

Drivers of Functional Diversity in Native Ericaceae Species Across Nova Scotia

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Abstract

Plant functional diversity is defined by variation in morphological, chemical, or phenological characteristics that influence the way a plant functions. Variation in such traits across different species can be influenced by evolutionary history and environmental factors. Functional traits can also vary within species, and the level of within-species trait plasticity can vary among species and habitats. This study investigates the relative influence of evolutionary history and environmental variation (light, nutrient availability, water) in driving plant functional diversity across 24 species from the Ericaceae family. Plants were sampled across three habitat types (barren, bog, and forest) in Nova Scotia. Morphological traits measured were specific leaf area (SLA), leaf dry matter content (LDMC), leaf thickness (Lth), leaf size (LS), and leaf arrangement (alternate or opposite). Chemical traits measured were leaf pH, and phenological traits were leaf lifespan (evergreen or deciduous) and flowering strategy (precocious or serotinous). Leaf arrangement, leaf lifespan, and leaf pH were influenced by evolutionary history, but the relative influence of evolutionary history was weaker at the family level than at a broader taxonomic scale. All traits were influenced by environmental factors and all traits except leaf pH and leaf arrangement are likely driven more by variation in light than soil water availability. In addition, some species exhibited higher trait plasticity than others. Understanding which environmental factors influence traits, which species had higher levels of plasticity, and the role that evolution and the environment play in shaping those traits is important to understand how species will cope with increasing environmental pressures from climate change.

Date: April 1, 2024

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1.0 Introduction

Plants possess characteristic functional traits that provide insight into their overall performance and function (Kearney et al., 2021). Understanding what factors drive trait differences among species is key to interpreting diversity in nature. Plant traits can vary among species and habitats due to evolutionary and environmental influences. Evolutionary drivers may cause closely related species to have similar traits as traits that were successful in the past are inherited by future generations; distantly related species may have different traits as traits are not being inherited by the same common ancestor (Calow, 1987). Environmental drivers can cause species within the same habitat to be similar due to shared environmental pressures and species in different habitats may be dissimilar as they are experiencing different environmental pressures (Cavender-Bares et al., 2004). The relative influence of evolutionary and environmental factors on plant functional traits can vary across different species and taxonomic groups (Goud and Sparks, 2018; Júnior and Torres Boeger, 2016).

1.1 Plant Functional Traits

Measuring plant functional traits has been an important method for understanding how species similarities and differences are driven by the environment (Pakeman and Stockan, 2014). Plant functional traits can be morphological (e.g., leaf size, leaf thickness), chemical (e.g., leaf pH, nutrient content), or phenological (e.g., flowering strategy, germination rate) (Pérez-Harguindeguy et al., 2013). Trait variation is often influenced by light, nutrients, and water availability because these resources are critical for plant growth and survival (Pérez-Harguindeguy et al., 2013).

Light is required for biochemical processes such as photosynthesis, which creates the energy necessary for plant function and survival (Clark et al., 2018). Photosynthesis is directly

influenced by light availability; however, some morphological traits can influence the amount of light a plant receives. These morphological traits include specific leaf area (SLA, the ratio of one-sided leaf area to dry mass), leaf size (LS, the average one-sided area of a leaf), and leaf thickness (Lth, the thickness or depth of a leaf in millimetres) (Goud & Roddy, 2022; Pérez-Harguindeguy et al., 2013). Larger SLA and LS are related to a higher index of light interception (the amount of solar radiation absorbed by a leaf) and therefore are more likely to be larger in lower-light habitats to maximize the amount of light they receive (Goud & Roddy, 2022). Lth increases with light intensity as thicker leaves have more layers to absorb solar radiation, and therefore are more efficient than thin leaves in habitats with intense sunlight (Burns, 2004). As critical as light is to plant function, nutrients also play a large role in shaping functional diversity within plants.

Soil nutrients such as nitrogen and potassium are important for growth and physiological processes (Clark et al., 2018), and nutrient availability influences morphological traits such as SLA, Lth, and LS, chemical traits such as leaf pH, and phenological traits such as leaf lifespan (evergreen or deciduous) (Aerts, 1995; Pérez-Harguindeguy et al., 2013). SLA tends to be smaller, and Lth tends to be larger when soil is more nutrient-poor, as these features conserve nutrients more effectively (Gong & Gao, 2019; Mooney & Dunn, 1970; Westoby et al., 2002; Wilson et al., 1999). Like SLA, LS tends to be smaller in resource-poor environments as resources for large leaf construction are unavailable (Ashton & Hall, 1992; Xu et al., 2009). The pH of a leaf tends to correlate with the type of nutrients present in the soil: high levels of cations such as calcium, magnesium, and potassium often lead to more alkaline or higher leaf pH, and the presence of organic acids often leads to more acidic or lower leaf pH (Pérez-Harguindeguy et al., 2013). Leaf lifespan (evergreen or deciduous) allows plants to have different strategies along

a nutrient gradient, and evergreen leaves are known to have low nutrient loss rates allowing them to be more adapted to living in a nutrient-poor environment (Aerts, 1995).

Water is also essential for plants, as it is required for many metabolic and physiological processes including photosynthesis and soil nutrient uptake (Clark et al., 2018). Morphological traits related to water use include SLA, LS, and leaf dry matter content (LDMC, the ratio of dry mass to fresh mass), and phenological traits related to water use include flowering strategy (precocious or serotinous)(Garnier et al., 2019; Markesteijn et al., 2011; Pérez-Harguindeguy et al., 2013). SLA is shown to be smaller in drier habitats (Laine et al., 2021) as smaller SLA decreases leaf evaporative water loss (Goud & Roddy, 2022). LS also tends to be smaller with limited water availability, as the construction of large leaves is structurally expensive and larger leaves provide more surface area for water evaporative loss (Goud & Roddy, 2022; Xu et al., 2009). The opposite is the case for LDMC, where studies have found that in stressful, drier environments, LDMC tends to be larger to combat drought (Garnier et al., 2019; Markesteijn et al., 2011). Earlier flowering times limit the exposure of flowers to water limitations, providing an advantage in drier habitats (Shavrukov et al., 2017).

1.2 Evolutionary Drivers

Evolutionary history may influence patterns of functional trait diversity in plants. Closely related species may share similar functional traits due to inheriting them from a common ancestor (Darwin, 1859; Webb et al., 2002). When closely related species share more similar traits than distantly related species the traits are considered phylogenetically conserved, while trait dissimilarity among close relatives is considered phylogenetic divergence (Figure 1.1) (Ávila-Lovera et. al 2023). Conserved traits are often less variable within species as evolutionary aspects play a large role in driving patterns of trait variation (Ávila-Lovera et. al 2023). For

example, a study on Ericaceae species across North America showed that leaf carbon (C) and nitrogen (N) stable isotope ratios were more similar between closely related species due to their shared evolutionary history, despite considerable variation in habitat preferences (Goud & Sparks, 2018). It is important however to take environmental factors into account when comparing evolutionary influences, as closely related species in a shared environment can display similar trait values due to shared responses to environmental drivers rather than evolutionary relatedness (Cavender-Bares et al., 2004).

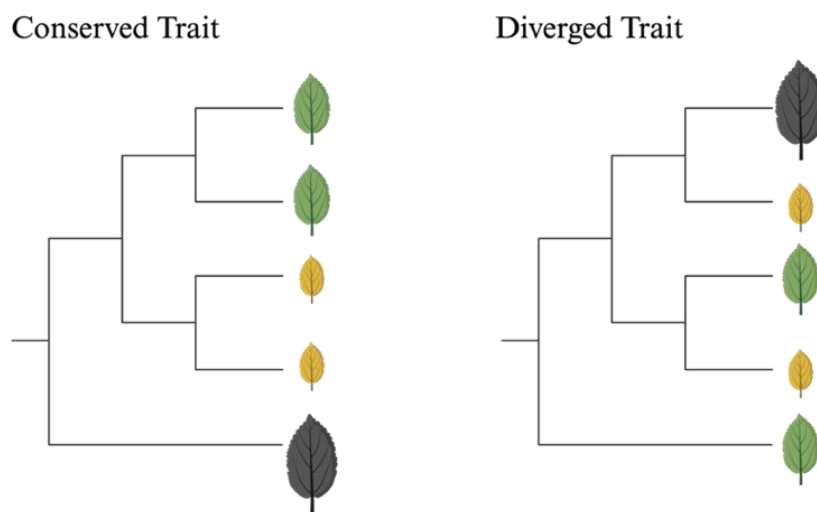


Figure 1.1. A visual representation of conserved vs diverged traits. The figure shows trait variation across a phylogenetic tree, where conserved traits are traits that are similar between closely related species, and diverged traits are trait differences between closely related species. Created with BioRender.com.

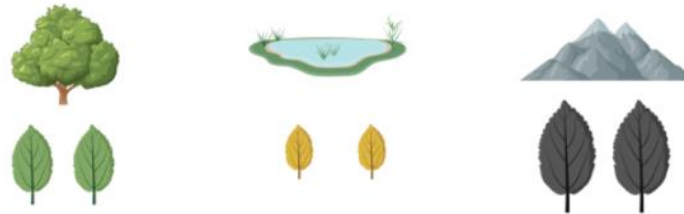
1.3 Environmental Drivers

Plasticity is the ability of a genotype to produce differing phenotypes in response to environmental change (Gratani, 2014). Species with plastic functional traits can adjust to multiple environments (Bradshaw, 2006), and the level of plasticity can vary between traits and species. For example, SLA may get larger within a species as water availability increases to increase transpiration (Goud & Roddy, 2022), whereas leaf arrangement (opposite or alternate)

often does not change across an environmental gradient as it is a genetically determined trait (Steeves & Sussex, 1989). Certain species may also have more plastic traits than others; for example, Júnior and Torres Boeger (2016) found that SLA had differing levels of plasticity across different shrub species in Southern Brazil.

A lack of trait plasticity can limit species from existing in a certain habitat, and the exclusion of an organism from a habitat due to environmental factors is called environmental filtering (Cavender-Bares et al., 2004). Evidence for environmental filtering is trait or phenotypic clustering, which is when species with similar traits occur together in an ecosystem (Figure 1.2) (Cavender-Bares et al., 2004; Cornwell et al., 2006; Weiher & Keddy, 1999). Phenotypically clustered traits within a habitat show evidence for environmental filtering, as similar traits within a habitat suggest such traits are essential for surviving in that habitat. For example, Prieto et al. (2017) observed phenotypic clustering in lichen species, where lichens with a high surface area to mass ratio occurred in drier habitats as this trait allows for better water capture. When traits are not predominantly within a habitat (phenotypic overdispersion), this suggests that environmental filtering is playing less of a role in shaping patterns of functional diversity and perhaps evolutionary aspects or niche partitioning may be driving trait diversity instead (Cavender-Bares et al., 2004).

a. Phenotypic Clustering



b. Phenotypic Overdispersion

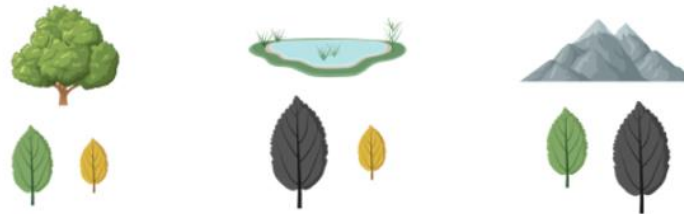


Figure 1.2. A visual representation of phenotypic clustering vs overdispersion. A shows phenotypic clustering, where traits such as leaf colour or size are similar within the same environment. B shows overdispersion, where traits of a plant are dispersed among the different habitats. Created with BioRender.com.

1.4 Research Objectives

The relative roles that evolutionary history and the environment have on shaping plant functional traits are often known when comparing broad taxonomic groups of plants such as bryophytes, gymnosperms, and angiosperms, however, the relative role of these drivers at smaller taxonomic scales such as within a family or clade is less clear (Goud et al., 2019). Understanding how evolutionary history and environmental factors interact to shape variation in plant traits within specific taxonomic groups is essential for predicting responses to environmental change and advancing our knowledge of trait evolution and functional diversity at finer taxonomic scales. The overarching goal of this work is to investigate patterns of functional diversity within the same family to determine the relative roles of environment and evolutionary history in shaping patterns of trait variation. My approach was to measure plant traits and

environmental variables for species within the Ericaceae family across three habitats in Nova Scotia that varied across light, nutrient, and water gradients: barrens, bogs, and hardwood forests.

1.4.1 Habitats and Species of Interest

Barrens are a type of heathland dominated by low shrubs and characterized by shallow, resource-limited soils (Porter et.al. 2020). Barren habitats often experience extreme temperatures and natural disturbances such as hurricanes or wildfires (Oberndorfer and Lundholm 2009). Different barren classifications experience unique environmental pressures, for example, coastal rock barrens experience high salinity and winds and have shallow soils which deter tree growth, whereas sand barrens have relatively deeper but sandy soils which can support some trees (Porter et.al., 2020).

Bogs are a type of peatland ecosystem, characterized by water-saturated organic soils (peat) with limited oxygen availability (Rydin & Jeglum, 2013). The soils are extremely nutrient-poor, acidic, and have low plant decomposability (Rydin and Jeglum 2013). The growth of many vascular plants such as trees is also limited within bogs (Breemen, 1995), which can lead to increased sun exposure.

Forests in Nova Scotia are temperate forests, which are classified as ecosystems dominated by winter-deciduous trees (Barbour & Christensen, 2019). These habitats are less harsh than barrens and bogs as they are sheltered by a tree canopy and generally have more nutrient-rich soils (Neily et al., 2010). However, specific forest sub-types experience different levels of environmental stressors. For instance, coastal forests (within 100km of the coast) experience salt stress and coastal winds, open woodlands have decreased tree density and increased exposure levels, and deciduous, coniferous, and mixed-wood forests have denser tree cover and less exposure (Neily et al., 2010).

Across all three habitat types, multiple species of Ericaceae are present. The Ericaceae family is widely distributed across North America, living in temperate, arctic, alpine, and tropical regions; there are approximately 4100 species of Ericaceae around the world, 212 of which occur in North America (Tucker, 2009). Of the North American species, there are four major clades, Monotropeoideae, Arbutoideae, Ericoideae, and Vaccinioideae. Within Nova Scotia, approximately 30 species of Ericaceae occur in a variety of habitats, with at least one member of each of the four major clades represented. In habitats where one species of Ericaceae occurs, there are often many Ericaceae species present. This family is an ideal study system for testing the relative influence of evolutionary and environmental drivers on functional diversity as species occur across a variety of habitat types that vary across multiple environmental gradients. The main research questions are:

1. What is the range of trait variation within and among Nova Scotia Ericaceae species?
2. What are the relative roles of evolutionary history and environmental variation in shaping functional diversity patterns within Nova Scotia Ericaceae?

Because barrens, bogs, and forests differ greatly in light, water, and soil nutrient availability, I predict that the environment will be the main driving factor of species differences. Due to SLA and LS often increasing with shade, nutrients, and water, I predict that SLA and LS will be largest in the forest and smallest in the barren. It is unclear whether these traits will be large in the bog due to a surplus of water, or small due to lack of nutrients. LDMC tends to increase with light and decrease with water availability, and Lth tends to increase with higher light and decreased nutrient availability. I predict that Lth will be largest in the barrens and bogs, and smallest in the forest, and LDMC will be largest in the barren and smallest in the forest. It is unclear if the LDMC will be large in the bog due to increased light, or small due to a surplus of

water. I predict that leaf pH will be highest in the barren due to increased salt in the soil from the ocean and the smallest in the bog due to the presence of acidic soils. Evergreen species tend to be more competitive than deciduous species in nutrient-poor environments, therefore I predict that there will be more evergreen species in the barren and bog, and the least in the forest. I predict that the most precocious species will occur in the barren and the least in the bog as earlier flowering periods often relate to drought avoidance. The functionality of leaf arrangement is unclear; therefore I predict that there will be no difference in the amount of opposite and alternate species between habitats.

2.0 Materials and Methods

2.1 Study System

Twenty-four species of Ericaceae from four major clades were collected between June-August of 2023 to represent diversity in functional traits and ecology. Of these species, five were found in all three habitats, 13 were found in only one habitat, and six were found in two out of three of the habitats (Table 2.1)

Table 2.1. Species of Ericaceae collected in this study and their major clade across habitats in Nova Scotia. Check marks represent which habitat types species were collected from, and rectangles represent which habitat types species are known to be present in, but were not collected from in this study.

Species	Clade	Bog	Forest	Barren
<i>Andromeda polifolia</i>	Vaccinioideae	✓		
<i>Arctostaphylos uva-ursi</i>	Arbutoideae			✓
<i>Chamaedaphne calyculata</i>	Vaccinioideae	✓	✓	✓
<i>Chimaphila umbellata</i>	Arbutoideae		✓	
<i>Corema condradii</i>	Ericoideae			✓
<i>Empetrum nigrum</i>	Ericoideae	✓	✓	✓
<i>Empetrum rubrum</i>	Ericoideae			✓
<i>Epigaea repens</i>	Ericoideae		✓	
<i>Gaultheria hispidula</i>	Vaccinioideae		✓	
<i>Gaultheria procumbens</i>	Vaccinioideae		✓	✓

<i>Gaylussacia baccata</i>	Vaccinioideae	✓	✓	✓
<i>Gaylussacia bigeloviana</i>	Vaccinioideae	✓		✓
<i>Kalmia angustifolia</i>	Ericoideae	✓	✓	✓
<i>Kalmia polifolia</i>	Ericoideae	✓		
<i>Monotropa hypopithys</i>	Monotropeoideae		✓	
<i>Monotropa uniflora</i>	Monotropeoideae		✓	
<i>Rhododendron canadense</i>	Ericoideae		✓	✓
<i>Rhododendron groenlandicum</i>	Ericoideae	✓	•	✓
<i>Vaccinium angustifolium</i>	Vaccinioideae	•	✓	✓
<i>Vaccinium corymbosum</i>	Vaccinioideae	•	✓	
<i>Vaccinium macrocarpon</i>	Vaccinioideae	✓	✓	✓
<i>Vaccinium myrtilloides</i>	Vaccinioideae	•	✓	
<i>Vaccinium oxycoccus</i>	Vaccinioideae	✓	✓	•
<i>Vaccinium vitis-idaea</i>	Vaccinioideae		•	✓

2.2 Phylogenetic Analysis

2.2.1 Evolutionary Relationships

Species evolutionary relationships were estimated using a multi-gene maximum likelihood molecular phylogeny. A pruned phylogenetic tree was created in R version 4.3.1 (R Core Team, 2023) by importing a previously published phylogenetic tree that was created with 106 Ericaceae species (Goud & Sparks, 2018). This tree is a maximum likelihood tree created using the genes matK, rbcL, and nrITS. The tree was pruned in R version 4.3.1 (R Core Team, 2023) by combining the larger phylogeny with a list of the 24 species of interest. Some species substitutions were made in this process, as the phylogeny did not include all the species of interest. The closest relative to the missing species was used as an approximation place, where *Allotropa virgata* was used in place of *Monotropa uniflora*, and *Gaylussacia dumosa* was used

instead of *Gaylussacia bigeloviana*.

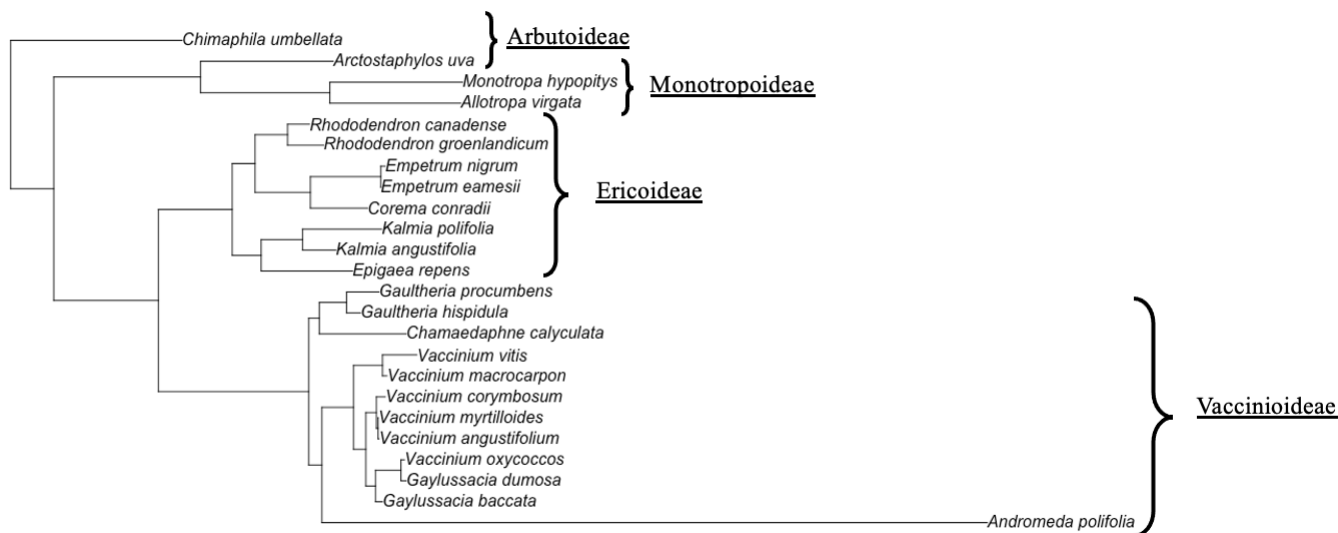


Figure 2.2. A pruned phylogenetic tree of the species of interest. The original tree had 106 species of Ericaceae that were made using genes *rbcL*, *nrITS* and *matK* (Goud and Sparks 2018). That larger tree was pruned to only include 24 species.

Some inconsistencies are shown within this tree when compared to other phylogenetic trees in the literature (Kron et al., 2002). The major clades are still shown within this tree, but *Vaccinium oxycoccus* is grouped with the *Gaylussacia* species rather than the other *Vaccinium* species. *Chimaphila* is also shown as the most ancestral species, when the *Monotropa* species are actually the most ancestral (Kron et al., 2002).

2.2.2 Phylogenetic Signal

Trait similarity due to common ancestry was evaluated using phylogenetic signal. Phylogenetic signal between species was tested by comparing trait values against the pruned phylogenetic tree. These analyses were done in R Version 4.3.1 (R Core Team, 2023), using packages “Geiger” (Pennell et al. 2014) and “phytools” (Revell 2024). Two variables were calculated for phylogenetic signal of continuous traits: Pagels’s lambda and Blomberg’s K. These tests use slightly different methods for assessing phylogenetic signal, therefore both were

used and results were compared. Only Pagel's lambda was calculated for discrete traits as Blomberg's K can only be used to measure continuous traits.

Pagel's lambda ranges from 0 to 1, where values near 0 suggest no phylogenetic signal and values close to 1 suggest a strong phylogenetic signal whereby traits are evolving according to Brownian motion (Pagel, 1999). Lambda was calculated using the "fitContinuous" and "fitDiscrete" functions from the Geiger package. Log-likelihood values and chi-squared tests were calculated for the lambda values to test if lambda is significantly different from 0 and 1 (LLR0, LLR1, respectively).

Blomberg's K values were calculated using the "phylosig" function in the phytools package. K values close to 0 indicate no phylogenetic signal, K values greater than 0 but less than 1 indicate weak phylogenetic signal, K close to 1 indicates as much phylogenetic signal as expected through Brownian motion, and K greater than 1 indicates more phylogenetic signal than expected based on Brownian motion (Blomberg et al. 2003).

2.3 Experimental Design

Field sites were chosen to capture a broad range of Ericaceae habitats. Sites were visited prior to collection to ensure the presence of species and to choose suitable habitats. At each site, 1m x 1m square plots were placed over one or multiple species of interest. The plots represented microsites within the habitat and each species collected in one plot shared a common soil sample. Instead of a set number of plots at each location, a minimum number of individuals were taken from each habitat type. Across one to three habitats, 9-12 individuals were taken of each species (two exceptions being *Vaccinium myrtilloides* and *Monotropa hypopithys* which only six and five samples were taken, respectively). Species that occurred in all three habitats such as Black Huckleberry (*Gaylussacia baccata*), had three to four individuals sampled from each habitat type

(forest, bog, barren). When a species occurred in two of the three habitat types such as Teaberry (*Gaultheria procumbens*), four to six individuals were sampled in both habitat types. Species that only occurred in one type of habitat such as Bog Rosemary (*Andromeda polifolia*) had all 9-12 samples taken from that one habitat type. Most species collected from one habitat type were still collected from multiple sites, however some species (*Vaccinium myrtilloides*, and *Monotropa hypopithys*) were only found at one site, therefore all samples were collected from the same site.

2.4 Site Descriptions

2.4.1 Barrens

Three different barren sites were visited to collect samples across Nova Scotia. Polly's Cove (44.2920 N, 63.5334) is a Broom Crowberry coastal barren that is dominated by Broom Crowberry (*Corema condradii*), Common Juniper (*Juniperus communis*), Fishnet lichen (*Cladonia boryi*), and Bearberry (*Arctostaphylos uva-ursi*) (Porter et al., 2020). This barren habitat is moderately sheltered to exposed. The sites in Duncan's Cove Nature Reserve are classified as Black Crowberry mesic coastal barrens and are dominated by Black Crowberry, Common Juniper, Lingonberry (*Vaccinium vitis-idaea*), and Lowbush Blueberries (*Vaccinium angustifolium*) (Porter et al., 2020). The third barren habitat is in Greenwood, Nova Scotia (44.9990 N, 64.94418 W). This barren is classified as a sand barren and the dominant species here are Broom Crowberry, Reindeer lichen (*Cladonia rangiferina*), Lowbush Blueberry, and Bearberry (Porter et al., 2020). This site has tree cover and was 9.5 km from the nearest coast. The soils here were deeper than the coastal rock barrens and consisted primarily of sand.

2.4.2 Bogs

Two bogs were visited to collect samples. The bog where the most samples were collected is approximately 200 km² and surrounded by dense forest in Goodwood, Nova Scotia

(44.3608 N, 63.4118 W). This bog is approximately 6.5km from the coast, and dominant species include Dwarf Huckleberries (*Gaylussacia bigeloviana*), Northern Pitcher Plants (*Sarracenia purpurea*), and Sundews (*Drosera rotundifolia*). This site was relatively undisturbed other than a small number of ATV trails. The second bog was located within Duncan's Cove Nature Reserve (44.3016 N, 63.3123 W). This bog was much smaller (approximately 1.1 km²), closer to the coast (150m) and is surrounded by a coastal barren. The dominant species at this site include Cottongrass (*Eriophorum angustifolium*), Northern Pitcher Plant, Bog Rosemary (*Andromeda polifolia*), Sundew, and Leatherleaf (*Chamaedaphne calyculata*).

2.4.3 Forests

Forest sites included Kejimikujik National Park (44.2607 N, 65.1243 W), Long Lake Provincial Park (44.3716 N, 63.3729 W), Taylor Head Provincial Park (44.4901 N, 62.3340 W), The Oaks on Saint Mary's University Campus (44.3732 N, 63.3453 W), a forest in Goodwood, Nova Scotia (44.3611 N, 63.4131 W) as well two other unnamed sites near Hemlock Ravine Park (44.6944 N, 63.6643 W) and Royal Oaks Park (45.0176 N, 63.5075 W). Kejimikujik and Long Lake Provincial Park sites are mixed-wood forests dominated by Red Oak (*Quercus rubra*), Red Maple (*Acer rubrum*), White Pine (*Pinus strobus*), and Spruce (*Picea spp.*). Taylor Head Provincial Park and The Oaks are classified as coastal forests, with Taylor Head stretching to the coastline and The Oaks being approximately 250 m from the coast. These areas experience more winds than the other inland forests (Neily et al., 2010). The dominant overstory species at Taylor Head include Fir (*Abies sp.*) and Spruce species, whereas The Oaks dominant overstory species are Red Oak and Red Maple. The forest in Goodwood is a wet deciduous forest with dominant overstory species being Striped Maple (*Acer pensylvanicum*), Red Maple, and

Tamarack (*Larix laricina*). The sampling site for this forest was close to a large bog, therefore soil contained peat and was relatively wet.



Figure 2.1. Barren, forest, and bog sites across Nova Scotia where plant and soil samples were collected between June-August 2023. Barren sites included Duncan’s Cover Nature Reserve, Polly’s Cove, and a sand barren in Greenwood, Nova Scotia. Forest sites included Kejimikujik National Park, Long Lake Provincial Park, Taylor’s Head Provincial Park, The Oak’s on Saint Mary’s University Campus, and three forests near Hemlock Ravine, Royal Oaks Park, and Greenwood, Nova Scotia. Bog sites included Duncan’s Cove Nature Reserve and a site near Goodwood, Nova Scotia.

2.5 Soil and Leaf Sampling

To determine the soil characteristics of each target individual’s habitat, a surface soil sample (top 5cm) was taken from the center of each plot using a garden shovel. Soil samples were placed in plastic containers to avoid water evaporation and leaf samples were stored in paper envelopes. Soil and leaf samples were stored in the fridge (approximately 2°C) to prevent chemical change or drying out until in-lab measurements could be made. Eight or more leaves were taken from each individual depending on the species, with some exceptions such as *Gaultheria procumbens* which do not often have more than three to five leaves per plant. Leaves were selected from the entire individual, capturing leaves of various ages to gain a representative sample of leaves on the entire plant. Leaves with damage were not chosen, as leaves were collected to measure leaf area and damage from herbivory or other environmental factors would have skewed the results. Five or more extra leaves were also taken from each plant to be used as

extra material for chemical analysis. The two *Monotropa* species collected in this study are leafless, and therefore the entire stem and flower were collected for chemical analysis. 47 samples from Duncan's Cove (barren) and Taylor's Head (forest) were from previous literature, those samples were collected using the same methods in September 2022 (Schofield, 2023).

2.5.1 Habitat Characteristics

To characterize environmental variation between habitats, soil water content and water-soluble chemical concentrations of potassium (K), calcium (Ca), sodium (Na), and nitrate (NO₃) ions (ppm), as well as soil pH and electrical conductivity (EC, mS/cm) were measured. The soils were weighed fresh (g) and then dried for over 48 hours at 75°C in a drying oven before being weighed again dry (g). These measurements were used to calculate gravimetric water content (θ_g) using the following equation:

$$\text{Gravimetric water content } (\theta_g) = \frac{[\text{Fresh mass } (g) - \text{Dry mass } (g)]}{\text{Dry mass } (g)}$$

Soil samples were then added to a mortar and pestle and ground into a fine powder. Analysis of water-soluble ions in the soils was conducted by creating a 1:2, soil to deionized water mixture. The mixture was then shaken and left for approximately 30 minutes to rest. The liquid was then pipetted onto portable ion-selective meters (LAQUAtwin from the Nutricheck Max kit by TestAgro, Phoenix, AZ) to test water-soluble K, Ca, Na, and NO₃ ions (ppm), pH, and EC. The same liquid was measured on each device. After every three samples, the machines were re-calibrated using the solutions from the kit, alternating between high and low calibrations to ensure accuracy. Light availability was not measured for each plot, but the bogs and barrens had more light than the forests due to the absence of canopy trees.

2.5.2 Leaf Morphology and Phenology

The area (cm^2) of fresh leaf samples was measured using a portable leaf area meter with conveyor attachment (LI-3000C and LI-3050C, LICOR, Lincoln, Nebraska). Fresh samples were then weighed (g), dried for 48 hours at 75°C , and then weighed again dry (g). Average leaf size (LS, cm^2) was calculated by dividing the total leaf area by the number of leaves. Specific leaf area (SLA, cm^2/g) was calculated as the average leaf area divided by average dry mass. Leaf thickness (Lth, mm) was calculated as average fresh leaf mass divided by average leaf area. Leaf dry matter content (LDMC, g/g) was calculated as average dry mass divided by average fresh mass. Information on leaf lifespan, leaf arrangement, and flowering strategies for each species were obtained from the literature (Chadde, 1998; Hinds et al., 2000).

2.5.3 Leaf Chemistry

Leaf pH was measured from dried leaf material. Dried leaf material was added to a mortar and pestle and ground into a fine powder using liquid nitrogen. In a microcentrifuge tube, a 1:2, leaf matter to deionized water solution was mixed. The mixture was then shaken and left for approximately 10 minutes to rest. The liquid portion was then pipetted into a portable ion-selective meter (LAQUAtwin pH-11 from the Nutricheck Max kit by TestAgro, Phoenix, AZ) to analyze leaf pH. After every three samples, the meter was re-calibrated using the included calibration solutions, alternating between high (pH 7) and low (pH 4) calibration to ensure accuracy.

2.6 Statistical Analysis

Differences in soil characteristics and differences in functional traits among species, habitats, and species in habitats were tested using analysis of variance (ANOVA). Data was first examined for normalcy using a histogram in R, and if the data for the given variable was

irregular, a log transformation was applied. Variables that were log-transformed included: soil gravimetric water content, soil EC, soil NO₃, soil K, soil Na, soil Ca, LDMC, LS, and Lth. An ANOVA was then performed using the “aov” function. To test which variables were significantly different from one another, a Tukey post-hoc test using the “HSD.test” function in the package “agricolae” was performed (De Mendiburu and Yaseen, 2020).

To compare the binary traits from the literature across habitats, a chi-squared test and post hoc test were conducted using the “chisq.posthoc.test” function from the “chisq.posthoc.test” package (Beasley & Schumacker, 1995) using the Bonferroni method. This test was conducted instead of ANOVA as traits are categorical rather than continuous. All analyses were conducted in R Version 4.3.1 (R Core Team, 2023).

3.0 Results

3.1 Functional Differences Between Species

All measured traits varied among species, habitat type, and among the same species in different habitat types (Table 3.1). Species differences had more of an influence on trait variance for Lth, LS, and leaf pH, and habitat differences had more of an influence on trait variance for SLA and LDMC (Table 3.1). Some species had similar average values for individual traits, but no two species were indistinguishable from each other across all measured traits (Table 3.2). Many species also exhibited high levels of intra-specific trait variation (plasticity), such as *Gaylussacia baccata*, *Chamaedaphne calyculata*, and *Kalmia angustifolia* (Figure 3.1).

Table 3.1. Analysis of variance of plant functional traits across 24 Ericaceae species, three main habitat types (barren, bog, forest) in Nova Scotia, and species across the three habitat types. Data is 276 samples (n=5-12 per species) and was collected in September 2022 and from June-August of 2023.

Leaf Trait		Df	Sum Sq	Mean Sq	F value	Pr(>F)
SLA (cm ² /g)	Species	21	662463	31546	38.869	p<0.0001
	Habitat Type	2	120128	60064	74.007	p<0.0001
	Species:Habitat Type	15	71595	4773	5.881	p<0.0001
	Residuals	219	177741	812		
Log(LDMC)	Species	21	7.052	0.3358	19.545	p<0.0001
	Habitat Type	2	0.917	0.4585	26.683	p<0.0001
	Species:Habitat Type	15	1.116	0.0744	4.331	p<0.0001
	Residuals	219	3.763	0.0172		
Log(Lth) (g/cm ²)	Species	21	38.78	1.8465	46.76	p<0.0001
	Habitat Type	2	3.10	1.5491	39.228	p<0.0001
	Species:Habitat Type	15	2.38	0.1584	4.011	p<0.0001
	Residuals	219	8.65	0.0395		
Log(LS) (cm ²)	Species	21	675.40	32.1600	301.566	p<0.0001
	Habitat Type	2	9.40	4.7000	44.033	p<0.0001
	Species:Habitat Type	15	8.50	0.5700	5.315	p<0.0001
	Residuals	220	23.50	0.1100		
Leaf pH	Species	23	76.30	3.3170	60.493	p<0.0001
	Habitat Type	2	2.34	1.1690	21.232	p<0.0001
	Species:Habitat Type	15	2.57	0.1710	3.121	0.000116
	Residuals	235	12.89	0.0550		

Table 3.2. Plant functional traits of 24 Ericaceae species in Nova Scotia. Data was collected from June-August of 2023. Data is trait means from 5-12 samples per species with standard deviation and post-hoc groupings from Tukey's HSD test. Vertical groups that share letters are statistically similar based on post-hoc groupings.

Species	SLA (cm ² /g)	LDMC	Lth (g/cm ²)	LS (cm ²)	Leaf pH
<i>Andromeda polifolia</i>	44.67 (3.92) ^g	0.48 (0.06) ^{bcdef}	0.05 (0.003) ^a	0.40 (0.09) ^{ef}	4.26 (0.21) ^{ghi}
<i>Arctostaphylos uva-ursi</i>	57.68 (14.15) ^{fg}	0.48 (0.03) ^{cdef}	0.04 (0.01) ^{ab}	0.63(0.15) ^{de}	4.25 (0.23) ^{ghi}

<i>Chamaedaphne calyculata</i>	111.44 (24.73) ^{def}	0.60 (0.11) ^{ab}	0.02 (0.004) ^{f^g}	1.59 (0.75) ^c	4.68 (0.20) ^{def}
<i>Chimaphila umbellata</i>	80.37 (7.28) ^{fg}	0.52 (0.01) ^{abcde}	0.02 (0.002) ^{cde}	2.96 (0.92) ^b	5.28 (0.10) ^a
<i>Corema condradii</i>	69.05 (11.09) ^{fg}	0.53 (0.04) ^{abcd}	0.03 (0.003) ^{bcd}	0.03 (0.01) ⁱ	4.62 (0.16) ^{defg}
<i>Empetrum nigrum</i>	105.86 (62.88) ^{defg}	0.54 (0.12) ^{abcd}	0.02 (0.01) ^{cdef}	0.03 (0.01) ⁱ	4.69 (0.18) ^{def}
<i>Empetrum rubrum</i>	65.40 (5.50) ^{fg}	0.52 (0.02) ^{abcde}	0.03 (0.002) ^{bc}	0.04 (0.01) ^{hi}	4.60 (0.17) ^{defg}
<i>Epigaea repens</i>	178.81 (48.95) ^{abc}	0.34 (0.07) ^h	0.02 (0.004) ^{efg}	9.37 (4.01) ^a	3.68 (0.19) ^k
<i>Gaultheria hispidula</i>	166.35 (43.18) ^{abcd}	0.41 (0.03) ^{efgh}	0.02 (0.003) ^{fgh}	0.16 (0.04) ^g	4.61 (0.22) ^{defg}
<i>Gaultheria procumbens</i>	77.35 (19.55) ^{f^g}	0.48 (0.04) ^{cdef}	0.03 (0.01) ^{bc}	3.63 (1.15) ^b	4.99 (0.33) ^{abcd}
<i>Gaylussacia baccata</i>	179.87 (64.97) ^{abc}	0.48 (0.08) ^{cdef}	0.01 (0.004) ^{ghi}	3.42 (1.21) ^b	3.96 (0.50) ^{ijk}
<i>Gaylussacia bigeloviana</i>	156.52 (20.39) ^{bcde}	0.36 (0.04) ^{gh}	0.02 (0.001) ^{ef}	1.38 (0.71) ^c	3.16 (0.10) ^l
<i>Kalmia angustifolia</i>	111.15 (56.26) ^{def}	0.52 (0.15) ^{abcde}	0.02 (0.004) ^{def}	2.00 (1.66) ^c	4.84 (0.17) ^{bcd}
<i>Kalmia polifolia</i>	76.75 (18.13) ^{fg}	0.46 (0.04) ^{cdef}	0.03 (0.01) ^{bc}	0.61 (0.37) ^e	4.22 (0.22) ^{ghi}

<i>Monotropa hypopithys</i>	N/A	N/A	N/A	N/A	4.52 (0.13) ^{defgh}
<i>Monotropa uniflora</i>	N/A	N/A	N/A	N/A	5.19 (0.09) ^{ab}
<i>Rhododendron canadense</i>	209.29 (65.72) ^{ab}	0.40 (0.05) ^{fgh}	0.01 (0.003) ^{ghi}	3.71 (1.43) ^b	4.32 (0.36) ^{fghi}
<i>Rhododendron groenlandicum</i>	91.62 (70.24) ^{efg}	0.58 (0.09) ^{abc}	0.03 (0.01) ^{cde}	1.49 (0.87) ^c	4.73 (0.55) ^{cde}
<i>Vaccinium angustifolium</i>	140.48 (38.03) ^{cde}	0.51 (0.08) ^{abcdef}	0.02 (0.004) ^{fgh}	1.54 (0.63) ^c	3.71 (0.34) ^k
<i>Vaccinium corymbosum</i>	216.79 (46.42) ^a	0.46 (0.08) ^{defg}	0.01 (0.002) ^{hi}	2.78 (0.58) ^b	3.76 (0.34) ^{jk}
<i>Vaccinium macrocarpon</i>	112.25 (28.13) ^{def}	0.45 (0.07) ^{defg}	0.02 (0.004) ^{cdef}	0.23 (0.07) ^{fg}	4.13 (0.14) ^{hij}
<i>Vaccinium myrtilloides</i>	163.11 (35.06) ^{abcde}	0.66 (0.07) ^a	0.01 (0.002) ⁱ	1.24 (0.31) ^{cd}	3.83 (0.15) ^{ijk}
<i>Vaccinium oxycoccus</i>	55.99 (6.76) ^{fg}	0.62 (0.10) ^a	0.03 (0.004) ^{bc}	0.06 (0.01) ^h	4.33 (0.22) ^{efghi}
<i>Vaccinium vitis-idaea</i>	71.52 (19.27) ^{fg}	0.66 (0.16) ^a	0.02 (0.005) ^{cde}	0.37 (0.10) ^{ef}	5.13 (0.11) ^{abc}

Table 3.3. Binary plant functional traits of 24 Ericaceae species in Nova Scotia. Data was collected from the literature.

Species	Leaf Lifespan	Flowering Strategy	Leaf Arrangement
<i>Andromeda polifolia</i>	Evergreen	Serotinous	Alternate

<i>Arctostaphylos uva-ursi</i>	Evergreen	Serotinous	Alternate
<i>Chamaedaphne calyculata</i>	Evergreen	Serotinous	Alternate
<i>Chimaphila umbellata</i>	Evergreen	Serotinous	Opposite
<i>Corema condradii</i>	Evergreen	Serotinous	Alternate
<i>Empetrum nigrum</i>	Evergreen	Serotinous	Alternate
<i>Empetrum rubrum</i>	Evergreen	Serotinous	Alternate
<i>Epigaea repens</i>	Evergreen	Serotinous	Alternate
<i>Gaultheria hispidula</i>	Evergreen	Serotinous	Alternate
<i>Gaultheria procumbens</i>	Evergreen	Serotinous	Alternate
<i>Gaylussacia baccata</i>	Deciduous	Precocious	Alternate
<i>Gaylussacia bigeloviana</i>	Deciduous	Serotinous	Alternate
<i>Kalmia angustifolia</i>	Evergreen	Serotinous	Opposite
<i>Kalmia polifolia</i>	Evergreen	Serotinous	Opposite
<i>Monotropa hypopithys</i>	N/A	N/A	N/A
<i>Monotropa uniflora</i>	N/A	N/A	N/A
<i>Rhododendron canadense</i>	Deciduous	Precocious	Alternate
<i>Rhododendron groenlandicum</i>	Evergreen	Serotinous	Alternate
<i>Vaccinium angustifolium</i>	Deciduous	Precocious	Alternate

<i>Vaccinium corymbosum</i>	Deciduous	Serotinous	Alternate
<i>Vaccinium macrocarpon</i>	Evergreen	Serotinous	Alternate
<i>Vaccinium myrtilloides</i>	Deciduous	Serotinous	Alternate
<i>Vaccinium oxycoccus</i>	Evergreen	Serotinous	Alternate
<i>Vaccinium vitis-idaea</i>	Evergreen	Serotinous	Alternate

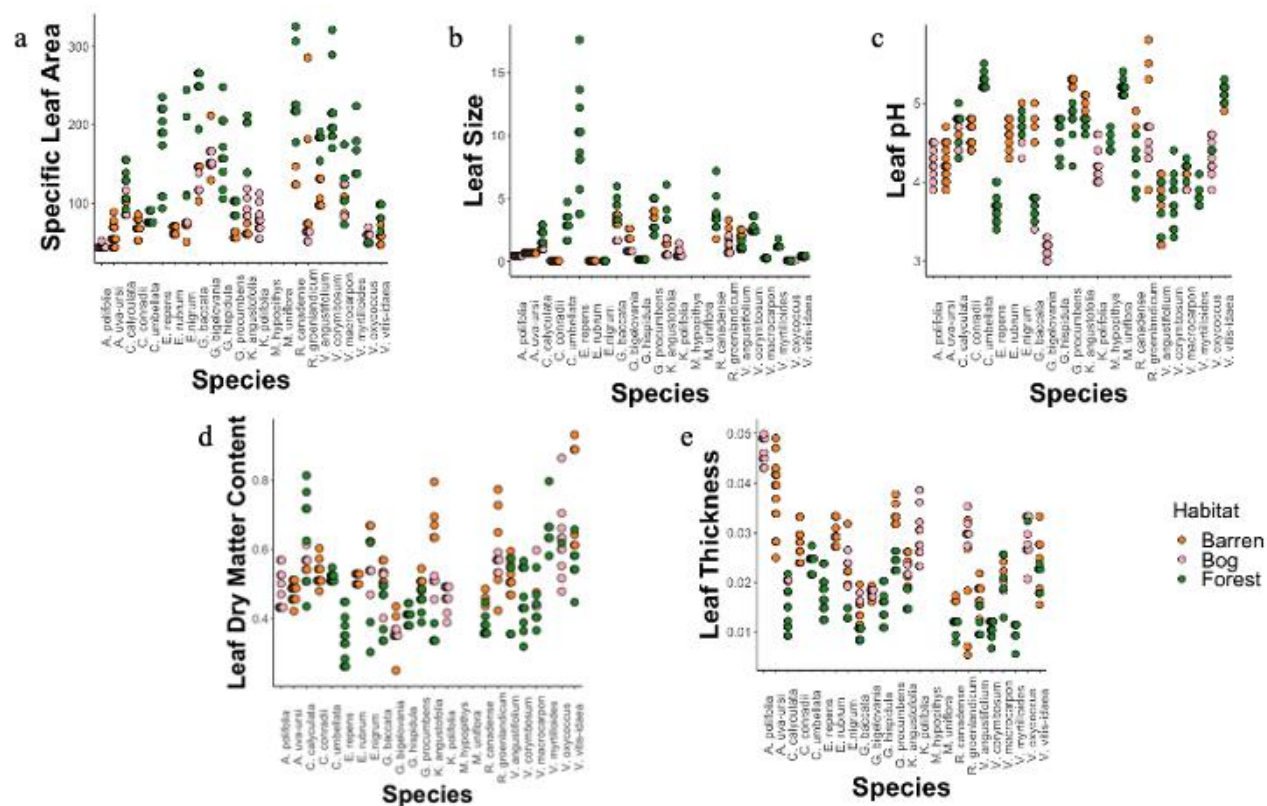


Figure 3.1. Variation in a) specific leaf area (SLA, cm²/g), b) leaf size (cm²), c) leaf pH, d) leaf dry matter content, and e) leaf thickness (mm) for 24 Ericaceae species across three habitat types (barren, bog, forest) in Nova Scotia. Data was collected in September 2022 and June-August of 2023 and are from individual plants (n = 5-12 per species).

3.2 Soil Characteristics

There were differences in soil water content and water-soluble nutrients between habitat types. Gravimetric water content was highest and Ca concentration was the lowest in the bogs compared to the other habitat types (Table 3.5). Gravimetric water content and Ca concentration in the barrens and forests were indistinguishable from each other (Table 3.5). Both EC and soil pH were highest in the barrens, and the bogs and forests were indistinguishable from each other (Table 3.5). Nitrate (NO₃) concentrations were significantly different between habitats (Table 3.4), where it was highest in the barrens and lowest in the bogs, but the forests were not different from either habitat type (Table 3.5). Sodium (Na) concentration also varied significantly between habitats (Table 3.4), where concentrations in the barrens were higher than in the forests, but the bogs were not different from either habitat type (Table 3.5). Potassium (K) concentrations showed no significant differences between any habitat type (Table 3.4, Table 3.5).

Table 3.4. Analysis of variance of soil characteristics across three main habitat types (barren, bog, forest) in Nova Scotia. Data is from 79 soil samples collected from September of 2022 and June-August 2023.

Soil Trait		Df	Sum Sq	Mean Sq	F value	Pr(>F)
Gravimetric water content (θg)	Habitat Type	2	43.070	21.535	23.910	9.80E-09
	Residuals	74	66.660	0.901		
pH	Habitat Type	2	4.491	2.246	12.040	2.87E-05
	Residuals	76	14.177	0.187		
K (ppm)	Habitat Type	2	0.045	0.023	0.066	0.936
	Residuals	76	26.112	0.344		
Ca (ppm)	Habitat Type	2	178.400	89.220	7.401	0.00118
	Residuals	74	892.100	12.060		
Na (ppm)	Habitat Type	2	12.060	6.029	13.360	1.07E-05
	Residuals	76	34.300	0.451		
NO ₃ (ppm)	Habitat Type	2	41.500	20.756	3.883	0.0248
	Residuals	76	406.300	5.346		
EC (mS/cm)	Habitat Type	2	2.224	1.112	4.989	0.00921
	Residuals	76	16.941	0.223		

Table 3.5. Soil characteristics between three habitat types (barren, bog, forest) in Nova Scotia. Data is 79 samples collected in September 2022 and from June-August of 2023. Data is soil characteristic means with standard deviation and post-hoc groupings using Tukey's HSD test. Columns that share letters are statistically indistinguishable based on post-hoc groupings.

Soil Variable	Bogs	Forests	Barrens
Gravimetric Water Content (θ_g)	12.99 (6.02) ^a	2.57 (2.38) ^b	2.00 (1.92) ^b
pH	4.17 (0.25) ^b	4.083 (0.44) ^b	4.61 (0.49) ^a
K (ppm)	36.67 (24.56) ^a	37.52 (20.96) ^a	35.68 (16.32) ^a
Ca (ppm)	2.75 (3.49) ^b	12.75 (23.18) ^a	7.88 (4.26) ^a
Na (ppm)	11.92 (5.18) ^{ab}	9.19 (5.81) ^b	29.80 (38.23) ^a
NO ₃ (ppm)	24.75 (18.20) ^b	26.36 (17.17) ^{ab}	63.36 (54.00) ^a
EC (mS/cm)	246.75 (142.34) ^b	235.69 (98.02) ^b	332.64 (161.08) ^a

3.3 Functional Trait Differences Among Habitats

Most of the functional traits measured were significantly different in the forests when compared to the barrens and bogs (Table 3.6). SLA and LS were significantly different between habitats (Table 3.1), where values were highest in the forests and indistinguishable between barrens and bogs (Table 3.6, Figure 3.2). LDMC and Lth were significantly different across habitats (Table 3.1), where values were lower in the forests and indistinguishable between the barrens and bogs (Table 3.6, Figure 3.2). Leaf pH was significantly different between habitats (Table 3.1) where values were higher in the barrens than in the bogs, and the forests were not different than either habitat type (Table 3.6, Figure 3.2).

Table 3.6. Plant functional traits between three habitat types (barren, bog, forest) in Nova Scotia. Data was collected from June-August of 2023. Data is trait means from 276 samples (n=5-12 per species) with standard deviation and post-hoc groupings from Tukey's HSD test. Groups that share letters are statistically indistinguishable based on post-hoc groupings.

Leaf Characteristic	Bogs	Forests	Barrens
SLA (cm ² /g)	81.60 (35.98)b	161.83 (64.35)a	85.64 (40.64)b
LDMC	0.51 (0.09)a	0.47 (0.12)b	0.54 (0.11)a
Lth (g/cm ²)	0.03 (0.01)a	0.02 (0.01)b	0.03 (0.01)a
LS (cm ²)	0.59 (0.50)b	2.97 (3.08)a	1.26 (1.34)b
Leaf pH	4.21 (0.48)b	4.41 (0.62)ab	4.50 (0.59)a

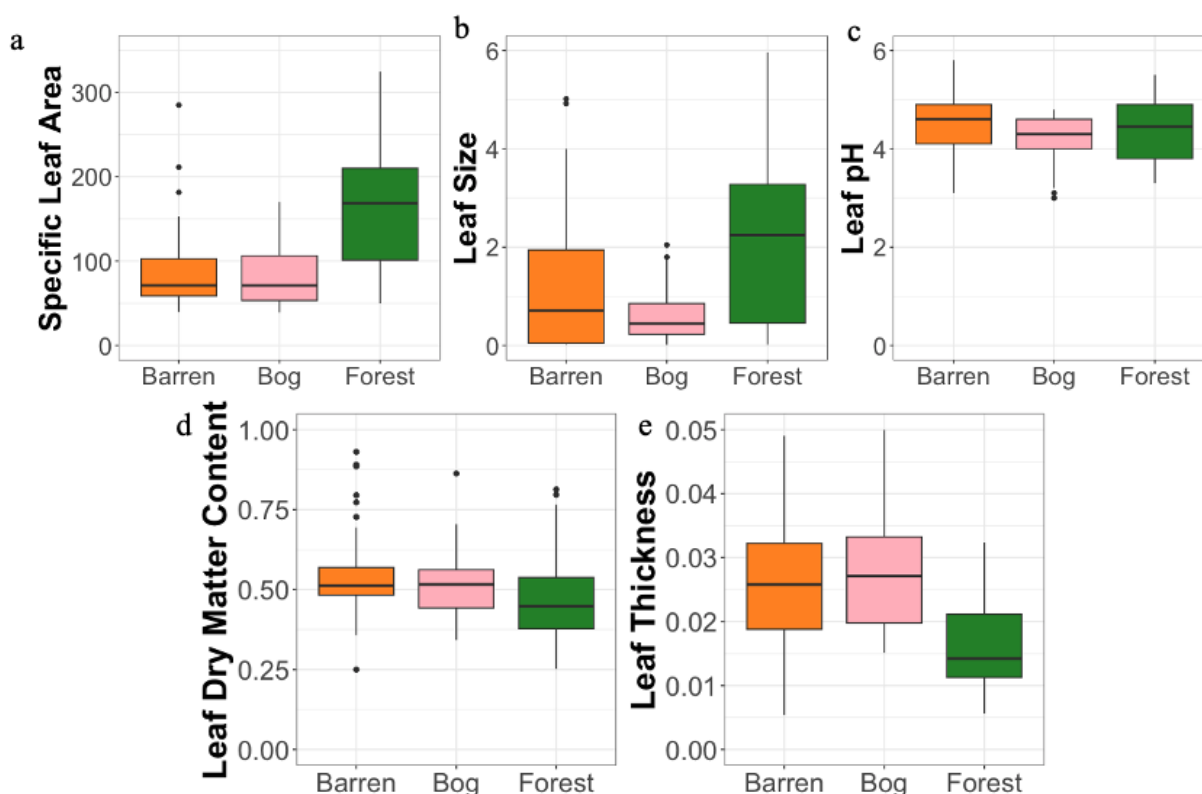


Figure 3.2. Variation in plant functional traits (a)SLA(cm²/g), b)leaf size (cm²), c)leaf pH, d)leaf thickness (mm), and e)leaf dry matter content) of Ericaceae species across three habitat types (barren, bog, forest) in Nova Scotia. Data is 276 samples (n=5-12 per species) collected in September 2022 and from June-August of 2023.

There was a difference in the amount of precocious and serotinous species, alternate and opposite species, and evergreen and deciduous species across habitat types (Table 3.7). There were significantly more serotinous, opposite, and evergreen species in the bogs (Table 3.7, Table 3.8, Figure 3.3). Forests had significantly more precocious and deciduous species but no difference in abundance of leaf arrangement (Table 3.7, Table 3.8, Figure 3.3). Barrens had significantly more alternate species but there was not a significant difference between flowering strategy or leaf lifespan (Table 3.7, Table 3.8, Figure 3.3).

Table 3.7. A chi-squared test calculating the difference in functional traits across three habitats (barren, bog, forest) in Nova Scotia. Traits were collected from the literature and added to the list of samples resulting in a sample size of 276. Flowering refers to precocious or serotinous, leaf arrangement refers to opposite or alternate, and leaf lifespan refers to evergreen or deciduous.

Trait	X squared	Df	P-value
Flowering	10.31	2	0.006
Leaf Arrangement	11.605	2	0.003
Leaf Lifespan	9.178	2	0.01

Table 3.8. A chi-squared post hoc test assessing differences in functional traits across three habitats (barren, bog, forest) in Nova Scotia. Traits were collected from the literature and added to the list of samples resulting in a sample size of 276. Flowering refers to precocious or serotinous, leaf arrangement refers to opposite or alternate, and leaf lifespan refers to evergreen or deciduous.

Trait		Bogs	Forests	Barrens
Flowering	Residuals	3.6748	-2.6726	-1.00223
	p-value	0.001428	0.0452	1
Leaf arrangement	Residuals	3.5773	-0.57699	-3.000355
	p-value	0.002083	1	0.01618
Leaf lifespan	Residuals	2.9099	-3.003757	0.09386
	p-value	0.021693	0.016	1

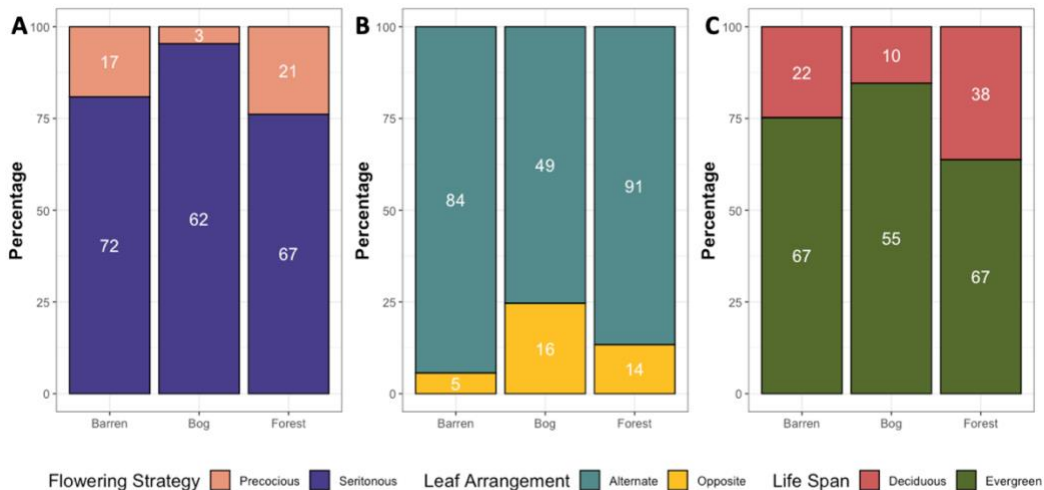


Figure 3.3: Variation of the percentage of species categorical traits (A: flowering strategy, B: leaf arrangement, C: leaf lifespan) across three habitats (barrens, bogs, forests) in Nova Scotia. The y-axis represents the percentage of samples with that trait and the sample counts are shown within the boxes.

3.4 Species Plasticity Across Habitats

To test species differences among different habitats, the five species that were present in all three habitat types were compared: *Chamaedaphne calyculata* ($n = 15$), *Empetrum nigrum* ($n = 11$), *Gaylussacia baccata* ($n = 16$), *Kalmia angustifolia* ($n = 4$), and *Vaccinium macrocarpon* ($n = 11$). Each trait measured was significantly different between species and habitats (Table 3.9), and traits had varying levels of plasticity depending on the species (Figure 3.4).

SLA did not vary across habitats for *Vaccinium macrocarpon*, whereas SLA was larger in the forests and similar in the barrens and bogs in the other four species (Table 3.10, Figure 3.4). LDMC was similar across all habitats for *Vaccinium macrocarpon*, *Gaylussacia baccata*, and *Chamaedaphne calyculata* (Table 3.10, Figure 3.4). *Kalmia angustifolia* had a lower LDMC in the forests than in other habitat types (Table 3.10, Figure 3.4). LDMC was larger in the barrens than the forests for *Empetrum nigrum*, but LDMC in the bogs was not different from either habitat (Table 3.10, Figure 3.4). LS did not vary across habitats for *Vaccinium macrocarpon* and *Empetrum nigrum* (Table 3.10, Figure 3.4). LS was largest in the forests and smallest in the bogs

for *Chamaedaphne calyculata* and *Gaylussacia baccata*, and the LS in the barrens did not differ from either habitat type (Figure 3.4). LS was different across all three habitat types for *Kalmia angustifolia*, where LS was largest in the forests and smallest in the bogs, and LS in the barrens was different from both habitats (Table 3.10, Figure 3.4). Lth was similar across all habitats for *Vaccinium macrocarpon*, *Kalmia angustifolia*, and *Chamaedaphne calyculata* (Table 3.10, Figure 3.4). Lth was larger in the barrens and bogs, and smaller in the forests for *Empetrum nigrum* and *Gaylussacia baccata* (Table 3.10, Figure 3.4). Leaf pH was similar across all habitats for *Vaccinium macrocarpon*, *Chamaedaphne calyculata*, *Kalmia angustifolia*, and *Empetrum nigrum* (Table 3.10, Figure 3.4). Leaf pH varied across habitats for *Gaylussacia baccata* where it was the highest in the barrens and the bogs and forests were indistinguishable from each other (Table 3.10, Figure 3.4).

Table 3.9. Analysis of variance of leaf functional traits of five Ericaceae species across three habitat types (barren, bog, forest) in Nova Scotia. Data was collected from June-August of 2023.

Leaf Trait		Df	Sum Sq	Mean Sq	F value	Pr(>F)
SLA (cm ² /g)	Species	4	59183	14796	22.447	8.23E-11
	Habitat Type	2	91515	45757	69.419	2.08E-15
	Species:Habitat Type	8	34687	4336	6.578	6.63E-06
	Residuals	52	34276	659		
Log(LDMC)	Species	4	0.6622	0.1655	7.407	8.45E-05
	Habitat Type	2	0.6488	0.3244	14.517	9.79E-06
	Species:Habitat Type	8	0.9536	0.1192	5.334	6.59E-05
	Residuals	52	1.1621	0.0223		
Log(Lth) (g/cm ²)	Species	4	2.6409	0.6602	19.487	7.55E-10
	Habitat Type	2	1.9511	0.9756	28.795	3.82E-09
	Species:Habitat Type	8	0.5328	0.0666	1.966	0.0696
	Residuals	52	1.7617	0.0339		
Log(LS) (cm)	Species	4	192.75	48.19	525.036	p<0.0001
	Habitat Type	2	7.11	3.56	38.734	4.29E-11
	Species:Habitat Type	8	5.67	0.71	7.724	8.43E-07
	Residuals	53	4.86	0.09		

Leaf pH	Species	4	8.699	2.1748	47.7	p<0.0001
	Habitat Type	2	1.246	0.6231	13.668	1.63E-05
	Species:Habitat Type	8	1.546	0.1932	4.239	0.000554
	Residuals	53	2.416	0.0456		

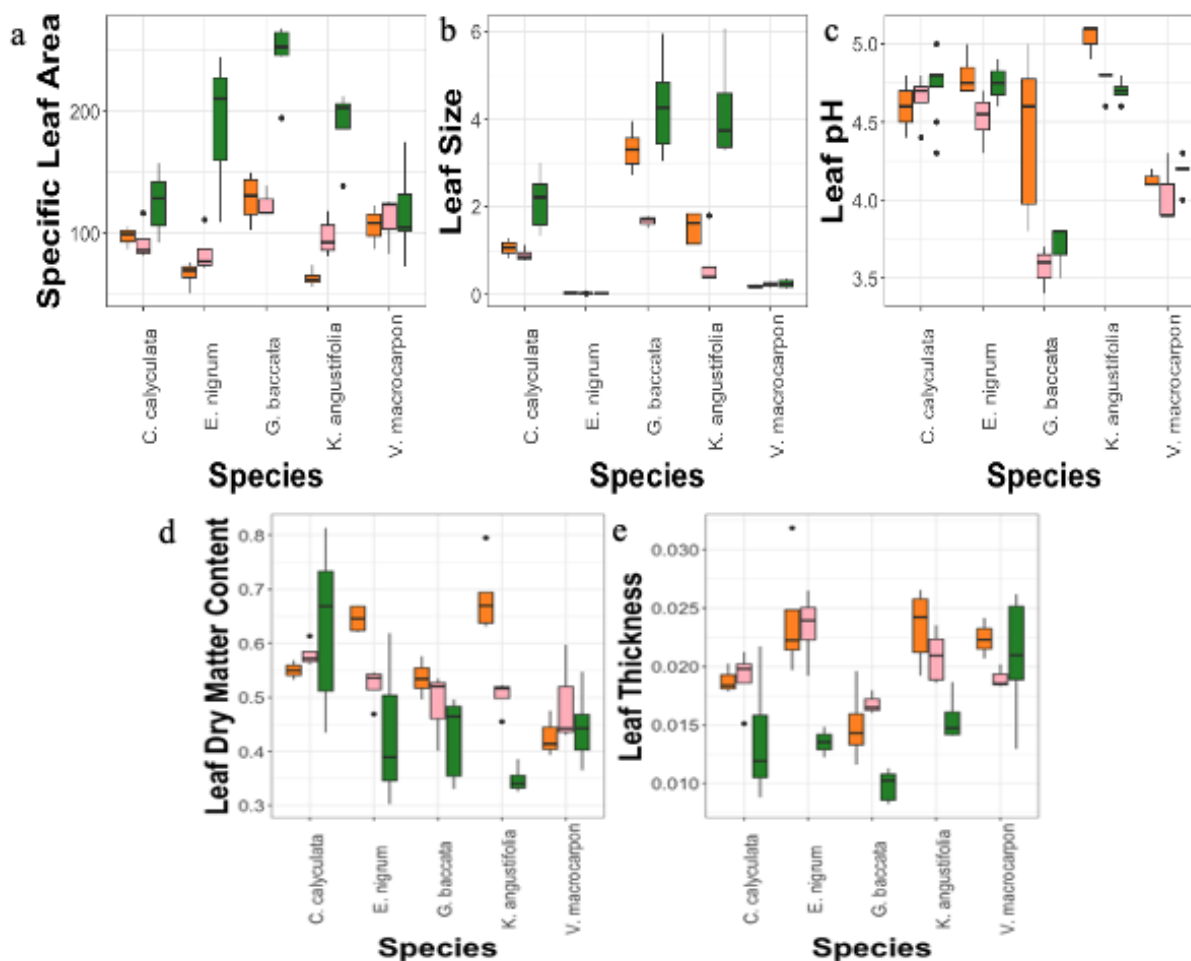


Figure 3.4: Variation in functional traits (a)SLA(cm²/g), b)leaf size (cm²), c)leaf pH, d)leaf thickness (mm), and e)leaf dry matter content) across five Ericaceae species present in all three habitat types (barren, bog, forest) in Nova Scotia. Data is from individual plants (n= 3-12 per species, per habitat).

Table 3.10. Plant functional traits between five species across three habitat types (barren, bog, forest) in Nova Scotia. Data was collected from June-August of 2023. Data is trait means with standard deviation and post-hoc groupings. Vertical groups that share letters are statistically similar based on post-hoc groupings.

Treatment	SLA (cm²/g)	LDMC	Lth (g/cm²)	LS (cm²)	Leaf pH
<i>Chacal-barrens</i>	97.00 (9.35) ^{de}	0.55 (0.02) ^{ab}	0.02 (0.001) ^{abc}	1.06 (0.23) ^{cde}	4.60 (0.20) ^{abcd}
<i>Chacal- bogs</i>	92.60 (16.08) ^{de}	0.58 (0.02) ^{ab}	0.02 (0.003) ^{abc}	0.90 (0.15) ^{de}	4.65 (0.17) ^{abc}
<i>Chacal-forests</i>	126.27 (23.33) ^{cd}	0.64 (0.14) ^a	0.01 (0.01) ^{cd}	2.14 (0.61) ^{bc}	4.73 (0.22) ^{ab}
<i>Empnig- barrens</i>	66.40 (11.11) ^e	0.65 (0.03) ^a	0.02 (0.01) ^a	0.03 (0.004) ^g	4.80 (0.14) ^{ab}
<i>Empnig- bogs</i>	83.92 (18.25) ^{de}	0.52 (0.04) ^{ab}	0.02 (0.003) ^a	0.03 (0.01) ^g	4.53 (0.17) ^{bcd}
<i>Empnig- forests</i>	187.72 (70.40) ^{bc}	0.44 (0.16) ^{bc}	0.01 (0.001) ^{bcd}	0.03 (0.01) ^g	4.75 (0.13) ^{ab}
<i>Gaybac- barrens</i>	128.70 (19.33) ^{cd}	0.54 (0.03) ^{ab}	0.02 (0.003) ^{bc}	3.30 (0.46) ^{ab}	4.43 (0.52) ^{bcd}
<i>Gaybac- bogs</i>	123.97 (12.74) ^{cde}	0.49 (0.07) ^{abc}	0.02 (0.001) ^{abc}	1.67 (0.14) ^{bcd}	3.57 (0.15) ^e
<i>Gaybac- forests</i>	247.68 (25.31) ^a	0.42 (0.07) ^{bc}	0.01 (0.001) ^d	4.26 (1.04) ^a	3.71 (0.12) ^e
<i>Kalang- barrens</i>	63.29 (6.86) ^e	0.69 (0.07) ^a	0.02 (0.003) ^a	1.52 (0.35) ^{cd}	5.04 (0.09) ^a
<i>Kalang- bogs</i>	96.86 (15.20) ^{de}	0.50 (0.03) ^{ab}	0.02 (0.002) ^{ab}	0.71 (0.61) ^e	4.76 (0.09) ^{ab}
<i>Kalang- forests</i>	188.85 (33.74) ^b	0.35 (0.03) ^c	0.02 (0.002) ^{abc}	4.21 (1.30) ^a	4.70 (0.08) ^{ab}
<i>Vacmac- barrens</i>	105.98 (17.98) ^{de}	0.43 (0.04) ^{bc}	0.02 (0.002) ^{ab}	0.19 (0.04) ^f	4.13 (0.06) ^{cde}
<i>Vacmac- bogs</i>	110.54 (23.90) ^{de}	0.49 (0.09) ^{abc}	0.02 (0.001) ^{abc}	0.23 (0.07) ^f	4.03 (0.23) ^{de}
<i>Vacmac- forests</i>	117.03 (38.34) ^{de}	0.45 (0.07) ^{bc}	0.02 (0.01) ^{ab}	0.24 (0.10) ^f	4.18 (0.11) ^{cd}

3.5 Phylogenetic Signal

The majority of traits measured did not show any phylogenetic signal (Table 3.11). Traits that showed phylogenetic signal based on Pagel's lambda include leaf arrangement ($\lambda = 1.000$, LLR0 = 0.010, LLR1= 1.000) and leaf lifespan ($\lambda= 0.700$, LLR0= 1.000, LLR1= 0.000), and traits that show phylogenetic signal based on Blomberg's K included leaf pH (K= 0.173, MLE= 0.007, p= 0.037).

Table 3.11: Phylogenetic signal values of *Ericaceae* traits in Nova Scotia. Bolded values represent significant phylogenetic signal. Phylogenetic signal of traits collected on these species were tested using both Pagel's lambda and Blomberg's K for continuous traits, and only Pagel's lambda for discrete traits. These values were tested using a pruned phylogenetic tree of 24 *Ericaceae* species. Continuous trait data was collected across barrens, bogs, and forests in Nova Scotia from June-August of 2023, and discrete trait data was collected from literature. LLR0 is the log-likelihood ratio that Lambda is different than 0, LLR1 is the log-likelihood ratio that Lambda is different than 1, and MLE maximum likelihood estimation used to calculate K.

Trait	Lambda (λ)	LLR0	LLR1	Blomberg's K	MLE	p-value
pH	0.528791	0.191866	0.000016	0.172967	0.006832	0.037000
SLA (cm ² /g)	0.000000	1.000000	0.000004	0.110269	65.628200	0.364000
LDMC	0.036418	0.999999	0.000000	0.034495	0.000380	0.879000
Lth (mm)	0.415370	0.688495	0.000015	0.136230	0.000001	0.099000
Leaf size (cm ²)	0.000000	1.000000	0.202765	0.215252	0.062985	0.092000
Leaf Lifespan	0.700000	0.9996546	0.0002146			
Leaf Arrangement	1.000000	0.0100627	1.000000			
Flowering Strategy	0.000000	1.000000	0.0046167			

4.0 Discussion

Functional traits of *Ericaceae* species varied across habitat types in Nova Scotia, and some species showed more intra-specific variation across habitats than others. The environment seemed to influence trait variation across these species more than evolutionary history, and variation in light availability appears to have a larger influence on *Ericaceae* functional diversity than differences in soil water content.

4.1 Influence of Environment:

Environmental variables shaped every functional trait measured in this study, either through trait plasticity or environmental filtering. Overall, bog habitats had higher water soil content than forests or barrens, and forests had the least light availability compared to bogs and barrens.

Across all species combined, specific leaf area was consistently larger in forests than in the barrens or bogs, while barrens and bogs had similar SLA. This is consistent with my predictions of SLA being largest in the forests and smallest in the barrens due to shade differences. Larger SLA increases light interception and is an important mechanism for plants in shaded areas (Goud & Roddy, 2022; Schieving & Poorter, 1999). SLA in the bogs was indistinguishable from the barrens and suggests that increased light availability may play a larger role in driving variation in SLA than soil water status. Consistent with this, Hodgson et al. (2011) also found SLA increased with shade when observing over 2000 species across Northern and Southern Europe. Another study observing Ericaceae species on Vancouver Island also found larger SLA in forests relative to bogs (Burns, 2004).

Similar to SLA, LS was also larger in the forests than in the barrens and bogs, and the barrens and bogs were indistinguishable from each other. This was consistent with my predictions of increased LS in the forests compared to the bogs and barrens due to light availability differences. The bogs and barrens having similar LS suggests that light plays a larger role in shaping LS than soil water status. LS plays a role in temperature regulation and photosynthetic ability, and similar to SLA, a smaller leaf size is favourable in areas with higher light availability as leaf temperature decreases with leaf size (Givnish and Vermeij, 1976; Parkhurst and Loucks, 1972; Ackerly et al., 2002). These are consistent with my findings of

smaller LS in the barrens and bogs where there was higher light intensity. Witkowski and Lamont (1991) found that LS increased with water availability; however, similar LS between the bog and barren in this study suggests that water may be a smaller driving factor than light for LS variation across Ericaceae within Nova Scotia.

Leaves were thinnest in the forests, and the bogs and barrens were indistinguishable from each other. This is consistent with my prediction of increased leaf thickness in the bogs and barrens due to nutrient limitations, however, soil nutrients may have played less of a role in shaping Lth in this study compared to the influence of light availability. Thicker leaves are also more efficient at absorbing irradiances in higher levels of sunlight (Burns, 2004). Previous studies found that increasing light and decreasing water caused an increase in the Lth of shrub species across multiple plant families (Carpenter & Smith, 1981; Witkowski & Lamont, 1991). These results are consistent with my findings of larger Lth in the bogs and barrens, likely due to increased sunlight in these habitats and less sunlight in the forests.

Similar to Lth, LDMC was also smallest in the forests, and the barrens and bogs were indistinguishable from each other. This is consistent with my prediction that LDMC would be smaller in the forests than in the barrens or bogs due to light availability differences, and LDMC was indistinguishable between barrens and bogs, which suggests differences between barrens and bogs, such as soil water content, may be less of a driving factor of LDMC than light availability. Higher LDMC is also linked to leaves being tougher or more resistant to physical hazards in general, and considering both the barrens and bogs are more exposed to hazards such as wind and precipitation than the forest (Oberndorfer & Lundholm, 2009), this may also account for the higher LDMC values observed in both the barrens and bogs (Pérez-Harguindeguy et al., 2013).

Leaves were the least acidic in the barrens, and the most acidic in the bogs. This is consistent with my predictions of decreased leaf acidity in the barrens due to exposure to salt that increases leaf pH and increased leaf acidity in the bogs due to their strongly acidic soils. Lu et al. (2022) found similar results when observing woody species across a water gradient in China, however, they also found a decrease in leaf pH when water availability increased. Decreasing leaf pH with increasing water availability is consistent with the results of this study, as the driest and wettest habitats have the highest and lowest leaf pH, respectively (Lu et al., 2022). These findings suggest that soil pH and water availability influence the variation in leaf pH for these Ericaceae species. Leaf pH has also been linked to palatability (Cornelissen et al., 2006), and differences in herbivore presences between these habitat types may also shape the differences seen in leaf pH.

Early flowering is often linked to drought avoidance (Shavrukov et al., 2017), suggesting precocious species should be more successful in drier habitats as early flowers are exposed less to dry conditions. There were more precocious species in the forests, more serotinous species in the bogs, and the flowering strategy of species in the barrens was not different than expected by random chance. This is partially consistent with my predictions of more serotinous species occurring in the bogs due to increased water supply; however, the relatively high abundance of precocious species in the forests and the barrens were not consistent with my predictions. Savage (2019) found that precocious species invest more in flowering buds the year before flowering, suggesting precocious buds are at higher risk of damage over the winter. A higher abundance of precocious species within the forests may be due to increased sheltering from snow, wind, and frost due to tree canopy (Carlsson & Callaghan, 1991). Barrens are dry and exposed (Oberndorfer & Lundholm, 2009), and opposing drivers of flowering strategy within the barren

may explain why one flowering strategy is not more prevalent than expected. Species that flower early also tend to have a competitive advantage against later-flowering species for pollinator availability as fewer plant species are flowering earlier in the season (Kehrberger & Holzschuh, 2019); the difference in types or abundance of pollinators across these habitats may also explain the differences in flowering strategy.

There was a higher percentage of species with opposite leaves in the bogs, and a higher percentage of alternate leaves in the barrens. Leaf arrangement in the forests was not different than what would be expected by random chance. This is not consistent with my predictions that leaf arrangement would not vary across habitat types. The functionality of leaf arrangement is unclear; however, the abundance of alternate leaves increases as water availability decreases, suggesting water may play a role in shaping leaf arrangement. A previous study on Tobacco plants found that water transfer between adjacent leaves was more difficult than water transfer between distant leaves (Fiscus et al. 1973). Opposite leaves may have a harder time transferring water between them than alternate leaves, resulting in fewer species with opposite leaves occurring in the barrens. Forests have higher water availability than barrens, but lower water availability than bogs, which could explain why leaf arrangement is not different than expected.

Evergreen leaves have a lower nutrient loss rate, which is advantageous in nutrient-poor environments (Aerts, 1995; Chabot & Hicks, 1982). There were more evergreen species in the bogs, more deciduous species in the forests, and the barrens did not have a significant difference in leaf lifespan strategy than expected. The bogs and forests are consistent with my prediction of nutrient-poor habitats having more evergreen species than nutrient-rich habitats, however, the barrens not being different than expected is not consistent with my predictions. Evergreen leaves are favoured in nutrient-poor environments, but deciduous species are favoured in habitats that

experience seasonal drought as deciduous leaves often reduce transpiration when water becomes limited (Givnish, 2002). A difference in water availability could explain why more of one leaf lifespan is not observed in the barren, as opposing forces are causing both leaf strategies to have an advantage. The soil samples from the barrens having some nutrients more prevalent than in forests may also explain why barren habitats had more deciduous species than expected.

Based on soil samples from this study it was unclear which habitat types had the most nutrients available. In general, forests tend to have more nutrients than barrens and bog (Oberndorfer & Lundholm, 2009; Rydin & Jeglum, 2013) and based on the Forest Classification for Nova Scotia (Neily et al., 2010) forests in Nova Scotia tend to have medium to nutrient-rich soils. It can be assumed that soil nutrients are greater in the forest than in the barren and bog, however in this study, the soil across all habitats had similar potassium (K) availability, the barrens tended to have the most sodium (Na) and nitrate (NO_3), and the forests and barrens tended to have the most calcium (Ca). The soil samples barrens containing more nutrients than forests could be because this was a short-term study and soil samples were only taken once from each plot, and temporary differences may have skewed the results. It could also be due to the barrens experiencing salt spray, or the water-soluble nutrients measured in the soil samples might not be the same nutrients accessible to plants. More in-depth soil samples testing plant-available nutrients are needed to understand the true effects of nutrient availability on these species.

4.2 Influence of Evolution:

Some traits had phylogenetic signal, meaning they were more similar among closely related species regardless of what habitat they were found in. These traits included leaf lifespan, leaf pH, and leaf arrangement. Goud and Sparks (2018) also found phylogenetic signal for leaf life span when observing Ericaceae species across North America. Another study found no

phylogenetic signal for leaf lifespan when looking at evergreen and deciduous tree species across 15 families; however, that study used leaf lifespan in terms of days rather than binary groupings, potentially accounting for the difference in results (Krishna et al., 2021). There were no previous studies found testing phylogenetic signal of leaf pH or leaf arrangement. A previous study found that leaf pH was species-driven rather than soil-driven; however, that study was conducted on herbaceous species which function differently and need to be separated from woody species (Cornelissen et al., 2011; Lu et al., 2022). These traits were likely driven more by evolutionary history and are more similar between more closely related species.

SLA did not have phylogenetic signal, which is supported by previous work from Basnett & Devy (2021) of 10 *Rhododendron* species in Sikkim Himalaya. When a trait has no phylogenetic signal, species are less similar than expected by Brownian motion, suggesting that evolutionary history is not the only mechanism driving trait evolution and environmental factors may be shaping differences in that trait (Ackerly, 2009). By contrast, Liu et al. (2023) and Akram et al. (2022) found that across multiple plant growth types (trees, shrubs, herbs) there was phylogenetic signal in SLA. These findings may suggest that at a larger taxonomic scale (across multiple plant growth types) evolution drives SLA, but at a finer scale (within a clade or genus) evolutionary history may play less of a role in structuring patterns of SLA (Donovan et al., 2011).

LS and Lth also showed no phylogenetic signal in this study, which implies that habitat preferences or environmental variation are playing a larger role in shaping trait variation in LS and Lth across these species. This finding is similar to Goud and Sparks (2018) for 57 Ericaceae species, and Akram et al. (2022) for 37 desert plant species of different growth types. However, Basnett and Devy's (2021) study of 10 *Rhododendron* species found phylogenetic signal for both

LS and Lth. Phylogenetic signal of traits is often more likely to be observed under stressful conditions due to increased constraints on growth (Burns & Strauss, 2012) and Basnett and Devy's (2021) study observed *Rhododendron* species at high and low elevations, which are stressful environments for plants. Elevational stress may explain why phylogenetic signal for LS and Lth is observed in Basnett & Devy's (2021) study, but not in other studies.

No phylogenetic signal was found for LDMC in this study. This is consistent with Akram et al. (2022) for 37 desert plant species and Liu et al. (2023) for boreal understory species. No phylogenetic signal for LDMC was also found when observing species in grasslands (Wang et al., 2021). Consistent results across multiple scales suggest that variation in LDMC is not strongly influenced by evolutionary aspects and is more likely influenced by environmental variation, such as differences in light availability between habitats.

No phylogenetic signal was found for flowering strategy in this study. Du et al. (2015) found that across multiple plant growth types, there was a phylogenetic signal for the flowering time. Neto-Bradley et al. (2021) also found that across 72 grass species, there was phylogenetic signal for flowering time. These studies, however, observed species across multiple plant growth types and used dates of flowering rather than the binary precocious-serotinous method used in this study. The difference in scale, plant growth type, and methods may explain why inconsistent results were found. Flowering strategy in terms of flowering date may be influenced by evolutionary history (Du et al., 2015; Neto-Bradley et al., 2021), but whether a species is precious or serotinous does not seem to be driven by evolutionary history, suggesting that environmental variables or perhaps biotic factors, such as pollinator interactions, influence the patterns of flowering strategy across *Ericaceae* species in Nova Scotia.

4.3 Relative Influence of Evolution and Environment

The impact of evolutionary history on driving plant functional traits is dependent on the taxonomic scale of the study, and intraspecific variation is dependent on the species. Closely related species are expected to be more similar due to shared evolutionary history (Darwin 1859), and coexisting species within a habitat should not be too similar or they will out-compete each other (Cavender-Bares et al., 2004). This duality offers a possible explanation as to why contrasting patterns of phylogenetic signals are observed at different scales, such as within SLA. When comparing species at a broad taxonomic scale, such as across multiple plant families, trait conservatism may be more prominent as closely related species within those families are going to be more similar to each other compared to distantly related clades (Ackerly, 2009). However, when examining species at a smaller scale such as within a clade, competition of species that occur together can drive differences between them (Mello et al., 2020), resulting in weak or no phylogenetic signal.

Environmental factors drive functional trait diversity in Ericaceae, and some environmental factors influence traits more than others. SLA, LS, Lth, LDMC, leaf lifespan, and flowering strategy appear to be relatively more influenced by environmental light availability than soil water content, based on their patterns between wetlands (bogs) and non-wetlands (forests, barrens). Leaf pH and leaf arrangement may be more influenced by water availability than light based on the patterns of traits across the water gradient.

Some species such as *Gaylussacia baccata* and *Chamaedaphne calyculata* were more plastic than others, suggesting these species may be able to acclimate to changing environmental variables more easily than non-plastic species (Mello et al., 2020). Understanding which traits are affected by, and which species are better equipped to face environmental change is important

as climate change progresses (Alba et al., 2019; Mello et al., 2020). Recent studies indicate that under rapid climate change, phenotypic plasticity will play a larger role in species acclimations than genetic diversity as short-term plasticity allows species to cope with rapid environmental change (Vitasse et al., 2010). In general, species traits were more influenced by environmental factors than evolutionary aspects at the clade level. Understanding the environmental gradients that traits respond to, and which species respond better to environmental pressures, is important for understanding how climate change will influence plant communities. More fine-scale studies of species plasticity across environmental gradients are required to understand how patterns of species diversity may be affected by climate change (Alba et al., 2019; Mello et al., 2020), and how the performance and function of species are going to change as environmental pressures increase.

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6.0 Appendix

Appendix 1. Analysis of variance of soil characteristics across three main habitat types (barren, bog, forest) in Nova Scotia. Data is from 79 soil samples collected from September of 2022 and June-August 2023.

Soil Trait		Df	Sum Sq	Mean Sq	F value	Pr(>F)
Gravimetric water content (θg)	Habitat Type	2	43.070	21.535	23.910	9.80E-09
	Residuals	74	66.660	0.901		
pH	Habitat Type	2	4.491	2.246	12.040	2.87E-05
	Residuals	76	14.177	0.187		
K (ppm)	Habitat Type	2	0.045	0.023	0.066	0.936
	Residuals	76	26.112	0.344		
Ca (ppm)	Habitat Type	2	178.400	89.220	7.401	0.00118
	Residuals	74	892.100	12.060		
Na (ppm)	Habitat Type	2	12.060	6.029	13.360	1.07E-05
	Residuals	76	34.300	0.451		
NO3 (ppm)	Habitat Type	2	41.500	20.756	3.883	0.0248
	Residuals	76	406.300	5.346		
EC (mS/cm)	Habitat Type	2	2.224	1.112	4.989	0.00921
	Residuals	76	16.941	0.223		

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