black spruce cover. This is because if plant traits affect soil nutrient availability, then they should be correlated. Furthermore, if soil nutrient availability determines the stability of *Kalmia* heath, then soil nutrient availability should increase as spruce cover increases. To test this, above-ground *Kalmia* traits related to litter quality (Table 1) and indicators of soil nutrient availability (Table 2) were measured in sites with differing amounts of black spruce cover. While past studies have compared *Kalmia* traits and soil chemistry in established forests and heaths, this study also examined heath and forest transitional sites with intermediate levels of spruce cover. The novelty of this study is that it examined sites representing a gradient of spruce cover rather than just the heath and forest states. This study tested whether the PSF maintaining nutrient-poor soil is (i) stronger as canopy cover decreases and (ii) stronger as *Kalmia* heath stability increases. *Kalmia* heath remains stable as long as ericaceous shrubs remain dominant, meaning post-fire black spruce cover expansion rate is a good proxy for heath stability. The rate of black spruce expansion is lowest in decades-old heath sites where there is very little increase in black spruce stem density after 15 years since fire (Mallik & Kravchenko, 2018). The expansion rate of black spruce is higher in the SS sites and in the heath sites transitioning to SS, due to black spruce canopy expansion via layering (St. James, 2023). Black spruce expansion rate is the highest in forest, since black spruce cover quickly increases to a closed canopy forest after fire. Therefore, a shift in vegetation type from heath to heath transitioning to SS (early-stage SS), to mature SS, and to black spruce forest is considered a heath stability gradient.

Table 1. Explanation of how four plant traits (LDMC, SLA, foliar C:N, and foliar total phenolics) are related to soil nutrient availability and litter quality.

Plant trait	Relationship to soil nutrient availability and litter quality
Leaf dry matter content (LDMC)	Leaves with high LDMC generally contain more non-labile structural components, such as lignin and fibres. They also contain more high-molecular-weight secondary metabolites, such as tannins (Chomel et al., 2016; Quested et al., 2007; Wright et al., 2004). Tannins can reduce N mineralisation by reducing the activity of N mineralisation enzymes (Joanisse et al., 2007), and by precipitating protein into protein-tannin complexes (Gundale et al., 2010; Hättenschwiler & Vitousek, 2000; Joanisse et al., 2008b). Furthermore, non-labile structural components and high-molecular-weight secondary metabolites are resistant to degradation. For this reason, high LDMC is often correlated with a lower decomposition rate of plant litter (Chomel et al., 2016). Lower litter decomposition rates can result in reduced N release and N mineralisation in soil (Hobbie, 2015). Therefore, high LDMC is associated with lower soil nutrient availability and poorer litter quality.
Specific Leaf Area (SLA)	SLA is related to soil nutrient availability, litter quality, and litter decomposition rates for similar reasons as LDMC. Leaves with higher SLA invest more in photosynthetic capacity and less in structural components and secondary metabolites (Pérez-Harguindeguy et al., 2013). This means that high SLA is often associated with a higher decomposition rate of plant litter (Chomel et al., 2016; Quested et al., 2007). Therefore, high SLA is associated with higher soil nutrient availability and better litter quality.
Foliar C:N ratio	High foliar C:N ratio results in plant litter with lower decomposition rates than plants with low foliar C:N (Chomel et al., 2016). Low-quality plant litter can therefore result in less N release and N mineralisation in soil (Hobbie, 2015) and is correlated with N mineralisation rate in many systems (Maithani et al., 1998; Satti et al., 2003; Scott & Binkley, 1997). Therefore, high foliar C:N is associated with lower soil nutrient availability and poorer litter quality.
Foliar total phenolics	Certain phenolic compounds can reduce N mineralisation by reducing the activity of N mineralisation enzymes (Joanisse et al., 2007) and by precipitating protein into protein-tannin complexes (Gundale et al., 2010; Hättenschwiler & Vitousek, 2000; Joanisse et al., 2008b). Furthermore, high-molecular-weight phenolic compounds are resistant to degradation and can reduce the decomposition rate of plant litter (Chomel et al., 2016). Therefore, high foliar total phenolics is associated with lower soil nutrient availability and poorer litter quality.

Table 2. Relationships between six soil properties and soil nutrient availability.

Soil Property	Relationship to soil nutrient availability
pH	Different soil nutrients have different relationships with soil pH. For most nutrients, there is a range where the nutrient is most available to plants and its availability drops above or below that range (Hartemink & Barrow, 2023; Kumaragamage et al., 2021). Since boreal forest soil is highly acidic (pH < 5; St. Martin & Mallik, 2021), most nutrients become more available as the pH increases. This is the case for nitrogen, phosphorus, and potassium (Hartemink & Barrow, 2023; Kumaragamage et al., 2021). Therefore, a higher pH is an indicator of higher nutrient availability.
Soil respiration	Higher soil respiration is associated with greater microbial activity and a higher rate of organic matter decomposition (Xiao et al., 2014). As a result, higher soil respiration is often associated with a greater rate of N mineralisation and concentration of plant-available inorganic N (Adhikari et al., 2023). Therefore, higher soil respiration is an indicator of higher nutrient availability.
Inorganic N	Inorganic N ions (NH_4^+ and NO_3^-) are directly available to plants and are generally more easily absorbed by plant roots than organic N sources (Adamczyk, 2021; Näsholm et al., 2009). Some organic N sources are only available to plants through mycorrhizal symbioses (Read et al., 2004). Since boreal forest soils are N-limited, greater inorganic N in soil is an indicator of higher nutrient availability.
Total N	While plants most readily use inorganic N ions, organic N can be used by plants through mycorrhizal symbioses or microbial activity that mineralises N into inorganic forms (Adamczyk, 2021; Read et al., 2004). Furthermore, some organic N sources are directly available to plants (Adamczyk, 2021; Näsholm et al., 2009). Since boreal forest soils are N-limited, higher total soil N is an indicator of higher nutrient availability.
Organic N to inorganic N ratio (DON:DIN ratio)	Inorganic N is typically more available to plants than organic N, so a lower DON:DIN ratio is an indicator of higher nutrient availability. This indicator is important in this study because *Kalmia* phenolic compounds are thought to prevent the conversion of organic N to inorganic N by inhibiting the activity of N mineralisation enzymes and by precipitating proteins in protein-tannin complexes (Chomel et al., 2016). If this is true, DON:DIN ratio would be highest in *Kalmia*-dominated sites.
Total phenolic compounds	Lower total phenolic compounds is an indicator of soil nutrient availability because of the ability of certain phenolic compounds to inhibit N mineralisation. This primarily happens either through the inhibition of N mineralisation enzymes (Chomel et al., 2016; Joanisse et al., 2007) or through the precipitation of protein into protein-tannin complexes that are resistant to degradation (Chomel et al., 2016; Gundale et al., 2010; Hättenschwiler & Vitousek, 2000; Joanisse et al., 2008b).

1.3 Hypotheses

I expect that along a vegetation type gradient of decreasing spruce cover and increasing heath stability, the PSF maintaining nutrient-poor soil conditions will become stronger. I expect that the PSF will be weakest in the black spruce forest state, strongest in the heath state, and have intermediate strength in vegetation states where spruce cover is intermediate to that of forest and heath (early-stage SS and mature SS). If the PSF is strongest in heath, then I expect to find the following: (1) as black spruce cover decreases and heath stability increases, *Kalmia* and community-weighted mean (CWM) traits will change indicating lower litter quality and higher production of phenolic compounds, (2) as black spruce cover decreases and heath stability increases, soil nutrient availability will decrease, and (3) *Kalmia* and CWM traits indicating low litter quality and high production of phenolic compounds will correlate with indicators of low soil nutrient availability. Litter quality and phenolic compounds are represented by four above-ground plant traits (specific leaf area, leaf dry matter content, foliar C:N, foliar total phenolics; Table 1) and soil nutrient availability is represented by six soil properties (pH, soil respiration, inorganic N, total N, organic N to inorganic N ratio, total phenolic compounds; Table 2).

2. Methods

2.1 Study Area

This study was conducted in and around Terra Nova National Park, Newfoundland, Canada (N 48° 33’, W 53° 59’). The area is located in the boreal region, but oceanic influences, resulting in higher precipitation and a shorter growing season, create unique vegetation patterns compared to inner-continental Canada (South, 1983). Forested areas are dominated by *Picea mariana*. *Abies balsamea*, *Betula papyrifera*, *Populus tremuloides*, *Larix laricina*, and *Acer rubrum* can also be present. The understory consists of ericaceous shrubs, including *Kalmia angustifolia*, *Rhododendron canadense*, *R. groenlandicum*, and *Vaccinium angustifolium*, as well as herbaceous plants such as *Gaultheria hispidula*, *Linnaea borealis*, *Cornus canadensis*, *Maianthemum canadense*, and *Clintonia borealis*. Heath areas are dominated by *Kalmia angustifolia* and, to a lesser extent, by other ericaceous shrubs (*Rhododendron canadense*, *R. groenlandicum*, and *Vaccinium angustifolium*). The average annual precipitation ranges from 801 to 1200mm, of which approximately 30% is snowfall. The mean summer and winter temperatures are 13 °C and -5 °C, respectively (Environment Canada, 2017). The soils of the area are classified as nutrient-poor podzolic gravel-loam (Soil Classification Working Group, 1998).

Data collection took place at eight sites in and around Terra Nova National Park (Figure 1; Table 3). Three sites were *Kalmia* heath with low black spruce density (< 500 black spruce stems/ha) and uniformly high *Kalmia* density and cover. One site was a heath site transitioning to SS (early-stage SS or eSS with ~4000 black spruce stems/ha).

Three sites were late-stage or mature SS (mSS). One site was a closed-canopy black spruce forest (Figure 1; Table 3). Hereafter, early-stage SS will be referred to as eSS, and mature SS will be referred to as mSS. These sites were chosen to compare *Kalmia* above-ground traits and soil chemistry along a gradient of spruce cover and in stable heath sites (the three heath sites with low black spruce density) versus sites with slow black spruce cover expansion (eSS and the three mSS sites). Only one forest site was chosen. I recognize the unbalanced study design but unfortunately this was the only post-fire closed canopy forest site of comparable age of *Kalmia* heaths available in the area (Siegwart Collier & Mallik, 2010). Besides, the main goal of this study was to determine how eSS and mSS are different from heath in terms of *Kalmia* traits and soil chemistry. It is already well established in the literature that *Kalmia* traits and soil chemistry are different in forest and heath (Bloom & Mallik, 2004; Bloom & Mallik, 2006; Joanisse et al., 2008a; Joanisse et al., 2018; St. Martin & Mallik, 2021).

Table 3. Information about the eight sites that were used for data collection in this study. The table shows the vegetation type (heath, early-stage SS, mature SS, and forest), coordinates, and time since fire for each of the sites. Data for time since fire is from St. Martin & Mallik (2021) and St. James (2023).

Site	**Vegetation type**	**Coordinates**	**Time since fire (years)**
Rocky Pond (RP)	Heath	N 48° 31' 58" W 53° 58' 55"	22
Triton Brook (TB)	Heath	N 48° 40′ 26″ W 54° 29′ 20″	26
Charlottetown (CT)	Heath	N 48° 27′ 08″ W 53° 59′ 55″	39
Dunphy's Pond (DP)	Early-stage SS	N 48° 26' 49.3" W 54° 08' 43.0"	61
Terra Nova Road SS (TRSS)	Mature SS	N 48° 30′ 44″ W 54° 00′ 36″	~80
Rocky Pond SS (RPSS)	Mature SS	N 48° 31′ 56″ W 53° 58′ 20″	~80
Ochre Hill SS (OH)	Mature SS	N 48° 30' 40" W 53° 59' 19"	~80
Gambo Forest (GF)	Forest	N 48° 42′ 26.7" W 54 7′ 55.2"	45

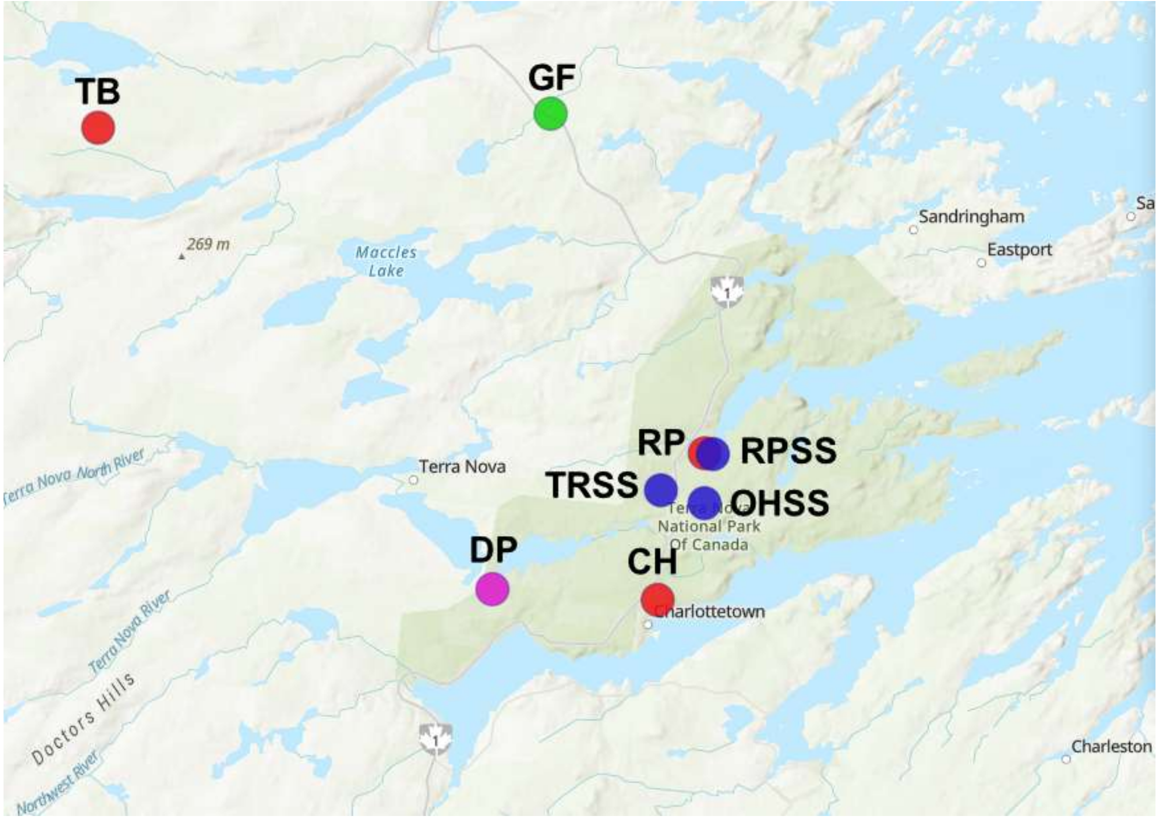

Figure 1. Map showing the location of the eight sites used for data collection in this study: Rocky Pond (RP), Triton Brook (TB), Charlottetown (CT), Dunphy's Pond (DP), Terra Nova Road SS (TRSS), Rocky Pond SS (RPSS), Ochre Hill SS (OHSS), and Gambo Forest (GF). Heath sites are in red, the eSS site is in purple, mSS sites are in blue, and the forest site is in green. Terra Nova National Park is located at N 48° 33', W 53° 59'.

2.2 Experimental design

2.2.1 Sampling procedure

In each heath site and SS site, 5 x 5 m plots were randomly placed in open heath (Figure 2). This was done within a 100 x 100 m area for each site. A random number generator was used to select points within the 100 x 100 m area, and these points were used as the corners of the 5 x 5 m plots. The 100 x 100 m area was divided into 10 x 10 m grids, resulting in 100 possible points for positioning the plots. Plots were considered in open heath if all parts of the plot were greater than 1 m from black spruce canopy. If this condition was not met, the plot was moved to the nearest open area. In mSS plots, 3 x 3 m plots were used if the open area was too small to contain a 5 x 5 m plot. Within each 5 x 5 m plot (or 3 x 3 m plot at some mSS locations), three 1 x 1 m subplots were placed at three corners of the larger plot. Four plots were placed in open heath at the RPSS, TRSS, OHSS, RP, TB, and CT sites. Twelve plots were placed in open heath at the DP site.

For each open heath plot, the nearest black spruce individual (in the case of heath and eSS sites) or the nearest black spruce island (in the case of mSS sites) was selected for placement of three additional 1 x 1 m subplots. For black spruce individuals in heath and eSS, three 1 x 1 m subplots were placed adjacent to the edge of the black spruce crown. For black spruce islands, three 1 x 1 m subplots were placed as follows: one subplot was randomly placed near the edge of the black spruce island, a second subplot was placed near the parent stem on the opposite side of the first subplot, and a third subplot was placed 1 m from the second subplot at a right angle to the first two subplots. This sampling method in spruce island ensured that sampling was done at the edge, middle, and centre of the spruce island. Figure 2 shows the placement of plots and subplots in the heath and SS sites.

In the forest site, twelve 5 x 5 m plots were randomly placed within a 200 x 100 m area. A random number generator was used to select points within the 200 x 100 m area randomly, and these points were used as a corner of the 5 x 5 m plots. Within each 5 x 5 m plot, 1 x 1 m subplots were placed at three corners of the larger plot. For all sites, parameters that were measured in each subplot were averaged to obtain one value per plot. All parameters were measured in each subplot, except for soil chemistry and *Kalmia* foliar chemistry, which were measured in each plot.

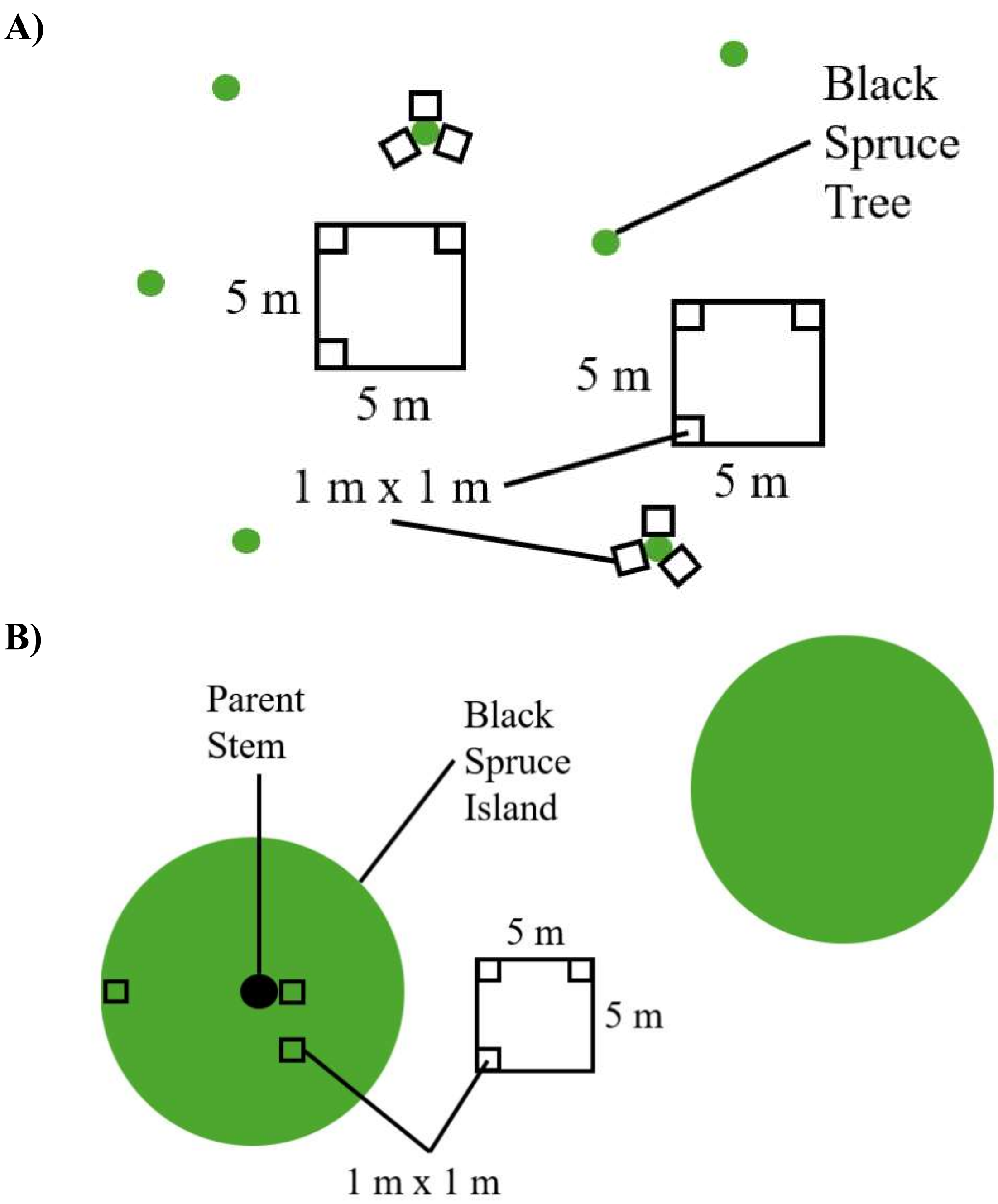

Figure 2. Placement of plots and subplots in **A)** heath and eSS sites, and **B)** mSS sites. At the RPSS, TRSS, OHSS, RP, TB, and CH sites, four 5 x 5 m plots were positioned in open heath. At the DP site, twelve 5 x 5 m plots were positioned in open heath. Within each plot, three 1 x 1 m subplots were sampled. At the heath and eSS sites, the areas adjacent to the black spruce stem closest to each open heath plot were sampled by placing three 1 x 1 m subplots adjacent to the canopy. At the mSS sites, three 1 x 1 m subplots were positioned in the spruce island closest to each open heath plot.

The number of plots at each site was selected to ensure a balanced design, allowing measured parameters to be compared across seven vegetation types. Each vegetation type consisted of 12 replicates at the level of 5 x 5 m plots (n = 84 total). The vegetation types were as follows: (1) open heath areas of heath, (2) black spruce patches of heath, (3) open heath areas of eSS, (4) black spruce patches of eSS, (5) open heath areas of mSS, (6) black spruce islands in mSS, (7) mature black spruce forest. Most plant traits and environmental variables did not show significant differences between vegetation types (1) and (2), and between vegetation types (3) and (4). Therefore, these vegetation types were grouped for most statistical analyses. The five vegetation types after grouping were as follows: (1) heath, (2) eSS, (3) open heath areas of mSS (also referred to as mSS open), (4) black spruce islands in mSS (also referred to as mSS island), (5) black spruce forest (also referred to as forest).

2.2.2 Soil samples

Soil samples of the organic layer were taken in each subplot and then combined to create one composite soil sample per 5 x 5 m plot. This means that a total of 84 soil samples were collected. Soil samples were taken by digging 30 x 30 cm holes with a shovel and extracting the soil profile to the mineral layer. The soil samples were air-dried at room temperature and sieved (2 mm diameter). Air-dried soil samples were transported to Lakehead University and stored at room temperature until analysis in the lab. For each soil sample, extractable nitrate (NO_3^-), extractable ammonia (NH_4^+), organic nitrogen, total carbon (C), total nitrogen (N), and total phenolics were measured. Before measuring each parameter, the soil samples were oven-dried (72 hours at 60 °C), ground using a mortar and pestle, and then sieved.

To measure the amount of ammonia and nitrate, 1.0 M KCl was used for extraction. For ammonia, using a SKALAR autoanalyzer, colour in the extract was developed using the Berthelot reaction, and absorbance was measured at 600 nm (Kalra & Maynard, 1991). For nitrate, using a SKALAR autoanalyzer, the nitrate in the extract was reduced to nitrite by a cadmium-copper reaction. The colour was developed using the Griess reaction, and absorbance was measured at 540 nm (Kalra & Maynard, 1991). Total carbon and nitrogen were determined via combustion. Total organic nitrogen was determined using the equation below.

$$DON = TN - DIN$$

Where *DON* is total organic nitrogen, *TN* is total nitrogen, and *DIN* is total inorganic nitrogen ($NH_4^+ + NO_3^-$).

For determining total phenolics, the Folin-Ciocalteu method was used (Waterman & Mole, 1994). Phenols were extracted twice from 100 mg of soil sample using 4 mL of 70% aqueous acetone. The soil sample and acetone were placed in 15 mL centrifuge tubes and homogenized for 1 minute. The samples were centrifuged for 10 minutes at 1500 x g. The supernatant was collected, and the extraction procedure was repeated a second time using the same 100 mg of soil. To determine total phenolics, the extract was diluted appropriately to a final volume of 1.5 mL (diluted either 3x, 3.75x, or 5x to ensure the measured absorbance was within the range of the calibration curve). The 1.5 mL extract was combined with 0.5 mL Folin-Ciocalteu reagent in test tubes. After 5 minutes, 2.5 mL of a sodium carbonate solution (prepared by dissolving 20 g of anhydrous sodium carbonate in 100 mL of distilled water) was added to the test tubes, and the test tubes were inverted several times to mix the solution. After 30 minutes, the absorbance of the reactants was determined at 760 nm using a spectrophotometer. Absorbances were compared to standards of 5, 10, 17.5, 25, 32.5, and 40 µg/mL of gallic acid.

2.2.3 Species composition and environmental variables

In each 1 x 1 m subplot, the following were measured: percent cover of mosses, lichens, herbs, shrubs, and trees, soil respiration rate, and soil pH. Percent cover of mosses and lichens was measured in 30 x 30 cm quadrats within the 1 x 1 m subplots. The percent cover of plant and lichen species was visually estimated. The percent cover of plant and lichen species was measured in each subplot and then averaged to obtain one value per plot. Soil respiration was measured as the rate of CO_2 emitted from the soil. This was done using a CO2 analyzer (PP Systems, model EGM-4, Amesbury, MA) and an SRC-1 soil respiration chamber (PP Systems, model ACS025, Amesbury, MA). One soil respiration measurement was taken per subplot and then averaged to obtain one value per plot. Soil pH was measured by soaking fresh soil collected from the organic layer in a 2:1 water-to-soil ratio by volume. The soil was allowed to soak in water for one hour, and then the pH was measured with a DeltaTRAK 24300 pH meter (Spectrum Technologies, Inc., Model IQ150) and an ISFET probe (Spectrum Technologies, Inc.). One soil pH reading was taken per subplot and then averaged to obtain one value per plot.

2.2.4 *Kalmia* traits

The following traits were measured in *Kalmia* individuals: specific leaf area (SLA), leaf dry matter content (LDMC), foliar C:N ratio, and foliar total phenolics. For SLA and LDMC, measurements were taken in two mature *Kalmia* individuals per subplot or six individuals per plot. The six SLA and six LDMC measurements in each plot were averaged to obtain one SLA and one LDMC value per plot. The above-ground biomass of *Kalmia* individuals was extracted by cutting the stem at the base. The base of the stem was then submerged in water for 24 hours to ensure complete hydration of all leaf tissues. Afterwards, twelve leaves were collected from each *Kalmia* individual. Leaf fresh weight was measured immediately using a Mettler Toledo XS4035 balance. Then, leaves were scanned at a resolution of 300 DPI using an HP Envy 4520 scanner. Leaf area was determined from scanned images using the black spot leaf area calculator (Varma & Osuri, 2013). Leaf dry weight was determined by drying the leaves at 70 °C for 72 hours, then weighing them using a Mettler Toledo XS4035 balance. SLA was calculated by dividing leaf area by leaf dry mass. LDMC was calculated by dividing leaf dry mass by leaf fresh mass.

For determining foliar C:N ratio and total phenolics in *Kalmia* leaves, leaf samples from each 5 x 5 m plot were combined (n = 80 across all sites, since four of the plots from the forest site had no *Kalmia* individuals and therefore *Kalmia* traits could not be measured). Leaves were turned into a fine powder using a Wiley Mill. For determining total phenolics in *Kalmia* leaves, the Folin-Ciocalteu method was used (Waterman & Cole, 1994). The same procedure was followed as for soil samples (see section 2.2.2), except 10 mg of powdered leaf samples were combined with 4 mL of 70% aqueous acetone for the extraction step. Total C and N in *Kalmia* leaves were determined by combustion.

2.3 Statistics

2.3.1 Intraspecific variation in above-ground *Kalmia* traits

PERMANOVA (Permutational multivariate analysis of variance) was used to determine if there were any significant differences between vegetation types based on four above-ground *Kalmia* traits: SLA, LDMC, foliar C:N, and foliar phenolics. Significant differences between vegetation types were determined by conducting pairwise PERMANOVA between each possible vegetation type pair and by using the Holm-Bonferroni correction for multiple comparisons. To determine the variance in *Kalmia* traits explained by the vegetation type gradient, redundancy analysis (RDA) was used. Furthermore, the 80 plots with *Kalmia* trait measurements were plotted on the first two RDA axes to visually represent the differences between plots based on the four *Kalmia* traits. To conduct PERMANOVA and post-hoc tests, the R packages “vegan” (Oksanen et al., 2025), “pairwiseAdonis” (Martinez Arbizu, 2017), and “multcompView” (Graves et al., 2024) were used. To conduct RDA, the R packages “vegan” (Oksanen et al., 2025), “dplyr” (Wickham, 2023), “ggplot2” (Wickham, 2016), and “tidyverse” (Wickham, 2019) were used. All statistical analyses in this study were done using R version 4.5.1 and RStudio (R Core Team, 2025).

Kruskal-Wallis tests (or single-factor ANOVA, if the assumptions were met) were used to determine if individual above-ground *Kalmia* traits differed based on vegetation type. Four above-ground traits were examined: SLA, LDMC, foliar C:N, and foliar phenolics concentration. These traits were compared across five vegetation types, as described in section 2.2.1. SLA and LDMC were measured in each 1 x 1 m subplot. Values obtained in the subplots were averaged to obtain one SLA and LDMC value per plot. Four of the black spruce forest (GF site) plots had no *Kalmia*, resulting in 80 observations for each trait. Significant differences between vegetation types were determined using a Dunn's test and a Holm-Bonferroni correction for multiple comparisons in the cases where a Kruskal-Wallis test was used. When single-factor ANOVA was used, Tukey's honest significant difference (HSD) test was used to determine significant differences between vegetation types. The R packages "car" (Fox, 2019) and "nortest" (Gross, 2015) were used to test the assumptions of single-factor ANOVA. The R packages "multcompView" (Graves et al., 2024), and "FSA" (Ogle et al., 2025) were used to conduct post-hoc tests for the Kruskal-Wallis tests. The R package "ggplot2" (Wickham, 2016) was used to plot the results of the Kruskal-Wallis and single-factor ANOVA tests.

In addition, single-factor ANOVA and Tukey's HSD test were used to determine if there were significant differences between vegetation types in a *Kalmia* litter quality index. A *Kalmia* litter quality index was calculated because there was a high degree of multicollinearity between the four *Kalmia* traits. The index was calculated by standardizing the values of the four traits and assigning equal weight to each trait. The *Kalmia* litter quality index in plot *i* was calculated as follows:

$$KLQ_i = \frac{1}{4}SLA_i^* - \frac{1}{4}LDMC_i^* - \frac{1}{4}CN_i^* - \frac{1}{4}Phen_i^*$$

Where *i* is the plot number, *KLQ* is the *Kalmia* litter quality index, SLA^* is the standardized value of *Kalmia* SLA, $LDMC^*$ is the standardized value of *Kalmia* LDMC, CN^* is the standardized value of *Kalmia* foliar C:N, and $Phen^*$ is the standardized value of *Kalmia* foliar total phenolics. All *Kalmia* traits were standardized to have a mean of zero and a standard deviation of one. Four indicators of *Kalmia* litter quality (SLA, LDMC, foliar C:N, and foliar phenolics; see Table 1) make equal contributions to the index. Equal weights were assigned since there was a high degree of multicollinearity between the four *Kalmia* traits and these traits are typically intercorrelated (Wright et al., 2004). This means there was no reason to believe any trait is a better indicator of litter quality than the others. The *Kalmia* litter quality index was set up to corroborate the results of PERMANOVA and univariate analyses.

2.3.2 Variation in CWM traits of understory plants

Differences in CWM traits of understory plants (hereafter referred to as CWM traits) between vegetation types were determined in the same way as for *Kalmia* traits (see section 2.3.2). Three above-ground traits were examined: SLA, LDMC, and foliar C:N. Trees were omitted from CWM calculations because comparing SLA between conifers (e.g., black spruce) and broadleaf shrubs and herbs give no information on the differences in litter quality between these two types of plants. Conifers typically have lower SLA than broadleaf plants not because they contain more recalcitrant leaf compounds, but because conifer needles are thicker than broadleaves (Witkowski & Lamont, 1991). CWM foliar total phenolics were not calculated because insufficient data were available in the literature and in databases to calculate them. CWM traits were determined for each plot for a total of 80 observations (four plots from the GF site had an insufficient amount of understory plants to calculate CWM traits). CWM traits in a given plot were calculated as follows:

$$CWM_i = \sum_{j=1}^{n} \frac{Cover_j}{\sum_{k=1}^{n} Cover_k} Trait_j$$

Where CWM_i is the community-weighted mean trait value for trait *i*, *n* is the number of understory plant species present in the plot, $Cover_j$ is the percent cover of species *j*, and $Trait_j$ is the trait value for species *j*. Trait values for *Kalmia* were assigned for each plot as measured in this study (see section 2.2.4). *Kalmia angustifolia* was the only species where intraspecific trait variation was considered when calculating CWM traits. For *Rhododendron groenlandicum*, *R. canadense*, and *Vaccinium angustifolia*, SLA and LDMC were assigned using my own measurements from heath sites in Terra Nova National Park. For the remaining species, trait values were obtained either from St. Martin & Mallik (2019) or the TRY database (Kattge et al., 2020). The TRY database was only used for species where traits were not measured by me or in St. Martin & Mallik (2019). Traits measurements in St. Martin & Mallik (2019) were for plants from heath sites in Terra Nova National Park. Traits values from St. Martin & Mallik (2019) were therefore considered a better source of trait values than TRY, since traits were measured in similar sites to those visited for this study. See Appendix 2 for the trait values of each species and the sources of the trait values assigned.

As for *Kalmia* traits, a CWM litter quality index was calculated. The CWM litter quality index in plot *i* was calculated as follows:

$$CLQ_i = \frac{1}{3}SLA_i^* - \frac{1}{3}LDMC_i^* - \frac{1}{3}CN_i^*$$

Where *i* is the plot number, *CLQ* is the CWM litter quality index, SLA^* is the standardized value of CWM SLA, $LDMC^*$ is the standardized value of CWM LDMC, and CN^* is the standardized value of CWM foliar C:N. All CWM traits were standardized to have a mean of zero and a standard deviation of one.

2.3.3 Variation in soil properties between vegetation types

PERMANOVA (Permutational multivariate analysis of variance) was used to determine if there were any significant differences between vegetation types based on six soil chemistry variables. Significant differences between vegetation types were determined by conducting pairwise PERMANOVA between each possible vegetation type pair and by using the Holm-Bonferroni correction for multiple comparisons. To determine the percentage of variance in soil chemistry explained by vegetation type, RDA was used. The 84 plots with soil chemistry measurements were plotted on the first two RDA axes to visually represent the differences between plots based on soil chemistry. The same R packages were used to conduct PERMANOVA and RDA as for *Kalmia* traits (section 2.3.1). The six soil chemistry variables were pH, soil respiration, inorganic N, total N, organic N to inorganic N ratio (DON:DIN ratio), and total phenolics. Values for inorganic N and total N were adjusted to account for mineral soil contamination of organic layer soil samples. There was high variability in the carbon content of soil samples within vegetation types, ranging from ~10-50% for the heath, SS open, and SS island vegetation types (see Appendix 3). Pure organic layer soil samples should have a carbon content of over 40% in *Kalmia* heath and black spruce forest ecosystems (Joanisse et al., 2018; St. James, 2023). To account for carbon content as a covariate affecting total N and inorganic N, the values were adjusted to what they would be if all soil samples had a carbon content of 50% and total N and inorganic N increased linearly with carbon content. This adjustment was done for all analyses.

Kruskal-Wallis tests (or single-factor ANOVA, if the assumptions were met) were used to determine if individual properties differed based on vegetation type. Significant differences between vegetation types were determined using a Dunn's test and a Holm-Bonferroni correction for multiple comparisons in the cases where a Kruskal-Wallis test was used. When single-factor ANOVA was used, Tukey's HSD test was used to determine significant differences between vegetation types. The same R packages were used to conduct Kruskal-Wallis tests, single-factor ANOVA, and post-hoc tests as for *Kalmia* traits (section 2.3.1).

2.3.4 Environment-*Kalmia* and environment-CWM trait relationships

Correlations between traits and soil properties were determined using canonical correlation analysis (CCA). CCA was performed separately for *Kalmia* traits and CWM traits. First CCA was performed between four *Kalmia* traits (SLA, LDMC, foliar C:N, and foliar total phenolics) and five soil nutrient availability indicators (soil respiration, pH, inorganic N, total N, and organic N to inorganic N ratio). Then, CCA was performed between three CWM traits (SLA, LDMC, foliar C:N) and the five soil nutrient availability indicators. The relationship between plant traits and soil nutrient availability was considered statistically significant if at least one of the correlations between canonical variate pairs was significant. Statistical significances of the correlations between canonical variate pairs were determined using the Wilks' Lambda test. To perform CCA, the R packages "CCA" (González & Déjean, 2023), "CCP" (Menzel, 2022), "ggplot2" (Wickham, 2016), and "dplyr" (Wickham et al., 2023) were used.

3. Results

3.1 Intraspecific variation in *Kalmia angustifolia* traits

PERMANOVA showed that there were significant differences between vegetation types based on four *Kalmia* traits: SLA, LDMC, foliar C:N, and foliar phenolics concentration ($F_{5,74} = 26.9$, $p < 0.001$). RDA showed that a large amount of the variance in *Kalmia* traits (64.5%) was explained by vegetation type. Almost all the variation (94.3%) in *Kalmia* traits explained by vegetation type was accounted for by a single axis (Figure 3). Furthermore, all *Kalmia* traits exhibited a high loading on the RDA1 axis and a small loading on other axes (Table 4). This indicates a high degree of multicollinearity among the four *Kalmia* traits. In general, as the vegetation type shifted from heath to eSS, to open areas of mSS, to spruce island of mSS, to forest, *Kalmia* traits changed as follows: SLA increased and LDMC, foliar C:N ratio, and foliar phenolics decreased (Figure 3). This means that *Kalmia* litter quality decreased and *Kalmia* phenolics production increased as the vegetation type shifted towards lower spruce cover and greater heath stability.

Table 4. Loadings of the four *Kalmia* traits with respect to the first two RDA axes. RDA was performed using *Kalmia* traits (SLA, LDMC, foliar C:N, and foliar total phenolics) as the response variables and vegetation type as the explanatory variable.

Kalmia Trait	RDA1 (loading)	RDA2 (loading)
SLA	1.95	-0.11
LDMC	-1.71	-0.19
Foliar C:N	-1.59	0.48
Foliar total phenolics	-1.25	-0.52

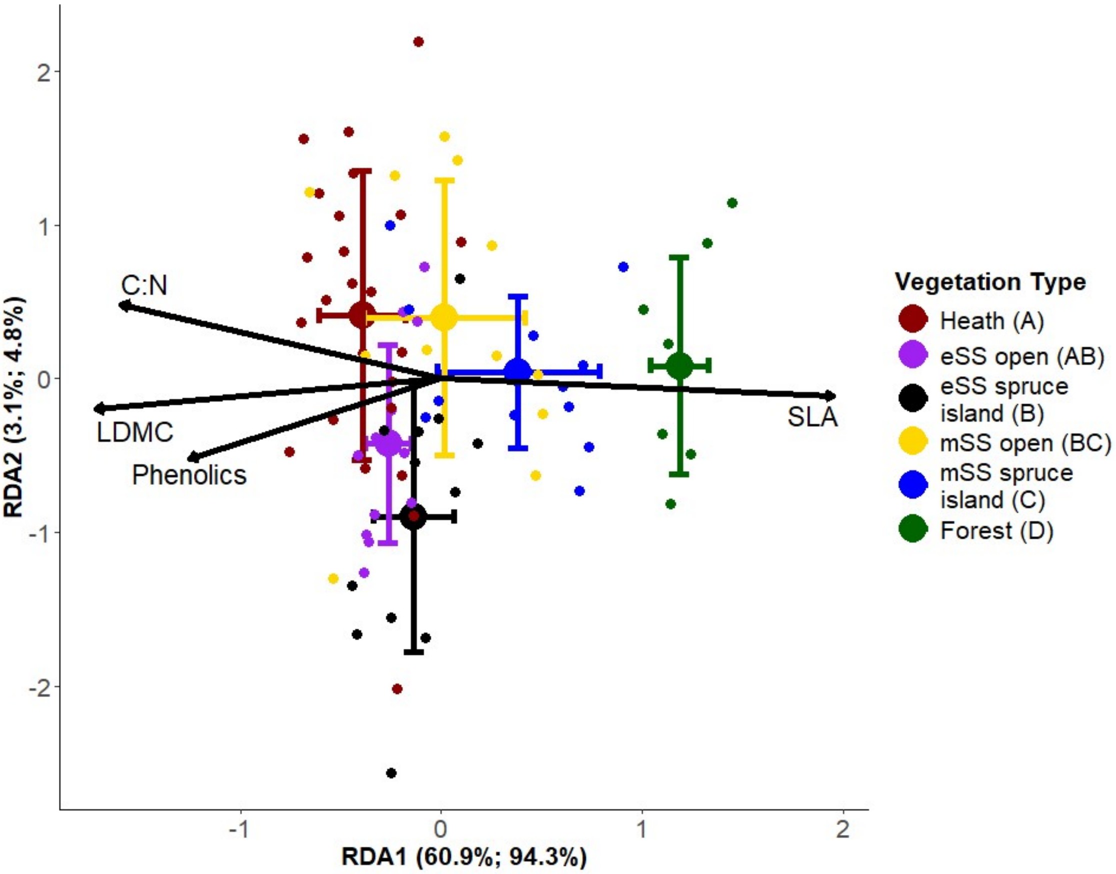

Figure 3. RDA plot showing how plots from six vegetation types were different based on four *Kalmia* traits: SLA, LDMC, foliar C:N ratio (C:N), and foliar phenolics concentration (Phenolics). Large dots are the mean value for each vegetation type, and the error bars are plus and minus one standard deviation. The percent of the total variance and the percent of constrained variance explained by each RDA axis are, respectively, shown in parentheses next to the axis title. The vectors represent the loadings of the four *Kalmia* traits with respect to the first two RDA axes. Different letters next to vegetation types indicate a statistically significant difference ($p < 0.05$) after conducting pairwise PERMANOVA and adjusting the p-values using a Bonferroni-Holm correction.

Kruskal-Wallis tests (or single factor ANOVA if assumptions were met) showed that SLA ($\chi^2_4 = 55.0$, $p < 0.001$), LDMC ($\chi^2_4 = 35.6$, $p < 0.001$), foliar C:N ($\chi^2_4 = 43.9$, $p < 0.001$), and foliar phenolics concentration ($F_{4,75} = 13.2$, $p < 0.001$) were significantly different between vegetation types. All *Kalmia* traits were significantly different in forest compared to heath (Figure 4). *Kalmia* SLA had values between heath and forest in eSS and open areas of mSS. *Kalmia* foliar C:N had values between heath and forest in eSS. *Kalmia* foliar phenolics concentration had values between heath and forest in open areas and spruce islands of mSS (Figure 4). In general, *Kalmia* SLA increased, and *Kalmia* LDMC, foliar C:N ratio, and foliar phenolics concentration decreased as spruce cover increased from heath to forest (Figure 4).

Given the high degree of multicollinearity between the four *Kalmia* traits, the same trend existed when the four traits were considered together as a *Kalmia* litter quality index. As the vegetation type shifted toward less spruce cover and greater heath stability, the quality of *Kalmia* litter decreased (Figure 5). *Kalmia* litter quality was significantly different in heath, mSS, and forest. Forest had the highest *Kalmia* litter quality, and mSS had a *Kalmia* litter quality intermediate to that of heath and forest (Figure 5).

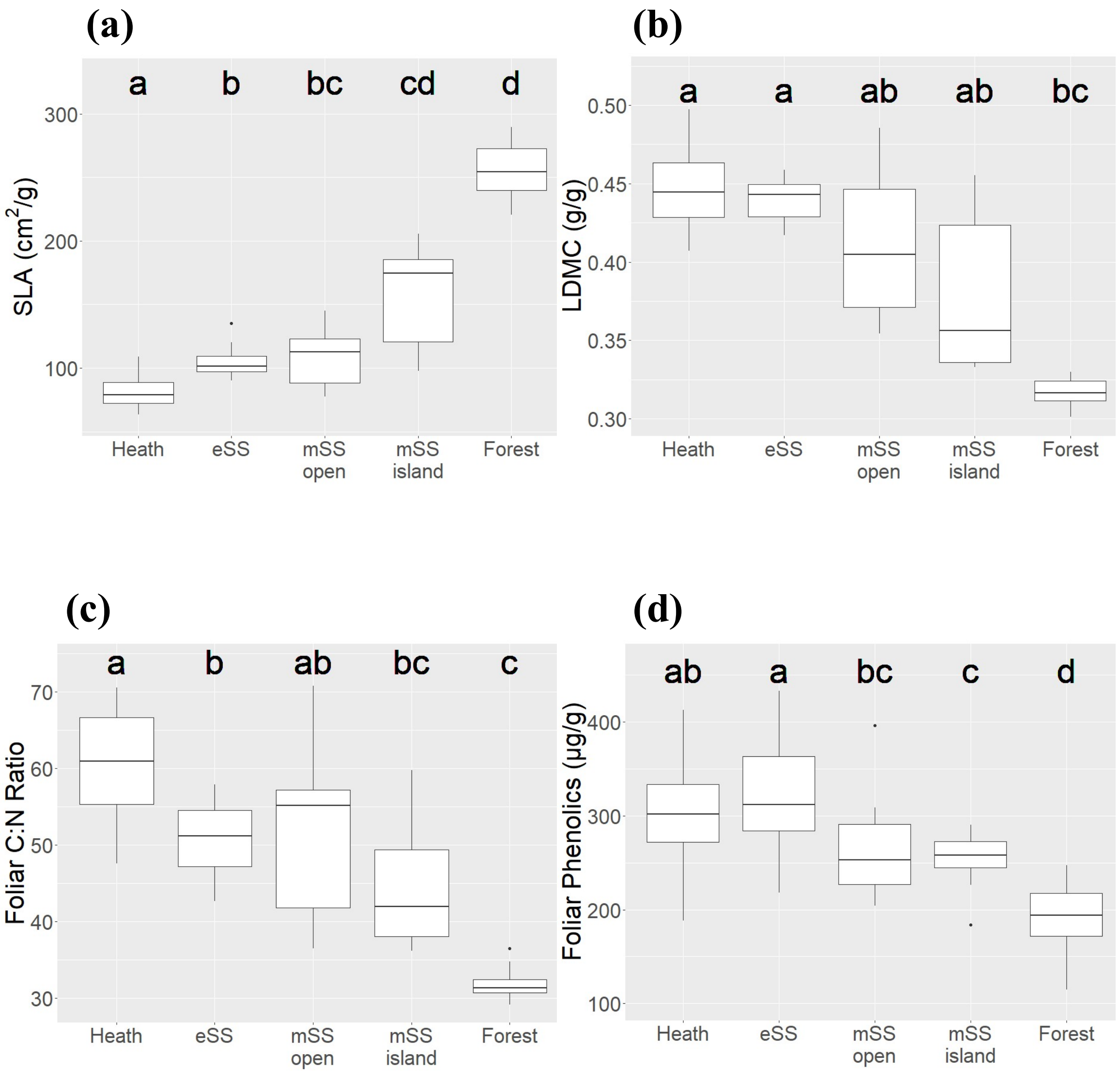

Figure 4. Variation in *Kalmia* **(a)** SLA, **(b)** LDMC, **(c)** foliar C:N, and **(d)** foliar phenolics concentration across five vegetation types: heath, early-stage SS (eSS), open areas of mature SS (mSS open), black spruce islands in mature SS (mSS island), and black spruce forest (forest). Shared letters indicate no significant difference ($p > 0.05$) between treatments using a Dunn's test with a Holm-Bonferroni correction (**a-c**) or a Tukey's HSD test (**d**).

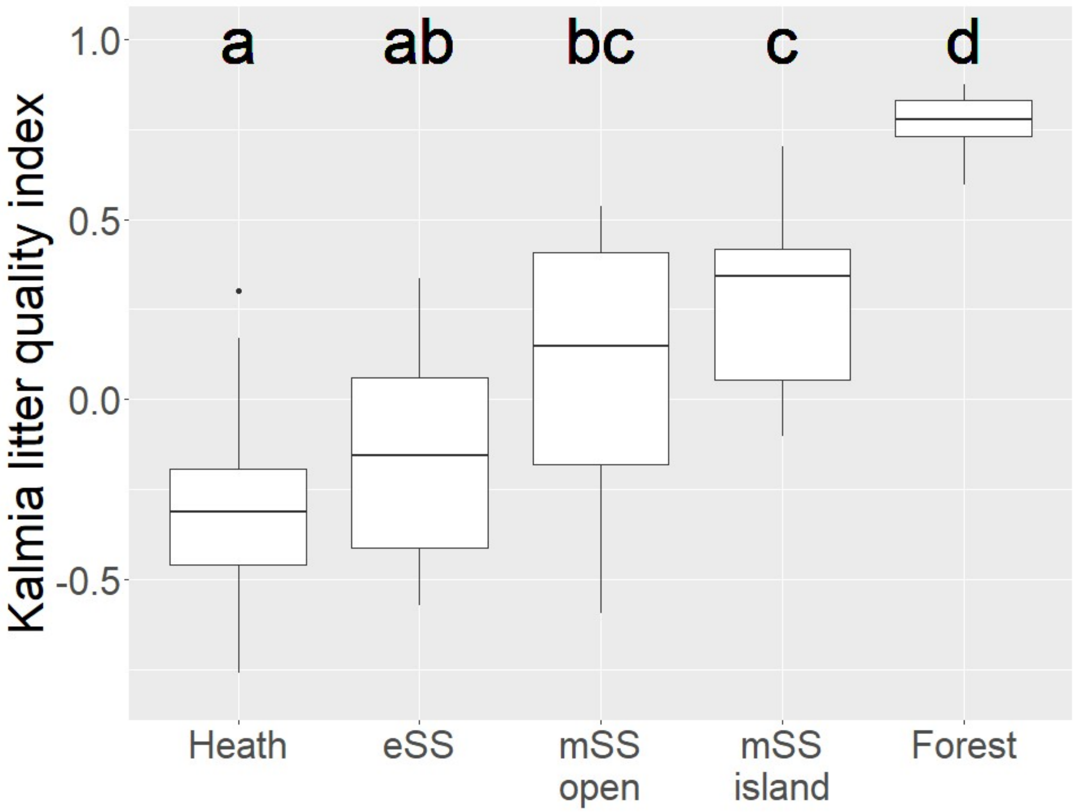

Figure 5. Variation in *Kalmia* litter quality index across five vegetation types: heath, early-stage SS (eSS), open areas of mature SS (mSS open), black spruce islands in mature SS (mSS island), and black spruce forest (forest). Shared letters indicate no significant difference ($p > 0.05$) between treatments using a Tukey's HSD test. Single-factor ANOVA showed that vegetation type had a significant impact on *Kalmia* litter quality index ($F_{4, 75} = 30.8$, $p < 0.001$).

3.2 CWM functional trait-vegetation type relationship

PERMANOVA showed that there were significant differences between vegetation types based on CWM traits ($F_{5,74} = 18.3$, $p < 0.001$). RDA showed that a large amount of the variance in CWM traits (55.2%) was explained by vegetation type. Almost all the variation (95.9%) in CWM traits explained by vegetation type was on a single axis (Figure 6). Furthermore, the loadings of the traits were high on the first RDA axis and low on the remaining RDA axes (Table 5). This suggests a high degree of multicollinearity among the three CWM traits. In general, as the vegetation type shifted from heath to eSS, to mSS, to forest, CWM traits changed as follows: SLA increased, LDMC decreased, and foliar C:N ratio decreased (Figure 6). This means that the litter quality of understory plants decreased as the vegetation type shifted towards lower spruce cover and greater heath stability.

Table 5. Loadings of the three CWM traits with respect to the first two RDA axes. RDA was performed using CWM traits (SLA, LDMC, and foliar C:N) as the response variables and vegetation type as the explanatory variable.

CWM Traits	RDA1 (Loading)	RDA2 (Loading)
SLA	1.79	0.04
LDMC	-1.54	-0.37
C:N Ratio	-1.60	0.40

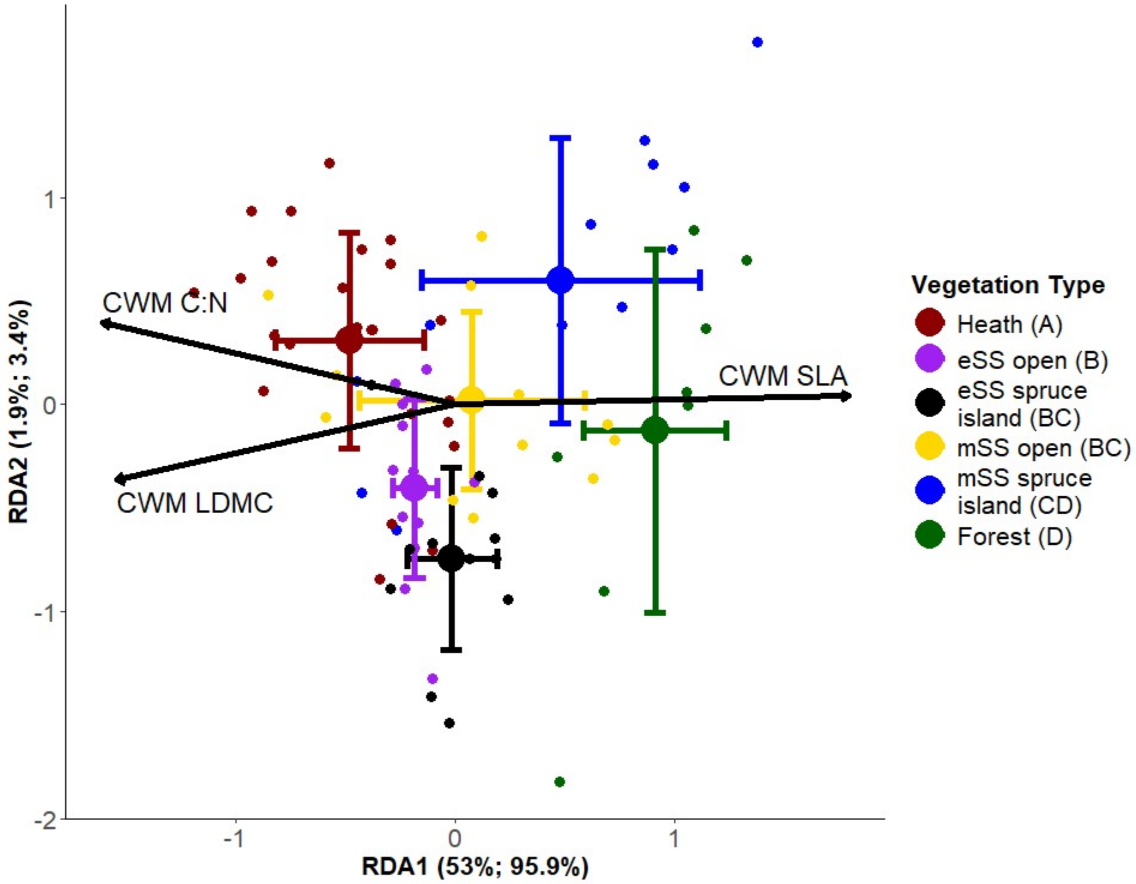

Figure 6. RDA plot showing how plots from five vegetation types were different based on three CWM traits: SLA, LDMC, and foliar C:N ratio (CWM C:N). Large dots represent the mean value for each vegetation type, and the error bars are plus and minus one standard deviation. The percent of total variance and percent of constrained variance explained by each RDA axis are, respectively, shown in parentheses next to the axis title. The vectors represent the loadings of the three CWM traits with respect to the first two RDA axes. Different letters next to vegetation types indicate a statistically significant difference ($p < 0.05$) after conducting pairwise PERMANOVA and adjusting the p-values using a Bonferroni-Holm correction.

Kruskal-Wallis tests showed that CWM SLA ($\chi^2_4 = 46.0$, $p < 0.001$), CWM LDMC ($\chi^2_4 = 29.3$, $p < 0.001$), and CWM foliar C:N ($\chi^2_4 = 39.1$, $p < 0.001$) were significantly different based on vegetation type. Each CWM trait was significantly different in heath compared to forest (Figure 6). CWM SLA had values between heath and forest in eSS. CWM foliar C:N had values between heath and forest in eSS and open areas of mSS (Figure 6). The direction of change in SLA, LDMC, and foliar C:N ratio as spruce cover increased from heath to forest was the same for CWM traits (Figure 6) and *Kalmia* traits (Figure 4).

Given the high degree of multicollinearity among the three CWM traits, the same trend existed when the three traits were considered together as a CWM litter quality index. As the vegetation type shifted towards less spruce cover and greater heath stability, CWM litter quality decreased (Figure 7). CWM litter quality was significantly different in heath, mSS, and forest. Forest had the highest CWM litter quality, and mSS had a CWM litter quality between that of heath and forest (Figure 7).

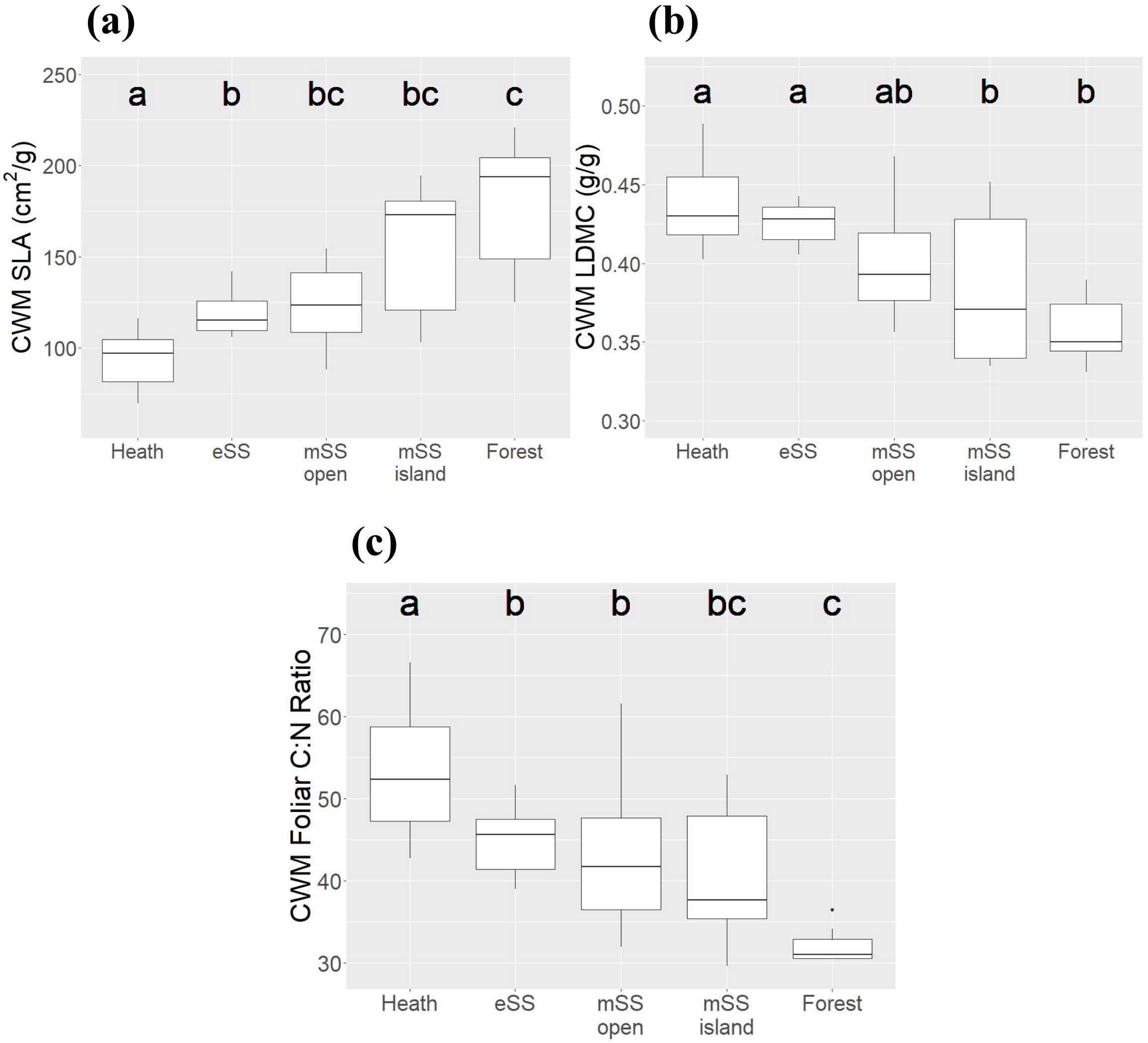

Figure 7. Variation in in community-weighted mean (CWM) **(a)** SLA, **(b)** LDMC, and **(c)** foliar C:N Ratio of understory shrubs, herbs, and ferns across five vegetation types: heath, early-stage SS (eSS), open heath areas of mature SS (mSS open), black spruce islands in mature SS (mSS island), and black spruce forest (forest). Shared letters indicate no significant difference between treatments using a Dunn's test with a Holm-Bonferroni correction.

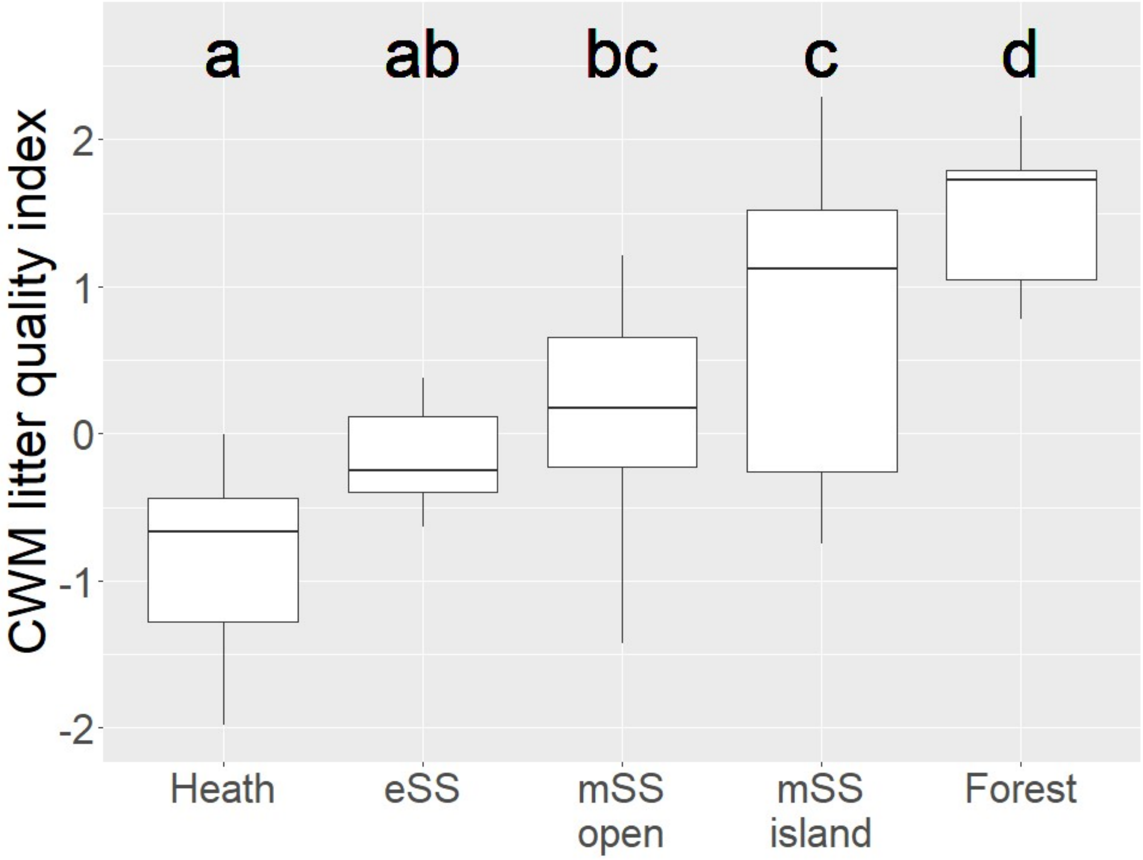

Figure 8. Variation in CWM litter quality index across five vegetation types: heath, early-stage SS (eSS), open heath areas of mature SS (mSS open), black spruce islands in mature SS (mSS island), and black spruce forest (forest). Shared letters indicate no significant difference ($p > 0.05$) between treatments using a Dunn's test with a Holm-Bonferroni correction. A Kruskal-Wallis test showed that vegetation type had a significant impact on CWM litter quality index ($\chi^2_4 = 38.4$, $p < 0.001$).

3.3 Environment-vegetation type relationship

PERMANOVA showed that there were significant differences between vegetation types based on soil nutrient availability ($F_{4, 79} = 9.7$, $p < 0.001$). RDA showed that the vegetation type gradient explained 41.3% of the variance in soil chemistry. This means that vegetation type was a worse predictor of soil chemistry than *Kalmia* traits since RDA showed that 64.5% of the variation in *Kalmia* traits was explained by vegetation type (section 3.1). Post-hoc tests revealed no significant differences between open areas and spruce islands of mSS in terms of soil chemistry. As the vegetation type shifted from heath, to SS, to forest, soil nutrient availability increased (higher soil respiration, pH, total N, inorganic N, and lower organic N to inorganic N ratio), and total phenolics increased (Figure 9). Soil respiration, pH, total N, inorganic N, and total phenolics had high loadings on the RDA1 axis (Table 6), indicating that these variables were important in distinguishing the forest vegetation type from the other vegetation types (Figure 9). Only inorganic N and organic N to inorganic N ratio had high loadings on the RDA2 axis (Table 6), which separated the mSS vegetation type from heath and eSS (Figure 9).

Table 6. Loadings of the six soil properties with respect to the first two RDA axes. RDA was performed using soil properties (soil respiration, pH, total N, inorganic N, organic N to inorganic N ratio, and total phenolics) as the response variables and vegetation type as the explanatory variable.

Soil property	RDA1 (Loading)	RDA2 (Loading)
Respiration	1.14	-0.02
pH	1.10	-0.03
Total N	1.68	-0.51
Inorganic N	0.74	0.81
Organic N to inorganic N ratio (DON:DIN)	-0.23	-1.01
Total phenolics	0.88	0.08

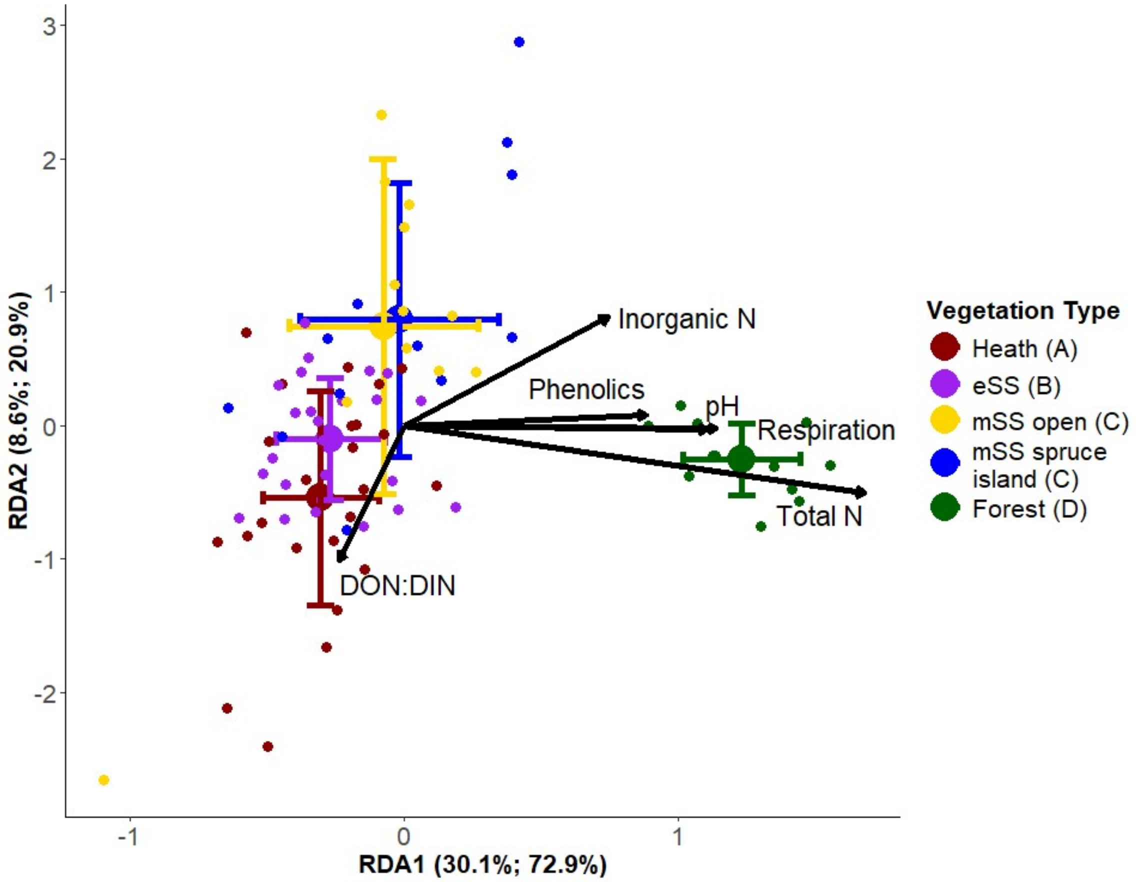

Figure 9. RDA plot showing how plots from five vegetation types were different based on six soil properties: pH, soil respiration, inorganic N, total N, total phenolics, and organic N to inorganic N ratio (DON:DIN). Large dots represent the mean value for each vegetation type, and the error bars are plus and minus one standard deviation. The percent of total variance and percent of constrained variance explained by each RDA axis are, respectively, shown in parentheses next to the axis title. The vectors represent the loadings of the six soil properties with respect to the first two RDA axes. Different letters next to vegetation types indicate a statistically significant difference ($p < 0.05$) after conducting pairwise PERMANOVA and adjusting the p-values using a Bonferroni-Holm correction.

Vegetation type was a weaker predictor of soil chemistry than *Kalmia* traits, as there was high site-to-site variability in soil chemistry within a given vegetation type (Figure 10). RDA showed that the site ID explained 59.3% of the variation in soil chemistry, which is an improvement on the 41.3% of variation in soil chemistry explained by vegetation type. Therefore, the site ID is a much better predictor of soil chemistry than vegetation type. Furthermore, there were heath sites (TB and CT) that were similar to eSS and mSS in terms of soil properties. This means that soil chemistry did not determine whether an ecosystem is in the *Kalmia* heath, eSS, or mSS state.

Table 7. Loadings of the six soil properties with respect to the first two RDA axes. RDA was performed using soil properties (soil respiration, pH, total N, inorganic N, organic N to inorganic N ratio, and total phenolics) as the response variables and the site ID as the explanatory variable.

Soil property	RDA1 (Loading)	RDA2 (Loading)
Respiration	1.14	-0.21
pH	1.35	0.23
Total N	1.54	-0.79
Inorganic N	1.05	0.89
Organic N to inorganic N ratio (DON:DIN)	-0.60	-1.18
Total phenolics	0.53	-0.93

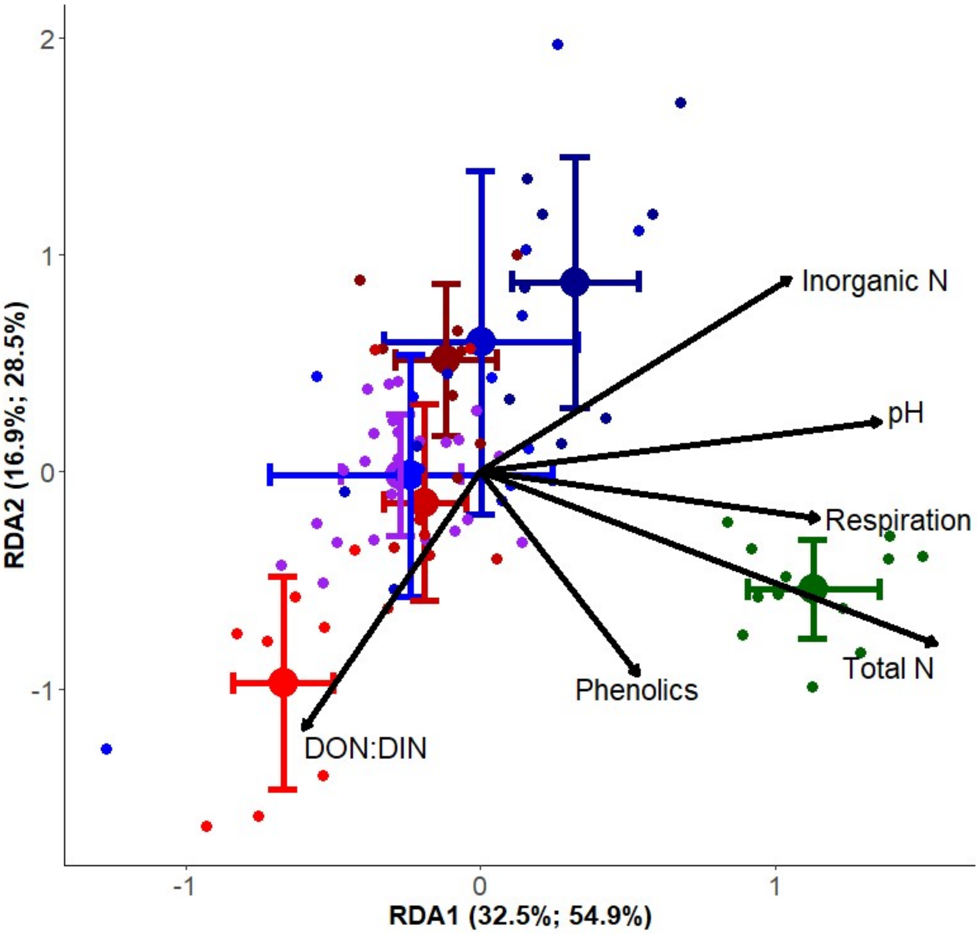

Figure 10. RDA plot showing how plots from eight sites were different based on six soil properties: pH, soil respiration, inorganic N, total N, total phenolics, and organic N to inorganic N ratio (DON:DIN). Large dots represent the mean value for each site, and the error bars are plus and minus one standard deviation. Heath sites are in red, the early-stage SS site is in purple, mature SS sites are in blue, and forest sites are in green. The percent of total variance and percent of constrained variance explained by each RDA axis are, respectively, shown in parentheses next to the axis title. The vectors represent the loadings of the six soil properties with respect to the first two RDA axes.

Kruskal-Wallis tests (or single factor ANOVA if assumptions were met) showed that soil respiration ($F_{4, 79} = 19.5$, $p < 0.001$), soil pH ($\chi^2_4 = 28.7$, $p < 0.001$), total N ($F_{4, 79} = 144.3$, $p < 0.001$), inorganic N ($\chi^2_4 = 37.8$, $p < 0.001$) organic N to inorganic N ratio ($\chi^2_4 = 28.0$, $p < 0.001$), total phenolics ($\chi^2_4 = 24.2$, $p < 0.001$) were significantly different between vegetation types. Each soil chemistry variable was significantly different in forest and heath, except for organic N to inorganic N ratio (Figures 11). None of the soil chemistry variables had values in eSS or mSS that were intermediate to and significantly different from those of forest and heath (Figures 11). Inorganic N was significantly higher in mSS open and mSS island than in heath, but not different than in forest (Figure 11d). Organic N to inorganic N ratio was significantly lower in mSS open and mSS island than in heath, but not different than in forest (Figure 11e). Early-stage SS was not different from heath in any of the soil nutrient availability indicators (Figures 11). This means that soil chemistry was not effective at distinguishing between the heath, eSS, and mSS states, but was effective at distinguishing between the forest state and other ecosystem states.

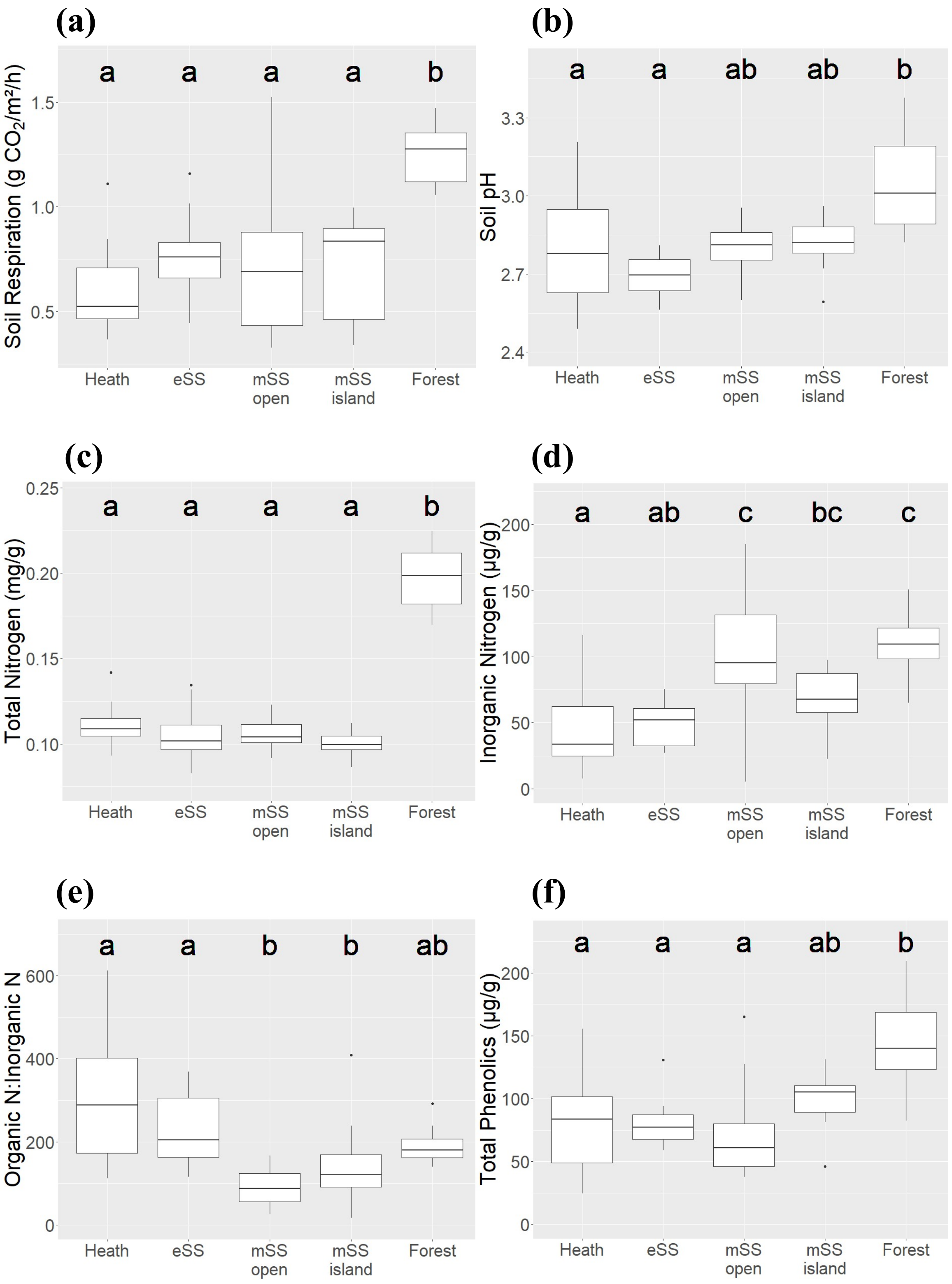
(a)
a a a a b
Soil Respiration (g CO_2/m²/h)
0.5
1.0
1.5
Heath
eSS
mSS open
mSS island
Forest
(b)
a a ab ab b
Soil pH
2.4
2.7
3.0
3.3
Heath
eSS
mSS open
mSS island
Forest
(c)
a a a a b
Total Nitrogen (mg/g)
0.10
0.15
0.20
0.25
Heath
eSS
mSS open
mSS island
Forest
(d)
a ab c bc c
Inorganic Nitrogen (µg/g)
0
50
100
150
200
Heath
eSS
mSS open
mSS island
Forest
(e)
a a b b ab
Organic N:Inorganic N
0
200
400
600
Heath
eSS
mSS open
mSS island
Forest
(f)
a a a ab b
Total Phenolics (µg/g)
0
50
100
150
200
Heath
eSS
mSS open
mSS island
Forest

Figure 11. Variation in soil **(a)** respiration, **(b)** pH, **(c)** total N, **(d)** inorganic N, **(e)** organic N to inorganic N ratio, and **(f)** total phenolics across five vegetation types: heath, early-stage SS (eSS), open heath areas of mature SS (mSS open), black spruce islands in mature SS (mSS island), and black spruce forest (forest). Shared letters indicate no significant difference ($p > 0.05$) between treatments using a Dunn's test with a Holm-Bonferroni correction (**b, d-f**) or a Tukey's HSD test (**a, c**).

3.4 Environment-*Kalmia angustifolia* trait relationships

Canonical correlation analysis (CCA) showed that indicators of low *Kalmia* litter quality (low SLA and high LDMC, foliar C:N, and foliar total phenolics) correlated with indicators of low soil nutrient availability (high organic to inorganic N ratio, and low soil respiration, pH, total N, and inorganic N; Figure 12). The first two canonical variate pairs of the CCA between four *Kalmia* above-ground traits (SLA, LDMC, foliar C:N, and foliar total phenolics) and five soil chemistry variables (respiration, pH, total N, inorganic N, and organic N to inorganic N ratio) were statistically significant (Table 8). The loadings of all variables except inorganic N and organic N to inorganic N ratio were high (> 0.50) with respect to the first canonical variate pair (Table 9; Figure 12). This means that soil respiration, pH, and total N made the most significant contributions to the correlations between soil nutrient availability and *Kalmia* traits. Additionally, inorganic N, foliar total phenolics, and LDMC had moderate loadings (> 0.20), and soil pH had a high loading (0.75) with respect to the second canonical variate pair (Table 9; Figure 12). Therefore, low LDMC and foliar total phenolics were correlated with high soil pH and inorganic N along the second canonical variate pair.

Table 8. Correlation coefficients and p-values for the relationships between the four canonical variate pairs of CCA between four *Kalmia* traits (SLA, LDMC, foliar C:N, and foliar total phenolics) and five soil chemistry variables (soil respiration, pH, total N, inorganic N, and organic N to inorganic N ratio).

	Canonical variate pair 1	Canonical variate pair 2	Canonical variate pair 3	Canonical variate pair 4
Correlation coefficient (r)	0.82	0.50	0.28	0.08
p-value	< 0.001	< 0.001	0.36	0.79

Table 9. Canonical loadings of the four *Kalmia* traits (SLA, LDMC, foliar C:N, and foliar total phenolics) and five soil chemistry variables (soil respiration, pH, total N, inorganic N, and organic N to inorganic N ratio) with respect to the first two canonical variate pairs.

Variable	Canonical loading (canonical variate pair 1)	Canonical loading (canonical variate pair 2)
SLA	-0.97	0.1
LDMC	0.83	-0.42
Foliar C:N	0.76	-0.06
Foliar total phenolics	0.62	-0.34
Soil respiration	-0.74	-0.21
Soil pH	-0.57	0.75
Total N	-0.90	-0.13
Inorganic N	-0.36	0.25
Organic N to inorganic N ratio	0.25	0.06

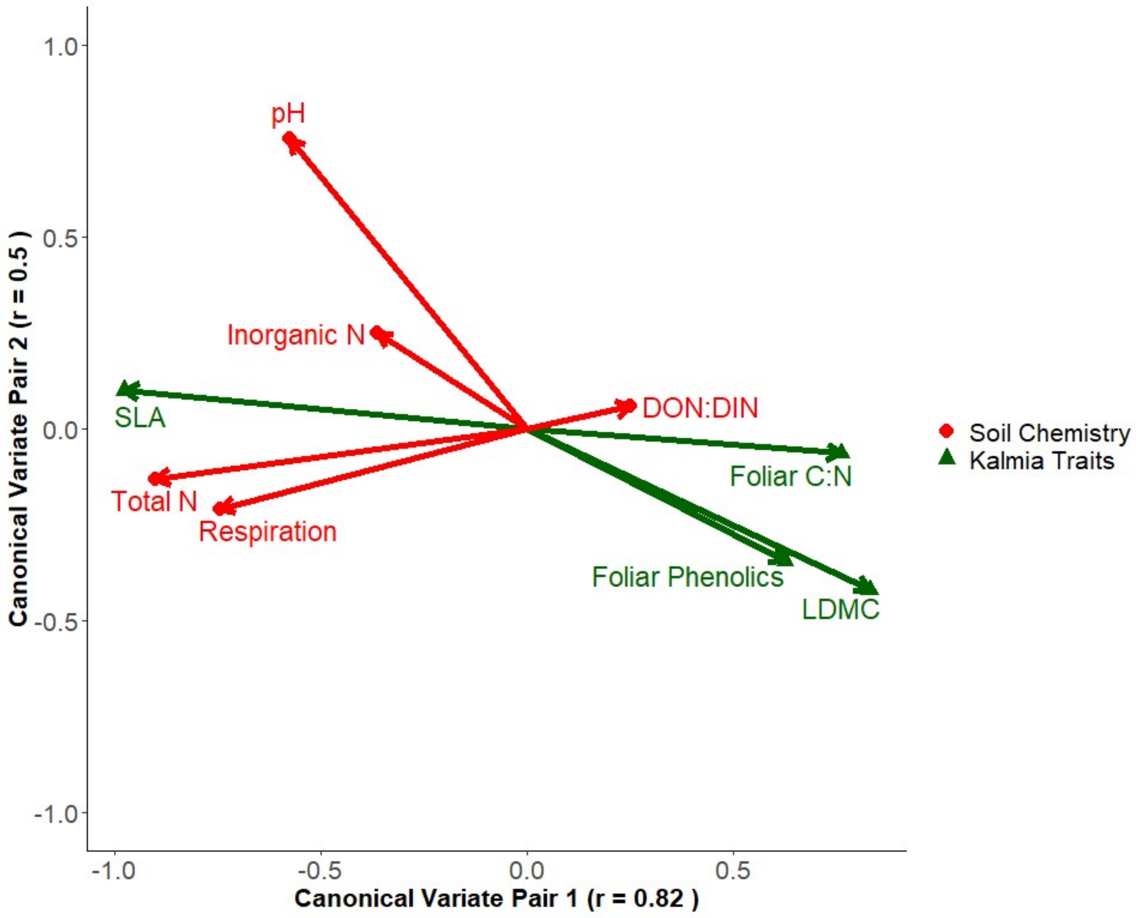

Figure 12. Plot of the canonical loadings of five soil chemistry variables and four *Kalmia* traits with respect to the first two canonical variate pairs obtained from canonical correlation analysis (CCA) between the *Kalmia* traits and soil chemistry variables. The x-axis represents the canonical loadings with respect to the first canonical variate pair, and the y-axis represents the canonical loadings with respect to the second canonical variate pair.

3.5 Environment-CWM trait relationships

CCA showed that indicators of low CWM litter quality (low SLA, high LDMC, and high foliar C:N) correlated with indicators of low soil nutrient availability (high organic to inorganic N ratio, and low soil respiration, pH, total N, and inorganic N; Figure 13). The first two canonical variate pairs of the CCA between three CWM above-ground traits (SLA, LDMC, and foliar C:N) and five soil chemistry variables (soil respiration, pH, total N, inorganic N, and organic N to inorganic N ratio) were statistically significant (Table 10). The loadings of all variables were high (≥ 0.50), meaning all soil properties correlated strongly with CWM traits (Table 11; Figure 13).

Table 10. Correlation coefficients and p-values for the relationships between the three canonical variate pairs of CCA between three CWM traits (SLA, LDMC, and foliar C:N) and five soil chemistry variables (soil respiration, pH, total N, inorganic N, and organic N to inorganic N ratio).

	Canonical variate pair 1	Canonical variate pair 2	Canonical variate pair 3
Correlation coefficient (r)	0.69	0.47	0.12
p-value	< 0.001	0.013	0.80

Table 11. Canonical loadings of the three CWM traits (SLA, LDMC, and foliar C:N) and five soil chemistry variables (soil respiration, pH, total N, inorganic N, and organic N to inorganic N ratio) against the first two canonical variate pairs.

Variable	Canonical loading (canonical variate pair 1)	Canonical loading (canonical variate pair 2)
SLA	-0.98	0.02
LDMC	0.95	0.33
Foliar C:N	0.95	-0.07
Soil respiration	-0.70	0.29
Soil pH	-0.71	-0.48
Total N	-0.64	0.44
Inorganic N	-0.59	-0.10
Organic N to inorganic N ratio	0.50	-0.22

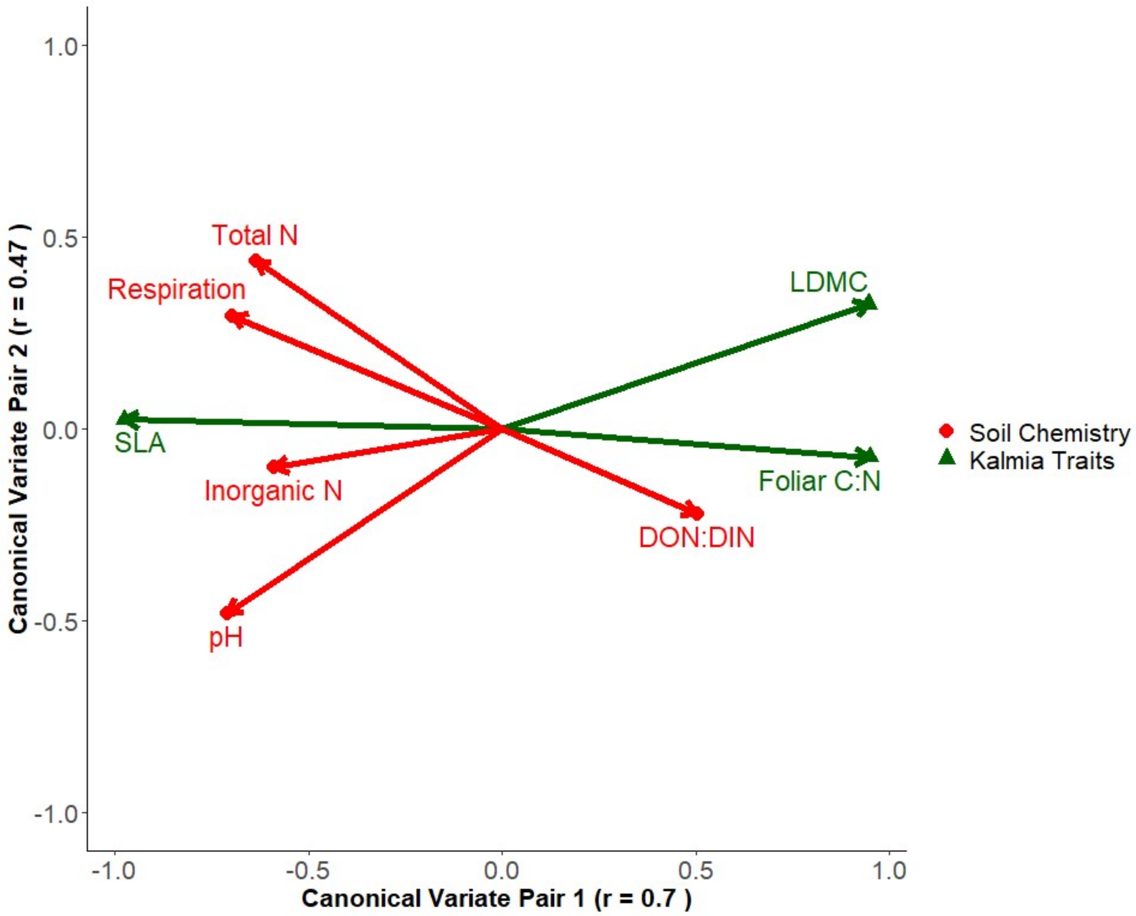

Figure 13. Plot of the canonical loadings of five soil chemistry variables and three CWM traits with respect to the first two canonical variate pairs obtained from canonical correlation analysis (CCA) between the CWM traits and soil chemistry variables. The x-axis represents the canonical loadings with respect to the first canonical variate pair, and the y-axis represents the canonical loadings with respect to the second canonical variate pair.

4. Discussion

The purpose of this study was to test under field conditions the presence of a positive PSF in *Kalmia* heath by measuring *Kalmia* traits and soil properties in sites that differ in black spruce cover and heath stability. Four vegetation types were sampled. In order of increasing spruce cover and decreasing heath stability, the vegetation types were *Kalmia* heath, early-stage shrub savanna (eSS), mature shrub savanna (mSS), and black spruce forest. The expectations were that as black spruce cover decreases and heath stability increases, (1) *Kalmia* and CWM above-ground litter quality (determined by measuring the traits SLA, LDMC, foliar C:N, and foliar total phenolics) decreases, and (2) soil nutrient availability (determined by measuring pH, soil respiration, inorganic N, total N, organic N to inorganic N ratio, and total soil phenolics) decreases. The third hypothesis was that indicators of soil nutrient availability are correlated with higher *Kalmia* and CWM litter quality. The results confirmed hypotheses 1 and 3 but not hypothesis 2. The results showed that soil nutrient availability was higher in the forest than in the other three ecosystem states (*Kalmia* heath, eSS, and mSS). However, there was little difference in soil nutrient availability between the *Kalmia* heath, eSS, and mSS ecosystem states.

4.1 Impact of vegetation type on *Kalmia* and CWM traits (hypothesis 1)

There is strong evidence in support of the first hypothesis, which states that *Kalmia* and CWM litter quality decreases as black cover decreases and heath stability increases. Evidence in support of this hypothesis comes from examining the relationships between four above-ground traits (SLA, LDMC, foliar C:N, and foliar phenolics) and vegetation type. RDA showed that 64.5% of the variation in *Kalmia* traits was explained by vegetation type, indicating that vegetation type was a strong predictor of *Kalmia* traits. RDA also showed a shift towards traits representing increased litter quality as the vegetation type transitioned from heath to eSS, to mSS, and finally to black spruce forest (Figure 4). PERMANOVA showed that these differences were statistically significant. *Kalmia* traits in heath were significantly different from *Kalmia* traits in the intermediately forested vegetation types (spruce patches of eSS, open areas of mSS, and mSS spruce islands), which were significantly different from *Kalmia* traits in black spruce forest (Figure 4). Variation in *Kalmia* traits in response to vegetation type was confirmed when examining each trait individually (Figure 5) and when examining variation in the *Kalmia* litter quality index (Figure 6). These results are consistent with past studies examining *Kalmia* trait variation in response to canopy cover (Bloom & Mallik, 2004; Joanisse et al., 2018; Mallik et al., 2012). The result regarding variation in *Kalmia* foliar total phenolics is also consistent with research showing that plants increase biosynthesis of phenolic compounds in response to increased UV-B exposure for protection (Alonso-Amelot et al., 2007; Gourlay et al., 2021). These findings are significant because they show that eSS and mSS are distinct from heath in terms of plant traits. In eSS and mSS, there is a slow rate of black spruce canopy expansion due to black spruce layering (St. James, 2023). Therefore, heath stability is slightly less in SS than in heath. For this reason, it was expected that eSS and mSS would have plant trait values between those of heath and forest.

CWM traits showed the same trends in relation to vegetation type as *Kalmia* traits (Figure 7-9). This is because CWM traits were largely influenced by the intraspecific variation in *Kalmia* traits. *Kalmia* respectively represented 75, 74, 59, 74, and 50% of the understory shrub and herb (combined) cover in heath, eSS, open areas of mSS, spruce islands of mSS, and black spruce forest (Appendix 1). Therefore, *Kalmia* trait values had by far a larger influence on CWM traits than other species. CWM traits having the same trend in relation to vegetation type as *Kalmia* traits showed that there are no differences in non-dominant species composition among the vegetation types that would cause the overall litter quality to be different. Nonetheless, it is important to measure CWM traits because the litters of all species, not just *Kalmia*, influence soil chemistry.

The results also showed a high degree of intercorrelation among the four *Kalmia* traits and the three CWM traits, which is consistent with the worldwide leaf economic spectrum hypothesis (Wright et al., 2004). A high degree of intercorrelation among plant traits was observed, as a large portion of the variation in plant traits was explained by the first constrained and unconstrained RDA axes (81.8% for *Kalmia* traits and 92.6% for CWM traits). As SLA increased, LDMC, foliar C:N, and foliar total phenolics decreased (Figure 4). This is consistent with the worldwide leaf economic spectrum, which predicts that there are several intercorrelated chemical and structural leaf traits that together signify a shift from a fast-growing, resource-acquisitive, and low investment in chemical defences strategy to a slow-growing, resource-conservative, and high investment in chemical defences strategy (Wright et al., 2004).

Relevant to this study is the shift in traits along the leaf economic spectrum that could be related to soil nutrient availability and cycling. The results showed that along a gradient of decreasing black spruce cover, there was a shift in leaf traits that signify an increase in production of tannins and phenolic compound (higher foliar total phenolics), a decrease in leaf litter quality (higher foliar C:N), and an increase in non-labile leaf structural components relative to total leaf mass (higher LDMC and lower SLA). These shifts in plant traits are relevant to soil nutrient availability and cycling. Nitrogen enters the soil in organic forms, such as protein and chitin, and is degraded by enzymes that convert organic N to plant-available inorganic forms (NH_4^+ or NO_3^-; Tabatabai et al., 2008). Plant tannins and phenolic compounds can slow this conversion (and therefore reduce plant N availability) if they are toxic to the microorganisms or fungi that produce the N mineralisation (Chomel et al., 2016). *Kalmia* tannins in particular are effective at reducing the activity of N mineralisation enzymes, and it has been shown that they are more effective than black spruce tannins (Joanisse et al., 2007; Joanisse et al., 2018). Plant tannins can also reduce N mineralisation rates by sequestering organic N into protein-tannin complexes that are resistant to decomposition by most decomposing organisms (Chomel et al., 2016; Hättenschwiler & Vitousek, 2000). As with the activity of N mineralisation enzymes, *Kalmia* tannins are more effective than black spruce tannins at precipitating protein in soil into protein-tannin complexes (Joanisse et al., 2008b). Therefore, the finding that *Kalmia* leaves contain higher total phenolic compounds and that *Kalmia* has the highest cover in the heath vegetation type is important because this suggests that inorganic N availability may be lowest in heath.

Two other plant traits in heath that are relevant to nutrient availability and cycling are low leaf litter quality and high LDMC. Leaf litter quality (either measured as foliar C:N ratio or lignin:N ratio) is correlated with soil N availability and net N mineralisation rates in many systems (Hobbie, 2015; Maithani et al., 1998; Satti et al., 2003; Scott & Binkley, 1997). This is because a lower concentration of N in litter has been shown to decrease decomposition rates and N release (Chomel et al., 2016). High LDMC is potentially associated with low soil N availability because it is associated with investment in non-labile leaf structural components, such as lignin and fibres (Pérez-Harguindeguy et al., 2013). These structural components resist degradation, meaning that high LDMC is often associated with slower litter degradation, reduced microbial activity, and lower N cycling (Chomel et al., 2016).

4.2 Impact of vegetation type and traits on soil chemistry (hypotheses 2 and 3)

The results showed that four *Kalmia* and CWM traits (SLA, LDMC, foliar C:N, and foliar total phenolics) shifted from trait values representing higher to lower litter quality as the vegetation type went from black spruce forest to mSS, to eSS, to *Kalmia* heath. In section 4.1, it was explained that each of these four traits and the direction in which they change as black spruce cover decreases are potentially related to lower soil nutrient availability in the heath state compared to more forested states. If this is true, then differences in soil nutrient availability indicators between vegetation types should show the same pattern as for plant traits. This means that soil nutrient availability should be lowest in *Kalmia* heath, highest in black spruce forest, and have intermediate values in the shrub savanna ecosystem states (eSS and mSS). The results showed that soil nutrient availability is higher in black spruce forest than in *Kalmia* heath. However, soil nutrient availability was not significantly different between the *Kalmia* heath, eSS, and mSS ecosystem states. This means that the strength of a plant-soil feedback implicating abiotic soil properties is important in distinguishing the black spruce forest state from other ecosystem states, but not in distinguishing between the *Kalmia* heath, eSS, and mSS states. This contradicts part of the second hypothesis, which was that soil nutrient availability should be higher in the eSS and mSS states than in the *Kalmia* heath state. This was the expectation because the rate of black spruce cover expansion is higher in eSS and mSS than in heath. In what follows, I will first explain the finding that soil nutrient availability is higher in the forest vegetation type than in the other vegetation types. Then, I will explain the finding that *Kalmia* heath, eSS, and mSS are not distinguishable in terms of soil nutrient availability.

There is strong evidence that nutrient availability is higher in black spruce forests than in the other vegetation types. Soil respiration and total N were significantly higher in the forest than in the other vegetation types (Figures 11a,c). Soil pH and inorganic N were significantly higher in the forest than the heath and eSS vegetation types (Figures 11b,d). Furthermore, PERMANOVA showed that forest was significantly different than the other vegetation types in terms of six soil properties (respiration, pH, total N, inorganic N, organic N to inorganic N ration, and total phenolics), and RDA showed that there was significant separation between forest plots and plots from other vegetation types in terms of the six soil properties (Figure 9). Together, this provides strong evidence that organic layer soils from black spruce forests have higher nutrient availability than those from less forested vegetation types. These findings are consistent with studies comparing soil properties in *Kalmia* heath and black spruce forest (Bloom & Mallik, 2004; Bloom & Mallik, 2006; Joanisse et al., 2008a; Joanisse et al., 2018; St. Martin & Mallik, 2021) and with a study comparing the impact of *Kalmia* and black spruce litter on nutrient availability under laboratory conditions (Joanisse et al., 2007). More specifically, studies have shown that greater *Kalmia* cover relative to black spruce cover is associated with the following soil properties: (i) lower rates of N mineralisation (Bloom & Mallik, 2006; Joanisse et al., 2007; Joanisse et al., 2018), (ii) higher organic N to inorganic N ratio (Joanisse et al., 2007), (iii) lower concentration of plant-available inorganic N (NH_4^+ and NO_3^-; Joanisse et al., 2007; Joanisse et al., 2018; St. Martin & Mallik, 2021), (iv) lower total N (St. Martin & Mallik, 2021), (v) lower pH (St. Martin & Mallik, 2021), and (vi) lower soil respiration (Bloom & Mallik, 2004).

While forest is distinguishable from other vegetation types based on soil nutrient availability, the heath, eSS, and mSS vegetation types are poorly distinguished by soil nutrient availability. This is because there was high site-to-site variability in soil nutrient availability within the heath and SS vegetation types (Figure 10). Some SS sites (RPSS and OHSS) were similar to heath sites (TB and CT) in terms of soil nutrient availability (Figure 10). This is inconsistent with the hypothesis that the strength of a PSF influencing nutrient availability controls vegetation type and heath stability in the boreal forest of eastern Newfoundland. If the extent of nutrient limitation controls whether a site is heath or SS, then these vegetation types should be distinguishable based on soil nutrient availability. Instead, there are sites with similarly nutrient-poor soils existing as heath, eSS, and mSS. This means there are factors other than what was measured in this study that determine whether a site is heath, eSS, or mSS. In eSS and mSS, *Kalmia* is less able to competitively exclude black spruce than in heath. Nitrogen in protein-tannin complexes is an important component of the N pool in *Kalmia* heath and SS, due to the protein-precipitating abilities of *Kalmia* phenolic compounds (Joanisse et al., 2008a). If either (i) less of the organic N pool is protein-tannin complexes in SS than heath and/or (ii) black spruce is better able to access N in protein-tannin complexes in SS than heath, then this might explain the differences in black spruce colonisation success between SS and heath.

An important difference between *Kalmia* and black spruce is that *Kalmia* associates with ericoid mycorrhizae, whereas black spruce associates with ectomycorrhizal fungi (Joanisse et al., 2008b; Read et al., 2004). A large body of research suggests that ectomycorrhizal fungi (ECM) can access little to no nitrogen from protein-tannin complexes, whereas ericoid mycorrhizae (ERM) are effective at utilizing complexed organic N (Bending & Read, 1996; Joanisse et al., 2008a; Rain et al., 2024; Read et al., 2004; Wu, 2011; Wu et al., 2003; Wu et al., 2005; Wurzburger & Hendrick, 2009). However, the result that ECM can access little to no nitrogen from protein-tannin complexes is not universal, and the extent to which ECM can access N in protein-tannin complexes is debated (Bennett & Prescott, 2004; Coq et al., 2022; Zhang & Adamczyk, 2025). Zhang & Adamczyk (2025) showed, using a greenhouse experiment and ^{15}N labelling, that *Pinus tabuliformis* utilized nitrogen from protein-tannin complexes when inoculated with ECM whether saprotrophic fungi were present or not. The results from Zhang & Adamczyk (2025) suggest that ECM can access complexed organic N directly without the help of saprotrophic fungi that mineralize protein-tannin complexes. However, simply being able to access complexed organic N does not mean that it is optimal for the growth of the plant to rely on protein-tannin complexes as an N source or that ERM plants can outcompete ECM for complexed organic N. For example, Coq et al. (2022) reported that *Pinus pinea* can utilize nitrogen from protein-tannin complexes, but that *P. pinea* grew 2-3 times better when mineral N or protein was the N source. Furthermore, Rain et al. (2024) reported that *Vaccinium ovatum* (an ERM species) accessed much more N from protein-tannin complexes than *Pinus muricata* (an ECM species) when grown individually. When grown together, there was a greater reduction in N acquisition for the ECM species than for the ERM species. This suggests that the ERM species outcompeted the ECM species for complexed organic N (Rain et al., 2024).

While there is debate on the extent to which ECM plants can utilize nitrogen from complexed organic N, most of the research shows that ERM plants are much better at utilizing N from this source than ECM plants (Bending & Read, 1996; Joanisse et al., 2008a; Rain et al., 2024; Read et al., 2004; Wu, 2011; Wu et al., 2003; Wu et al., 2005; Wurzburger & Hendrick, 2009). Even if ECM plants can access complexed organic N, it is likely that ERM plants outcompete ECM plants for nitrogen from protein-tannin complexes (Rain et al., 2024). Therefore, while it is possible that black spruce can improve its nutrient acquisition in nutrient-poor heathland through associations with ECM, it is unlikely that associations with ECM alone could allow spruce to overcome its competitive disadvantage with *Kalmia*. For example, St. Martin & Mallik (2016) demonstrated that black spruce individuals in heath with a normal growth rate exhibit a higher amount of ECM colonisation and a distinct ECM community composition compared to black spruce individuals with stunted growth. ECM colonisation improves black spruce growth in heath, but the site remains heath. Sampling the amount of ECM colonisation of spruce and the community composition of ECM and other fungi in *Kalmia* heath, eSS, and mSS would help determine if these sites are distinguishable based on the ERM, ECM, and saprotrophic fungi present in the soil biota. Perhaps spruce has a better competitive ability in SS than in heath due to interactions with specific ECM that access complexed organic N or with saprotrophic fungi that mineralize complexed organic N. It is also possible that protein-tannin complexes are a less important part of the N pool in SS than heath. Therefore, a more detailed investigation of the N pool in heath, eSS, and mSS should be done. Determining the amount of organic N that is complexed with polyphenols versus the amount that is not is important, since ECM plants are effective at utilizing non-complexed organic N (Read et al., 2004).

Another unexpected result was that total soil phenolics increased from less to more forested vegetation types (Figure 11f). This was unexpected since black spruce foliar phenolics concentration is about a third that of *Kalmia* (Joanisse et al., 2018), and the results showed *Kalmia* foliar phenolics concentration to be highest in the unforested vegetation types (Figure 4d). Thus, as black spruce cover increases relative to *Kalmia* cover and *Kalmia* foliar phenolics concentration decreases, soil phenolics concentration should decrease. However, this might not be the case if black spruce biomass in forest is much greater than *Kalmia* biomass in heath. While *Kalmia* leaves have about three times as many phenolic compounds per unit of dry mass compared to spruce needles, if *Kalmia* biomass in heath is much less than a third that of black spruce in forest, then it would be expected that more phenolics leach into the soil in forest. Another potential reason for this finding is that *Kalmia* tannins are more effective than black spruce tannins at precipitating soil N into protein-tannin complexes (Joanisse et al., 2008b), and these tannins are less extractable by the Folin-Ciocalteu method than non-precipitated tannins (Joanisse et al., 2008a; Nierop & Verstraten, 2006). More tannins forming protein-tannin complexes in heath than forest would explain less total phenolics being detected in heath using the Folin-Ciocalteu method. St. Martin (2018) also found, using the Folin-Ciocalteu method, that black spruce organic layer soil contains more total phenolic compounds than

Kalmia heath organic layer soil. Although, the differences were not statistically significant in St. Martin (2018).

The third hypothesis was that *Kalmia* and CWM traits related to low litter quality correlate with indicators of low soil nutrient availability. This study showed support for this hypothesis. Low *Kalmia* and CWM litter quality (low SLA, and high LDMC, foliar C:N, and foliar total phenolics) were related to high soil organic N to inorganic ratio and low soil respiration, pH, total N, and inorganic N (Figures 12 & 13). Soil respiration, pH, and total N contributed the most to the relationship between litter quality and soil nutrient availability (Tables 9 & 11). The third hypothesis was formulated based on the assumption that if the strength of a PSF determines whether a site is classified as a *Kalmia* heath, eSS, mSS, or black spruce forest, then plant traits should correlate with soil nutrient availability. This is because PSF, by definition, means that plant traits influence soil properties. However, the more important finding is that soil nutrient availability was not different in the *Kalmia* heath, eSS, and mSS ecosystems. Since these three ecosystems were not distinguishable based on soil nutrient availability, the strength of a PSF implicating the soil nutrient indicators measured in this study cannot be said to determine whether the ecosystem state is heath, eSS, or mSS.

4.3 Connections to other ecological systems

This study shows the potential for internal ecosystem dynamics (plant-soil feedback) to reinforce a shift in ecosystem state caused by disturbance. In the boreal forest of eastern Newfoundland, three alternative stable states are recognized, each defined by its unique species composition. *Kalmia* heath is characterized by ericaceous shrub dominance, forest is dominated by black spruce, and SS is characterized by patchy dominance of ericaceous shrubs and black spruce (Appendix 1). There are two ways that state shifts can happen in the *Kalmia*-black spruce system: (i) disturbances such as forest fire, and (ii) weakening of internal dynamics (plant-soil feedback) that maintain the current vegetation state. The role of forest fire severity in causing state shifts in the *Kalmia*-black spruce system had been studied by others and was not the focus of this study. Forest fire severity is an abiotic filter that determines post-fire species composition, where low-severity fires lead to *Kalmia* heath, high-severity fires lead to black spruce forests, and patchy high/low-severity fires lead to SS (Siegwart Collier & Mallik, 2010; Mallik, 2022). The long-term persistence of a state shift caused by fire is then determined by the strength of plant-soil feedback that maintains the new vegetation state. If plant-soil feedback is strong enough to prevent any meaningful change in species composition within the fire return interval, then the new vegetation state is likely to persist long-term.

There are other examples of ecological systems where disturbance, such as fire, causes a shift from a forested to a non-forested state, and where plant-soil feedback leads to the long-term persistence of the non-forested state after the regime shift occurs. Fletcher et al. (2014) examined pollen and charcoal in sediments to recreate the vegetation and fire history at a site in Tasmania, Australia. They found that 7,000 years ago, there was a shift in species composition from an *Eucalyptus* forest to non-forested moorland, which coincided with a forest fire, and that this non-forested moorland state has persisted for the past 7,000 years. Fletcher et al. (2014) proposed that the moorland state is maintained because low transpiration rates and the rhizomatous nature of moorland plants cause waterlogging, which prevents tree colonisation. This represents a positive PSF where moorland plants alter the physical properties of soil (root density and water content) in a way that prevents their replacement by tree species. This moorland system in Tasmania is analogous to *Kalmia* heath in that a fire disturbance explains a shift from a forested to non-forested state, and then the non-forested state persists due to PSF. The difference is that the PSF maintaining moorland involves changes to the physical properties of the soil, whereas the PSF in *Kalmia* heath involves changes to nutrient cycling and the composition of mycorrhizal fungi.

While PSF explains the stability of non-forested ecosystems in some instances, this result is not universal. In some instances, the non-forested state is maintained because dominant species alter the disturbance regime. This is the case in many grassland and savanna ecosystems, where frequent fires are necessary to maintain the ecosystem state, and the dominant plants favour frequent fire. In these systems, dominant species are pyrophytic plants that possess traits associated with flammability and high growth rates, enabling them to take advantage of post-fire conditions. Examples of such systems are Longleaf Pine savannas of the southeastern United States (Beckage et al., 2009; Hopkins et al., 2023, Platt et al., 2016), pine barrens of the northeastern United States (Quigley et al., 2020), and tropical savannas in the Brazilian Cerrado (Dantas et al., 2013). In other cases, changes to climate (Hirota et al., 2011), herbivory (Filbee-Dexter & Scheibling, 2014), or human intervention (Sühs et al., 2020) explain the persistence of a non-forested state. Even in the case of heathland ecosystems, it is not universally the case that PSF alone explains heath stability. Heathland ecosystems in northwestern Europe, dominated by ericaceous plants such as *Calluna vulgaris* or *Empetrum nigrum*, were traditionally maintained by humans through practices including prescribed burning, livestock grazing, and vegetation cutting (Webb, 1998). Over the past 100 years, these traditional management activities have been significantly reduced, causing many, but not all (Ransijn et al., 2014), northern European heathland areas to be replaced by grassland or forest (Curt et al., 2003; Løvschal et al., 2022; Mitchell et al., 1997; Vikane et al., 2013). Therefore, there are examples of heathland ecosystems where PSFs are insufficient to maintain the heathland state and instead require human intervention to be maintained. This suggests that whether PSF explains stability in heathland ecosystems or in non-forested ecosystems more broadly is context-dependent. To determine whether a non-forested ecosystem is likely to persist in the long term, it is important to consider all factors that may impact the stability of these ecosystems. The stability of non-forested ecosystems may be explained, depending on the context, by one or more of the following factors: PSFs (abiotic and/or biotic), plant-fire feedback, disturbance regimes, climate, herbivory, and/or human influences.

5. Conclusion

This study tested whether four ecosystem states in the *Kalmia*-black spruce system of eastern Newfoundland could be distinguished based on above-ground *Kalmia* traits and soil nutrient availability. The four ecosystem states were *Kalmia* heath, early-stage shrub savanna (eSS), mature shrub savanna (mSS), and black spruce forest. The four ecosystem states were found to be different based on four above-ground *Kalmia* traits related to litter quality (SLA, LDMC, foliar C:N, and foliar phenolics). *Kalmia* litter quality decreased from black spruce forest to mSS, to eSS, to *Kalmia* heath. Black spruce forest had higher soil nutrient availability (based on the indicators soil respiration, pH, inorganic N, total N, organic N to inorganic N ratio, and total phenolics) than the mSS, eSS, and *Kalmia* heath ecosystem states. The mSS, eSS, and *Kalmia* heath ecosystem states were not distinguishable based on indicators of soil nutrient availability. This shows that a PSF that creates nutrient-poor soil conditions explains the difference between the black spruce forest and the mSS, eSS, and *Kalmia* heath ecosystem states in eastern Newfoundland. This is because *Kalmia* litter quality and soil nutrient availability were significantly lower in the mSS, eSS, and *Kalmia* heath states than in the black spruce forest state. The mSS, eSS, and *Kalmia* heath ecosystem states must be distinguished by soil properties that were not measured in this study. Differences in mycorrhizal community composition or in the amount of organic N in protein-tannin complexes may be what distinguishes mSS, eSS, and *Kalmia* heath.

6. References

Adamczyk, B. (2021). How do terrestrial plants access high molecular mass organic nitrogen, and why does it matter for Soil Organic Matter Stabilization? *Plant and Soil*, *465*(1–2), 583–592. https://doi.org/10.1007/s11104-021-05022-8

Adhikari, K., Anderson, K. R., Smith, D. R., Owens, P. R., Moore, P. A., & Libohova, Z. (2023). Identifying key factors controlling potential soil respiration in agricultural fields. *Agricultural & Environmental Letters*, *8*(2). https://doi.org/10.1002/ael2.20117

Alonso-Amelot, M. E., Oliveros-Bastidas, A., & Calcagno-Pisarelli, M. P. (2007). Phenolics and condensed tannins of high altitude *Pteridium arachnoideum* in relation to sunlight exposure, elevation, and rain regime. *Biochemical Systematics and Ecology*, *35*(1), 1–10. https://doi.org/10.1016/j.bse.2006.04.013

Beckage, B., Platt, W. J., & Gross, L. J. (2009). Vegetation, fire, and feedbacks: A disturbance mediated model of savannas. *The American Naturalist*, *174*(6), 805 818. https://doi.org/10.1086/648458

Beisner, B., Haydon, D., & Cuddington, K. (2003). Alternative stable states in ecology. *Frontiers in Ecology and the Environment*, *1*(7), 376–382. https://doi.org/10.1890/1540 9295(2003)001[0376:assie]2.0.co;2

Bending, G. D., & Read, D. J. (1996). Nitrogen mobilization from protein-polyphenol complex by ericoid and ectomycorrhizal fungi. *Soil Biology and Biochemistry*, *28*(12), 1603–1612. https://doi.org/10.1016/s0038-0717(96)00258-1

Bennett, J. N., & Prescott, C. E. (2004). Organic and inorganic nitrogen nutrition of Western Red Cedar, western hemlock and Salal in mineral n-limited cedar–hemlock forests. *Oecologia*, *141*(3), 468–476. https://doi.org/10.1007/s00442-004-1622-3

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*(1–2), 279–293. https://doi.org/10.1007/s11104-005-0508-4

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*(1–2), 211–226. https://doi.org/10.1007/s11104-006-9130-3

Curt, T., Prévosto, B., Klesczewski, M., & Lepart, J. (2003). Post-grazing Scots pine colonization of mid-elevation heathlands: Population structure, impact on vegetation composition and diversity. *Annals of Forest Science*, *60*(7), 711–724. https://doi.org/10.1051/forest:2003065

Chomel, M., Guittonny-Larchevêque, M., Fernandez, C., Gallet, C., DesRochers, A., Paré, D., Jackson, B. G., & Baldy, V. (2016a). Plant secondary metabolites: A key driver of litter decomposition and soil nutrient cycling. *Journal of Ecology*, *104*(6), 1527–1541. https://doi.org/10.1111/1365-2745.12644

Chung, Y. A., Collins, S. L., & Rudgers, J. A. (2019). Connecting plant–soil feedbacks to long-term stability in a desert grassland. *Ecology*, *100*(8). https://doi.org/10.1002/ecy.2756

Coq, S., Cárdenas, R. E., Mousain, D., Selosse, M.-A., Richard, F., & Hättenschwiler, S. (2022). Acquisition of nitrogen from tannin protein complexes in ectomycorrhizal pine seedlings. *Pedobiologia*, *93–94*, 150817. https://doi.org/10.1016/j.pedobi.2022.150817

Dantas, V. de L., Batalha, M. A., & Pausas, J. G. (2013). Fire drives functional thresholds on the savanna–forest transition. *Ecology*, *94*(11), 2454–2463. https://doi.org/10.1890/12-1629.1

de Bello, F., Lavorel, S., Hallett, L. M., Valencia, E., Garnier, E., Roscher, C., Conti, L., Galland, T., Goberna, M., Májeková, M., Montesinos-Navarro, A., Pausas, J. G., Verdú, M., E-Vojtkó, A., Götzenberger, L., & Lepš, J. (2021). Functional trait effects on ecosystem stability: Assembling the jigsaw puzzle. *Trends in Ecology & Evolution*, *36*(9), 822–836. https://doi.org/10.1016/j.tree.2021.05.001

De Deyn, G. B., Raaijmakers, C. E., Zoomer, H. R., Berg, M. P., de Ruiter, P. C., Verhoef, H. A., Bezemer, T. M., & van der Putten, W. H. (2003). Soil invertebrate fauna enhances grassland succession and diversity. *Nature*, *422*(6933), 711–713. https://doi.org/10.1038/nature01548

Environment Canada. Canadian Climate Normals 1981–2010: Gambo, NL. 2017. Available online: http://climate.weather.gc.ca/ (accessed on 5 October 2025).

Fernández-Martínez, M., Vicca, S., Janssens, I. A., Carnicer, J., Martín-Vide, J., & Peñuelas, J. (2018). The consecutive disparity index, *d*: A measure of temporal variability in ecological studies. *Ecosphere*, *9*(12), e02527. https://doi.org/10.1002/ecs2.2527

Filbee-Dexter, K., & Scheibling, R. E. (2014). Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. *Marine Ecology Progress Series*, *495*, 1–25. https://doi.org/10.3354/meps10573

Fletcher, M.-S., Wood, S. W., & Haberle, S. G. (2014). A fire-driven shift from forest to non-forest: Evidence for alternative stable states? *Ecology*, *95*(9), 2504–2513. https://doi.org/10.1890/12-1766.1

Fox J, Weisberg S (2019). _An R Companion to Applied Regression_, Third edition. Sage, Thousand Oaks CA. <https://www.john-fox.ca/Companion/>.

González I, Déjean S (2023). _CCA: Canonical Correlation Analysis_. doi:10.32614/CRAN.package.CCA <https://doi.org/10.32614/CRAN.package.CCA>, R package version 1.2.2, <https://CRAN.R-project.org/package=CCA>.

Gourlay, G., Hawkins, B. J., Albert, A., Schnitzler, J., & Peter Constabel, C. (2021). Condensed tannins as antioxidants that protect poplar against oxidative stress from drought and UV B. *Plant, Cell & Environment*, *45*(2), 362–377. https://doi.org/10.1111/pce.14242

Graves S, Piepho H, Dorai-Raj LSwhfS (2024). _multcompView: Visualizations of Paired Comparisons_. doi:10.32614/CRAN.package.multcompView <https://doi.org/10.32614/CRAN.package.multcompView>, R package version 0.1-10, <https://CRAN.R-project.org/package=multcompView>.

Gross J, Ligges U (2015). _nortest: Tests for Normality_. doi:10.32614/CRAN.package.nortest <https://doi.org/10.32614/CRAN.package.nortest>, R package version 1.0-4, <https://CRAN.R-project.org/package=nortest>.

Gundale, M. J., Sverker, J., Albrectsen, B. R., Nilsson, M.-C., & Wardle, D. A. (2010). Variation in protein complexation capacity among and within six plant species across a borealforest chronosequence. *Plant Ecology*, *211*(2), 253–266. https://doi.org/10.1007/s11258010-9787-9

Hartemink, A. E., & Barrow, N. J. (2023). Soil PH - nutrient relationships: The diagram. *Plant and Soil*, *486*(1–2), 209–215. https://doi.org/10.1007/s11104-022-05861-z

Hättenschwiler, S., & Vitousek, P. M. (2000). The role of polyphenols in terrestrial ecosystem nutrient cycling. *Trends in Ecology & Evolution*, *15*(6), 238–243. https://doi.org/10.1016/s0169-5347(00)01861-9

Hirota, M., Holmgren, M., Van Nes, E. H., & Scheffer, M. (2011). Global resilience of tropical forest and savanna to critical transitions. *Science*, *334*(6053), 232–235. https://doi.org/10.1126/science.1210657

Hobbie, S. E. (2015). Plant species effects on nutrient cycling: Revisiting litter feedbacks. *Trends in Ecology & Evolution*, *30*(6), 357–363. https://doi.org/10.1016/j.tree.2015.03.015

Hopkins, J. R., Huffman, J. M., Jones, N. J., Platt, W. J., & Sikes, B. A. (2023). Pyrophilic plants respond to postfire soil conditions in a frequently burned longleaf pine savanna. *The American Naturalist*, *201*(3), 389–403. https://doi.org/10.1086/722569

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

Inderjit, & 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. https://doi.org/10.1016/s0378-1127(01)00463-7

Ingrisch, J., & Bahn, M. (2018). Towards a comparable quantification of resilience. *Trends in Ecology & Evolution*, *33*(4), 251–259. https://doi.org/10.1016/j.tree.2018.01.013

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. https://doi.org/10.1111/j.1469-8137.2007.02113.x

Joanisse, G. D., Bradley, R. L., & Preston, C. M. (2008a). Do late-successional tannin-rich plant communities occurring on highly acidic soils increase the DON/DIN ratio? *Biology and Fertility of Soils*, *44*(6), 903–907. https://doi.org/10.1007/s00374-008-0297-z

Joanisse, G. D., Bradley, R. L., Preston, C. M., & Bending, G. D. (2008b). 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. https://doi.org/10.1111/j.1469-8137.2008.02622.x

Joanisse, G. D., Bradley, R. L., & Preston, C. M. (2018). The spread of *Kalmia angustifolia* on Black Spruce Forest cutovers contributes to the spatial heterogeneity of Soil Resources. *PLOS ONE*, *13*(6), e0198860. https://doi.org/10.1371/journal.pone.0198860

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., Cornips, N. J., van Kempen, M. M., Bakx-Schotman, J. M., & van der Putten, W. H. (2007). Microbe-mediated plant–soil feedback causes historical contingency effects in Plant Community Assembly. *Ecological Monographs*, *77*(2), 147–162. https://doi.org/10.1890/06-0502

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. https://doi.org/10.1111/j.1461-0248.2006.00953.x

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., ... & Cornelissen, J. H. (2020). TRY plant trait database – enhanced coverage and open access. *Global Change Biology*, *26*(1), 119–188. https://doi.org/10.1111/gcb.14904

Kéfi, S., Domínguez-García, V., Donohue, I., Fontaine, C., Thébault, E., & Dakos, V. (2019). Advancing our understanding of ecological stability. *Ecology Letters*, *22*(9), 1349–1356. https://doi.org/10.1111/ele.13340

Kumaragamage, D., Warren, J., & Spiers, G. (2021). Soil chemistry. In M. Krzic, F. L. Walley, A. Diochon, M. C. Paré, & R. E. Farrell (Eds.), *Digging into Canadian soils: An introduction to soil science*. Canadian Society of Soil Science.

Løvschal, M., & Damgaard, C. F. (2022). Mapping the ecological resilience of Atlantic Postglacial Heathlands. *Journal of Applied Ecology*, *59*(11), 2825–2838. https://doi.org/10.1111/1365-2664.14278

Maithani, K., Arunachalam, A., Tripathi, R. S., & Pandey, H. N. (1998). Influence of leaf litter quality on N mineralization in soils of subtropical humid forest regrowths. *Biology and Fertility of Soils*, *27*(1), 44–50. https://doi.org/10.1007/s003740050398

Mallik, A.U. (1987). Allelopathic potential of *Kalmia angustifolia* to black spruce (*Picea mariana*). *Forest Ecology and Management*, *20*(1–2), 43–51. https://doi.org/10.1016/0378-1127(87)90149-6

Mallik, A. U. (2022). Post-fire habitat heterogeneity leads to black spruce–*Kalmia* L. Shrub savannah alternate state. *Forests*, *13*(4), 570. https://doi.org/10.3390/f13040570

Mallik, A., & Kayes, I. (2018). Lichen matted seedbeds inhibit while moss dominated seedbeds facilitate black spruce (*Picea mariana*) seedling regeneration in post-fire boreal forest. *Forest Ecology and Management*, *427*, 260–274. https://doi.org/10.1016/j.foreco.2018.05.064

Mallik, A., & Kravchenko, D. (2018). Recruitment and ontogenic patterns of stunting and growth release of black spruce (*Picea mariana*) in post-fire *Kalmia* Heaths. *Forest Ecology and Management*, *407*, 135–144. https://doi.org/10.1016/j.foreco.2017.09.068

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*, *85*(4), 513–522. https://doi.org/10.1093/forestry/cps047

Martinez Arbizu P (2017). _pairwiseAdonis: Pairwise Multilevel Comparison using Adonis_. R package version 0.4.1, commit cb190f7668a0c82c0b0853927db239e7b9ec3e83, <https://github.com/pmartinezarbizu/pairwiseAdonis>.

Menzel U (2022). _CCP: Significance Tests for Canonical Correlation Analysis (CCA)_. doi:10.32614/CRAN.package.CCP <https://doi.org/10.32614/CRAN.package.CCP>, R package version 1.2, <https://CRAN.R-project.org/package=CCP>.

Mitchell, R. J., Marrs, R. H., Duc, M. G., & Auld, M. H. (1997). A study of succession on lowland heaths in Dorset, southern England: Changes in vegetation and soil chemical properties. *The Journal of Applied Ecology*, *34*(6), 1426–1444. https://doi.org/10.2307/2405259

Näsholm, T., Högberg, P., Franklin, O., Metcalfe, D., Keel, S. G., Campbell, C., Hurry, V., Linder, S., & Högberg, M. N. (2013). Are ectomycorrhizal fungi alleviating or aggravating nitrogen limitation of tree growth in boreal forests? *New Phytologist*, *198*(1),214–221. https://doi.org/10.1111/nph.12139

Näsholm, T., Kielland, K., & Ganeteg, U. (2009). Uptake of organic nitrogen by plants. *New Phytologist*, *182*(1), 31–48. https://doi.org/10.1111/j.14698137.2008.02751.x

Nierop, K. G., & Verstraten, J. M. (2006). Fate of tannins in Corsican pine litter. *Journal of Chemical Ecology*, *32*(12), 2709–2719. https://doi.org/10.1007/s10886-006-9194-9

Ogle DH, Doll JC, Wheeler AP, Dinno A (2025). _FSA: Simple Fisheries Stock Assessment Methods_. doi:10.32614/CRAN.package.FSA <https://doi.org/10.32614/CRAN.package.FSA>, R package version 0.10.0, <https://CRAN.R-project.org/package=FSA>

Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Borman T, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill M, Lahti L, Martino C, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A, Ter Braak C, Weedon J (2025). _vegan: Community Ecology Package_. doi:10.32614/CRAN.package.vegan <https://doi.org/10.32614/CRAN.package.vegan>, R package version 2.7-1, <https://CRAN.R-project.org/package=vegan>.

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., … Cornelissen, J. H. (2013). New Handbook for Standardised Measurement of plant functional traits worldwide. *Australian Journal of Botany*, *61*(3), 167. https://doi.org/10.1071/bt12225

Platt, W. J., Ellair, D. P., Huffman, J. M., Potts, S. E., & Beckage, B. (2016). Pyrogenic fuels produced by savanna trees can engineer humid savannas. *Ecological Monographs*, *86*(3), 352–372. https://doi.org/10.1002/ecm.1224

Qu, Q., Xu, H., Wang, M., Liu, G., & Xue, S. (2022). Plant–soil feedback plays an important role in the progression of Plant Community Succession. *Journal of Plant Nutrition and Soil Science*, *186*(2), 169–176. https://doi.org/10.1002/jpln.202200292

Quested, H., Eriksson, O., Fortunel, C., & Garnier, E. (2007). Plant traits relate to whole community litter quality and decomposition following land use change. *Functional Ecology*, *21*(6), 1016–1026. https://doi.org/10.1111/j.1365 2435.2007.01324.x

Quigley, K. M., Kolka, R., Sturtevant, B. R., Dickinson, M. B., Kern, C. C., Donner, D. M., & Miesel, J. R. (2020). Prescribed burn frequency, vegetation cover, and management legacies influence soil fertility: Implications for restoration of imperiled pine barrens habitat. *Forest Ecology and Management*, *470–471*, 118163. https://doi.org/10.1016/j.foreco.2020.118163

Rains, K. C., Bledsoe, C., Kraus, T. E., & Wurzburger, N. (2024). Evidence that ericoid mycorrhizal shrubs can outcompete ectomycorrhizal trees for nitrogen in tannin-rich litter. *Ecosphere*, *15*(3), e4818. https://doi.org/10.1002/ecs2.4818

Ransijn, J., Kepfer-Rojas, S., Verheyen, K., Riis-Nielsen, T., & Schmidt, I. K. (2014). Hints for alternative stable states from long-term vegetation dynamics in an unmanaged heathland. *Journal of Vegetation Science*, *26*(2), 254–266. https://doi.org/10.1111/jvs.12230

R Core Team (2025). _R: A Language and Environment for Statistical Computing_. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R project.org/>.

Read, D. J., Leake, J. R., & Perez-Moreno, J. (2004). Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes. *Canadian Journal of Botany*, *82*(8), 1243–1263. https://doi.org/10.1139/b04-123

Rocha, M. R., Gaedke, U., & Vasseur, D. A. (2011). Functionally similar species have similar dynamics. *Journal of Ecology*, *99*(6), 1453–1459. https://doi.org/10.1111/j.1365-2745.2011.01893.x

Satti, P., Mazzarino, M. J., Gobbi, M., Funes, F., Roselli, L., & Fernandez, H. (2003). Soil N dynamics in relation to leaf litter quality and soil fertility in north-western Patagonian forests. *Journal of Ecology*, *91*(2), 173–181. https://doi.org/10.1046/j.13652745.2003.00756.x

Scott, N. A., & Binkley, D. (1997). Foliage litter quality and annual net N mineralization: Comparison across North American Forest Sites. *Oecologia*, *111*(2), 151–159. https://doi.org/10.1007/s004420050219

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. https://doi.org/10.1007/s00442-010-1642-0

Soil Classification Working Group. 1998. The Canadian System of Soil Classification, 3rd ed. Agriculture and Agri-Food Canada Publication 1646, 187 pp.

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

St. James, C. (2023). *Floristic composition and functional stability of black spruce-Kalmia shrub savannah* (thesis). Lakehead University. Retrieved from https://lurepository.lakeheadu.ca/handle/2453/5080.

St Martin, P. (2018). *A functional trait analysis of successional pathway dynamics* (thesis). Retrieved from https://lurepository.lakeheadu.ca/bitstream/handle/2453/4404/St.%20MartinP2018d-1b.pdf?sequence=1&isAllowed=y.

St. Martin, P., & Mallik, A. U. (2016). Growth release of stunted black spruce (*Picea mariana*) in *Kalmia* heath: The role of ectomycorrhizal fungi and near-ground microclimate. *Canadian Journal of Forest Research*, *46*(5), 666–673. https://doi.org/10.1139/cjfr-2015-0267

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. https://doi.org/10.1007/s00442-021-04864-4

Sühs, R. B., Giehl, E. L., & Peroni, N. (2020). Preventing traditional management can cause grassland loss within 30 years in southern Brazil. *Scientific Reports*, *10*(1). https://doi.org/10.1038/s41598-020-57564-z

Tabatabai, M. A., Ekenler, M., & Senwo, Z. N. (2010). Significance of enzyme activities in soil nitrogen mineralization. *Communications in Soil Science and Plant Analysis*, *41*(5), 595–605. https://doi.org/10.1080/00103620903531177

van der Putten, W. H., Bardgett, R. D., Bever, J. D., Bezemer, T. M., Casper, B. B., Fukami, T., Kardol, P., Klironomos, J. N., Kulmatiski, A., Schweitzer, J. A., Suding, K. N., Van de Voorde, T. F., & Wardle, D. A. (2013). Plant–soil feedbacks: The past, the present and future challenges. *Journal of Ecology*, *101*(2), 265–276. https://doi.org/10.1111/1365-2745.12054

Van Meerbeek, K., Jucker, T., & Svenning, J. (2021). Unifying the concepts of stability and resilience in ecology. *Journal of Ecology*, *109*(9), 3114–3132. https://doi.org/10.1111/1365-2745.13651

Varma, V & Osuri, A.M. (2013). Black Spot: a platform for automated and rapid estimation of leaf area from scanned images. *Plant Ecology*, *214*, 1529-1534. https://doi.org/10.1007/s11258-013-0273-z

Vikane, J. H., Vandvik, V., & Vetaas, O. R. (2013). Invasion of *Calluna* heath by native and non-native conifers: The role of succession, disturbance and allelopathy. *Plant Ecology*, *214*(7), 975–985. https://doi.org/10.1007/s11258-013-0223-9

Walker, L. C. (2021). *All fired up: A long-term fire history of the coastal boreal forest of Newfoundland, Canada* (thesis). Retrieved from https://memorial.scholaris.ca/server/api/core/bitstreams/af973751-ea35-4d58-b1d0-db295da4f898/content.

Wickham H, Averick M, Bryan J, Chang W, McGowan LD, François R, Grolemund G, Hayes A, Henry L, Hester J, Kuhn M, Pedersen TL, Miller E, Bache SM, Müller K, Ooms J, Robinson D, Seidel DP, Spinu V, Takahashi K, Vaughan D, Wilke C, Woo K, Yutani H (2019). “Welcome to the tidyverse.” _Journal of Open Source Software_, *4*(43), 1686. doi:10.21105/joss.01686 <https://doi.org/10.21105/joss.01686>.

Wickham H, François R, Henry L, Müller K, Vaughan D (2023). _dplyr: A Grammar of Data Manipulation_. doi:10.32614/CRAN.package.dplyr <https://doi.org/10.32614/CRAN.package.dplyr>, R package version 1.1.4, <https://CRAN.R-project.org/package=dplyr>.

Witkowski, E. T., & Lamont, B. B. (1991). Leaf specific mass confounds leaf density and thickness. *Oecologia*, *88*(4), 486–493. https://doi.org/10.1007/bf00317710

Whittle, C. A., Duchesne, L. C., & Needham, T. (1997). The impact of broadcast burning and fire severity on species composition and abundance of surface vegetation in a jack pine (pinus banksiana) clear-cut. *Forest Ecology and Management*, *94*(1–3), 141–148. https://doi.org/10.1016/s0378-1127(96)03969-2

Wood, S. W., & Bowman, D. M. (2011). Alternative stable states and the role of fire–vegetation–soil feedbacks in the temperate wilderness of Southwest Tasmania. *Landscape Ecology*, *27*(1), 13–28. https://doi.org/10.1007/s10980-011-9677-0

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., … Villar, R. (2004). The Worldwide Leaf Economics Spectrum. *Nature*, *428*(6985), 821–827. https://doi.org/10.1038/nature02403

Wu, T. (2011). Can ectomycorrhizal fungi circumvent the nitrogen mineralization for plant nutrition in temperate forest ecosystems? *Soil Biology and Biochemistry*, *43*(6), 1109–1117. https://doi.org/10.1016/j.soilbio.2011.02.003

Wu, T., Kabir, Z., & Koide, R. T. (2005). A possible role for saprotrophic microfungi in the N nutrition of ectomycorrhizal *Pinus resinosa*. *Soil Biology and Biochemistry*, *37*(5), 965–975. https://doi.org/10.1016/j.soilbio.2004.10.015

Wu, T., Sharda, J. N., & Koide, R. T. (2003). Exploring interactions between saprotrophic microbes and ectomycorrhizal fungi using a protein–tannin complex as an n source by red pine (*Pinus resinosa*). *New Phytologist*, *159*(1), 131–139. https://doi.org/10.1046/j.1469-8137.2003.00800.x

Wurzburger, N., & Hendrick, R. L. (2009). Plant Litter Chemistry and mycorrhizal roots promote a nitrogen feedback in a temperate forest. *Journal of Ecology*, *97*(3), 528–536. https://doi.org/10.1111/j.1365-2745.2009.01487.x

Xiao, W., Ge, X., Zeng, L., Huang, Z., Lei, J., Zhou, B., & Li, M. (2014). Rates of litter decomposition and soil respiration in relation to soil temperature and water in different aged *Pinus massoniana* forests in the Three Gorges Reservoir area, China. *PLOS ONE*, *9*(7). https://doi.org/10.1371/journal.pone.0101890

Yamasaki, S. H., Fyles, J. W., & Titus, B. D. (2002). Interactions among *Kalmia angustifolia*, soil characteristics, and the growth and nutrition of black spruce seedlings in two boreal Newfoundland plantations of contrasting fertility. *Canadian Journal of Forest Research*, *32*(12), 2215–2224. https://doi.org/10.1139/x02-119

Zhang, Z., & Adamczyk, B. (2025). Independent of saprotrophic interactions, ectomycorrhizal fungi facilitate nitrogen utilization from protein-tannin complex by Chinese pine (*Pinus tabuliformis*). *Applied Soil Ecology*, *214*, 106372. https://doi.org/10.1016/j.apsoil.2025.106372

Zhu, H., & Mallik, A. U. (1994). Interactions Between *Kalmia* and black spruce: Isolation and identification of allelopathic compounds. *Journal of Chemical Ecology*, *20*(2), 407–421. https://doi.org/10.1007/bf02064447

Appendix 1: Mean species abundances (percent cover) in the seven vegetation types: heath open area (HO), heath spruce patch (HS), Dunphy's Pond open area (DPO), Dunphy's Pond spruce patch (DPS), SS open area (SSO), SS black spruce island (SSI), and mature black spruce forest (F).

Species	HO	HS	DPO	DPS	SSO	SSI	F
Trees							
Picea mariana	0	5.22	0.17	16.67	0	61.67	72.22
Larix laricina	0	0	0	0	3.39	4.67	0
Shrubs							
Alnus viridis	0.06	0	0	0	0	0	4.75
Amelanchier spp.	0.14	0.14	0	0.25	0.25	0.86	0
Chamaedaphne calyculata	0.28	0.56	0	0	0	0	0
Ilex mucronata	1.03	0.83	0.97	1.08	1.81	1.67	0
Kalmia angustifolia	30.14	29.5	43.47	44.17	32.36	30.39	5.17
Rhododendron canadense	2.22	3.42	6.53	9.00	9.89	1.67	0.08
Rhododendron groenlandicum	1.19	1.36	0.22	0.28	1.28	0.42	0
Vaccinium angustifolium	3.14	3.44	5.28	4.19	4.47	1.83	0.42
Vaccinium vitis-idaea	0	0	0	0	0	0.11	0
Viburnum spp.	0.08	0	0.08	0.14	0.22	0.22	0
Juniperus communis	0	0	0.06	0.28	0	0	0
Herbs							
Cornus canadensis	0.83	0.61	0.72	1.03	4.42	3.89	0
Maianthemum canadense	0.08	0.11	0.03	0.06	0	0	0
Trientalis borealis	0	0	0	0.06	0	0.17	0
Ferns							
Pteridium aquilinum	0	0	1.61	0.94	0.47	0	0
Lichens							
Cladonia stellaris	9.00	7.50	9.31	10.58	58.89	20.06	0
Cladonia rangiferina	28.61	25.72	30.97	26.50	4.36	3.58	0.03
Cladonia mitis	9.53	7.64	11.72	10.25	3.25	2.03	0.36

Species	HO	HS	DPO	DPS	SSO	SSI	F
Cladonia unicialis	18.67	10.92	1.39	0.64	0	0	0
Cladonia cristatella	0.33	0.67	0	0	0	0	0
Cladonia chlorophaea	0.14	0.14	0	0	0	0.03	0
Cladonia fimbriata	0	0.06	0	0	0	0.17	0.22
Cladonia verticillata	0	0	0	0	0	0.19	0.33
Cladonia cornuta	0	0.14	0	0	0	0	0
Cladonia cenotea	0	0.22	0	0	0	0	0
Platismatia glauca	0.03	0.33	0	0.25	0.06	12.39	2.78
Hypogymnia physodes	1.22	1.42	1.00	1.36	1.50	8.75	3.39
Usnea spp./Alectoria sarmentosa	0	0.03	0	0.19	0.06	5.47	0.39
Bryoria trichodes	0.03	0.19	0	0.39	0.14	9.08	1.00
Icmadophila ericetorum	0	0.42	0	0	0	0	0
Mosses							
Dicranum polysetum	1.75	2.06	2.19	3.06	3.89	3.11	5.03
Dicranum scoparium	0	0.42	0	0	0	2.22	3.22
Dicranum spp.	1.83	1.25	0.97	0.72	0	0	0
Polytrichum juniperinum	0.92	2.75	0	0	0	0	0.47
Ptilium crista-castrensis	0	0	0.03	0	0	0	3.53
Hylocomium splendens	0	0	0.14	0	0.06	1.11	2.50
Pleurozium schreberi	2.81	3.67	22.78	23.25	14.58	37.92	62.00
Sphagnum spp.	1.39	1.67	0	0	0	0	0

Appendix 2: Functional trait matrix for three traits: specific leaf area (SLA), leaf dry matter content (LDMC), and foliar C:N ratio (C:N). Trait values for *Kalmia angustifolia* are not shown since intraspecific trait variation was considered when calculating CWM traits. The table also shows the source used to obtain values for SLA and LDMC. All values for foliar C:N ratio came from the TRY database (Kattge et al., 2020). Uncertainty ranges are one standard deviation, and *n* represents the sample size. There is no information on the uncertainty range and on the sample size for the data from St. Martin & Mallik (2019).

Species	Source (SLA & LDMC)	SLA (cm^2/g)	LDMC (g/g)	C:N
Alnus viridis	St. Martin & Mallik (2019)	114.4	0.394	N/A
Amelanchier spp.	St. Martin & Mallik (2019)	167.2	0.397	19.3 ± 3.2 n = 55
Chamaedaphne calyculata	Kattge et al. (2020)	129.2 ± 10.6 n = 13	0.501 ± 0.017 n = 10	39.52 ± 2.1 n = 2
Ilex mucronata	St. Martin & Mallik (2019)	183.6	0.375	29.7 ± 0.8 n = 3
Rhododendron canadense	Personal measurement	137.9 ± 45.1 n = 34	0.418 ± 0.036 n = 34	30.1 ± 1.5 n = 2
Rhododendron groenlandicum	Personal measurement	69.2 ± 10.1 n = 18	0.476 ± 0.029 n = 18	35.6 ± 4.2 n = 10
Vaccinium angustifolium	Personal measurement	135.7 ± 26.4 n = 42	0.402 ± 0.041 n = 42	26.3 ± 5.1 n = 78
Vaccinium vitis-idaea	St. Martin & Mallik (2019)	65.1	0.469	48.1 ± 14.8 n = 151
Viburnum spp.	St. Martin & Mallik (2019)	144.9	0.327	31.5 ± 13.7 n = 18
Cornus canadensis	St. Martin & Mallik (2019)	204.2	0.206	23.3 ± 4.2 n = 32
Maianthemum canadense	St. Martin & Mallik (2019)	305.6	0.206	22.0 ± 3.6 n = 92
Pteridium aquilinum	Kattge et al. (2020)	285.9 ± 15.1 n = 15	0.282 ± 0.144 n = 88	20.2 ± 6.1 n = 79
Trientalis borealis	St. Martin & Mallik (2019)	253.0	0.296	22.4 ± 8.2 n = 18
Juniperus communis	Kattge et al. (2020)	102.2 ± 9.8 n = 27	0.490 ± 0.098 n = 131	42.0 ± 9.8 n = 51

Appendix 3: Variation in soil carbon percentage in plots from five vegetation types: heath, Dunphy's Pond, open areas of SS (SS open), black spruce islands in SS (SS island), and black spruce forest (forest).