# Examining Species Coexistence Through the Functional Trait Lens

By

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## Abstract

**Introduction:** I investigate several key knowledge gaps and inconsistencies observed in coexistence literature, specifically gaps associated with spatial heterogeneity, functional trait divergence, and the storage effect. For spatial heterogeneity, empirical research has resulted in all possible heterogeneity-biodiversity patterns, positive, negative, and neutral. The lack of consistency between studies indicates a need to further explore this topic and piece together why various patterns can occur. Although trait divergence has been associated with species coexistence, work is still needed to understand which specific traits play the greatest role in plant communities, how intraspecific trait variation influences coexistence, and to incorporate trait data into community and ecosystem processes. Furthermore, there is a lack of empirical evidence regarding modern coexistence theory and the storage effect, so research is needed to determine if these theories hold true in the natural world.

**Methods:** In order to address questions surrounding coexistence and plant community assembly, I created the first functional trait database for Nova Scotia, Canada. In total, this database contains 13,458 trait values from 203 species comprising 130 genera and 53 families (Chapter 1). Using this database, I conducted one observational and three experimental studies. The observational study relies on six coastal barren vegetation datasets to determine how spatial heterogeneity and environmental stress influence biodiversity and plant community assembly in turn coexistence (Chapter 3). I examined how soil depth heterogeneity and environmental stress influence plant community assembly over time in an experimental green roof system (Chapter 4). The purpose of the final two experiments was to address questions regarding coexistence and functional trait divergence. I created a greenhouse study examining coexistence under a dynamic watering regime, and a green roof study examining coexistence at low density (Chapter 5).

**Main Findings:** Environmental stress, rather then spatial heterogeneity, led to an increase in functional trait diversity. Since species with more divergent traits are less likely to compete for limiting resources, this finding indicates the presence of a filter, encouraging coexistence between species that differ in stress tolerant strategies. This finding is further emphasised when specific functional traits are examined. Specifically, coexistence in water-limited environments is possible when species differ in plant height and leaf dry matter content. This dissertation also demonstrates the importance of analysing the functional diversity of individual traits. This analysis allows researchers to understand which specific strategies encourage coexistence and co-occurrence.

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# Chapter 1

# Introduction: Coexistence and Plant Functional Traits

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## Coexistence Theory

Plant community ecology is the study of the factors driving the assembly of plant communities (Jackson and Blois, 2015). These factors can be biotic, abiotic, or even due to chance (demographic stochasticity). Although there is much theoretical literature detailing the processes behind community assembly (Vellend, 2010), more empirical evidence is necessary in order to validate the inferences drawn from theoretical simulations (Diaz and Cabido, 2001; Chesson, 2011; Letten et al., 2017). Of particular interest to many community ecologists are questions regarding species coexistence, defined as co-occurrence of species' populations over an extended period of time (Chesson, 2008). Furthermore, competitive coexistence, found at finer spatial scales, refers to coexistence maintained through interaction and/or competition between neighboring individuals. This topic is not only of ecological interest; insights can be used to assist with rare species conservation, the control of invasive species, and forecasting the effects of climate change on plant populations (Adler et al., 2018).

Our current understanding of plant coexistence comes from modern coexistence theory, which is based on the work of Peter Chesson, specifically Chesson (1994) and (2000ab). This work incorporates niche theory (heterogeneity, resource-ratio hypothesis, storage effect, facilitation), neutral theory, and the Lotka-Volterra competition model, providing the mathematical framework necessary to quantify the diverse variables contributing to coexistence (Ellner et al., 2019). Modern coexistence theory states that species coexistence can only occur if three conditions are met (Chesson, 2000b; Chesson, 2018; Godwin et al., 2020):

1. Intraspecific competition must be greater than interspecific competition (Lotka-Volterra competition model),
2. Species must have niche differences (niche theory)
3. Relative fitness differences must be present (niche theory)

Although this coexistence framework has greatly influenced how plant ecologists understand coexistence, with Chesson (2000b) cited at least 3,401 times (Web of Science, 2021), it lacks empirical support (Ellner et al., 2019).

For researchers to understand coexistence, there is a need to grasp the competitive relationship between co-occurring species. Without this knowledge, researchers cannot predict how a plant community will change over time. The Lotka-Volterra competition model can be used to understand how inter/intraspecific competition varies between two plant species (Chesson, 2000b). Modern variations of the model are based on equations contributed by two academics, Alfred J. Lotka and Vito Volterra, who in 1925 independently created a series of equations to simulate predator-prey interactions (Kingsland, 2015). When applied to plant ecology, the model demonstrates that stable coexistence between species can occur if intraspecific competition is greater than interspecific competition (Silvertown, 2004). For example, if a community contains a competitive fast-growing species (species A) and a less competitive slow-growing species (species B), then coexistence is possible if species A limits its own population, enabling species B to persist. A literature review by Adler et al., (2018) found 39 studies pertaining to this topic. When examined, the authors found that intraspecific competition was four to five times stronger than interspecific competition. Although inter/intraspecific competition plays a central role in modern coexistence theory, it is not the only factor that must be present for coexistence to occur (Chesson, 2000b).

Two of the three conditions for coexistence proposed by modern coexistence theory are based on niche theory, which was first introduced in 1917 by Joseph Grinnell. It was further developed in 1927 by Charles Sutherland Elton, and in 1957 our modern understanding of niche theory was proposed by George Evelyn Hutchinson (Grinnell, 1917; Hutchinson, 1957; Chase and Leibold, 2003). The Hutchinsonian niche (hereafter referred to as niche theory) defines a species' niche as the biotic and abiotic factors that allow a species to maintain its population within a community (Hutchinson, 1957; Silvertown, 2004). According to niche theory, a species' fundamental niche is a hypervolume composed of n-dimensional axes where the axes are the boundaries in which a species can maintain its population (Blonder, 2017). For example, environmental gradients (varied soil depth, shade, nutrients), temporal gradients (changes in temperature, precipitation, light), a species' morphological traits (height, photosynthetic pathway, drought tolerance), a species' physical development (timing for dormancy, seed set, growth), and density-independent factors (disturbance) can all be considered axes defining a species' niche, several of which are likely involved in maintaining a species' population within a community (Grubb, 1977; Chesson, 2000b; Chesson, et al. 2004; Grime, 2006; Pierce et al., 2007; Lavorel et al., 2011; Pauw, 2013). A species' traits play an important role in niche theory, as co-occurring species with more divergent traits should differ in resource acquisition strategies (spatially or temporally), encouraging co-existence (Macarthur and Levins, 1967; Levine and Hille Ris Lambers, 2009). Over time, niche theory has been divided into multiple key categories, each of which describes how variation in plant functional traits, the morphological, physiological, and phenological characteristics expressed in the phenotypes of individual organisms (Violle et al., 2007; Diaz et al., 2013; Garnier et al., 2016), encourages coexistence.

Spatial and temporal heterogeneity encourage coexistence through the formation of different microsites, or time periods, favorable to different plant species (MacArthur and Levins, 1967; Grubb, 1977; Tilman, 1982; Chesson, 2008). Spatial heterogeneity can occur when features such as soil, water, nutrients, and/or shade vary across the environment. A grassland study by Maire et al. (2012) found that heterogeneity in soil nutrients encouraged coexistence between tall and short species, with shorter species inhabiting the low-nutrient patches and taller species inhabiting the high-nutrient patches. Temporal heterogeneity, associated with seasonal changes as well as variation in plant phenologies, encourages coexistence, as species use resources at different times. A study conducted in grassland communities in Northern Greece found that $C_3$ annuals and perennials grew from autumn to spring and co-occurring $C_4$ species grew from winter to summer. Since these species were growing and using resources at different times, coexistence between them was possible (Mamolos, 2006). Even though heterogeneity is predicted to increase biodiversity, by increasing the available niche space and allowing more species to find their niche requirements within a given area (MacArthur and Levins, 1967; Grubb, 1977; Tilman 1982), researchers have observed both neutral associations

(Reynolds et al., 2007; Questad and Foster, 2008; Lundholm, 2009; Tamme et al., 2010) and negative associations between species diversity and heterogeneity (Tamme et al., 2010; Gazol et al., 2013; Laanisto et al., 2013; Yang et al., 2015). Due to these disparate observations, there is a need to increase understanding of how environmental heterogeneity influences biodiversity.

Interspecies coexistence is not exclusive to heterogenous ecosystems. In more homogeneous environments, coexistence may be due to variation in how a species acquires resources. Tilman’s resource-ratio hypothesis describes this phenomenon (Tilman, 1982; Silvertown, 2004). For example, if a community has one species limited by phosphorous (species A) and a second species limited by nitrogen (species B), coexistence is possible if each species limits their desired resources in favor of the other. If this hypothetical community is currently limited by nitrogen, then species A will be dominant. Over time, as species A depletes the phosphorous, the nutrient levels in the community begin to favor nitrogen. This nutrient shift leads to species B having the competitive advantage. This variation in nutrient quantities continues over time, leading to coexistence between species A and B (Tilman, 1982). This can be taken further to describe coexistence between species that differ in how/where they acquire nutrients. This has been observed in the natural environment between species that differ in how they acquire nitrogen (Fargione and Tilman, 2005; Mamolos, 2006), access light (Price et al., 2014), and where in the soil column they access resources (Wang et al., 2018). The resource-ratio hypothesis demonstrates the importance of trait variation in the maintenance of species diversity. It also touches on concepts fully defined under the storage effect.

The storage effect is a term used to describe coexistence in instances where species store resources from a productive period in order to survive an unproductive period. For coexistence to occur through the storage effect, three components need to be present in a community: species must have divergent traits that lead to different environmental responses (germination temperature, drought-tolerant strategies), species' competitive ability must change as a response to environmental conditions (covariance between species), and species must be capable of surviving unfavorable conditions (Chesson, 2000b). For example, if two desert annuals germinate under different temperatures but similar moisture regimes, annual variation in temperature will influence which species has the competitive advantage. So long as both species can survive unfavorable conditions, this annual variation can lead to coexistence (Chesson et al., 2004). Angert et al. (2009) observed the storage effect in winter annuals with divergent traits related to water-use efficiency. During short but frequent rainfall events, species with low water-use efficacy excelled and species with high water-use efficacy excelled during periods of long but infrequent rainfall events. Coexistence between species was possible due to a yearly variation in rainfall supporting the growth of each species in turn (Angert et al., 2009). Within year variation can also lead to coexistence via the storage effect. This was observed by Mathias and Chesson (2013), who examined the influence of seasonal temperature variation on the germination and seed set of winter annuals. They found that seasonal temperature variation resulted in variation in the competitive ability of winter annuals, leading to co-existence between these species (Mathias and Chesson, 2013). Due to their short life cycles, annual plant communities offer an ideal environment to test coexistence mechanisms. However, there is still a need to empirically test the storage effect in long-lived plant communities.

In some plant communities, coexistence is possible due to interspecific facilitation, where the presence of one species alters the environment in a way that supports the growth of another. For example, plants can shade the soil (reducing soil temperatures and evaporation), create toxins (discouraging the presence of herbivores), or have symbiotic associations with nitrogen-fixing bacteria (increasing soil nutrient availability) (Greenlee and Callaway, 1996; Wright et al., 2017). This facilitative association is frequently used in agriculture, with nitrogen-fixing legumes planted alongside, or before, species with a high nitrogen demand (Oelmann et al., 2011). Within the natural environment, facilitation is usually observed in environments under environmental stress. In a Kenyan savannah, where species are exposed to water and thermal stress, Scholes and Archer (1997) observed trees facilitating herbaceous vegetation. In these sites, shade from the tree canopy resulted in lower soil temperature and reduced water stress. Researchers also found that the soil underneath tree canopies contained more organic soil, nitrogen availability, and microbial biomass than neighboring vegetation lacking in tree canopies (Scholes and Archer, 1997). Another natural occurrence of facilitation can be observed between seedlings of *Carnegiea gigantea* and neighboring vegetation (nurse plants). The shade provided by nurse plants cools the soil, enabling *C. gigantea* seedlings to survive the harsh desert sun (Turner et al., 1966). In these examples, variation in plant functional traits encouraged coexistence and species diversity. However, as environmental conditions change, a facilitative relationship can become a competitive one. For instance, as *C. gigantea* seedlings grow, competition occurs between the seedlings and the former nurse plant, which can result in death or decreased biomass (Turner et al., 1966). This trend is common, with facilitation often present during unfavorable conditions and competition present during favorable conditions (Greenlee and Callaway, 1996). As with the storage effect and the resource-ratio hypothesis, variation in this facilitative interaction could lead to coexistence.

The examples above have touched on how divergence in multiple traits can encourage coexistence. Here I further explore this topic and discuss the occurrence of trait divergence and convergence within the same plant community. Research has found that species naturally occurring in the same habitat will likely possess some trait similarity, allowing them to persist in that habitat (Grime, 2006; Maire et al., 2012; Price et al., 2017). For example, the majority of plants in Israel's Central Negev Desert are winter annuals, which allows them to survive as seeds during the dry summer and grow and reproduce during the wet winter (Lortie and Turkington, 2002). Another study, conducted on plant communities in the Córdoba Mountains in Central Argentina, found three distinct vegetative groups, each associated with specific environmental conditions. Tall grass was found in environments high in potassium, short grass was found in the driest environments, and wet turf was found in saturated environments (Cantero et al., 2003). However, even in functionally similar plant communities, distinct differences between species can be observed. For example, desert annuals that are similar in terms of their senescence but differ in the timing of germination can coexist, as they use resources at different times (Chesson et al., 2004). For this reason, research incorporating multiple niche axes into the analysis are better suited to catching the nuanced patterns that occur in habitats where species must be convergent in specific traits (Clark et al., 2007).

Although the theory itself has rarely been supported in the natural environment, neutral theory has played an important role in the development of modern coexistence theory. Neutral theory was first proposed by Hubbell in 2001 and states that the composition of species within a community is a result of demographic stochasticity, with all species sharing the same average fitness (Hubbell, 2001; Silvertown, 2004; Hubbell, 2006; Chesson, 2011). According to this theory, the presence of divergent or convergent traits within a community is irrelevant, as species are essentially equivalent. Since Hubbell first proposed this theory, the concept has been heavily debated, leading to a flood of academic papers tackling the disparity between neutral theory and conventional coexistence theory (niche theory) (Chase, 2014). Research has found rare cases in which neutral models do adequately explain patterns in the natural environment (Volkov et al., 2007; Chesson, 2011). However, the majority of empirical studies demonstrate that neutral models alone do not explain the patterns behind coexistence in many plant communities (Adler, 2004; Chu et al., 2007; Chesson, 2011). Additionally, the trends predicted by neutral models can also be predicted by non-neutral models (Chesson, 2011). Nevertheless, neutral theory has played an important role in the development of modern coexistence theory, providing researchers a null model from which to test coexistence

(Kraft et al., 2008). Furthermore, neutral theory has forced ecologists to justify the claims made by non-neutral models (Adler et al., 2007).

Plant functional traits, the morphological, physiological, and phenological features that influence plant fitness (Violle et al., 2007), are an ideal tool for examining coexistence in plant communities. They can be used to tease apart which aspects of the community have shared ecological strategies and which aspects have divergent ecological strategies, with divergent strategies indicating how plant species can coexist. For example, Gross et al., (2015) used a functional trait approach to examine coexistence between alien and native species in a grassland community. The authors found that the array of traits possessed by particular species allowed the invaders to either outcompete or coexist with native vegetation (Gross et al., 2015). Another study used functional plant traits to examine coexistence between two co-occurring tropical plant guilds, lianas and trees. The authors found that the two guilds significantly differed in mean functional trait values for four of the ten traits examined. The findings indicate that these two guilds may coexist due to differences in survival strategies (Mello et al., 2020). Although research has found associations between traits and variations in the structure and function of plant communities, empirical evidence is still needed to understand which traits influence coexistence in natural and constructed ecosystems (Funk et al., 2017).

## Plant Functional Traits

Community ecologists often cluster vegetation into specific groups based on attributes such as habitat, traits, or growth form in order to see if patterns emerge between particular vegetation clusters and abiotic/biotic variables. This method has been used to answer key ecological questions that have shaped the way ecologists understand plant community assembly (Grime, 2006; Flynn et al., 2011; Rowe and Speck, 2005; Díaz and Cabido, 2001; Chesson et al., 2004). For example, research has found that species in high-stress environments tend to share similar traits (Katabuchi et al., 2012), the first species that colonize after disturbance tend to be ruderals (Turner et al., 1998), and plant species are more likely to coexist if they use resources in a different way or at a different time (Chesson et al., 2004). In these examples, plant functional traits play a key role in understanding ecological patterns. Furthermore, plant functional traits can be used to divide a single species into multiple variables (plant height, leaf size, root length), allowing researchers to fully investigate plant interactions (Spasojevic et al., 2012).

Published trait guidelines, such as the works by Pérez-Harguindeguy et al. (2016) and Cornelissen et al. (2003), provide instructions on how to collect specific traits and how many individuals specific traits should be collected from. Although trait divergence can exist between individuals of the same species, on average, between-species variation is greater than within-species variation (Kattge et al., 2011). This methodology has allowed researchers to create functional trait databases with standardized trait variables at the species level. Furthermore, resources and study questions determine whether researchers incorporate trait values from a database that is global, regional, or from their specific experiment. Each of these different database types has strengths and weaknesses.

Global trait databases are a useful tool when examining traits across large spatial scales (across continents and biomes) and when resources are not available for researchers to gather traits themselves. One of the largest global databases, the TRY database, has been operating for 12 years. It has been used in 350 scientific publications and currently contains 11,850,781 trait records and 279,875 plant taxa (TRY, 2021). However, this resource is limited in that it only contains data contributed by researchers. This means that there is an overabundance of data from specific regions, plant species, and functional traits (Stahl 2013). In situations where trait data pertinent to the study are not available in global databases, researchers can create regional, research-specific databases. In this way, average species trait values can be determined from individuals growing in the study system. Regional databases are useful tools for research incorporating high species richness and when applying functional traits to previously collected data. Regional trait databases have been curated for vegetation from locations such as China, Australia, the Mediterranean, and tundra biomes (Bjorkman 2018; Tavşanoğlu and Pausas, 2018; Wang et al., 2018; Falster et al., 2021). Since the majority of global and regional databases rely on functional trait averages, analysis can only examine interspecific variation. For researchers interested in intraspecific variation, a trait database is not the ideal option. Rather, researchers tend to collect trait values directly from their experiment or study system (Rosas et al., 2019). However, this method is often not feasible for projects that incorporate high species richness, contain rare species, or have limited resources. For this reason, the use of global or regional datasets is a widely accepted alternative for functional trait researchers (Bjorkman 2018; Tavşanoğlu and Pausas, 2018; Wang et al., 2018; Falster et al., 2021; TRY, 2021).

Functional plant traits can be used to understand where a plant grows, how a plant interacts with neighbors, and how a plant influences their environment (Reich, 2014). Extensive research has led to the development of functional trait correlations, describing associations between specific trait values, physiological processes, and environmental variables (Poorter and Garnier, 1999; Niinemets 2001; Wright et al., 2001; Liira et al., 2002; Vile et al., 2005; Moles et al., 2009; Ogburn et al., 2010; Tardy et al., 2015; Wang et al., 2019). The patterns associated with specific trait values are often described in terms of cost-income models, or economic spectrums, where energy use in plants is explained in terms of energy investment (energy used to create an organ) and return (energy produced due to that organ) (Orians and Solbrig, 1977; Westoby, 1998; Wright et al., 2004; Freschet et al., 2010; Kong et al., 2016). For example, the leaf-height-seed scheme (Westoby, 1998), leaf economic spectrum (Wright et al., 2004), root economic spectrum (Kong et al., 2019), and whole-plant economic spectrum (Freschet et al., 2010) describe the relationship between specific trait values and ecological strategies (competitive, stress-tolerant). In these schemes, stress-tolerant species tend to build energy-intensive organs adapted to high-stress environments, such as thick leaves in areas exposed to drought (Niinemets, 2001). Competitive species, such as those found in low-stress environments, build organs with low energy-demands, such as thin, wide leaves (Wright et al., 2004). The organs created by stress-tolerant species do not have a high carbon return, but these species are able to persist through unfavorable conditions. Competitive species can quickly gain carbon, but their organs are susceptible to environmental stress (Orians and Solbrig, 1977; Westoby, 1998; Wright et al., 2004; Freschet et al., 2010;

Kong et al., 2016). This trade-off in plant strategies allows species to favor different environmental conditions, increasing biodiversity and encouraging coexistence between species (Chesson et al., 2004).

Although numerous plant functional traits could be included in ecological analysis, most researchers limit themselves to traits that reflect plant energy use and those associated with the study system or research question. For many plant species, the central organ involved in photosynthesis, and thus carbon acquisition, is the leaf (He et al., 2018). Three leaf traits: specific leaf area (leaf area/dry mass), leaf dry matter content (leaf dry mass/ leaf wet mass), and leaf thickness are frequently used to provide insight into plant community dynamics. The leaves of fast-growing, more competitive species tend to have higher specific leaf areas, lower leaf dry matter content, and tend to be thinner (Poorter and Garnier, 1999; Niinemets, 2001; Vile et al., 2005; Freschet et al., 2010; Tardy et al., 2015; Griffith et al., 2016; Kramer et al., 2016). However, these leaves are more susceptible to herbivory and physical stress, such as drought and high wind (Edwards et al., 2014). For this reason, species in infertile and stressful environments tend to create more carbon-expensive leaves which live longer and are more resilient to physical hazards while being less efficient at acquiring resources (Freschet et al., 2010; Griffith et al., 2016; Kramer et al., 2016). When examined as individual traits, specific leaf area is associated with leaf lifespan, net photosynthetic rate, relative growth rate, and leaf nitrogen content (Wright et al., 2001); leaf dry matter content is associated with nutrient and water conservation (Poorter and Garnier, 1999; Tardy et al., 2015); and leaf thickness is associated with water conservation, light absorption, CO2 dispersion, construction costs, longevity, and salt tolerance (Niinemets 2001; Vile et al., 2005; Ogburn et al., 2010). For specific leaf area, the pattern described above does not apply to succulent species. Due to the quantity of water stored in succulent leaves, these species usually have a higher specific leaf area than is expected from a stress-tolerant individual (Vendramini et al., 2002).

Roots play an integral role in plant growth and survival. However, functional root traits are not as prevalent in the literature as aboveground organs. This is partly due to the difference between how these traits are gathered, with root traits requiring more time and resources to collect and measure (Pérez-Harguindeguy et al., 2016). Even so, two root traits, specific root length (fine root length/dry mass) and root diameter, have proven useful in understanding species interactions. Research has found that species with smaller root diameters and higher specific root length have greater hydraulic conductivity due to the increased contact between the root and soil. This trend leads to a greater prevalence of species with small root diameters and higher specific root lengths in dry environments (Comas et al., 2013).

For many species, seed traits influence reproductive success, with germination and survival only possible if the seed reaches a suitable environment (Gallien et al., 2015). Seed mass plays an important role in dispersal, with lighter seeds capable of dispersing farther then larger seeds. Furthermore, the species that produce lighter seeds tend to produce more per capita, increasing the likelihood that these seeds will reach a viable location. Heavier seeds also have advantages as they are more efficient at surviving undesirable conditions such as drought, shade, and herbivory (Viard-Crétat et al., 2011; Jimenez-Alfaro et al., 2016).

Canopy width and plant height are whole-plant traits that provide insights concerning survival strategies. Canopy width is associated with light acquisition (Liira et al., 2002) and can be used to differentiate habitats, such as tree stands and *Sphagnum* bogs. For example, on the coastal barrens of Nova Scotia species with narrow canopies are dominant in the seaside-plantain-rocky-coastal-shoreline associations (vegetative communities) and species with wider canopies are dominant in the black-spruce-highland-heath associations (Porter et al., 2020). Plant height at maturity plays a central role in how plant species survive, grow, and reproduce. It is associated with several key leaf and reproduction traits, including canopy area, leaf area ratio, leaf mass fraction, leaf nitrogen content, seed mass, time to reproduction, seed longevity, and the number of seeds a plant can produce per year (Moles et al., 2009; Wang et al., 2019). Furthermore, this trait can be used to understand variation in fitness and ecological strategies; taller individuals are more efficient at accessing light and soil resources and they have a greater seed and pollen dispersal distance. In the natural environment, taller plants tend to be more competitive, as the shade from tall species can suppress the growth of neighboring species (Moles et al., 2009). However, taller plants are more vulnerable to drought, high winds, and extreme temperature, leading to a greater prevalence of short species in harsh environments (Wang et al., 2019; Nagashima and Hikosaka, 2011).

## Functional Trait Indices

Although the equations differ, the indices used in both functional trait analysis and taxonomic analysis provide similar insights, with equations available to understand richness, evenness, and diversity (Table 1.1). These different indices are calculated by combining trait data (quantitative and/or qualitative) with community abundance data (Lavorel et al., 2008). Depending on the question, a researcher may use one or more traits in their analysis (Laliberté and Legendre, 2010). For example, a study by Dobert et al. (2017) on tropical forest degradation found that logging was associated with an increase in the trait diversity of understory vegetation. In order to understand the ecological strategy of these plants, the authors included 10 functional traits in their calculations (Dobert et al., 2017). Another study by de Vries et al. (2012) found that in a grassland ecosystem, the ratio between fungal/bacterial biomass decreased as the specific leaf area increased. Since low specific leaf area is associated with slow-growing N-conservative grassland species, this finding highlights the relationship between rhizosphere microbial communities and species with low specific leaf areas (de Vries et al., 2012).

There are three indices that can be used to calculate functional diversity: Rao's quadratic entropy (Botta-Dukát, 2005), functional divergence (Villéger et al., 2008), and functional dispersion (Laliberté and Legendre, 2010). The purpose of these formulas is to understand how similar or different species within the community are to each other. For example, if plot A has higher functional diversity than plot B, then the species in plot A have more divergent trait values than the species in plot B. Each equation takes a slightly different approach to calculate functional diversity: Rao's quadratic entropy incorporates species relative abundance and pairwise functional difference between species (Botta-Dukát, 2005), functional divergence shows abundance along a trait axis (Villéger et al., 2008), and functional dispersion is the mean distance from a species' position in multidimensional trait space to the centroid (calculated as the average value of trait(s) across all species). Functional dispersion incorporates species abundance, shifting the centroid towards the more abundant species. The index researchers use to calculate functional diversity depends on the data, with functional dispersion the most flexible. Specifically, functional dispersion can be used to calculate functional diversity for datasets containing abundance data collected in a presence/absence format (data not suited to Rao’s quadratic entropy) and for datasets containing fewer species than traits (data not suited to functional divergence) (Anderson 2006; Laliberté and Legendre, 2010; Laliberté et al., 2015).

In addition to functional diversity, researchers frequently use community weighted mean, functional richness, and functional evenness to examine plant community dynamics. Community weighted mean incorporates species abundance and population-based trait measurements to calculate a mean trait value for each sample (Lavorel et al., 2008). Functional richness describes the range of functional traits filled by the community. This index is determined by calculating the convex hull volume using the Quickhull algorithm (Villéger et al., 2008). Finally, functional evenness describes how evenly traits are distributed in an n-dimensional trait space (Villéger et al., 2008).

**Table 1.1.** Formulas for functional trait indices and corresponding references.

| Formula | Equation | Legend | Reference |
|---|---|---|---|
| Community Weighted Mean | $\sum_{i=1}^{n} p_i \times trait_i$ | $p_i$ is the relative contribution of species *i* to the community and $\text{trait}_i$ is the trait value of species *i* | Lavorel et al., 2008 |
| Functional Richness | $[ta_1 + (1\text{-}t)b_1, ta_2 + (1\text{-}2)b2 \ldots ta_n + (1\text{-}t)b_n]$ | *t* is the coordinates in this multidimensional space, a and b are trait values for individual *j* and *i* | Barber et al., 1996; Villéger et al., 2008; Cornwell et al., 2006 |
| Weighted Evenness ($EW_l$) | $\frac{dist(i,j)}{w_i + w_j}$ | *i and j* are the species involved, dist(*i*,*j*) is the Euclidean distance between them, and $W_i$ is the relative abundance of species *i* along branch *l* (distribution on axis) | Villéger et al., 2008 |
| Partial Weighted Evenness ($PEW_l$) | $\frac{EW_l}{\sum_{l=1}^{S-1} EW_l}$ | *S* is species, *l* is distribution on axis, $EW_l$ is weighted evenness | Villéger et al., 2008 |
| Functional Evenness | $\frac{\sum_{l=1}^{S-1} min\left(PEW_l, \frac{1}{S-1}\right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}}$ | *S* is species, *l* is distribution on axis, $PEW_l$ is partial weighted evenness | Villéger et al., 2008 |
| Rao's Quadratic Entropy | $\sum_{k=1}^{n}\sum_{l=1}^{n} w_{kl}\,(X_{ik} - X_{jk})(X_{il} - X_{jl})$ | species are *i* and *j*, $w_{kl}$ is the inverse of variance-covariance matrix of traits, n is the number of traits, and $X_{ik}$ is the value of trait *k* for species *i* | Botta-Dukát, 2005 |
| Center of Gravity | $\frac{1}{V}\sum_{i=1}^{V} X_{ik}$ | *V* is the center of gravity for the species forming the vertices of the convex hull, $X_{ik}$ is the coordinate of species *i* on trait *k* | Villéger et al., 2008 |

| | | | |
|---|---|---|---|
| Euclidean Distance | $\sqrt{\sum_{k=1}^{T}(X_{ik} - g_k)^2}$ | $T$ is trait, $X_{ik}$ is the coordinate of species $i$ on trait $k$, $g_k$ is the center of gravity for the species forming the convex hull | Villéger et al., 2008 |
| Mean Distance to the Center of Gravity ($\overline{dG}$) | $\frac{1}{S}\sum_{i=1}^{S} dG_i$ | $S$ is species, $dG_i$ is the Euclidean distance to the center of gravity | Villéger et al., 2008 |
| Abundance-Weighted Deviance ($\Delta d$) | $\sum_{i=1}^{S} w_i \times (dG_i - \overline{dG})$ | $S$ is species, $dG_i$ is the Euclidean distance to the center of gravity, $\overline{dG}$ is the mean distance to the center of gravity, $w_i$ is the relative abundance of species $i$ | Villéger et al., 2008 |
| Absolute Abundance-Weighted Deviances ($\Delta\|d\|$) | $\sum_{i=1}^{S} w_i \times \lvert dG_i - \overline{dG} \rvert$ | $S$ is species, $dG_i$ is the Euclidean distance to the center of gravity, $\overline{dG}$ is the mean distance to the center of gravity, $w_i$ is the relative abundance of species $I$, $\Delta d$ is abundance-weighted deviance | Villéger et al., 2008 |
| Functional Divergence | $\frac{\Delta d + \overline{dG}}{\Delta\lvert d\rvert + \overline{dG}}$ | $dG_i$ is the Euclidean distance to the center of gravity, $\overline{dG}$ is the mean distance to the center of gravity, $\Delta d$ is abundance-weighted deviance, $\Delta\lvert d\rvert$ is the absolute abundance-weighted deviances | Villéger et al., 2008 |
| Functional Dispersion | $\frac{\sum a_j z_j}{\sum a_j}$ | $a_j$ is the abundance of species $j$ and $z_j$ is the distance of species $j$ to the weighted centroid. | Laliberté and Legendre, 2010 |

## Study Ecosystems

Heathland plant communities are dominated by shrub species possessing sclerophyllous leaves, which are evergreen, leathery, low in nutrient and water content, and commonly found in infertile environments (Morrow, 1983; Clarkson et al., 2011). Heathland ecosystems are diverse, with some communities seasonally waterlogged, containing well drained soil, or maintained by fire (Clarkson et al., 2011). This unique landscape is under threat worldwide, with agriculture, urbanization, and afforestation leading to the loss of habitat and species (Clarkson et al., 2011). This development has led to fragmented heathland ecosystems susceptible to colonizing species, nutrient enrichment, and unnaturally frequent fires (Oberndorfer and Lundholm, 2009; Clarkson et al., 2011). In order to maintain the diverse ecosystem services provided by these landscapes, such as water production, recreation, cultural services, and rare species habitat (Steven et al., 1997; Burley et al., 2010), restoration and conservation is required. Nova Scotian heathlands, coastal barrens, inland barrens, and highland barrens cover roughly 2.17% of the province (Porter, 2013). They are dominated by shrubby Ericaceous vegetation and contain unique plant communities that can be divided into 22 distinct plant associations, communities with relatively uniform plant and environmental variables (Porter et al., 2020). This ecosystem provides habitat to rare and endangered species (Porter et al., 2020), cultural services, and recreation (Burley et al., 2010). Research into the vegetative composition of Nova Scotia’s coastal barrens is a recent endeavor, beginning with the publication of Oberndorfer (2006). It is only now, with the completion of Porter et al. (2020), that we have a comprehensive set of plant community and environmental data. Insights gained through the analysis of Nova Scotian barrens can be used to protect and restore this unique landscape.

In addition to the ecosystem services described above, coastal barrens contain vegetation suitable to manmade ecosystems, specifically green roofs. Since both environments are exposed to harsh environmental conditions including high winds, drought, and extreme temperatures, species found in one environment can thrive in the other (Lundholm, 2006). This shared species profile means that ecological insights from the green roof environment may be applicable to the coastal barren environment, and vice versa. However, creating green roof populations from native populations should only be done in a sustainable manner, so as not to damage local populations (Pedrini et al., 2020).

Green roofs are a composite of layers, usually constructed with a vegetation layer, substrate layer, and root barrier/water retention layer placed on top of the roof surface (Molineux et al., 2009; Castleton et al., 2010). This manmade ecosystem is generally separated into two categories, with those with a deep substrate called intensive green roofs (substrate depth ≥ 20 cm), and those with a shallow substrate called extensive green roofs (substrate depth < 20 cm) (Carter and Butler, 2008; Olly et al., 2011). Due to weight restrictions, the majority of green roofs are extensive, with the shallow substrate depth limiting the type of vegetation that can be used. Succulents, especially *Sedum spp*., are the most common growth form, with drought-tolerant forbs, shrubs, and graminoids seen at lower frequencies (Dunnett and Kingsbury, 2004).

Due to variation in plant functional traits, green roof species differ in their ability to reduce storm water runoff, cool the substrate, filter air pollution, and attract pollinators (Lundholm et al., 2015; Heim et al., 2021). Since these ecosystem services are the main reasons why green roofs are built (Oberndorfer et al., 2007), it is important to incorporate a specific plant profile into the green roof design. However, just because researchers know which species are proficient at a particular function does not mean that all desired species will be able to persist together for an extended period of time. Research is needed to understand which functional trait combinations will provide the greatest ecosystem services while fostering coexistence for the duration of the roof lifespan.

## Dissertation Structure

I investigate several key knowledge gaps and inconsistencies observed in coexistence literature, specifically gaps associated with spatial heterogeneity, functional trait divergence, and the storage effect. For spatial heterogeneity, empirical research has resulted in all possible heterogeneity-biodiversity patterns, positive, negative, and neutral (Chesson et al., 2004; Löbel et al., 2006; Reynolds et al, 2007; Questad and Foster 2008; Angert et all., 2009; Lundholm 2009; Tamme et al., 2010; Gazol et al., 2013; Laanisto et al., 2013; Yang et al., 2015; Stein et al., 2014; Stark et al., 2017). The lack of consistency between studies indicates a need to further explore this topic and piece together why various patterns can occur. Since functional plant traits are associated with specific physiological processes they may shed more light on heterogeneity/biodiversity patterns then can be garnered from traditional approaches which rely solely on species richness. Although trait divergence has been associated with species coexistence, work is still needed to understand which specific traits play the greatest role in plant communities, how, and to incorporate trait data into community and ecosystem processes (Funk et al., 2017). Furthermore, there is a lack of empirical evidence regarding modern coexistence theory and the storage effect (Ellner et al., 2019), so research is needed to determine if these theories hold true in the natural world. Functional plant traits can be used to address these knowledge gaps. This method allows researchers to incorporate a multidimensional approach, essential for understanding how biodiversity is maintained (Clark et al., 2007). Furthermore, plant functional traits can be used to determine if a community meets the requirements for coexistence outlined by Chesson (Chesson, 2000b; Chesson, 2018).

# Chapter 2: Functional Trait Database for Nova Scotian Coastal Barren, Green Roof, and Ruderal Flora

In Chapter 2 I provide a summary of the trait database used in this dissertation. Detailed information on how individuals were collected, where they were collected from, and how they were processed is provided. Additionally, this chapter contains a table of mean trait values for all species in the trait database.

### Chapter 3: Multiple Assembly Processes Form Coastal Barren Plant Communities

In Chapter 3 I explore community assembly on the coastal barrens of Nova Scotia, an ecosystem that contains wide variations in spatial heterogeneity, environmental stress, and plant associations (Porter et al., 2020). This distinct landscape offers an ideal space to examine how functional traits influence plant community assembly, as environmental variables play a crucial role in determining which functional traits are necessary to survive. In this chapter I have two objectives:

1. How does spatial heterogeneity influence functional trait diversity?

My hypothesis is that increased spatial heterogeneity will lead to increased functional trait diversity. This will occur as increased heterogeneity will lead in an increase in the number of distinct types of microsites, allowing species with different functional traits to coexist.

### Chapter 4: Changes in Plant Community Composition and Functional Plant Traits Over a Four-Year Period on an Extensive Green Roof

In Chapter 4 I examine plant community assembly on an extensive green roof over a four-year period. Here, the same suite of 14 species were planted into four substrate depth treatments, allowing me to examine how assembly processes differ between more and less productive habitats, and between more and less heterogenous habitats. Additionally, these 14 species incorporated a range of functional types, allowing me to examine the trait response to these four substrate depth treatments. In this chapter I had one objective:

1. How do spatial heterogeneity influence functional trait diversity and coexistance over time?

I hypothesized that decreased stress, due to increased substrate depth, will lead to greater functional diversity, richness, and evenness. This will occur because the low stress environment will be capable of supporting more species than the high stress environment. In order to coexist in this more productive environment, species will need divergent traits allowing them to occupy different niches. Furthermore, increased niche space, due to increased substrate depth heterogeneity, will also result in greater functional diversity, richness, and evenness. This will occur as spatial heterogeneity will lead to different microsites favorable to different species. Finally, distinct community weighted means will be observed between high/low stress treatments and high/low heterogeneity treatments due to the formation of distinct plant communities.

## Chapter 5: Functional Trait Divergence Encourages Coexistence

In Chapter 5, I conduct two experiments to determine how trait divergence influences competition and coexistence. Both experiments compare communities that vary in trait divergence, with species combinations possessing functional traits that are similar, different, and of intermediate similarity. The first experiment was conducted in a controlled greenhouse environment and examined how trait divergence influences coexistence in an environment with a dynamic watering regime. Experiment two was conducted on a green roof, and I examined how trait divergence influences a species' potential to persist at low density. These experiments use three indices to determine coexistence potential: (1) an analysis testing for the presence of facilitation, with increased facilitative values associated with lower competition and greater potential coexistence; (2) the ability to increase when rare (low density) should be higher when the mixture is more functionally diverse, used to determine if co-occurrence could occur for an extended period of time, the definition of coexistence; (3) intraspecific competition should be stronger than interspecific competition; larger differences between species as indicated by FD are expected to reduce interspecific competition. In this chapter I had one objective:

1. How do trait convergence and divergence influence coexistence?

I hypothesized that species pairs that differ in growth due to the fluctuating environment will be more likely to coexist, with coexistence possible due to the storage effect. Furthermore, I believe that species with divergent traits will be the least antagonistically competitive, increasing the potential for them to coexist.

## Chapter 6: Research Application: Extensive Green Roofs

Through the incorporation of functional plant traits, each chapter of this dissertation provides insights that can be directly applied to green roof construction. Specifically, the functional trait database used in chapter two can be used to determine which native species can be used on green roofs in Nova Scotia, chapter two provides insights into how soil depth heterogeneity can influence community assembly and ecosystem services; and chapter three provides information on which trait combinations will likely coexist and provide the greatest ecosystem services.

## Chapter 7: Synthesis

Here I highlight the findings from each chapter and discuss how the results from this dissertation assist in our understanding of coexistence in relation to spatial heterogeneity and functional trait divergence/convergence

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# Chapter 2

# Functional Trait Database for Nova Scotian Coastal Barrens, Green Roof, and Ruderal Flora

## Abstract

This is the first plant functional trait database for Nova Scotia, Canada. The data contained here were collected between 2016 and 2019 from locations around Halifax, Nova Scotia. The species selected for trait collection were chosen based on species inventories taken across Nova Scotian coastal barrens and from green roof projects hosted at Saint Mary's University. The majority of coastal barrens species were collected from open (non-forested) dwarf heath coastal barrens sites. Species that do not grow in dwarf heath habitat, such as *Drosera* ssp., were collected from the coastal barrens community type they are most dominant in. However, in the rare instances where a species could not be found at a coastal barrens location, species were collected from forests, abandoned lots, and salt marshes. For those species solely identified in the green roof inventory, individuals were mainly collected from the green roof at Saint Mary's University. In total, this database contains 13,458 trait values from 203 species comprising 130 genera and 53 families. The majority of species are commonly found on coastal barrens (n=84 species), disturbed sites (n=48), and forests (n=27). Additionally, this database contains trait data for 30 species that have been successfully established on green roofs in Nova Scotia. This database contains eight plant functional traits: leaf thickness (203 species), leaf area (203 species), specific leaf area (203 species), leaf dry matter content (203 species), plant height (203 species), canopy width (203 species), seed weight (77 species), and root radius (22 species). The species in this database can be subdivided into 10 growth forms, with the majority of species characterised as forbs (n=75), shrubs (n=56), or graminoids (n=33).

## Introduction

Plant functional traits, the morphological, physiological, and phenological features that influence plant fitness (Violle et al., 2007), are an ideal tool for examining coexistence in plant communities. They can be used to tease apart which aspects of the community have shared ecological strategies and which aspects have divergent ecological strategies, with divergent strategies indicating how plant species can coexist. However, due to regional genetic differences trait analysis should incorporate values from individuals within the study system. For this reason I created the first plant functional trait database for Nova Scotia, Canada. The data contained here were collected between 2016 and 2019 from locations around Halifax, Nova Scotia (Figure 2.1 and Table 2.1). In total, the database contains 13,458 trait values from 203 species comprising 130 genera and 53 families. The majority of species are commonly found on coastal barrens (n=84 species), disturbed sites (n=48), and forests (n=27). Additionally, this database contains trait data for 30 species that have been successfully established on green roofs in Nova Scotia (Table 2.2). This database contains eight plant functional traits: leaf thickness (203 species), leaf area (203 species), specific leaf area (203 species), leaf dry matter content (203 species), plant height (203 species), canopy width (203 species), seed weight (77 species), and root radius (22 species) (Table 2.3). The species in this database can be subdivided into 10 growth forms, with the majority of species characterised as forbs (n=75), shrubs (n=56), or graminoids (n=33) (Table 2.4). Detailed information on each species can be found in Tables 2.5, 2.6, and 2.7.

## Methods

The species selected for trait collection were chosen based on species inventories taken across Nova Scotian coastal barrens (Porter et al., 2020) and from green roofs at Saint Mary's University (Chapter 4). Nomenclature follows VASCAN (Brouillet et al. 2010+). Since intraspecific trait variation can increase as variation in environmental conditions increases, the majority of traits were gathered from individuals located from the habitats examined in this dissertation, coastal barrens, and green roofs. Since this dissertation is purely focused on interspecific relationships, trait averages were used for analysis. The coastal barrens species, identified in Porter et al. (2020), were collected from open (non-forested) dwarf heath coastal barrens sites. Species that do not grow in dwarf heath habitat, such as *Drosera ssp.*, were collected from the coastal barrens community type they are most dominant in (salt spray zone, rocky outcrop, *Sphagnum* bog, tall shrub, and tree island) (Porter et al., 2020). However, in the rare instances where a species could not be found at a coastal barrens location, species were collected from forests, abandoned lots, and saltmarshes. For those species solely identified in the green roof inventory (Chapter 4), individuals were mainly collected from the green roof at Saint Mary's University. For plant height, canopy width, leaf area, leaf dry matter content, seed weight, and specific leaf area, traits from 10 individuals of a species were collected from naturally occurring populations within one hour's drive of Saint Mary's University, Halifax, Nova Scotia (44°37"N 63°34"W). Traits were collected based on the guidelines established by Pérez-Harguindeguy et al. (2016).

Plant height was determined by measuring from the base of the plant to the top of the crown. In situations where a species drooped, they were held up during measurement. Canopy width was determined by measuring the widest width of the plant canopy. In situations where the canopy was oblong, the larger diameter was measured. All leaf traits were taken from one leaf collected from the target individual. The leaf chosen was required to be healthy and of average size. Leaf collection occurred in the field, with leaves stored in a moist, sealed bag until processing could occur. All leaves were processed the day they were collected. Leaf thickness was determined using a caliper and by avoiding the midrib. Leaf area was determined by scanning the leaf and then measuring the leaf in ImageJ (Image Processing and Analysis in Java, http://rsbweb.nih.gov/ij/). After these measurements, the leaf fresh weight was measured and then dried in a drying oven at 21°C for at least two days. After drying, leaves were weighed again. Specific leaf area was calculated by dividing the leaf area by the leaf dry mass, and leaf dry matter content was calculated by dividing the leaf dry mass by the fresh mass. Seed weight was determined by collecting as many seeds as possible from an individual, with 1-50 seeds collected for each. Immediately after collection, seeds were dried in a drying oven at 21°C for at least two days. The seeds were then weighed. Seed weight was determined by dividing the weight of all the seeds collected for an individual by the number of seeds weighed. The number of seeds used for each individual are listed in the functional trait database as “# seeds weighed”.

For the majority of species, root radius was collected from five healthy individuals from the greenhouse experiment at the end of August 2019 (Chapter 3). Roots were stored in a 70/30 ethanol/water solution at 4ºC until November 2019, at which time traits were calculated. Roots from *Phedimus spurius* and *Festuca rubra* were collected from five healthy adult individuals growing on a green roof at Saint Mary’s University while roots for *Avenella flexuosa* were collected from five individuals grown to adulthood from seed (collected from Chebucto Head). Root radius was determined by scanning one fine root (root thickness ≤ 2 mm) and then measuring the average radius in ImageJ (Image Processing and Analysis in Java, http://rsbweb.nih.gov/ij/).

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## Figures

**Figure 2.1.** Map of Nova Scotia highlighting the 17 locations surrounding Halifax that species were collected from.

## Tables

**Table 2.1.** Table depicting the locations in Nova Scotia species were collected from, the types of habitats species were collected from, and the number of species collected from each location.

| Location | Habitat | Species | Coordinates |
|---|---|---|---|
| Chebucto Head | Coastal Barrens | 84 | 34°30′ N, 63°31′W |
| Saint Mary’s University | Urban Lawn | 10 | 44°39′N, 63°35′W |
| Saint Mary’s University | Green Roof | 27 | 44°39′N, 63°35′W |
| Saint Mary’s University | Urban Forest | 1 | 44°39′N, 63°35′W |
| Point Pleasant Park | Urban Forest | 30 | 44°37′ N, 63°34′W |
| Crystal Crescent | Coastal Barrens | 6 | 44°27′ N, 63°37′W |
| Crystal Crescent | Coastal Dune | 8 | 44°27′ N, 63°37′W |
| Polly’s Cove | Coastal Barrens | 9 | 44°29′ N, 63°53′W |
| Dalhousie University | Urban Field | 8 | 44°38′N, 63°35′W |
| Frog Pond | Urban Forest | 6 | 44°37′ N, 63°36'W |
| Chain of Lakes Trail | Disturbed Site | 5 | 44°38′ N, 63°40′W |
| York Redoubt National Historic Site | Forest | 2 | 44°35′ N, 63°33′W |
| York Redoubt National Historic Site | Tall Shrub | 2 | 44°35′ N, 63°33′W |
| Conrad's Beach | Salt Marsh | 2 | 44°38′ N, 63°22′W |
| Ardmore Park | Urban Lawn | 1 | 44°39′N, 63°36′W |
| Hemlock Ravine | Urban Forest | 1 | 44°41′ N, 63°39'W |
| Herring Cove | Coastal Barrens | 1 | 44°34′N, 63°33′W |
| Lawrence Town Beach | Coastal Dune | 1 | 44°38′ N, 63°20′W |
| Otter Lake | Disturbed Field | 1 | 44°38′ N, 63°42′W |
| Rainbow Haven | Salt Marsh | 1 | 44°39′ N, 63°25′W |
| Titanium Crescent Park | Inland Barrens | 1 | 44°36′ N, 63°35′W |

**Table 2.2.** The type of habitat the species included in the trait database are commonly found in.

| Common Habitat | Species |
|---|---:|
| Coastal Dune, Wetlands | 1 |
| Forest Edge, Wetlands | 1 |
| Forest, Disturbed Sites | 1 |
| Coastal Barrens, Disturbed Sites | 2 |
| Salt Marsh | 3 |
| Green Roof | 5 |
| Coastal Dune | 7 |
| Roof and Barrens | 25 |
| Forest | 27 |
| Disturbed Sites | 48 |
| Coastal Barrens | 84 |

**Table 2.3.** The total number of samples, species, genera, and families in the trait database for each plant functional trait.

| Trait | Samples | Species | Genus | Family |
|---|---:|---:|---:|---:|
| Leaf Thickness | 2,088 | 203 | 130 | 53 |
| Leaf Area | 2,088 | 203 | 130 | 53 |
| Specific Leaf Area | 2,088 | 203 | 130 | 53 |
| Leaf Dry Matter Content | 2,088 | 203 | 130 | 53 |
| Plant Height | 2,121 | 203 | 130 | 53 |
| Canopy Width | 2,121 | 203 | 130 | 53 |
| Seed Weight | 744 | 77 | 60 | 27 |
| Root Radius | 120 | 22 | 18 | 9 |

**Table 2.4.** The 208 plant species included in the trait database, separated by growth form.

| **Growth Form** | **Species** |
|---|---:|
| Hemiparasite | 1 |
| Vine | 1 |
| Carnivorous | 3 |
| Seedlings | 6 |
| Fern | 7 |
| Succulent | 7 |
| Tree | 19 |
| Graminoid | 33 |
| Shrub | 56 |
| Forb | 75 |

**Table 2.5.** The mean ± the standard error for leaf thickness, leaf area, specific leaf area, leaf dry matter content, plant height, and canopy width for each species in the trait database.

| Species | Leaf Thickness (cm) | Leaf Area (cm) | Specific Leaf Area (cm$^2$g$^{-1}$) | Leaf Dry Matter Content (g) | Plant Height (cm) | Canopy Width (cm) |
|---|---|---|---|---|---|---|
| *Abies balsamea* | 0.0405±0.002 | 0.239±0.02 | 89.2±9.8 | 0.4427±0.0308 | 697.5±94.77 | 332.5±42.5 |
| *Acer platanoides* | NA | NA | NA | NA | NA | NA |
| *Acer platanoides* seedling | 0.1408±0.053 | 7.718±1.46 | 222.8±9.1 | 0.4029±0.0251 | 4.64±0.27 | 8±0.83 |
| *Acer rubrum* | 0.021±0.002 | 50.757±5.29 | 127.6±11.4 | 0.4773±0.0121 | 437.5±79.69 | 415±80.29 |
| *Achillea millefolium* | 0.1172±0.015 | 3.568±0.96 | 164.7±10.2 | 0.314±0.0385 | 29.88±2.75 | 29.88±2.75 |
| *Agalinis neoscotica* | 0.0337±0.002 | 0.305±0.03 | 188±20.1 | 0.2467±0.0084 | 9.26±0.87 | 3.26±0.29 |
| *Agrostis scabra* | 0.0109±0.001 | 4.22±0.53 | 373.7±22.3 | 0.3449±0.0083 | 41.34±3.36 | 6.05±0.64 |
| *Agrostis stolonifera* | 0.0211±0.001 | 4.301±0.79 | 652.2±25.7 | 0.2442±0.0119 | 17.4±3.31 | 23.5±4.57 |
| *Alnus alnobetula* | 0.0279±0.001 | 36.254±6.24 | 117.4±6.5 | 0.3145±0.0118 | 68.3±5.3 | 102.7±16.14 |
| *Alnus incana* | 0.0375±0.001 | 16.622±2.19 | 151.9±7.7 | 0.4269±0.0079 | 190±24.78 | 153.5±15.24 |
| *Amelanchier spicata* | 0.0288±0.001 | 11.702±0.81 | 118.7±4.8 | 0.4344±0.0116 | 67.26±8.16 | 56.21±13.73 |
| *Anaphalis margaritacea* | 0.643±0.04 | 2.838±0.25 | 143.3±7.5 | 0.2299±0.0102 | 30.11±4.31 | 20.85±3.13 |
| *Andromeda polifolia* | 0.6526±0.098 | 0.842±0.09 | 49±3.3 | 0.488±0.0229 | 16.25±1.74 | 9±1.11 |
| *Aralia hispida* | 0.0191±0.001 | 4.501±0.55 | 216.8±10.2 | 0.2861±0.0083 | 51.95±4.12 | 16.9±2.2 |
| *Aralia nudicaulis* | 0.165±0.012 | 9.426±2.78 | 191.4±19.6 | 0.6936±0.2963 | 25.6±3.46 | 15.69±2.4 |
| *Arctostaphylos uva-ursi* | 0.55±0.017 | 0.621±0.03 | 45.6±3.3 | 0.4771±0.0116 | 5.7±0.67 | 123.3±20.1 |
| *Arethusa bulbosa* | 0.0319±0.004 | 2.25±0.22 | 422.3±47.6 | 0.1305±0.015 | 16±1.06 | 2.6±0.18 |
| *Aronia arbutifolia* | 0.0326±0.001 | 8.979±0.93 | 133.8±3 | 0.3015±0.006 | 53.85±5.11 | 21.5±2.38 |
| *Aronia melanocarpa* | 0.3442±0.087 | 7.961±0.91 | 101.6±2.9 | 0.3758±0.009 | 18.9±3.91 | 7.25±1.23 |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Aronia x prunifolia* | 0.303±0.01 | 14.966±1.28 | 110.4±4 | 0.3577±0.0094 | 136.4±5.38 | 38.4±7.08 |
| *Artemisia stelleriana* | 0.0472±0.006 | 4.468±0.72 | 140±9.5 | 0.2678±0.0113 | 11.68±0.8 | 26.83±4.03 |
| *Avenella flexuosa* | 0.0206±0.002 | 1.829±0.23 | 612.8±43.3 | 0.4205±0.0179 | 33.09±2.31 | 12.65±1.72 |
| *Betula papyrifera* | 0.0276±0.001 | 34.052±2.84 | 172.5±14 | 0.3237±0.0142 | 635±39.75 | 232.5±14.48 |
| *Betula populifolia* | 0.0383±0.002 | 25.522±4.39 | 179.7±9.8 | 0.3519±0.0082 | 335±69.94 | 200±28.87 |
| *Cakile edentula* | 0.403±0.026 | 1.446±0.17 | 172.6±14.1 | 0.1071±0.0044 | 19.39±4.31 | 42.98±5 |
| *Calamagrostis breviligulata* | 0.0548±0.002 | 31.132±2.22 | 93.6±3.4 | 0.3938±0.0111 | 65.75±3.8 | 40.7±3.22 |
| *Calamagrostis canadensis* | 0.0248±0.001 | 15.531±2.08 | 194±20.9 | 0.4025±0.017 | 83.9±5.25 | 19.4±2.5 |
| *Calamagrostis pickeringii* | 0.0175±0.001 | 3.506±0.6 | 182.9±11.6 | 0.3645±0.0136 | 34.73±1.22 | 5.72±0.99 |
| *Calopogon tuberosus* | 0.0268±0.002 | 3.476±0.4 | 264.1±11.3 | 0.146±0.0042 | 11.5±1.32 | 3.55±0.31 |
| *Campanula intercedens* | 0.0267±0.001 | 1.106±0.08 | 208.2±17 | 0.2651±0.0151 | 23.06±2.57 | 7.25±1.08 |
| *Carex echinata* | 0.0346±0.005 | 4.785±0.43 | 223.6±10.8 | 0.3621±0.0115 | 13.9±1.09 | 6.21±1.16 |
| *Carex exilis* | 0.0589±0.003 | 0.893±0.11 | 54±3.3 | 0.4281±0.0136 | 37.22±1.11 | 0.94±0.06 |
| *Carex folliculata* | 0.0231±0.002 | 13.583±1.27 | 208.6±10.4 | 0.3116±0.0084 | 22.8±2.43 | 16.4±2.64 |
| *Carex magellanica* | 0.0301±0.001 | 6.893±0.46 | 291±22.2 | 0.4037±0.0153 | 39.6±2.81 | 11.9±2.58 |
| *Carex nigra* | 0.0121±0.001 | 0.95±0.12 | 218.6±17.9 | 0.3492±0.0111 | 39.99±3.02 | 3.24±0.63 |
| *Carex paleacea* | 0.0375±0.003 | 11.33±1.65 | 156.3±19.3 | 0.322±0.0094 | 32.15±2.57 | 13.8±4.25 |
| *Carex pauciflora* | 0.0192±0.001 | 0.642±0.04 | 162.1±7.4 | 0.4204±0.0113 | 15.87±1.91 | 1.14±0.28 |
| *Carex silicea* | 0.0198±0.002 | 4.136±0.38 | 118.7±8.9 | 0.6867±0.0201 | 21.2±3.37 | 26.5±2.53 |
| *Carex trisperma* | 0.025±0.013 | 1.664±0.26 | 498.7±51.7 | 0.378±0.0201 | 32.91±2.37 | 51.45±8.93 |
| *Carex viridula* | 0.0313±0.002 | 1.284±0.22 | 245.3±15.2 | 0.261±0.0119 | 5.3±0.59 | 0.23±0.02 |
| *Centaurea nigra* | 0.0403±0.002 | 15.28±2.59 | 237.9±12.1 | 0.2024±0.0053 | 71.72±5.54 | 31.2±3.98 |
| *Cerastium fontanum* | 0.032±0.001 | 0.546±0.07 | 364.5±31 | 0.137±0.0119 | 13.35±1.21 | 2.88±0.97 |
| *Chamaedaphne calyculata* | 0.245±0.005 | 1.685±0.19 | 90.2±3.1 | 0.5077±0.0123 | 30.45±3.6 | 11.6±1.49 |

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| *Chamaenerion angustifolium* | 0.0176±0.001 | 23.428±1.89 | 206.9±7.2 | 0.2577±0.0034 | 98.2±8.65 | 24.45±2 |
| *Clintonia borealis* | 0.301±0.008 | 45.533±8.9 | 241.8±10.1 | 0.119±0.0059 | 13.02±1.07 | 10.59±2.6 |
| *Comptonia peregrina* | 0.0252±0.003 | 3.244±0.52 | 235.7±9.2 | 0.2142±0.0112 | 46.2±4.36 | 33.8±5.48 |
| *Convolvulus arvensis* | 0.0276±0.001 | 20.093±3.75 | 214.5±13.9 | 0.22±0.0089 | 33.26±5.46 | 95.5±13.67 |
| *Coptis trifolia* | 0.0239±0.001 | 2.266±0.28 | 259±9.2 | 0.3128±0.0132 | 3.75±0.45 | 3.51±0.79 |
| *Corema conradii* | 0.0412±0.005 | 0.042±0 | 74±9 | 0.5558±0.0863 | 9.89±1.38 | 90±17.25 |
| *Cornus canadensis* | 0.0244±0.001 | 6.058±0.48 | 181.9±12.1 | 0.3234±0.0232 | 13.5±0.91 | 7.28±0.38 |
| *Crataegus monogyna Seedling* | 0.0099±0 | 2.086±0.12 | 280.7±13.6 | 0.3927±0.0145 | 4.65±0.36 | 4.62±0.31 |
| *Cypripedium acaule* | 0.0304±0.002 | 101.299±9.84 | 253.7±7.5 | 0.1319±0.0038 | 31.8±2.69 | 24.7±1.14 |
| *Danthonia spicata* | 0.0126±0.001 | 0.851±0.07 | 152.1±13.5 | 0.3851±0.0083 | 18.83±3.96 | 12.47±0.97 |
| *Dennstaedtia punctilobula* | 0.0201±0.002 | 18.092±1.67 | 546±22 | 0.2314±0.0061 | 60±0 | 60±0 |
| *Diervilla lonicera* | 0.0277±0.002 | 20.293±2.69 | 194.6±8.8 | 0.3281±0.0076 | 57.2±5.29 | 33.7±5.37 |
| *Doellingeria umbellata* | 0.0265±0.002 | 21.362±1.86 | 352.1±45.3 | 0.2704±0.0455 | 105.69±5.6 | 26.9±2.09 |
| *Drosera Intermedia* | 0.278±0.021 | 0.171±0.02 | 161.6±16.9 | 0.1701±0.0235 | 5.8±0.33 | 7.1±0.19 |
| *Drosera rotundifolia* | 0.252±0.017 | 0.509±0.03 | 333.8±22.2 | 0.1374±0.0178 | 3.2±0.33 | 5.9±0.35 |
| *Dryopteris carthusiana* | 0.0182±0.001 | 22.2±1.4 | 387.9±27 | 0.2163±0.006 | 50.89±2.14 | 63.62±2.7 |
| *Elymus repens* | 0.0286±0.002 | 6.103±0.39 | 157±5.7 | 0.3851±0.0076 | 55.37±3.46 | 15.6±2.89 |
| *Empetrum eamesii* | 0.0424±0.011 | 0.063±0.01 | 81.6±8.6 | 0.4929±0.0201 | 8.24±1.95 | 75.6±29.31 |
| *Empetrum nigrum* | 0.0338±0.004 | 0.066±0.01 | 112.9±17.8 | 0.4925±0.0567 | 9.3±1.21 | 167.1±60.65 |
| *Epigaea repens* | 0.027±0.001 | 18.776±1.66 | 127.3±17 | 0.4353±0.0316 | 11.91±5.43 | 13.85±2.51 |
| *Epilobium ciliatum* | 0.0195±0.001 | 3.126±0.3 | 218.7±8.6 | 0.2803±0.0129 | 17.27±2.21 | 6±2.27 |
| *Equisetum arvense* | 0.0496±0.007 | 1.061±0.1 | 192.8±9.6 | 0.2861±0.0079 | 26.37±2.25 | 13.65±0.95 |
| *Erigeron Annuus* | 0.0267±0.001 | 10.037±1.14 | 188.9±6.2 | 0.2253±0.0075 | 31.77±2.77 | 7.31±0.77 |
| *Erigeron canadensis* | 0.0226±0.002 | 1.872±0.42 | 287.7±18.8 | 0.1837±0.0093 | 21.32±4.25 | 8.82±1.28 |
| *Eriophorum vaginatum* | 0.0423±0.002 | 0.999±0.09 | 50.8±3.3 | 0.4462±0.0112 | 42.43±3.79 | 16.8±2.49 |

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| *Eriophorum virginicum* | 0.0312±0.001 | 10.23±2.23 | 73.7±14.8 | 0.3622±0.0184 | 56.55±3.33 | 13.7±1.77 |
| *Euphrasia stricta* | 0.0272±0.002 | 0.563±0.1 | 144±12.1 | 0.2593±0.029 | 10.62±1.44 | 2.23±0.33 |
| *Festuca filiformis* | 0.0221±0.002 | 0.138±0.02 | 62.7±5.8 | 0.4997±0.0513 | 6.7±1.02 | 8.65±1.46 |
| *Festuca rubra* | 0.0051±0 | 0.652±0.12 | 97.5±6.8 | 0.396±0.0287 | 35.99±3.22 | 5.8±1.73 |
| *Fragaria virginiana* | 0.0266±0.001 | 10.084±2.88 | 185.2±28.4 | 0.3663±0.0063 | 10.46±1.27 | 52.58±9.24 |
| *Fraxinus americana* | 0.0325±0.004 | NA | NA | 0.3629±0.0415 | 264.5±85.5 | 142.75±57.25 |
| *Fraxinus excelsior* | NA | NA | NA | NA | NA | NA |
| *Fraxinus excelsior Seedling* | 0.03±0.003 | 1.433±0.12 | 246±20 | 0.3153±0.0252 | 4.94±0.43 | 3.58±0.09 |
| *Galium mollugo* | 0.0345±0.002 | 0.329±0.03 | 374.1±28.3 | 0.2251±0.0181 | 31.05±3.46 | 22.3±4.15 |
| *Gaultheria hispidula* | 0.0341±0.002 | 0.271±0.03 | 153.9±16 | 0.3851±0.0418 | 1.5±0.2 | 8.15±1.11 |
| *Gaultheria procumbens* | 0.0472±0.003 | 4.062±0.43 | 94.4±17.9 | 0.3626±0.0367 | 10.64±1 | 4.73±0.46 |
| *Gaylussacia baccata* | 0.0212±0.002 | 4.232±0.46 | 205.9±15.8 | 0.2924±0.0232 | 49.1±4.99 | 19.58±2.16 |
| *Gaylussacia bigeloviana* | 0.0282±0.001 | 3.932±0.38 | 152.4±12.3 | 0.2985±0.0131 | 24.35±2.61 | 10.05±0.68 |
| *Hamamelis virginiana* | 0.0205±0.001 | 66.447±6.68 | 199.7±3.2 | 0.3862±0.0074 | 282±40.96 | 237.5±33.18 |
| *Hudsonia ericoides* | 0.0165±0.002 | 0.027±0 | 328.6±39 | 0.4836±0.0669 | 4.4±0.67 | 15.35±2.75 |
| *Hylotelephium telephium* | 0.0845±0.006 | 2.546±0.22 | 150.1±6.6 | 0.0984±0.0031 | 10.4±1.51 | 8.1±1.43 |
| *Hypericum perforatum* | 0.0372±0.018 | 0.742±0.11 | 166.3±10.7 | 0.3275±0.0066 | 30.42±2.63 | 11.31±2.74 |
| *Ilex glabra* | 0.0349±0.001 | 1.894±0.14 | 72.7±2.2 | 0.4924±0.0285 | 56±6.1 | 40.9±5.92 |
| *Ilex mucronata* | 0.1757±0.023 | 6.496±0.94 | 151.2±7.2 | 0.3955±0.0078 | 100.7±8.54 | 38.45±8.27 |
| *Ilex verticillata* | 0.216±0.01 | 9.299±0.64 | 120.8±8.5 | 0.3845±0.008 | 171.9±6.79 | 159.7±19.27 |
| *Impatiens capensis* | 0.0351±0.003 | 12.989±1.22 | 368.8±10.3 | 0.2012±0.0054 | 48.9±1.89 | 14.6±1.38 |
| *Iris setosa* | 0.0678±0.005 | 6.697±0.51 | 133.3±9.6 | 0.2219±0.0103 | 28.25±1.16 | 12.15±1.49 |
| *Iris versicolor* | 0.0754±0.013 | 38.107±4.01 | 124.6±6.6 | 0.1617±0.0103 | 45.4±2.03 | 10.7±2.03 |
| *Juncus arcticus* | 0.1009±0.005 | 4.478±0.36 | 31.5±2 | 0.47±0.0124 | 46.8±2.16 | 9.4±1.02 |
| *Juncus bufonius* | 0.0305±0.005 | 0.476±0.06 | 239.9±29.8 | 0.2534±0.0251 | 9.35±0.85 | 5±1.51 |

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| *Juncus gerardi* | 0.0485±0.004 | 2.082±0.45 | 111.2±9.9 | 0.3883±0.0102 | 49.43±2.49 | 2.69±0.49 |
| *Juniperus communis* | 0.0326±0.002 | 0.149±0.01 | 88.5±7.4 | 0.4688±0.036 | 10.1±0.6 | 184.4±48.6 |
| *Juniperus horizontalis* | 0.0414±0.005 | 0.041±0.01 | 108.1±10.5 | 0.3471±0.0704 | 13.5±2.72 | 249.1±22.04 |
| *Kalmia angustifolia* | 0.0204±0.001 | 2.624±0.29 | 95.4±2.8 | 0.4232±0.0113 | 24.27±2.1 | 16.67±1.8 |
| *Kalmia polifolia* | 0.544±0.061 | 0.874±0.14 | 102.1±11.1 | 0.4214±0.0122 | 16.74±1.29 | 5.14±0.79 |
| *Larix laricina* | 0.0312±0.002 | 0.138±0.01 | 113.3±8.8 | 0.4361±0.031 | 582.5±92.5 | 277.5±48.94 |
| *Lathyrus japonicus* | 0.0305±0.002 | 8.499±1.01 | 277.5±17 | 0.208±0.0046 | 38.33±3.22 | 74.2±2.96 |
| *Ligusticum scoticum* | 0.0342±0.001 | 2.221±0.18 | 199.1±6.3 | 0.2123±0.0069 | 9.53±0.52 | 13.93±3.24 |
| *Limonium carolinianum* | 0.037±0.002 | 32.434±3.18 | 123.3±9.4 | 0.2244±0.011 | 26.05±3.11 | 29.1±1.97 |
| *linnaea borealis* | 0.0378±0.003 | 0.861±0.08 | 201.1±9.9 | 0.2919±0.007 | 7.8±0.66 | 12.3±1.54 |
| *Luzula multiflora* | 0.0168±0.002 | 1.039±0.07 | 290.3±14.3 | 0.2368±0.0103 | 21.83±2.19 | 10.65±1.2 |
| *Lysimachia borealis* | 0.019±0.001 | 3.394±0.32 | 223.7±15.9 | 0.248±0.0126 | 19.2±1.62 | 8.46±0.65 |
| *Maianthemum canadense* | 0.0234±0.003 | 13.509±1.73 | 193.1±12.2 | 0.2553±0.0101 | 9.62±0.89 | 2.76±0.28 |
| *Maianthemum stellatum* | 0.0328±0.001 | 6.707±0.95 | 159.4±6.6 | 0.2413±0.0039 | 24.7±2.29 | 8.7±0.98 |
| *Maianthemum trifolium* | 0.181±0.006 | 12.37±1.26 | 223.4±72.9 | 0.2647±0.0242 | 10.73±1.17 | 9.04±0.57 |
| *Melampyrum lineare* | 0.0772±0.05 | 0.698±0.1 | 254.5±45.7 | 0.2062±0.0222 | 12.95±0.97 | 7.3±1.77 |
| *Mitchella repens* | 0.0178±0.001 | 1.468±0.12 | 78.1±23.3 | 4.4511±1.915 | 3±0.77 | 20.7±2.4 |
| *moehringia laterflora* | 0.0265±0.002 | 0.505±0.05 | 216.8±18.3 | 0.3509±0.0325 | 9.1±1.09 | 1.17±0.14 |
| *Mononeuria groenlandica* | 0.0384±0.005 | 0.107±0.02 | 247.4±20.6 | 0.1717±0.0105 | 7±0.49 | 32.6±30.27 |
| *Morella pensylvanica* | 0.0183±0.004 | 6.48±0.72 | 186.2±15.9 | 0.3022±0.014 | 25.37±1.7 | 23.85±2.5 |
| *Myrica gale* | 0.268±0.023 | 3.852±0.42 | 127.5±8.9 | 0.4105±0.0067 | 30.3±3.63 | 22.1±3.83 |
| *Nabalus trifoliolatus* | 0.0346±0.002 | 15.203±1.72 | 197.4±11.8 | 0.2047±0.0057 | 11.98±1.23 | 7.42±0.94 |
| *Oclemena acuminata* | 0.0391±0.002 | 15.814±1.49 | 371.1±21.4 | 0.196±0.0062 | 32.5±2.19 | 11.6±0.79 |
| *Oclemena nemoralis* | 0.0402±0.004 | 0.55±0.07 | 152.3±17.8 | 0.0005±0.0001 | 27.7±2.94 | 3.55±0.39 |
| *Oclemena x blakei* | 0.023±0.001 | 3.993±0.16 | 190.3±7 | 0.3002±0.006 | 25.67±1.36 | 5.56±0.39 |
| *Oenothera biennis* | 0.27±0.015 | 8.326±1.34 | 177.4±14.5 | 0.1997±0.0055 | 39.71±3.58 | 35.12±7.3 |

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| *Onoclea sensibilis* | 0.0198±0.002 | 31.322±4.36 | 455.1±31.7 | 0.212±0.0074 | 38.4±3.45 | 30.7±2.32 |
| *Osmundastrum cinnamomeum* | 0.0305±0.002 | 0.424±0.06 | 185.9±19.2 | 0.2409±0.0151 | 46.88±6.48 | 30.6±4.97 |
| *Oxalis stricta* | 0.0121±0.001 | 0.708±0.11 | 598.9±60.4 | 0.1453±0.0152 | 5.65±0.33 | 3.76±0.29 |
| *Parathelypteris noveboracensis* | 0.0173±0.002 | 4.322±0.99 | 627.6±36.5 | 0.1557±0.019 | 29.8±2.84 | 16.8±3.07 |
| *Phedimus spurius* | 0.0976±0.006 | 1.4±0.2 | 142.9±8.4 | 0.0878±0.0036 | 4.88±0.46 | 17.6±1.71 |
| *Phleum pratense* | 0.0189±0.001 | 6.511±1.35 | 192.4±20 | 0.3258±0.0111 | 100.05±7.15 | 11.4±1.66 |
| *Picea glauca* | 0.5904±0.139 | 0.092±0.01 | 32.8±2.5 | 0.4677±0.0173 | 286.2±33.9 | 239.8±19.65 |
| *Picea mariana* | 0.729±0.037 | 0.096±0.01 | 44±4.7 | 0.5374±0.0808 | 339.8±44.56 | 237.6±30.48 |
| *Picea rubens* | 0.063±0.004 | 0.131±0.01 | 43.1±2.2 | 0.5584±0.0353 | 69.2±22.6 | 275±23.86 |
| *Pilosella caespitosa* | 0.0446±0.004 | 11.723±1.63 | 272.3±10 | 0.1531±0.0065 | 4.6±0.45 | 18.8±2.86 |
| *Pilosella flagellaris* | 0.0274±0.001 | 4.931±0.59 | 211.9±19.5 | 0.1765±0.0107 | 13.65±1.36 | 8.93±0.5 |
| *Pilosella officinarum* | 0.0368±0.002 | 3.731±0.73 | 197.9±27.2 | 0.1742±0.011 | 2.38±0.36 | 5.1±0.36 |
| *Pinus banksiana* | 0.0607±0.001 | 0.527±0.04 | 53.7±4.3 | 0.4344±0.02 | 345.63±30.18 | 189.38±16.31 |
| *Pinus resinosa* | 0.0601±0.002 | 1.158±0.06 | 35.9±3.3 | 0.4141±0.0108 | 745±42.46 | 380±28.09 |
| *Pinus strobus* | 0.0442±0.004 | 0.329±0.02 | 69±5.3 | 0.4035±0.0239 | 794.31±125.16 | 389.31±58.96 |
| *Pinus sylvestris* | 0.0563±0.002 | 0.881±0.11 | 59.8±4.7 | 0.4111±0.0171 | 850±104.88 | 455±43.11 |
| *Pinus sylvestris Seedling* | 0.0345±0.002 | 0.355±0.04 | 106.2±14.5 | 0.4299±0.0556 | 16.12±2.22 | 12.4±2.28 |
| *Plantago major* | 0.0309±0.001 | 18.385±1.9 | 232.6±29.9 | 0.1553±0.0103 | 13.2±1.38 | 13.4±1.89 |
| *Plantago maritima* | 0.138±0.007 | 2.808±0.41 | 90.3±9.5 | 0.1216±0.009 | 7.04±0.63 | 14.99±0.54 |
| *Poa annua* | 0.0098±0.001 | 0.514±0.06 | 410.8±57.2 | 0.3309±0.0274 | 4.85±0.94 | 5.72±0.74 |
| *Poa compressa* | 0.0179±0.001 | 2.52±0.43 | 305.9±17.2 | 0.2667±0.0138 | 39.34±2.44 | 16.45±3.22 |
| *Poa palustris* | 0.0136±0.001 | 3.54±0.44 | 226.4±26.4 | 0.2937±0.0125 | 27.1±2.1 | 3.15±0.29 |
| *Populus grandidentata* | 0.0241±0.001 | 41.628±4.51 | 131.7±4.1 | 0.4443±0.009 | 970±87.31 | 425±34.36 |
| *Populus tremuloides* | 0.0329±0.003 | 17.002±2.86 | 128.8±16.2 | 0.3841±0.0201 | 735±47.17 | 280±36.67 |
| *Potentilla anserina* | 0.0307±0.001 | 3.989±0.49 | 194.7±5.7 | 0.3251±0.0046 | 17.11±3.63 | 22.38±5.42 |

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| *Potentilla simplex* | 0.0161±0.001 | 1.659±0.24 | 261.9±23.3 | 0.3057±0.0142 | 14.2±1.49 | 4.7±0.67 |
| *Prunus pensylvanica* | 0.0467±0.004 | 6.046±0.85 | 240.6±9 | 0.2841±0.0045 | 168±22.6 | 98±13.48 |
| *Pteridium aquilinum* | 0.0271±0.004 | 9.902±1.03 | 152.3±10 | 0.2457±0.0128 | 47.42±3.25 | 23.75±1.66 |
| *Quercus rubra* | 0.0711±0.005 | 99.197±9.57 | 151.7±8.6 | 0.3915±0.0148 | 800±91.59 | 385±36.55 |
| *Ranunculus repens* | 0.0289±0.001 | 4.046±0.26 | 355.4±23.6 | 0.1496±0.0085 | 7.28±0.59 | 4.58±0.21 |
| *Rhinanthus minor* | 0.0458±0.001 | 3.488±0.32 | 227.1±9.4 | 0.1819±0.0062 | 47.52±2.95 | 10.05±0.62 |
| *Rhodiola rosea* | 0.0505±0.009 | 1.451±0.19 | 172.6±9 | 0.0818±0.0098 | 15.8±3.3 | 27.55±5.18 |
| *Rhododendron canadense* | 0.0179±0.001 | 4.972±0.61 | 152.8±23.3 | 0.4089±0.0118 | 58.37±4.74 | 18.87±2.02 |
| *Rhododendron groenlandicum* | 0.0733±0.007 | 2.247±0.23 | 73±4.8 | 0.3793±0.0088 | 11.15±2.17 | 29.45±2.25 |
| *Rhus typhina* | 0.0228±0.001 | 21.688±2.18 | 224.1±16.2 | 0.3307±0.0123 | 100.1±5.72 | 46.55±3.88 |
| *Rhynchospora alba* | 0.0241±0.002 | 1.143±0.2 | 159.8±8.5 | 0.5295±0.0422 | 255±32.23 | 170±21.34 |
| *Rosa multiflora* | 0.2236±0.137 | 1.698±0.17 | 239±40.9 | 0.4602±0.1023 | 13.65±0.9 | 1.14±0.17 |
| *Rosa nitida* | 0.0162±0.001 | 3.436±0.39 | 200.1±11.1 | 0.3536±0.007 | 55.35±4.09 | 68.5±11.69 |
| *Rosa virginiana* | 0.0125±0 | 3.291±0.39 | 180±17.6 | 0.499±0.1401 | 36.01±3.25 | 13.05±1.33 |
| *Rubus allegheniensis* | 0.034±0.03 | 84.034±8.13 | 221.8±16.4 | 0.3523±0.0132 | 42±5.17 | 36.8±4.77 |
| *Rubus canadensis* | 0.0306±0.002 | 56.877±10.1 | 320.5±28.6 | 0.2879±0.015 | 136.1±8.57 | 77.3±6.92 |
| *Rubus chamaemorus* | 0.528±0.034 | 12.923±1.7 | 127.5±10.7 | 0.3516±0.0073 | 98.6±8.89 | 66.55±10.18 |
| *Rubus hispidus* | 0.0267±0.002 | 6.196±0.97 | 232.1±9.6 | 0.3411±0.0116 | 6.47±0.78 | 7.69±0.96 |
| *Rubus idaeus* | 0.0347±0.003 | 42.149±6.87 | 281.8±23.6 | 0.3151±0.0079 | 9±1.06 | 13.08±2.78 |
| *Rubus pubescens* | 0.0597±0.006 | 9.579±0.94 | 242.6±6.4 | 0.3226±0.0044 | 13.03±0.9 | 15.28±2.3 |
| *Rumex acetosella* | 0.0325±0.001 | 1.711±0.55 | 225±20.2 | 0.1344±0.0072 | 17.69±2.78 | 5.95±1.18 |
| *Rumex crispus* | 0.0678±0.008 | 157.851±26.5 | 245.8±15.9 | 0.1633±0.0092 | 107±6.63 | 29.8±2.73 |
| *Sagina procumbens* | 0.0229±0.002 | 0.047±0.01 | 217.6±17.5 | 0.5539±0.0734 | 3±0.43 | 6.1±1.02 |
| *Sarracenia purpurea* | 0.0668±0.005 | 71.617±5.47 | 135.5±11.6 | 0.1775±0.0121 | 41.4±1.65 | 26.55±2 |
| *Scorzoneroides autumnalis* | 0.0312±0.004 | 11.956±2.47 | 256.6±8.8 | 0.1697±0.0072 | 4.45±0.63 | 15.95±2.28 |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Sedum acre* | 0.0853±0.024 | 0.116±0.02 | 204.3±14.7 | 0.0604±0.0064 | 5.31±0.41 | 16.77±1.79 |
| *Sedum album* | 0.3155±0.035 | 0.452±0.04 | 80.9±6 | 0.062±0.0032 | 4.17±1.27 | 14.8±4.5 |
| *Sedum sexangulare* | 0.0783±0.012 | 0.112±0.03 | 111±7.9 | 0.1363±0.018 | 3.81±0.55 | 19.96±3.6 |
| *Senecio viscosus* | 0.055±0.003 | 5.727±0.86 | 298.6±16.2 | 0.1027±0.006 | 6.37±0.85 | 7.05±0.59 |
| *Sibbaldia tridentata* | 0.033±0.002 | 1.292±0.15 | 89.2±3 | 0.3952±0.0052 | 9.01±1.52 | 5.14±0.5 |
| *Sisyrinchium montanum* | 0.0292±0.002 | 0.713±0.29 | 43.5±18.5 | 0.2114±0.006 | 23.75±3.49 | 19.11±3.9 |
| *Solidago bicolor* | 0.0278±0.001 | 6.451±0.61 | 110.4±6.8 | 0.3093±0.03 | 28.19±1.81 | 14.07±1.28 |
| *Solidago canadensis* | 0.0294±0.002 | 14.386±1.74 | 325.1±34.8 | 0.2209±0.0176 | 101.16±8.08 | 22.15±0.94 |
| *Solidago nemoralis* | 0.0259±0.002 | 3.036±0.77 | 142.9±8.5 | 0.3574±0.0131 | 35.46±4.09 | 16.46±2.94 |
| *Solidago puberula* | 0.0206±0.001 | 3.718±0.7 | 152.1±7.4 | 0.3024±0.013 | 35.25±2.19 | 16.15±1.74 |
| *Solidago rugosa* | 0.0359±0.002 | 16.043±1.8 | 238.8±10.2 | 0.255±0.0082 | 81.7±6.87 | 13.3±0.79 |
| *Solidago sempervirens* | 0.0743±0.005 | 11.826±1.44 | 90.3±5.7 | 0.2066±0.0349 | 39.41±3.66 | 21.48±1.67 |
| *Solidago uliginosa* | 0.301±0.035 | 11.752±2.34 | 115.8±6.2 | 0.299±0.0141 | 31.76±2.33 | 14.55±1.23 |
| *Sonchus arvensis* | 0.0541±0.004 | 57.276±7.05 | 218.6±13.1 | 0.1514±0.0062 | 65.46±7.7 | 32.3±1.7 |
| *Sorbus americana* | 0.0201±0.001 | 13.619±1.36 | 168.3±10.4 | 0.4235±0.0111 | 405±41.63 | 232.5±36.71 |
| *Spiraea alba* | 0.0227±0.008 | 4.672±0.5 | 212.4±7.5 | 0.3719±0.0084 | 49.5±5.28 | 29.1±3.37 |
| *Stellaria media* | 0.015±0.001 | 0.779±0.11 | 740±36.5 | 0.0943±0.0051 | 7.7±1.09 | 4.4±0.64 |
| *Symphyotrichum lateriflorum* | 0.02±0.001 | 3.971±1.05 | 271.5±19.83 | 0.2496±0.011 | 68.96±4.14 | 25±3.44 |
| *Symphyotrichum novi-belgii* | 0.019±0.001 | 9.95±1.34 | 275.2±18 | 0.251±0.006 | 50.39±5.72 | 32.6±4.53 |
| *Tanacetum vulgare* | 0.0269±0.002 | 3.826±0.57 | 326.7±21.9 | 0.1664±0.008 | 22.89±3.55 | 16.9±2.35 |
| *Taraxacum officinale* | 0.0515±0.003 | 15.498±2.46 | 278.4±12.1 | 0.1575±0.006 | 19.99±1.83 | 13.75±0.81 |
| *Thalictrum pubescens* | 0.0317±0.002 | 3.829±0.47 | 321.2±32.8 | 0.2656±0.0128 | 57±6.86 | 33.4±4.06 |
| *Trichophorum cespitosum* | 0.0811±0.007 | 1.054±0.13 | 37.9±3.7 | 0.4072±0.0146 | 23.85±1.12 | 61.2±3.93 |
| *Trifolium arvense* | 0.0429±0.022 | 0.225±0.02 | 145.3±13 | 0.7253±0.2697 | 11.7±0.91 | 3.4±0.32 |
| *Trifolium dubium* | 0.0462±0.017 | 0.28±0.03 | 407.1±25.1 | 0.4087±0.181 | 11.54±2.34 | 5.27±1.11 |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Trifolium pratense* | 0.0174±0.001 | 4.362±0.49 | 252.1±13.9 | 0.2388±0.0099 | 38.5±4.49 | 12.48±1.29 |
| *Trifolium repens* | 0.017±0.001 | 2.046±0.21 | 342.7±21.3 | 0.1857±0.0193 | 8.47±0.43 | 3.6±0.18 |
| *Tussilago farfara* | 0.0464±0.002 | 104.476±33.63 | 309.3±29.7 | 0.111±0.0062 | 17.02±4.72 | 26.5±4.98 |
| *Ulmus glabra* | NA | NA | NA | NA | NA | NA |
| *Ulmus glabra seedling* | 0.0246±0.004 | 1.165±0.19 | 282±23.1 | 0.3063±0.0191 | 3.4±0.64 | 2.58±0.26 |
| *Vaccinium angustifolium* | 0.0222±0.001 | 2.132±0.15 | 135.6±7.9 | 0.3648±0.0116 | 18.2±2.32 | 12.9±1.17 |
| *Vaccinium macrocarpon* | 0.0238±0.003 | 0.358±0.03 | 90.6±5.6 | 0.5262±0.0215 | 7.88±0.69 | 7.78±2.12 |
| *Vaccinium myrtilloides* | 0.0206±0.003 | 3.868±0.27 | 365.3±28.6 | 0.2575±0.0161 | 32.1±3.28 | 24.7±2.84 |
| *Vaccinium oxycoccos* | 0.3632±0.044 | 0.134±0.01 | 115.1±10.5 | 0.4743±0.0294 | 3.99±0.59 | 7.91±1.49 |
| *Vaccinium vitis-idaea* | 0.0429±0.003 | 0.601±0.06 | 64.9±3.9 | 0.4832±0.0369 | 7.33±1.14 | 3.22±0.42 |
| *Veronica serpyllifolia* | 0.0173±0.001 | 0.432±0.09 | 250.3±15.4 | 0.2726±0.015 | 2.68±0.29 | 3.9±0.57 |
| *Viburnum cassinoides* | 0.276±0.015 | 15.693±1.45 | 98.5±2.7 | 0.3936±0.0094 | 99.4±4.2 | 57.4±9.35 |
| *Viola sororia* | 0.0319±0.002 | 12.71±2.04 | 368.6±20 | 0.1864±0.0109 | 8.71±0.9 | 9.78±0.95 |

**Table 2.6.** The mean ± the standard error for seed weight and root radius for species in the trait database.

| Species | Seed Weight (mg) | Root Radius (mm) |
|---|---|---|
| *Acer platanoides* | 13.162±0.4418 | NA |
| *Agrostis scabra* | 0.045±0.0146 | NA |
| *Alnus alnobetula* | 0.205±0.0201 | NA |
| *Aralia nudicaulis* | 5.209±1.655 | NA |
| *Arctostaphylos uva-ursi* | 9.382±1.1379 | NA |
| *Aronia melanocarpa* | 1.064±0.0833 | NA |
| *Avenella flexuosa* | 0.223±0.0342 | 0.22±0.02 |
| *Calamagrostis pickeringii* | 0.281±0.0706 | NA |
| *Carex exilis* | 0.772±0.1044 | NA |
| *Carex nigra* | 0.32±0.0658 | NA |
| *Carex paleacea* | NA | NA |
| *Cerastium fontanum* | 0.115±0.0085 | 0.44±0.09 |
| *Chamaedaphne calyculata* | 0.046±0.0072 | NA |
| *Clintonia borealis* | 5.261±0.1752 | NA |
| *Corema conradii* | 0.755±0.0541 | NA |
| *Cornus canadensis* | 6.098±0.3412 | NA |
| *Danthonia spicata* | 0.697±0.0634 | 0.34±0.06 |
| *Elymus repens* | 3.483±0.1846 | NA |
| *Empetrum eamesii* | 0.457±0.0361 | NA |
| *Empetrum nigrum* | 0.595±0.0418 | 0.22±0.02 |
| *Epilobium ciliatum* | 0.089±0.0412 | NA |

| | | |
|---|---|---|
| *Erigeron annuus* | 0.038±0.0107 | NA |
| *Festuca rubra* | 0.306±0.0401 | 0.12±0.01 |
| *Fragaria virginiana* | 0.416±0.0497 | NA |
| *Fraxinus excelsior* | 52.087±5.9391 | NA |
| *Gaultheria procumbens* | 0.718±0.5271 | 0.19±0.02 |
| *Gaylussacia baccata* | NA | NA |
| *Gaylussacia bigeloviana* | 1.168±0.0833 | NA |
| *Ilex mucronata* | 9.069±0.4956 | NA |
| *Ilex verticillata* | 4.764±1.585 | NA |
| *Juniperus communis* | 13.354±1.6839 | NA |
| *Juniperus horizontalis* | 8.629±0.8251 | NA |
| *Kalmia angustifolia* | NA | NA |
| *Larix laricina* | 1.109±0.2416 | NA |
| *Luzula multiflora* | 0.413±0.027 | NA |
| *Lysimachia borealis* | 0.516±0.0387 | NA |
| *Maianthemum canadense* | 8.565±1.0114 | NA |
| *Mitchella repens* | 3.131±0.1303 | NA |
| *Mononeuria groenlandica* | 0.125±0.0107 | NA |
| *Morella pensylvanica* | 9.495±0.8257 | NA |
| *Nabalus trifoliolatus* | 0.714±0.0994 | NA |
| *Oenothera biennis* | 0.44±0.0513 | NA |
| *Oxalis stricta* | 0.176±0.0081 | NA |
| *Phedimus spurius* | 0.013±0.0049 | 0.23±0.03 |
| *Picea mariana* | 0.781±0.0983 | NA |
| *Pilosella caespitosa* | NA | NA |
| *Pilosella flagellaris* | 19.771±5.2904 | 0.73±0.09 |
| *Pilosella officinarum* | 0.099±0.0157 | NA |

| | | |
|---|---|---|
| *Pinus sylvestris* | 2.461±0.596 | NA |
| *Plantago major* | 0.302±0.0164 | 0.7±0.08 |
| *Plantago maritima* | 0.198±0.0212 | 0.32±0.09 |
| *Poa annua* | 0.221±0.0137 | NA |
| *Poa compressa* | 0.197±0.0074 | 0.47±0.08 |
| *Poa palustris* | 0.205±0.0175 | NA |
| *Prunus pensylvanica* | 26.644±4.4897 | NA |
| *Ranunculus repens* | NA | 0.71±0.06 |
| *Rhodiola rosea* | 0.104±0.0129 | NA |
| *Rosa nitida* | 2.829±0.2707 | NA |
| *Rubus pubescens* | 2.086±0.1371 | NA |
| *Sagina procumbens* | 0.006±0.0007 | NA |
| *Sarracenia purpurea* | 0.347±0.048 | NA |
| *Sedum acre* | 0.031±0.0029 | 0.38±0.05 |
| *Sedum album* | 0.039±0.006 | 0.3±0.02 |
| *Sedum sexangulare* | 0.069±0.0269 | 0.21±0.02 |
| *Senecio viscosus* | 0.462±0.0401 | NA |
| *Sibbaldia tridentata* | 0.302±0.037 | 0.29±0.03 |
| *Solidago bicolor* | 0.166±0.0222 | 0.31±0.04 |
| *Solidago nemoralis* | 0.049±0.0057 | NA |
| *Solidago puberula* | 0.071±0.0075 | 0.4±0.09 |
| *Solidago sempervirens* | 0.171±0.043 | NA |
| *Sorbus americana* | 3.535±0.2821 | NA |
| *Symphyotrichum novi-belgii* | 0.228±0.02 | 0.36±0.03 |
| *Tanacetum vulgare* | 0.113±0.0045 | NA |
| *Taraxacum officinale* | 0.443±0.0312 | 0.97±0.03 |

| | | |
|---|---|---|
| *Trichophorum cespitosum* | 0.437±0.011 | NA |
| *Trifolium arvense* | 0.43±0.0417 | NA |
| *Trifolium dubium* | 0.359±0.0366 | NA |
| *Trifolium repens* | 0.394±0.0331 | 0.76±0.05 |
| *Ulmus glabra* | 15.655±4.9924 | NA |
| *Vaccinium angustifolium* | 0.249±0.0242 | NA |
| *Vaccinium macrocarpon* | 0.774±0.0779 | 0.26±0.03 |
| *Vaccinium vitis-idaea* | 0.246±0.0128 | NA |

**Table 2.7.** Information on age, growth form, and habitat for each species in the functional trait database.

| Family | Genus | Species | Age | Growth Form | Common Habitat | Collected Habitat | Location |
|---|---|---|---|---|---|---|---|
| Adoxaceae | *Viburnum* | *cassinoides* | Adult | Shrub | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Anacardiaceae | *Rhus* | *typhina* | Adult | Shrub | Disturbed Sites | Disturbed Field | Chain of Lakes Trail |
| Apiaceae | *Ligusticum* | *scoticum* | Adult | Forb | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Aquifoliaceae | *Ilex* | *glabra* | Adult | Shrub | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Aquifoliaceae | *Ilex* | *mucronata* | Adult | Shrub | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Aquifoliaceae | *Ilex* | *verticillata* | Adult | Shrub | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Araliaceae | *Aralia* | *hispida* | Adult | Forb | Disturbed Sites | Disturbed Field | Chain of Lakes Trail |
| Araliaceae | *Aralia* | *nudicaulis* | Adult | Shrub | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Asparagaceae | *Maianthemum* | *canadense* | Adult | Forb | Roof and Barrens | Coastal Barrens | Chebucto Head |
| Asparagaceae | *Maianthemum* | *stellatum* | Adult | Forb | Coastal Dune | Coastal Dune | Lawrence Town Beach |
| Asparagaceae | *Maianthemum* | *trifolium* | Adult | Forb | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Asteraceae | *Achillea* | *millefolium* | Adult | Forb | Disturbed Sites | Disturbed Field | Chain of Lakes Trail |
| Asteraceae | *Anaphalis* | *margaritacea* | Adult | Forb | Disturbed Sites | Disturbed Field | Otter Lake |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Asteraceae | *Artemisia* | *stelleriana* | Adult | Forb | Coastal Dune | Coastal Barrens | Crystal Crescent |
| Asteraceae | *Centaurea* | *nigra* | Adult | Forb | Disturbed Sites | Coastal Barrens | Crystal Crescent |
| Asteraceae | *Doellingeria* | *umbellata* | Adult | Forb | Disturbed Sites | Urban Lawn | Saint Mary’s University |
| Asteraceae | *Erigeron* | *canadensis* | Adult | Forb | Disturbed Sites | Green Roof | Saint Mary’s University |
| Asteraceae | *Erigeron* | *annuus* | Adult | Forb | Disturbed Sites | Green Roof | Saint Mary’s University |
| Asteraceae | *Nabalus* | *trifoliolatus* | Adult | Forb | Roof and Barrens | Coastal Barrens | Chebucto Head |
| Asteraceae | *Oclemena* | *acuminata* | Adult | Forb | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Asteraceae | *Oclemena* | *nemoralis* | Adult | Forb | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Asteraceae | *Oclemena* | *x blakei* | Adult | Forb | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Asteraceae | *Pilosella* | *flagellaris* | Adult | Forb | Disturbed Sites | Green Roof | Saint Mary’s University |
| Asteraceae | *Pilosella* | *caespitosa* | Adult | Forb | Disturbed Sites | Urban Field | Dalhousie University |
| Asteraceae | *Pilosella* | *officinarum* | Adult | Forb | Disturbed Sites | Urban Field | Dalhousie University |
| Asteraceae | *Scorzoneroides* | *autumnalis* | Adult | Forb | Disturbed Sites | Urban Field | Dalhousie University |
| Asteraceae | *Senecio* | *viscosus* | Adult | Forb | Disturbed Sites | Green Roof | Saint Mary’s University |
| Asteraceae | *Solidago* | *bicolor* | Adult | Forb | Roof and Barrens | Coastal Barrens | Chebucto Head |

|  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|
| Asteraceae | *Solidago* | *canadensis* | Adult | Forb | Coastal Barrens | Urban Forest | Point Pleasant Park |
| Asteraceae | *Solidago* | *nemoralis* | Adult | Forb | Coastal Barrens and Disturbed Sites | Disturbed Field | Chain of Lakes Trail |
| Asteraceae | *Solidago* | *puberula* | Adult | Forb | Coastal Barrens and Disturbed Sites | Disturbed Field | Chain of Lakes Trail |
| Asteraceae | *Solidago* | *rugosa* | Adult | Forb | Coastal Barrens | Urban Forest | Point Pleasant Park |
| Asteraceae | *Solidago* | *sempervirens* | Adult | Forb | Roof and Barrens | Coastal Barrens | Chebucto Head |
| Asteraceae | *Solidago* | *uliginosa* | Adult | Forb | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Asteraceae | *Sonchus* | *arvensis* | Adult | Forb | Disturbed Sites | Urban Field | Dalhousie University |
| Asteraceae | *Symphyotrichum* | *lateriflorum* | Adult | Forb | Disturbed Sites | Urban Lawn | Saint Mary’s University |
| Asteraceae | *Symphyotrichum* | *novi-belgii* | Adult | Forb | Roof and Barrens | Coastal Barrens | Chebucto Head |
| Asteraceae | *Tanacetum* | *vulgare* | Adult | Forb | Disturbed Sites | Green Roof | Saint Mary’s University |
| Asteraceae | *Taraxacum* | *officinale* | Adult | Forb | Disturbed Sites | Urban Lawn | Saint Mary’s University |
| Asteraceae | *Tussilago* | *farfara* | Adult | Forb | Disturbed Sites | Coastal Barrens | Chebucto Head |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Balsaminaceae | *Impatiens* | *capensis* | Adult | Forb | Forest | Urban Forest | Point Pleasant Park |
| Betulaceae | *Alnus* | *incana* | Adult | Shrub | Forest edge, Wetlands | Urban Forest | Point Pleasant Park |
| Betulaceae | *Alnus* | *alnobetula* | Adult | Shrub | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Betulaceae | *Betula* | *papyrifera* | Adult | Tree | Forest | Urban Forest | Point Pleasant Park |
| Betulaceae | *Betula* | *populifolia* | Adult | Tree | Forest | Urban Forest | Point Pleasant Park |
| Brassicaceae | *Cakile* | *edentula* | Adult | Succulent | Coastal Dune | Coastal Dune | Crystal Crescent |
| Campanulaceae | *Campanula* | *intercedens* | Adult | Forb | Roof and Barrens | Coastal Barrens | Chebucto Head |
| Caprifoliaceae | *Diervilla* | *lonicera* | Adult | Shrub | Forest | Urban Forest | Point Pleasant Park |
| Caprifoliaceae | *Linnaea* | *borealis* | Adult | Forb | Roof and Barrens | Coastal Barrens | Polly’s Cove |
| Caryophyllaceae | *Cerastium* | *fontanum* | Adult | Forb | Disturbed Sites | Green Roof | Saint Mary’s University |
| Caryophyllaceae | *Moehringia* | *laterflora* | Adult | Forb | Coastal Dune | Coastal Dune | Crystal Crescent |
| Caryophyllaceae | *Mononeuria* | *groenlandica* | Adult | Forb | Roof and Barrens | Green Roof | Saint Mary’s University |
| Caryophyllaceae | *Sagina* | *procumbens* | Adult | Forb | Disturbed Sites | Green Roof | Saint Mary’s University |
| Caryophyllaceae | *Stellaria* | *media* | Adult | Forb | Disturbed Sites | Urban Lawn | Saint Mary’s University |
| Cistaceae | *Hudsonia* | *ericoides* | Adult | Shrub | Coastal Barrens | Coastal Barrens | Chebucto Head |

|  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|
| Convolvulaceae | *Convolvulus* | *arvensis* | Adult | Vine | Disturbed Sites | Urban Forest | Point Pleasant Park |
| Cornaceae | *Cornus* | *canadensis* | Adult | Shrub | Roof and Barrens | Coastal Barrens | Chebucto Head |
| Crassulaceae | *Hylotelephium* | *telephium* | Adult | Succulent | Green Roof | Green Roof | Saint Mary's University |
| Crassulaceae | *Phedimus* | *spurius* | Adult | Succulent | Green Roof | Green Roof | Saint Mary's University |
| Crassulaceae | *Rhodiola* | *rosea* | Adult | Succulent | Roof and Barrens | Coastal Barrens | Chebucto Head |
| Crassulaceae | *Sedum* | *acre* | Adult | Succulent | Green Roof | Green Roof | Saint Mary's University |
| Crassulaceae | *Sedum* | *album* | Adult | Succulent | Green Roof | Green Roof | Saint Mary's University |
| Crassulaceae | *Sedum* | *sexangulare* | Adult | Succulent | Green Roof | Green Roof | Saint Mary's University |
| Cupressaceae | *Juniperus* | *communis* | Adult | Shrub | Roof and Barrens | Coastal Barrens | Chebucto Head |
| Cupressaceae | *Juniperus* | *horizontalis* | Adult | Shrub | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Cyperaceae | *Carex* | *echinata* | Adult | Graminoid | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Cyperaceae | *Carex* | *exilis* | Adult | Graminoid | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Cyperaceae | *Carex* | *folliculata* | Adult | Graminoid | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Cyperaceae | *Carex* | *magellanica* | Adult | Graminoid | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Cyperaceae | *Carex* | *nigra* | Adult | Graminoid | Roof and Barrens | Coastal Barrens | Chebucto Head |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Cyperaceae | *Carex* | *paleacea* | Adult | Graminoid | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Cyperaceae | *Carex* | *pauciflora* | Adult | Graminoid | Coastal Barrens | Coastal Barrens | Polly’s Cove |
| Cyperaceae | *Carex* | *silicea* | Adult | Graminoid | Salt Marsh | Salt Marsh | Rainbow Haven |
| Cyperaceae | *Carex* | *trisperma* | Adult | Graminoid | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Cyperaceae | *Carex* | *viridula* | Adult | Graminoid | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Cyperaceae | *Eriophorum* | *vaginatum* | Adult | Graminoid | Coastal Barrens | Coastal Barrens | Polly’s Cove |
| Cyperaceae | *Eriophorum* | *virginicum* | Adult | Graminoid | Coastal Barrens | Coastal Barrens | Polly’s Cove |
| Cyperaceae | *Rhynchospora* | *alba* | Adult | Graminoid | Coastal Barrens | Coastal Barrens | Polly’s Cove |
| Cyperaceae | *Trichophorum* | *cespitosum* | Adult | Graminoid | Disturbed Sites | Coastal Barrens | Chebucto Head |
| Dennstaedtiaceae | *Dennstaedtia* | *punctilobula* | Adult | Fern | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Dennstaedtiaceae | *Pteridium* | *aquilinum* | Adult | Fern | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Droseraceae | *Drosera* | *intermedia* | Adult | Carnivorous | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Droseraceae | *Drosrea* | *rotundifolia* | Adult | Carnivorous | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Dryopteridaceae | *Dryopteris* | *carthusiana* | Adult | Fern | Forest | Urban Forest | Point Pleasant Park |
| Equisetaceae | *Equisetum* | *arvense* | Adult | Fern | Coastal Barrens | Urban Forest | Point Pleasant Park |

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|---|---|---|---|---|---|---|---|
| Ericaceae | *Andromeda* | *polifolia* | Adult | Shrub | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Ericaceae | *Arctostaphylos* | *uva-ursi* | Adult | Shrub | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Ericaceae | *Coremi* | *conradii* | Adult | Shrub | Roof and Barrens | Coastal Barrens | Chebucto Head |
| Ericaceae | *Empetrum* | *eamesii* | Adult | Shrub | Roof and Barrens | Coastal Barrens | Chebucto Head |
| Ericaceae | *Empetrum* | *nigrum* | Adult | Shrub | Roof and Barrens | Coastal Barrens | Chebucto Head |
| Ericaceae | *Epigaea* | *repens* | Adult | Shrub | Coastal Barrens | Urban Forest | Frog Pond |
| Ericaceae | *Gaultheria* | *hispidula* | Adult | Shrub | Coastal Barrens | Urban Forest | Hemlock Ravine |
| Ericaceae | *Gaultheria* | *procumbens* | Adult | Shrub | Roof and Barrens | Coastal Barrens | Chebucto Head |
| Ericaceae | *Gaylussacia* | *baccata* | Adult | Shrub | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Ericaceae | *Gaylussacia* | *bigeloviana* | Adult | Shrub | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Ericaceae | *Kalmia* | *angustifolia* | Adult | Shrub | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Ericaceae | *Kalmia* | *polifolia* | Adult | Shrub | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Ericaceae | *Rhododendron* | *canadense* | Adult | Shrub | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Ericaceae | *Rhododendron* | *groenlandicum* | Adult | Shrub | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Ericaceae | *Vaccinium* | *angustifolium* | Adult | Shrub | Roof and Barrens | Coastal Barrens | Chebucto Head |

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|---|---|---|---|---|---|---|---|
| Ericaceae | *Vaccinium* | *macrocarpon* | Adult | Shrub | Roof and Barrens | Coastal Barrens | Chebucto Head |
| Ericaceae | *Vaccinium* | *myrtilloides* | Adult | Shrub | Coastal Barrens | Urban Forest | Point Pleasant Park |
| Ericaceae | *Vaccinium* | *oxycoccos* | Adult | Shrub | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Ericaceae | *Vaccinium* | *vitis-idaea* | Adult | Shrub | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Fabaceae | *Lathyrus* | *japonicus* | Adult | Forb | Coastal Dune | Coastal Dune | Crystal Crescent |
| Fabaceae | *Trifolium* | *arvense* | Adult | Forb | Disturbed Sites | Green Roof | Saint Mary’s University |
| Fabaceae | *Trifolium* | *dubium* | Adult | Forb | Disturbed Sites | Green Roof | Saint Mary’s University |
| Fabaceae | *Trifolium* | *pratense* | Adult | Forb | Disturbed Sites | Coastal Dune | Crystal Crescent |
| Fabaceae | *Trifolium* | *repens* | Adult | Forb | Disturbed Sites | Green Roof | Saint Mary’s University |
| Fagaceae | *Quercus* | *rubra* | Adult | Tree | Forest | Urban Forest | Frog Pond |
| Hamamelidaceae | *Hamamelis* | *virginiana* | Adult | Shrub | Forest | Urban Forest | Saint Mary’s University |
| Hypericaceae | *Hypericum* | *perforatum* | Adult | Forb | Disturbed Sites | Green Roof | Saint Mary’s University |
| Iridaceae | *Iris* | *setosa* | Adult | Forb | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Iridaceae | *Iris* | *versicolor* | Adult | Forb | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Iridaceae | *Sisyrinchium* | *montanum* | Adult | Forb | Coastal Barrens | Urban Forest | Point Pleasant Park |

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|---|---|---|---|---|---|---|---|
| Juncaceae | *Juncus* | *arcticus* | Adult | Graminoid | Coastal Barrens | Coastal Barrens | Crystal Crescent |
| Juncaceae | *Juncus* | *bufonius* | Adult | Graminoid | Coastal Barrens | Coastal Barrens | Crystal Crescent |
| Juncaceae | *Juncus* | *gerardi* | Adult | Graminoid | Salt Marsh | Salt Marsh | Conrad's Beach |
| Juncaceae | *Luzula* | *multiflora* | Adult | Graminoid | Coastal Barrens | Urban Forest | Point Pleasant Park |
| Liliaceae | *Clintonia* | *borealis* | Adult | Forb | Coastal Barrens | Coastal Barrens | Polly’s Cove |
| Myricaceae | *Comptonia* | *peregrina* | Adult | Shrub | Forest | Urban Forest | Point Pleasant Park |
| Myricaceae | *Morella* | *pensylvanica* | Adult | Shrub | Roof and Barrens | Coastal Barrens | Chebucto Head |
| Myricaceae | *Myrica* | *gale* | Adult | Shrub | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Oleaceae | *Fraxinus* | *americana* | Adult | Tree | Forest | Urban Lawn | Saint Mary’s University |
| Oleaceae | *Fraxinus* | *excelsior* | Adult | Tree | Forest | Urban Lawn | Saint Mary’s University |
| Oleaceae | *Fraxinus* | *excelsior* | seedling | Tree | Forest | Urban Lawn | Saint Mary’s University |
| Onagraceae | *Chamaedaphne* | *calyculata* | Adult | Shrub | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Onagraceae | *Chamaenerion* | *angustifolium* | Adult | Forb | Disturbed Sites | Urban Forest | Point Pleasant Park |
| Onagraceae | *Epilobium* | *ciliatum* | Adult | Forb | Disturbed Sites | Green Roof | Saint Mary’s University |
| Onagraceae | *Oenothera* | *biennis* | Adult | Forb | Coastal Dune | Coastal Barrens | Chebucto Head |

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|---|---|---|---|---|---|---|---|
| Onocleaceae | *Onoclea* | *sensibilis* | Adult | Fern | Forest | Urban Forest | Point Pleasant Park |
| Orchidaceae | *Arethusa* | *bulbosa* | Adult | Forb | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Orchidaceae | *Calopogon* | *tuberosus* | Adult | Forb | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Orchidaceae | *Cypripedium* | *acaule* | Adult | Forb | Forest | Urban Forest | Point Pleasant Park |
| Orobanchaceae | *Agalinis* | *neoscotica* | Adult | Forb | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Orobanchaceae | *Euphrasia* | *stricta* | Adult | Forb | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Orobanchaceae | *Melampyrum* | *lineare* | Adult | Hemiparasite | Coastal Barrens | Coastal Barrens | Polly’s Cove |
| Orobanchaceae | *Rhinanthus* | *minor* | Adult | Forb | Coastal Barrens | Coastal Barrens | Crystal Crescent |
| Osmundaceae | *Osmundastrum* | *cinnamomeum* | Adult | Fern | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Oxalidaceae | *Oxalis* | *stricta* | Adult | Forb | Disturbed Sites | Green Roof | Saint Mary’s University |
| Pinaceae | *Abies* | *balsamea* | Adult | Tree | Forest | Urban Forest | Frog Pond |
| Pinaceae | *Larix* | *laricina* | Adult | Tree | Coastal Barrens | Coastal Barrens | Polly’s Cove |
| Pinaceae | *Picea* | *glauca* | Adult | Tree | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Pinaceae | *Picea* | *mariana* | Adult | Tree | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Pinaceae | *Picea* | *rubens* | Adult | Tree | Forest | Urban Forest | Point Pleasant Park |

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|---|---|---|---|---|---|---|---|
| Pinaceae | *Pinus* | *banksiana* | Adult | Tree | Forest | Inland Barrens | Titanium Crescent Park |
| Pinaceae | *Pinus* | *resinosa* | Adult | Tree | Forest | Urban Lawn | Saint Mary’s University |
| Pinaceae | *Pinus* | *strobus* | Adult | Tree | Forest | Urban Forest | Point Pleasant Park |
| Pinaceae | *Pinus* | *sylvestris* | Adult | Tree | Forest | Urban Forest | Frog Pond |
| Pinaceae | *Pinus* | *sylvestris* | Seedling | Tree | Forest | Urban Forest | Frog Pond |
| Plantaginaceae | *Plantago* | *major* | Adult | Forb | Disturbed Sites | Green Roof | Saint Mary’s University |
| Plantaginaceae | *Plantago* | *maritima* | Adult | Forb | Roof and Barrens | Coastal Barrens | Chebucto Head |
| Plantaginaceae | *Veronica* | *serpyllifolia* | Adult | Forb | Disturbed Sites | Green Roof | Saint Mary’s University |
| Plumbaginaceae | *Limonium* | *carolinianum* | Adult | Shrub | Salt Marsh | Salt Marsh | Conrad's Beach |
| Poaceae | *Agrostis* | *scabra* | Adult | Graminoid | Disturbed Sites | Coastal Barrens | Polly’s Cove |
| Poaceae | *Agrostis* | *stolonifera* | Adult | Graminoid | Coastal Barrens | Urban Forest | Point Pleasant Park |
| Poaceae | *Avenella* | *flexuosa* | Adult | Graminoid | Roof and Barrens | Coastal Barrens | Chebucto Head |
| Poaceae | *Calamagrostis* | *breviligulata* | Adult | Graminoid | Coastal Dune | Coastal Dune | Crystal Crescent |
| Poaceae | *Calamagrostis* | *Canadensis* | Adult | Graminoid | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Poaceae | *Calamagrostis* | *pickeringii* | Adult | Graminoid | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Poaceae | *Danthonia* | *spicata* | Adult | Graminoid | Roof and Barrens | Coastal Barrens | Chebucto Head |

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|---|---|---|---|---|---|---|---|
| Poaceae | *Elymus* | *repens* | Adult | Graminoid | Roof and Dune | Coastal Dune | Crystal Crescent |
| Poaceae | *Festuca* | *filiformis* | Adult | Graminoid | Disturbed Sites | Green Roof | Saint Mary’s University |
| Poaceae | *Festuca* | *rubra* | Adult | Graminoid | Roof and Barrens | Coastal Barrens | Chebucto Head |
| Poaceae | *Phleum* | *pratense* | Adult | Graminoid | Disturbed Sites | Coastal Dune | Crystal Crescent |
| Poaceae | *Poa* | *annua* | Adult | Graminoid | Disturbed Sites | Green Roof | Saint Mary’s University |
| Poaceae | *Poa* | *compressa* | Adult | Graminoid | Disturbed Sites | Green Roof | Saint Mary’s University |
| Poaceae | *Poa* | *palustris* | Adult | Graminoid | Disturbed Sites | Urban Field | Dalhousie University |
| Polygonaceae | *Rumex* | *acetosella* | Adult | Forb | Disturbed Sites | Coastal Barrens | Chebucto Head |
| Polygonaceae | *Rumex* | *crispus* | Adult | Forb | Disturbed Sites | Urban Forest | Frog Pond |
| Primulaceae | *Lysimachia* | *borealis* | Adult | Forb | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Ranunculaceae | *Coptis* | *trifolia* | Adult | Forb | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Ranunculaceae | *Ranunculus* | *repens* | Adult | Forb | Disturbed Sites | Green Roof | Saint Mary’s University |
| Ranunculaceae | *Thalictrum* | *pubescens* | Adult | Forb | Disturbed Sites | Coastal Barrens | Chebucto Head |
| Rosaceae | *Amelanchier* | *spicata* | Adult | Shrub | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Rosaceae | *Aronia* | *arbutifolia* | Adult | Shrub | Coastal Barrens | Tall Shrub | York Redoubt National Historic Site |

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|---|---|---|---|---|---|---|---|
| Rosaceae | *Aronia* | *melanocarpa* | Adult | Shrub | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Rosaceae | *Aronia* | *x prunifolia* | Adult | Shrub | Coastal Barrens | Tall Shrub | York Redoubt National Historic Site |
| Rosaceae | *Crataegus* | *monogyna* | seedling | Shrub | Forest | Urban Lawn | Saint Mary's University |
| Rosaceae | *Fragaria* | *virginiana* | Adult | Shrub | Forest, Disturbed Sites | Urban Field | Dalhousie University |
| Rosaceae | *Potentilla* | *anserina* | Adult | Forb | Disturbed Sites | Coastal Dune | Crystal Crescent |
| Rosaceae | *Potentilla* | *simplex* | Adult | Forb | Disturbed Sites | Urban Field | Dalhousie University |
| Rosaceae | *Prunus* | *pensylvanica* | Adult | Shrub | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Rosaceae | *Rosa* | *multiflora* | Adult | Shrub | Disturbed Sites | Urban Field | Dalhousie University |
| Rosaceae | *rosa* | *nitida* | Adult | Shrub | Coastal Barrens | Coastal Barrens | Herring Cove |
| Rosaceae | *Rosa* | *virginiana* | Adult | Shrub | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Rosaceae | *Rubus* | *allegheniensis* | Adult | Shrub | Coastal Barrens | Urban Forest | Point Pleasant Park |
| Rosaceae | *Rubus* | *canadensis* | Adult | Shrub | Coastal Barrens | Urban Forest | Point Pleasant Park |
| Rosaceae | *Rubus* | *chamaemorus* | Adult | Shrub | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Rosaceae | *Rubus* | *hispidus* | Adult | Shrub | Coastal Barrens | Coastal Barrens | Chebucto Head |

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|---|---|---|---|---|---|---|---|
| Rosaceae | *Rubus* | *idaeus* | Adult | Shrub | Coastal Barrens | Urban Forest | Point Pleasant Park |
| Rosaceae | *Rubus* | *pubescens* | Adult | Shrub | Coastal Barrens | Urban Forest | Point Pleasant Park |
| Rosaceae | *Sibbaldia* | *tridentata* | Adult | Shrub | Roof and Barrens | Coastal Barrens | Chebucto Head |
| Rosaceae | *Sorbus* | *americana* | Seedling | Shrub | Forest | Urban Lawn | Saint Mary’s University |
| Rosaceae | *Spiraea* | *alba* | Adult | Shrub | Disturbed Sites | Urban Forest | Point Pleasant Park |
| Rubiaceae | *Galium* | *mollugo* | Adult | Forb | Coastal Dune, Wetland | Coastal Barrens | Crystal Crescent |
| Rubiaceae | *Mitchella* | *repens* | Adult | Shrub | Coastal Barrens | Urban Forest | Point Pleasant Park |
| Salicaceae | *Populus* | *grandidentata* | Adult | Tree | Forest | Forest | York Redoubt National Historic Site |
| Salicaceae | *Populus* | *tremuloides* | Adult | Tree | Forest | Forest | York Redoubt National Historic Site |
| Sapindaceae | *Acer* | *platanoides* | Adult | Tree | Forest | Urban Forest | Point Pleasant Park |
| Sapindaceae | *Acer* | *platanoides* | Seedling | Tree | Forest | Urban Forest | Point Pleasant Park |
| Sapindaceae | *Acer* | *rubrum* | Adult | Tree | Forest | Urban Forest | Point Pleasant Park |
| Sarraceniaceae | *Sarracenia* | *purpurea* | Adult | Carnivorous | Coastal Barrens | Coastal Barrens | Chebucto Head |
| Thelypteridaceae | *Parathelypteris* | *noveboracensis* | Adult | Fern | Forest | Urban Forest | Point Pleasant Park |

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|---|---|---|---|---|---|---|---|
| Ulmaceae | *Ulmus* | *glabra* | Adult | Tree | Forest | Green Roof | Saint Mary’s University |
| Ulmaceae | *Ulmus* | *glabra* | Seedling | Tree | Forest | Green Roof | Saint Mary’s University |
| Violaceae | *Viola* | *sororia* | Adult | Forb | Disturbed Sites | Urban Lawn | Ardmore Park |

# Chapter 3

## Multiple Assembly Processes Form Coastal Barren Plant Communities

### Abstract

According to theory, increased heterogeneity should lead to an increase in coexistence and diversity due to an increase in microsites favorable to different species. Positive heterogeneity-diversity relationships have been demonstrated in the natural environment across geographic regions and community types. However, spatial/temporal heterogeneity has also been shown to have neutral and negative associations with species diversity. Since functional plant traits are associated with specific physiological processes, they may shed more light on heterogeneity/biodiversity patterns then can be garnered from traditional approaches which rely solely taxonomic diversity. Furthermore, high diversity in plant traits could be an indicator of potential coexistence as trait diversity indicates species are using resources in a different way. In order to address the disparities observed in heterogeneity-biodiversity literature, I use six coastal barren vegetation datasets to determine how spatial heterogeneity influences the functional trait profile of coastal barren plant communities.. Using a multiple linear regressions, I found that multiple assembly processes are active on Nova Scotia's coastal barrens. Both high (limiting similarity) and low (habitat filtering) functional diversity were observed in environments with higher values of environmental heterogeneity and stress. Nevertheless, most associations follow the patterns indicated in the literature, namely higher functional diversity in environments with higher environmental heterogeneity and lower environmental stress. Overall, environmental stress had far more associations with functional diversity than environmental heterogeneity, an indication that, on Nova Scotia's coastal barrens, environmental stress is the main driver of plant community composition.

## Introduction

Heterogeneity-diversity theory predicts that increases in spatial heterogeneity will result in increases in species richness and functional diversity. The general explanation of this hypothesis is that areas with greater environmental heterogeneity provide more niche space, encouraging coexistence between(MacArthur and Levins, 1967; Grubb, 1977; Tilman 1982). Positive heterogeneity-diversity relationships have been demonstrated in the natural environment across geographic regions and community types (Chesson et al., 2004; Löbel, 2006; Angert et all., 2009; Stein et al., 2014; Stark et al., 2017). However, environmental heterogeneity has also been shown to have neutral associations (Reynolds et al, 2007; Questad and Foster 2008; Lundholm 2009; Tamme et al. 2010) and negative associations with species diversity (Tamme et al., 2010; Gazol et al., 2013; Laanisto et al., 2013; Yang et al., 2015). Due to these disparate associations, there is a need to increase understanding of how environmental heterogeneity influences biodiversity.

Negative and neutral heterogeneity-biodiversity relationships are usually attributed to situations where spatial heterogeneity does not create enough variation in the environment to support different species (Lundholm 2009; Tamme et al. 2010). These situations can occur when the scale of spatial heterogeneity is too small to create separate niches and when environmental stress reduces the diversity of species that can exist in the heterogeneous environment (Tamme et al. 2010; Gazol et al., 2013). A meta-analysis conducted by Tamme et al. (2010) found that negative correlations between heterogeneity and diversity were more common at smaller spatial scales. The authors reason that this negative relationship could be due to micro-fragmentation (leading to low population size, with stochastic processes resulting in species exclusion) and heterogeneity at scales smaller than the size of individuals (roots from the same individual accessing resources from different microsites) (Tamme et al., 2010; Gazol et al. 2013; Price et al., 2017). However, negative, and neutral heterogeneity-biodiversity relationships could also occur in situations were taxonomic diversity and is high but functional trait diversity is low. In these scenarios species have similar resource requirements, limiting their ability to persist in different microsites. For this reason functional diversity rather then taxonomic diversity may be better suited to examining the relationship between heterogeneity and biodiversity.

Functional traits, the morphological, physiological, and phenological characteristics expressed in the phenotypes of individual organisms (Violle et al., 2007; Diaz et al., 2013; Garnier et al., 2016), are a valuable tool that can be used to identify the underlying factors influencing plant community assembly. This is possible partly due to an extensive body of literature that provides insight into which trait values are most common in specific environments and which traits are associated with key physiological processes. For example, species under drought stress tend to have smaller, thicker leaves and grow more slowly than those in more favorable environments. This adaptation occurs because these types of leaves are less vulnerable to evapotranspiration. However, these drought-adapted leaves are also more costly to produce, resulting in a slower growth rate than observed in species with larger, thinner leaves (Niinemets 2001; Wright et al., 2001; Vile et al., 2005; Tardy et al., 2015). These insights are not limited to drought-prone environments. Examining associations between environmental variables and functional traits has been a global endeavour leading to the development of plant economic spectrums, which describe the relationship between functional plant traits and carbon acquisition/survival strategies (e.g. leaf economic spectrum (Wright et al., 2004). Due to these associations, functional trait diversity can be used to understand whether coexistence is due to spatial heterogeneity (high trait diversity and high spatial heterogeneity) or a filtering effect associated with environmental stress (low trait diversity).

Two assembly processes that can be deduced from examining the diversity of functional traits within a plant community include habitat filtering and limiting similarity. Habitat filtering is associated with low functional diversity, as the habitat filters out species that lack the functional traits needed for survival. This process is usually associated with stressful, more homogenous environments or environments where high stress renders heterogeneity irrelevant in community assembly (Katabuchi et al., 2012; Cross et al., 2015). In contrast, limiting similarity is associated with high functional diversity, as species require different functional traits to coexist among competitors (Spasojevic et al., 2012; Katabuchi et al., 2012; Cross et al., 2015). Limiting similarity occurs when species occupy different niches, where a niche can be defined as the biotic and abiotic factors that allow a species to maintain their population within a community (Hutchinson 1957; Silvertown, 2004). This niche separation can occur in heterogenous environments where spatial variation allows species with different functional traits to coexist and in more homogenous environments where differences in functional traits allow species to acquire resources or resist stress in a different manner (Tilman, 1982;

Chesson et al., 2004; Silvertown, 2004). For example, a study on mountain and alpine plant communities found that increased soil moisture heterogeneity was associated with increased variation in leaf dry matter content (dry leaf mass/wet leaf mass) (Stark et al., 2017), a trait associated with water conservation (Poorter and Garnier, 1999). Support for limiting similarity can also be found in less heterogenous environments. Wilson and Stubbs (2012) examined functional trait variation in a salt marsh rush community at a fine spatial scale and discovered that species with deep and shallow roots were commonly found together. This pattern likely occurred as these functional root differences allowed species to acquire resources from different locations, encouraging co-existence (Wilson and Stubbs, 2012). Furthermore, when limiting similarity occurs in high stress environments, one species may be facilitating the survival of a second species (Chesson, 2000; Callaway 2007; Spasojevic et al., 2012; He et al., 2013). This facilitative effect can occur in several different ways: in an environment under thermal stress, the canopy of one species could reduce soil temperatures, allowing less heat-tolerant species to survive (Turner et al. 1966); in a nutrient poor environment, the symbiotic relationship between legumes and nitrogen-fixing bacteria can increase soil nutrient availability, allowing species with greater nutrient requirements to survive (Oelmann et al. 2011); and, in environments with pressure from herbivores, the presence of unpalatable species can reduce herbivory on the more palatable species neighboring them (Danet et al., 2017).

Even though habitat filtering and limiting similarity represent opposite functional diversity patterns, they are not mutually exclusive. A single habitat can filter for specific traits while encouraging diversity in other traits (Spasojevic et al., 2012; Cross et al., 2015). For example, a plant community exposed to high winds would have low plant height functional diversity. However, multiple species may be able to coexist in this environment because they possess different root lengths- high functional diversity- leading to a reduction in the competition for soil resources. For this reason, community assembly analysis should not only include total functional diversity (one value calculated from multiple traits) but also the functional diversity of individual traits (Spasojevic et al., 2012; Li et al., 2018).

The goal of this chapter was to examine how functional traits influence plant community assembly and coexistence.  This study was conducted on the coastal barrens of Nova Scotia, an ecosystem that contains wide variation in spatial heterogeneity, environmental stress, and plant associations (Porter et al., 2020). This distinct landscape offers an ideal space to examine how functional traits influence plant community assembly, as environmental variables play a crucial role in determining which functional traits are necessary to survive. Using six coastal barren vegetation datasets, my objective was to determine how spatial heterogeneity and environmental stress influence the functional trait profile of coastal barren plant communities.

Analysing multiple datasets that differ in their experimental design presented a unique challenge as well as an opportunity. These datasets represent 12 years of data collection from multiple investigators. Research into the vegetative composition of Nova Scotia's coastal barrens is also a recent endeavor, beginning with the publication of Oberndorfer (2006). It is only now, with the completion of coastal barren plant association guidebook by Porter et al., (2020), that we have a comprehensive set of plant community and environmental data from which we can begin to understand the mechanisms behind the composition of this unique ecosystem.

## Methods

### *Study System*

The coastal barrens on the Atlantic coast of Nova Scotia are characterized by cool temperatures, persistent fog, and frequent precipitation with shallow, acidic, and nutrient poor soil (Oberndorfer and Lundholm 2009; Neily et al 2017). The landscape is exposed to harsh environmental conditions, high winds, and salt spray, and is dominated by shrubby Ericaceous vegetation (Oberndorfer and Lundholm 2009). This ecosystem supports 21 distinct plant associations (Porter et al., 2020), which I generalized into six vegetation types according to Oberndorfer and Lundholm (2009), Porter (2013) and Cameron and Bondrup-Neilsen (2013): (1) salt spray zone (sparse vegetation on exposed bedrock adjacent to the coast and regularly exposed to salt spray), (2) rocky outcrop (inland bedrock exposures not subject to regular salt spray), (3) dwarf heath (dominated by dwarf shrubs of the genera *Empetrum*, *Corema*, and *Juniperus*), (4) *Sphagnum* bog (wetlands dominated by a bryophyte layer of the genus *Sphagnum*), (5) tall shrub (taller shrubland communities dominated by a variety of families), and (6) tree island communities (isolated patches of trees under 1 ha in area with greater than 30% tree cover) within a largely treeless landscape (Burley et al., 2010) (Figure 3.1 and 3.2). In this region, mean winter (December-February) precipitation is 131.6 mm and mean winter temperature is -1.6 °C. Mean summer (June-August) precipitation is 106.2 mm and mean summer temperature is 17.6 °C (Government of Canada, 2020).

**Figure 3.1.** Polly's Cove coastal barren site.

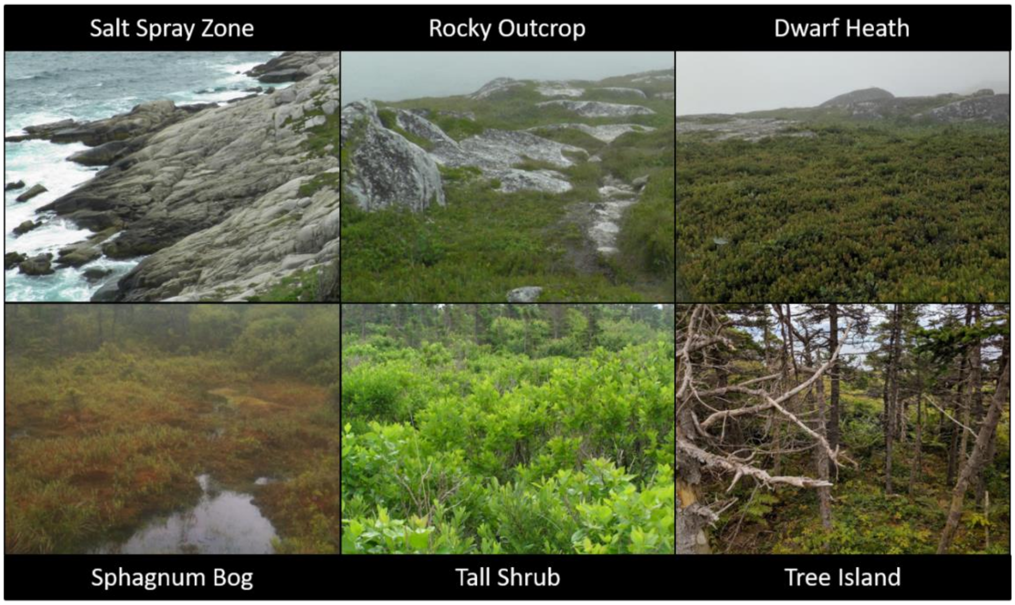


**Figure 3.2.** Six common vegetation types found within Nova Scotia coastal barrens: salt spray zone, rocky outcrop, dwarf heath, *Sphagnum* bog, tall shrub, and tree island. Photo credit: the photographs of the *Sphagnum* bog and tall shrub community were taken by Jeremy Lundholm, all other photographs were taken by Amy Heim.

### ***Datasets***

I analyzed six separate datasets collected in 2005 (Oberndorfer, 2006; Oberndorfer and Lundholm 2009), 2008 (Burley et al., 2010), 2010 (Porter et al., 2020), 2011 (Porter, 2013; Porter et al., 2020), 2016 (Appendix A), and 2017 (Clarke, 2018). Each dataset contains plant species abundance estimates (measured by frequency (2017), density (2005, 2008, 2011, 2016) and % cover (2010)) in plots and encompasses a range of vegetation types found within the barrens landscape (see appendix for detailed descriptions). Although several of these datasets included data from the same general location, the same plots were not measured across years. Due to relatively harsh environmental conditions, community dynamics are slow in this system, with major changes only evident at time scales greater than 70 years (Burley et al., 2010). Each dataset contains data on species abundance, and all but the 2016 dataset contain data on the following environmental variables: soil moisture, soil depth, elevation, distance to the coast, slope, soil variables (phosphorus, organic matter, and nitrogen content), wind exposure, leaf litter cover, and leaf litter thickness. I considered gradients in these variables to correspond with environmental stress, with high stress indicated by low soil nutrients, high winds, low soil depth, low soil moisture, proximity to the coast (increased exposure to high winds and salt spray), low elevation (closer to the coast), steep slopes (erosion), and low leaf litter cover and thickness (indicating low leaf turnover, more common in stress-tolerant leaves) (Balsdon et al., 2011; Nagashima and Hikosaka , 2001; Walter et al., 2020).

Stress variables were quantified as the average of each environmental variable, and heterogeneity variables as the interquartile range of each environmental variable. For all but the 2010 and 2016 datasets, the data were analyzed at multiple spatial scales.

The broadest spatial scale was calculated from all plots at each site or along each transect (1-85 sites; 6-25 transects), the fine spatial scale was calculated from individual plot data (1x1 m-5x5 m), and the very fine spatial scale was calculated from individual plots divided into four equal subplots (0.5 x 0.5 m). For each dataset, I only included plot data that contained vascular species, with the majority of plots included in the analysis (Tables 3.1 and 3.2).

**Table 3.1.** Breakdown of the datapoints used for each dataset. Plots for which I could not collect functional plant traits for every species were excluded from analysis.

| Dataset | # Sites | # Transects | Plot size | # Broad values (transects*sites) | # Fine values (# plots) | # Very fine values (# plots*4) |
|---|---|---|---|---|---|---|
| 2017 | 1 | 25 | 1x1 m | 25 | 237 | 858 |
| 2016 | 1 |  | 4x4 m |  | 35 |  |
| 2011 | 20 |  | 1x1 m | 20 | 366 |  |
| 2010 | 85 |  | 5x5 m |  | 85 |  |
| 2008 | 3 | 18 | 2x8 m | 18 | 73 |  |
| 2005 | 6 | 6 | 1x1 m | 6 | 106 |  |

**Table 3.2.** The environmental variables available for each dataset.

| | **Dataset** | | | | | |
|---|---|---|---|---|---|---|
| **Environmental Variables** | **2017** | **2016** | **2011** | **2010** | **2008** | **2005** |
| Soil Moisture | x | | | x | | x |
| Soil Depth | x | | x | x | x | x |
| Elevation | x | | | x | | |
| Coast Distance | | | x | x | | x |
| Slope | | | x | x | | |
| Phosphorous | | | | | x | x |
| Organic Matter | | | | | x | x |
| Nitrogen | | | | | x | |
| Wind Exposure | | | | | | x |
| Litter Cover | x | | | | | |
| Litter Thickness | | | x | | | |

### *Functional Plant Traits*

Between 2016 and 2019, functional plant traits were measured for 146 vascular species from naturally occurring populations within one hour's drive of Saint Mary's University, Halifax, Nova Scotia (44°37"N 63°34"W). The majority of individuals were collected from open (non-forested) dwarf heath coastal barren sites. Additionally, species that do not grow in dwarf heath habitat, such as *Drosera ssp.*, were collected from the coastal barren community type they are most dominant in (salt spray zone, rocky outcrop, *Sphagnum* bog, tall shrub, and tree island) (Porter et al., 2020). However, in the rare instances where a species could not be found at a coastal barren location, species were collected from forests, abandoned lots, and saltmarshes. For each species, traits were collected from 10 healthy non-dormant, sexually mature adult individuals according to protocols described in Pérez-Harguindeguy et al., (2016). Traits measured included plant height, canopy width, specific leaf area (leaf area/dry weight), leaf dry matter content (dry weight/wet weight), and leaf thickness. These traits were selected due to their ecological significance and their observed association with coastal barren plant communities (Table 3.3). Due to resource constraints and species rarity, traits could not be collected for every species in the study. Plots for which I could not collect functional plant traits for every species were excluded from analysis.

Both the 2011 and 2005 datasets contained abundance data for individuals that could not be identified to species. If a species from the same genus as these individuals was present at the site, then these individuals that could not be identified to species were counted as belonging to the same species as the identified individual. Additionally, I were unable to collect traits for one species from the 2011 dataset (*Euphrasia randii* (n=6 plots)) and one species from the 2005 dataset (*Amelanchier bartramiana* (n=2 plots)), both of which have very similar characteristics to species for which we were able to collect traits (*Euphrasia stricta* and *Amelanchier spicata*) (Roland, 1998). Therefore, during analysis, *E. randii* was counted as *E. stricta* and *A. bartramiana* was counted as *A. spicata*.

**Table 3.3.** Ecological significance of the functional plant traits used in this study and the values these traits would likely have in high stress environments.

| Trait | Ecological Significance | High Stress | Reference |
|---|---|---|---|
| **Plant Height** | Acquisition of light and soil resources, seed mass, and dispersal distance | Short plants | Moles et al., 2009;<br>Wang et al., 2019 |
| **Canopy Width** | Light acquisition | No clear relationship | Liira et al., 2002 |
| **Specific Leaf Area** | Leaf lifespan, net photosynthetic rate, relative growth rate, leaf nitrogen | Low specific leaf area | Wright et al., 2001 |
| **Leaf Dry Matter Content** | Nutrient and water conservation | High leaf dry matter content | Tardy et al., 2015;<br>Poorter and Garnier, 1999 |
| **Leaf Thickness** | Water conservation, light absorption, $CO_2$ dispersion, construction costs and longevity, salt tolerance | Thick leaves | Vile et al., 2005;<br>Niinemets 2001;<br>Ogburn et al., 2010 |

### *Statistical Methods*

Two functional trait analyses were conducted for the plant communities in all broad, fine, and very fine scale samples: community weighted mean (CWM) and functional dispersion (Fdis). CWM incorporates species abundance and population-based trait measurements to calculate a mean trait value for each sample (Lavorel et al., 2008). The trait values used in this calculation came from the trait database created for this study. Six different CWM variables were calculated: plant height CWM, canopy width CWM, specific leaf area CWM, leaf dry matter content CWM, and leaf thickness CWM. Since CWM represents the average trait value for each datapoint, it was used to determine which values for each trait were associated with specific environmental variables. CWM was calculated using the FD package (Laliberté et al., 2015) in R version 3.6.0.

Fdis is the mean distance from a species' position in multidimensional trait space to the centroid (calculated as the average value of trait(s) across all species). This measurement incorporates species abundance, shifting the centroid towards the more abundant species (Laliberté and Legendre, 2010). In this study, six different Fdis variables were calculated: plant height Fdis, canopy width Fdis, specific leaf area Fdis, leaf dry matter content Fdis, leaf thickness Fdis, and total Fdis. Total Fdis incorporated all five traits in the equation and all others only included one trait in the equation (the trait mentioned). Fdis was calculated using the FD package (Laliberté et al., 2015) in R version 3.6.0.

Eleven multiple linear regression analyses were run for each spatial scale for the 2017, 2011, 2010, 2008, and 2005 datasets (n=110 separate regressions). The 11 response variables were: plant height CWM, canopy width CWM, specific leaf area CWM, leaf dry matter content CWM, leaf thickness CWM, plant height Fdis, canopy width Fdis, specific leaf area Fdis, leaf dry matter content Fdis, leaf thickness Fdis, and total Fdis. The explanatory variables were the environmental variables, environmental stress (average environmental variable), and environmental heterogeneity (interquartile range of environmental variable). Explanatory variables were checked for normalcy using the Shapiro-Wilk test and transformed as needed. Before running the models, I examined the data graphically to determine if there was an interaction between stress and heterogeneity variables on functional diversity, but no interactions were observed. The Akaike Information Criterion was used to determine if all response variables were needed in the model. If the regression model had multiple delta scores below seven, all models with a delta score below seven were averaged together to create the final model (R version 3.6.0, library: MuMIn). For those datasets with nested datapoints, nesting was incorporated into the models as random effects. Positive associations refer to cases where model-averaged regression coefficients had 95% confidence intervals above 0, negative associations refer to cases where coefficients had 95% confidence intervals below 0, and no association refers to cases where 95% confidence intervals overlapped 0.

For the 2016 dataset, one-way ANOVAs and Tukey post-hoc tests were used to compare differences in CWM and Fdis between vegetation types. This analysis was only conducted on the 2016 dataset because it was the only one which separated plant community data into specific vegetative communities.

In the 2005 dataset, only six sites were available for analysis at the broad spatial scale. In order to reduce dimensions in this one dataset, factor analysis was performed on average environmental variables at the fine scale (n=106) (R version 3.6.0), with the output used to calculate environmental stress and heterogeneity at the broad scale. For each site (n=6), the average of each factor was used as an indicator of environmental stress, and the interquartile range was used as an index of spatial heterogeneity. Factor analysis was chosen as it accounts for variation among multiple variables while excluding variation unique to single variables (Suarez-Rubio and Krenn, 2018) (Table 3.4). In order to reduce the influence overfitting would have on the model, a single linear regression was run for each response and explanatory variable.

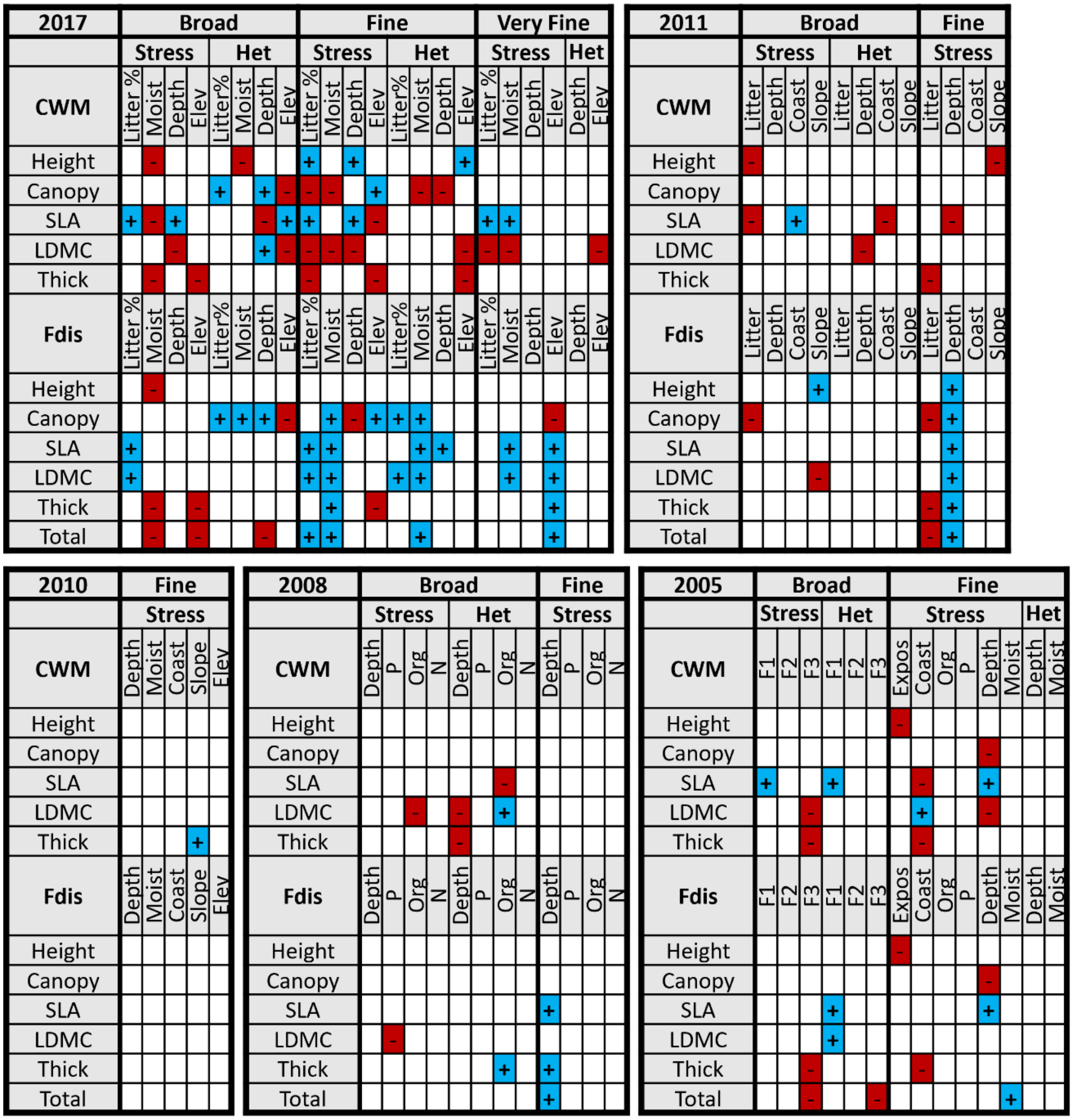
**Table 3.4.** Factor analysis conducted on environmental variables in the 2005 dataset on the 1x1 m plots. These factors were used to calculate environmental heterogeneity and stress variables for the broad spatial scale in the 2005 dataset. Stress value indicates whether high or low values of the environmental variable led to stressful growing conditions. For all variables, a Tukey's ladder of powers transformation was used.

| | **2005 Fine scale (1x1 m)** | | | |
|---|---|---|---|---|
| **Factor Loadings** | **Stress** | **Factor 1** | **Factor 2** | **Factor 3** |
| Distance to Coast | Low | **0.94** | 0.03 | 0.02 |
| Organic Matter | Low | -0.02 | **0.89** | -0.04 |
| Soil Depth | Low | 0.23 | **0.54** | 0.01 |
| Soil Moisture | Low | 0.04 | 0.14 | **-0.64** |
| Wind Exposure | High | 0.16 | -0.03 | **0.58** |
| Phosphorous | Low | -0.40 | 0.21 | 0.41 |

## Results

At the fine spatial scale, specific leaf area Fdis (Datasets: 2017, 2011, 2008, and 2005), total Fdis, and leaf thickness Fdis increased with average soil depth (Datasets: 2017, 2011). Canopy width Fdis was lower in habitats with a low average soil depth in the 2011 dataset, and higher in habitats with a low average soil depth for the 2017 and 2005 datasets. Total Fdis increased as soil moisture decreased for both the 2017 and 2005 datasets.

At broader spatial scales, greater leaf dry matter content CWM was associated with less soil depth heterogeneity for the 2011 and 2008 datasets, with the inverse pattern observed for the 2017 dataset. When spatial scale was compared within the same dataset, both similar and contrasting associations were observed. For the 2017 dataset, canopy width CWM was was positively associated with soil depth heterogeneity at the broad spatial scale (2x24 m transect) and negatively associated at the fine spatial scale (1x1 m). Leaf thickness Fdis was negatively associated with average soil moisture at the broad scale and positively associated at the fine scale. Leaf thickness Fdis was negatively associated with average elevation at the broad and fine spatial scale and positively associated at the very fine spatial scale (0.5 x 0.5 m). For the 2011 dataset, canopy width Fdis was negatively associated with leaf litter thickness at both the broad (site) and fine (1x1 m) spatial scales (Figure 3.3).



| 2017 | Broad | | | | | | | | Fine | | | | | | | | Very Fine | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Stress | | | | Het | | | | Stress | | | | Het | | | | Stress | | | | Het | |
| **CWM** | Litter % | Moist | Depth | Elev | Litter% | Moist | Depth | Elev | Litter % | Moist | Depth | Elev | Litter% | Moist | Depth | Elev | Litter % | Moist | Depth | Elev | Depth | Elev |
| Height | | - | | | | - | | | + | | + | | | | | + | | | | | | |
| Canopy | | | | | + | | + | - | - | - | | + | | - | - | | | | | | | |
| SLA | + | - | + | | | | - | + | + | | + | - | | | | | + | + | | | | |
| LDMC | | | - | | | | + | - | - | - | - | | | | | - | - | - | | | | - |
| Thick | | - | | - | | | | | - | | | - | | | | - | | | | | | |
| **Fdis** | Litter % | Moist | Depth | Elev | Litter% | Moist | Depth | Elev | Litter % | Moist | Depth | Elev | Litter% | Moist | Depth | Elev | Litter % | Moist | Depth | Elev | Depth | Elev |
| Height | | - | | | | | | | | | | | | | | | | | | | | |
| Canopy | | | | | + | + | + | - | | + | - | + | + | + | | | | | | - | | |
| SLA | + | | | | | | | | + | + | | | | + | + | | | + | | + | | |
| LDMC | + | | | | | | | | + | + | | | + | + | | | | + | | + | | |
| Thick | | - | | - | | | | | | + | | - | | | | | | | | + | | |
| Total | | - | | - | | | - | | + | + | | | | + | | | | | | + | | |

| 2011 | Broad | | | | | | | | Fine | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Stress | | | | Het | | | | Stress | | | |
| **CWM** | Litter | Depth | Coast | Slope | Litter | Depth | Coast | Slope | Litter | Depth | Coast | Slope |
| Height | - | | | | | | | | | | | - |
| Canopy | | | | | | | | | | | | |
| SLA | - | | + | | | | - | | | - | | |
| LDMC | | | | | | - | | | | | | |
| Thick | | | | | | | | | - | | | |
| **Fdis** | Litter | Depth | Coast | Slope | Litter | Depth | Coast | Slope | Litter | Depth | Coast | Slope |
| Height | | | | + | | | | | | + | | |
| Canopy | - | | | | | | | | - | + | | |
| SLA | | | | | | | | | | + | | |
| LDMC | | | | - | | | | | | + | | |
| Thick | | | | | | | | | - | + | | |
| Total | | | | | | | | | - | + | | |

| 2010 | Fine | | | | |
|---|---|---|---|---|---|
| | Stress | | | | |
| **CWM** | Depth | Moist | Coast | Slope | Elev |
| Height | | | | | |
| Canopy | | | | | |
| SLA | | | | | |
| LDMC | | | | | |
| Thick | | | | + | |
| **Fdis** | Depth | Moist | Coast | Slope | Elev |
| Height | | | | | |
| Canopy | | | | | |
| SLA | | | | | |
| LDMC | | | | | |
| Thick | | | | | |
| Total | | | | | |

| 2008 | Broad | | | | | | | | Fine | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Stress | | | | Het | | | | Stress | | | |
| **CWM** | Depth | P | Org | N | Depth | P | Org | N | Depth | P | Org | N |
| Height | | | | | | | | | | | | |
| Canopy | | | | | | | | | | | | |
| SLA | | | | | | | - | | | | | |
| LDMC | | | - | | - | | + | | | | | |
| Thick | | | | | - | | | | | | | |
| **Fdis** | Depth | P | Org | N | Depth | P | Org | N | Depth | P | Org | N |
| Height | | | | | | | | | | | | |
| Canopy | | | | | | | | | | | | |
| SLA | | | | | | | | | + | | | |
| LDMC | | - | | | | | | | | | | |
| Thick | | | | | | | + | | + | | | |
| Total | | | | | | | | | + | | | |

| 2005 | Broad | | | | | | Fine | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Stress | | | Het | | | Stress | | | | | | Het | |
| **CWM** | F1 | F2 | F3 | F1 | F2 | F3 | Expos | Coast | Org | P | Depth | Moist | Depth | Moist |
| Height | | | | | | | - | | | | | | | |
| Canopy | | | | | | | | | | | - | | | |
| SLA | + | | | + | | | | - | | | + | | | |
| LDMC | | | - | | | | | + | | | - | | | |
| Thick | | | - | | | | | - | | | | | | |
| **Fdis** | F1 | F2 | F3 | F1 | F2 | F3 | Expos | Coast | Org | P | Depth | Moist | Depth | Moist |
| Height | | | | | | | - | | | | | | | |
| Canopy | | | | | | | | | | | - | | | |
| SLA | | | | + | | | | | | | + | | | |
| LDMC | | | | + | | | | | | | | | | |
| Thick | | | - | | | | | - | | | | | | |
| Total | | | - | | | - | | | | | | + | | |

**Figure 3.3.** Results of the multiple linear regressions conducted on each dataset (2017, 2011, 2010, 2008, 2005) at each spatial scale (broad, fine, very fine). Response variables are rows and include the community weighted mean (CWM) and functional dispersion (Fdis) of plant height (Height), canopy width (Canopy), specific leaf area (SLA), leaf dry matter content (LDMC), leaf thickness (Thick), and total Fdis (total). Explanatory variables are columns and include environmental stress (Stress) and environmental heterogeneity (Het): soil moisture (Moist), soil depth (Depth), elevation (Elev), distance to the coast (Coast), slope (Slope), soil phosphorus (P), soil organic matter (Org), soil nitrogen (N), wind exposure (Expos), leaf litter cover (Litter %), and leaf litter thickness (Litter). Factor 1 (F1) is positively associated with distance to the coast, factor 2 (F2) is positively associated with soil organic matter and soil depth, and factor 3 (F3) is positively associated with wind exposure and negatively associated with soil moisture (Table 4). Positive associations (95% intervals all above 0) are indicated by a "+", negative associations (95% intervals all below 0) are indicated by a "-", and a blank indicates 95% intervals were both above and below 0.

### ***Vegetation Type Comparison***

When the tree island, dwarf heath, tall shrub, *Sphagnum* bog, rocky outcrop, and salt spray vegetation types were compared (2016 dataset), the tree island habitat contained the tallest and widest species, the tall shrub habitat contained species with the highest specific leaf area, and the salt spray habitat contained species with the thickest leaves and highest leaf dry matter content. The tree island habitat had the greatest diversity of species height, canopy width, and specific leaf area and the salt spray habitat had the greatest diversity of leaf dry matter content and leaf thickness. The greatest total functional diversity was observed in the tree island habitat, followed by the salt spray habitat (Figures 3.4 and 3.5).

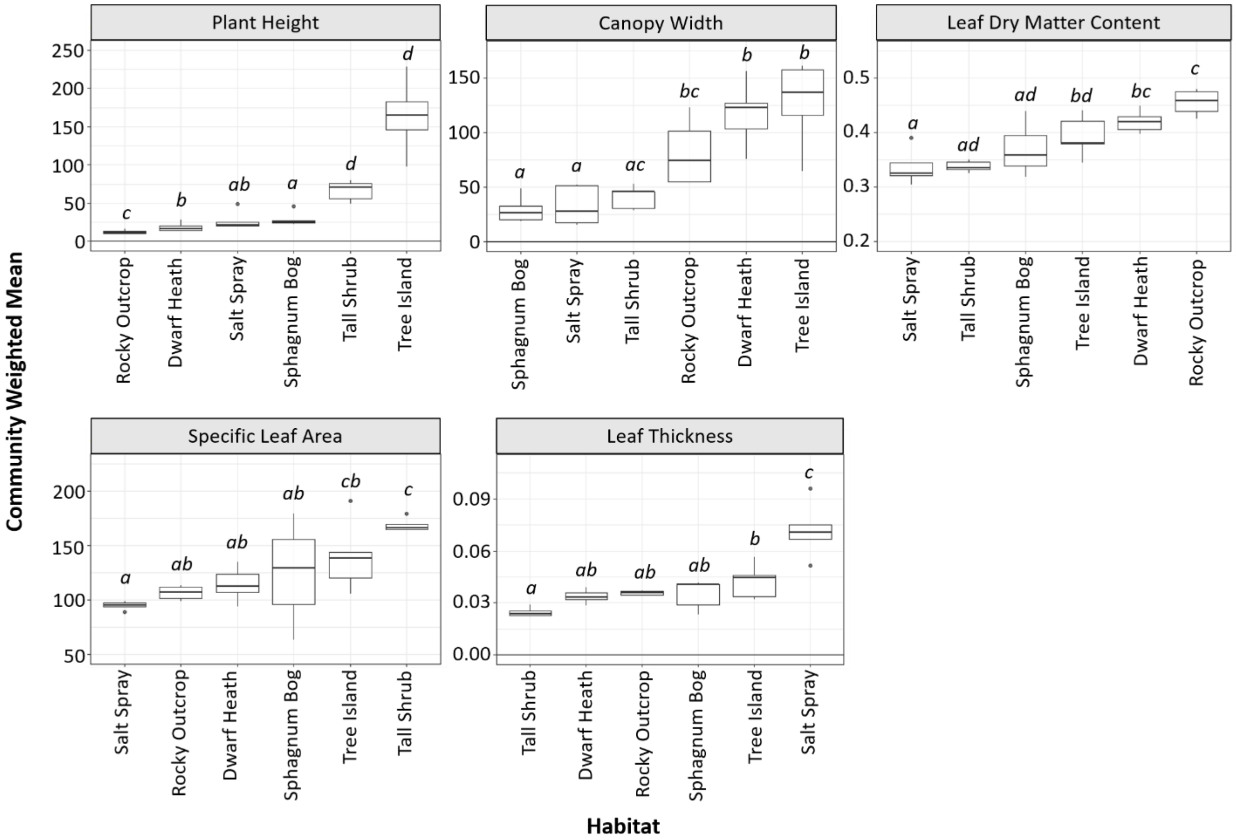


**Figure 3.4.** Box and whisker graphs for the community weighted mean (CWM) of each trait for each habitat type in the 2016 dataset. The figures list species in order of lowest to highest CWM. The letters represent results from Tukey post-hoc tests for which functional traits are the independent variables and habitat is the dependent variable. Bars that share a letter are p>0.0).

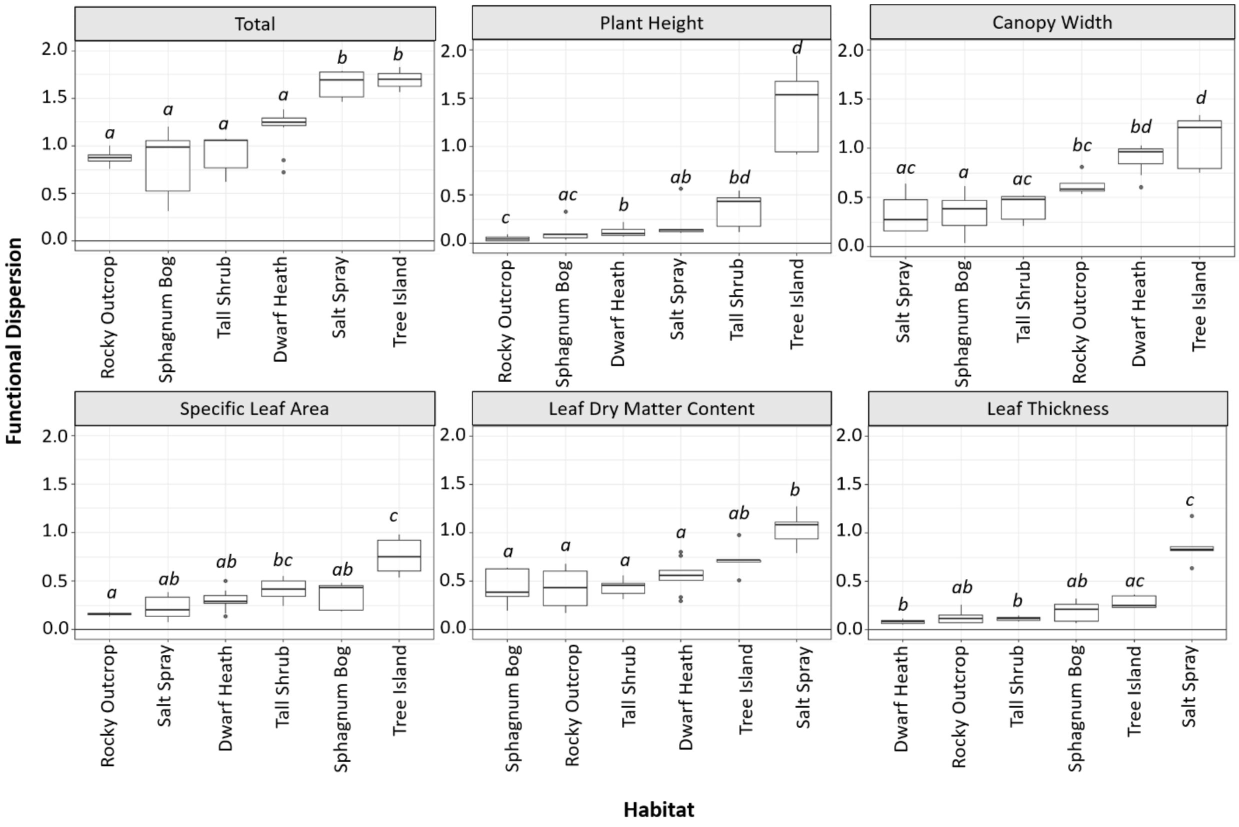


**Figure 3.5.** Box and whisker graphs for the functional dispersion  of each trait and the combination of all traits (total) for each habitat type in the 2016 dataset. The figures list species in order of lowest to highest functional dispersion. The letters represent results from Tukey post-hoc tests for which functional traits are the independent variables and habitat is the dependent variable. Bars that share a letter p>0.05.

## Discussion

Using coastal barrens as the target environment, the goal of this chapter was to examine whether heterogeneity is the main driver of coexistence on the coastal barrens of Nova Scotia. Overall, positive associations between functional trait diversity and spatial heterogeneity were observed across spatial scales and datasets, an indication that heterogeneity is encouraging interspecies coexistence. These findings reflect biodiversity patterns observed in European heathland communities, with increased landscape spatial/temporal heterogeneity associated with an increase in species richness (Vandvik et al., 2005; Mobaied et al., 2016; ). However, the datasets in my study also revealed negative associations between functional trait diversity and heterogeneity as well aa positive associations between functional trait diversity and environmental stress. In these situations, a filtering effect may limit which species can persist, with coexistence possible due to variation in those functional traits capable of variation within the filtered environment.

In addition to the coexistence patterns described above also I found that each of the six vegetation types (salt spray zone, rocky outcrop, dwarf heath, *Sphagnum* bog, tall shrub, and tree island) contained distinct functional trait and diversity values, likely due to the distinct environmental variables associated with these habitats (Oberndorfer and Lundholm, 2009; Porter (2013); Cameron and Bondrup-Neilsen, 2013). Future research should apply the functional diversity variables examined here to the 21 plant associations identified in Porter et al., 2020 (a guidebook which classifies heathlands based on biotic and abiotic variables). Doing so would allow researchers to understand how this region's species pool organises around environmental variables. That is, different environments likely encourage coexistence through variation in specific traits. Furthermore, this study found the relationships between functional traits and plant diversity patterns to be complex, with different associations observed between datasets. Specifically, I found patterns consistent with both limiting similarity (associated with high functional diversity), and habitat filtering (associated with low functional diversity) shared between datasets and spatial scales and distinct to specific datasets and spatial scales. This finding indicates that coastal barrens are not governed by one overreaching principle. Rather, multiple factors are at play, all leading to the development of a specific vegetative community.

### *Plant Community Assembly on Nova Scotia's Coastal Barrens*

For the most part, the trait-environmental patterns observed mirror findings from other plant diversity studies. Specifically, high functional diversity (trait and total) was usually associated with low-stress environments that also had a high degree of heterogeneity (Chesson et al., 2004; Katabuchi et al., 2012; Spasojevic et al., 2012; Cross et al., 2015). Additionally, the majority of CWM associations (n=24) reflected findings from the literature, where areas with characteristics associated with high stress had shorter plants with lower specific leaf area, higher leaf dry matter content, and thicker leaves (MacArthur and Levins, 1967; Grubb, 1977; Tilman 1982; Chesson, 2000; Wright et al., 2001; Chesson et al., 2004; Moles et al., 2009; Spasojevic et al., 2012; Pérez-Harguindeguy et al., 2016). However, there were several exceptions to these patterns.

Five CWM associations do not reflect what is expected in stressful environments (resource conservation strategies), a result which can be explained by taking a closer look at the data. In the 2005 dataset, species closest to the coast had low leaf dry matter content and high specific leaf area, values associated with large thin leaves and increased susceptibility to drought and salt stress. This pattern may have occurred for two reasons. Firstly, the 2005 dataset did not include the vegetation type closest to the coast: the salt spray zone. Since species in the salt spray zone are in a high stress environment (low soil depth, low soil moisture, high wind), this exclusion likely led to this unexpected pattern.

Secondly, coastal barren locations differ in topography, with some containing sheltered areas along the coast. These sheltered areas allow larger species, such as those belonging to tall shrub and tree island habitats, to survive closer to the coast than would otherwise be possible (Porter et al., 2020).

The last two surprising associations were: low soil moisture associated with taller plants and higher specific leaf area (2017 dataset broad scale) and low soil depth associated with higher specific leaf area (2011 dataset fine scale). For the 2017 dataset, the dominant plant community in the low-moisture environment was a tall shrub association, *Gaylusaccia baccata* shrubland (Porter et al., 2020), and the dominant plant community in the high moisture environment was a different tall shrub association, *Kalmia angustifolia* inland heath (Porter et al., 2020). Because the average height of *G. baccata* was 49 cm and mean specific leaf area was 206 $cm^2 g^{-1}$, and the average height of *K. angustifolia* was 24.27 cm and the average specific leaf area was 95 $cm^2 g^{-1}$, the associations observed here are likely due to differences in the dominant species of these distinct tall shrub communities. As these trends are not observed in the 2017 dataset for the fine or very fine scale, the findings for the broad scale likely reflects a landscape pattern that is influenced by the species common in the most dominant plant associations. That is, at the smaller spatial scales the mean is derived from fewer species and more likely to contain species specific to particular habitats and, at the broader spatial scales, the mean incorporates species present in all habitats. For the 2011 dataset, the plots with the lowest soil depth contained species indicative of the salt spray zone, specifically the *Plantago maritima* rocky coastal shoreline association (Porter et al., 2020). On the coastal barrens of Nova Scotia, only plant communities in the salt spray zone contain species exhibiting leaf succulence, a trait prominent in areas under salt stress (Ogburn et al., 2010).

In this study we did not expect environmental heterogeneity to be associated with the CWM of any trait, as CWMs are usually linked to specific stress values and not environmental heterogeneity. Therefore, the observed associations between heterogeneity and CWMs may imply that these heterogeneity values are associated with specific stress variables. For example, if mean soil depth in a more heterogenous habitat is lower than the mean soil depth in a more homogenous habitat, then mean soil depth (rather than soil depth heterogeneity) may be the main limiting factor.

For environmental stress and functional diversity, associations that differed from the expected pattern were also observed. Specifically, high stress due to shallow soil was associated with an increase in the functional diversity of canopy widths, and high stress due to low soil moisture was associated with an increase in the functional diversity of plant height and leaf thickness. This increase in functional diversity could be due to a facilitative effect, the physical nature of some of our moisture-limited sites (rocky outcrops and salt spray zone), and/or limiting similarity. The possible facilitative effect is expressed in the composition of the dwarf heath vegetation type, where species of different heights and canopy widths commonly co-occur. In dwarf heaths, the wide canopies provided by particular species may protect neighboring species from the elements (e.g. high winds). Additionally, in drier dwarf heaths, shade provided by species with large canopies may facilitate functionally diverse neighbors through the reduction of evaporation from the soil surface. Similar facilitative effects have been observed in desert ecosystems, with shrubby vegetation shading the soil and protecting annuals from high winds (Berg et al., 2012), and in arctic dwarf shrub communities, where shrub canopies facilitate neighbors through wind protection and by creating a warmer, moister microclimate (Olofsson, 2004). The second explanation pertains to the physical nature of some of our moisture-limited sites and addresses the way in which data were collected. Specifically, data collected within each plot do not fully capture the total area an individual can acquire resources from. As our most water-limited habitats contain soil crevices (i.e. salt spray zone, rocky outcrop), taller species with deeper roots may be able to access resources not available to shorter species with smaller roots, resulting in co-existence and an increase in the functional diversity of height. This root strategy is a common occurrence in other rocky outcrop systems, such as granite (Poot et al., 2012) and ironstone (Poot and Lambers, 2008) plant communities, and likely occurs on Nova Scotia's coastal barrens. This root strategy may also happen in deeper soil, but the overall higher productivity in such areas likely results in the competitive exclusion of shorter species, lowering plant height functional diversity. Finally, the third explanation reflects the salt spray zone, which was the only habitat containing succulents. Here, increased functional diversity of leaf thickness likely reflects the divergent strategies used to persist in regions of low soil moisture and high exposure to salt spray (limiting similarity).  For example, the salt spray zone contains co-occurring thick leaved species such as *Rhodiola rosea* and *Plantago maritima*, as well as thin-leafed species such as *Festuca rubra* and *Campanula intercedens* (Porter et al., 2020).

For the functional diversity of leaf dry matter content, high stress due to low soil phosphorus was associated with greater functional diversity. This association was only found for the 2008 dataset in plots located in the transition zone between the tree island and dwarf heath habitats. In part, this increase in functional diversity could be due to the incorporation of species from two distinct habitats. Furthermore, since leaf dry matter content plays an important role in nutrient conservation (Poorter and Garnier, 1999; Tardy et al., 2015), possessing a slightly different leaf dry matter content may increase a species' competitive advantage (limiting similarity). Previous research on wetland/upland ecotones also found higher biodiversity in the transition zone between habitats (Kirkman et al., 1998; Traut, 2005). However, it is important to note that this pattern is not observed in all wetland/upland ecotones (Harper et al., 2021).

In this study, only one environmental variable had a negative heterogeneity-functional diversity relationship: soil depth in the 2017 dataset at the broad spatial scale. This pattern likely occurred because the broad scale incorporated species from across the landscape, leading to an increase in the number of functionally similar species (habitat filtering). ***Inconsistency across Spatial Scales and Datasets***

No dataset had the same associations at every spatial scale, an indication that scale plays a major role in how data should be interpreted. This finding has been expressed in previous species richness research (Bond and Chase, 2002; Ma and Zhang, 2015; Neves et al., 2019) and holds true for functional trait diversity (Bello et al. 2013; Biswas et al., 2015). In terms of community assembly, broad spatial scales reflect the average of all plant associations in the landscape, and analysis at finer spatial scales reflect individual interactions (Lundholm, 2009). For example, in the 2017 dataset, total functional diversity was negatively correlated with average soil moisture at the broad scale, with the inverse observed at the fine scale. At the broad scale, the presence of specific habitats with lower total functional diversity and higher soil moisture likely contributed to this pattern. Based on data from the 2016 dataset, both *Sphagnum* bog and tall shrub communities fit this description. At the fine scale, individuals are directly competing for resources. Therefore, the positive association found at this scale could be due to a limiting similarity filter where coexistence is only possible if species have different resource acquisition strategies in this competitive environment.

In this study, differences observed between datasets may also be due to differences in the way data were collected. Specifically, differences in the number of sites (n=1-105), plot selection (random vs specific habitat), and the calculation of species abundance can influence trait and environmental associations, as different locations can draw from different species pools and differ in environmental variables (Oberndorfer and Lundholm, 2009). Consequently, studies from a larger range of sites likely incorporate greater species richness and geographical range,. Furthermore, since the coastal barrens are a mosaic of vegetation types, the exclusion or overinclusion of certain vegetation types can influence the observed trends, as each vegetation type likely has a different size and composition of species pool, due to substantial environmental differences among vegetation types (Porter 2013; Porter et al. 2020). Similar patterns are present in other heterogenous landscapes, where the increased inclusion of different environments leads to an increase in species richness (Auerbach and Shmida, 1987). The influence that differential abundance of distinct vegetation types has on community assembly patterns is particularly obvious between the 2011 and 2005 datasets. The positive association between soil depth and the functional diversity of canopy width in the 2011 dataset was likely due to a greater inclusion of tree island habitat with the inverse association in the 2005 dataset likely due to a greater inclusion of dwarf heath habitats. Both tree island and dwarf heath habitats tend to have higher canopy functional diversity, with soil depth usually higher in tree island communities and lower in dwarf heath communities, and little overlap in dominant plant species (Burley et al. 2010).

The calculation of species abundance is another component that likely influenced variation between datasets. Since species abundance plays an integral role in the calculation of Fdis and CWM, the differences in how abundance was calculated can lead to different associations among the environmental variables between datasets. For example, even though plot size was equal (1x1 m), the 2017 dataset had more associations than the 2011 dataset. This may be due to measuring abundance with frequency (2017 dataset) as opposed to density (2011 dataset). The method used in the 2017 dataset may have led to overweighting smaller and less abundant species. Since the 2011 dataset used a density-based method, potential overweighting is much reduced as this abundance measurement covers more physical space.

## Conclusion

Multiple assembly processes are active on Nova Scotia’s coastal barrens. Both high (limiting similarity) and low (habitat filtering) functional diversity were observed in environments with higher values of environmental heterogeneity and stress. Nevertheless, most associations follow the patterns indicated in the literature, namely higher functional diversity in environments with higher environmental heterogeneity and lower environmental stress. Overall, functional diversity had far more associations with environmental stress than environmental heterogeneity, an indication that, on Nova Scotia’s coastal barrens, environmental stress is the main driver of plant community composition.

The use of multiple functional trait analysis (CWM, Fdis) allowed me to understand community assembly to a degree that would not have been possible with only a single analysis. Fdis provided insight into which traits played a key role within each community, with different traits desired in each habitat type. Additionally, Fdis allowed us to observe the general trends that occur within this landscape, with analysis indicating community assembly on the coastal barrens is influenced by limiting similarity, habitat filtering, and facilitation. Finally, CWM allowed us to understand which functional traits were associated with which environmental variables and vegetation types. Sequentially, this allowed us to determine which habitats were associated with the observed diversity patterns. Spatial scale also played an important role in understanding our study system, with the broad scale associated with landscape patterns, such as habitat diversity, and the fine scale associated with individual interactions, such as competition. Based on the results of this study, I highly recommend the incorporation of multiple functional trait analysis for research aiming to understand the community assembly rules present within a given landscape.

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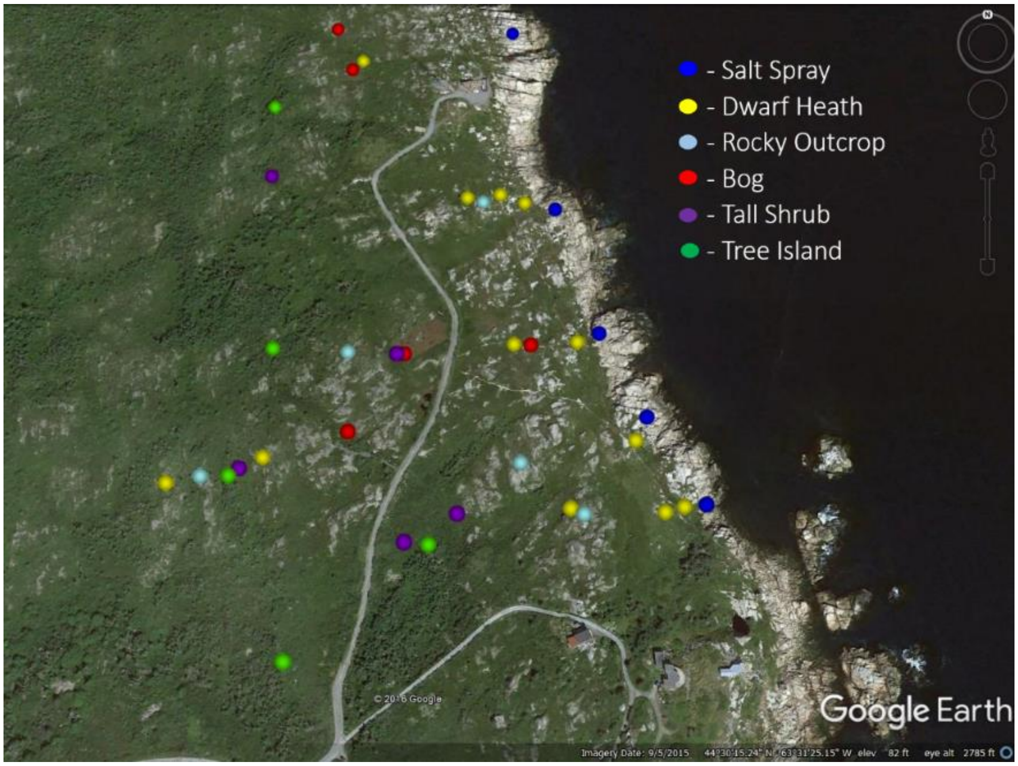
## Appendices

**Appendix 3.A.** Map showing plot locations in the 2016 dataset. The 2016 dataset was collected in July 2016 from the Chebucto Head coastal barren site (40°30’15 N, 63°31’25 W). At this site 35, 4x4 m habitat plots were placed along six 500 m transects, which were perpendicular to the coast, and 100 m apart. Each plot was placed on uniform ground (vegetation and environment) belonging to one of the following habitats: tree island and (n=5), tall shrub (n=5), dwarf heath (n=11), *Sphagnum* bog (n=5), rocky outcrop (n=4), or the salt spray zone (n=5) (Appendix 3). Habitat type was determined based on previous coastal barren research (Oberndorfer, 2006; Porter, 2013; Burley et al., 2010). Species composition in this dataset was determined by gathering the percent cover of each species in each plot, with a total of 74 different vascular species observed.



**Appendix 3.B.** For the 2016 dataset this table shows average(+/- standard error) community weighted mean, trait functional dispersion and total functional dispersion for the following habitats: salt spray zone (n=5), rocky outcrop (n=4), dwarf heath (n=11), *Sphagnum* bog (n=5), tall shrub (n=5), and tree island (n=5).

| **Community Weighted Mean** | **Salt Spray** | **Rocky Outcrop** | **Dwarf Heath** | **Sphagnum Bog** | **Tall Shrub** | **Tree Island** |
|---|---|---|---|---|---|---|
| Plant Height | 27.14(±12.35) | 12.10(±2.82) | 18.12(±4.68) | 28.98(±9.73) | 66.01(±13.25) | 181.77(±61.54) |
| Canopy Width | 32.83(±17.90) | 81.70(±33.33) | 117.28(±23.96) | 29.45(±12.25) | 40.82(±10.65) | 127.17(±39.24) |
| Specific Leaf Area | 94.94(±3.58) | 106.66(±6.92) | 114.65(±12.17) | 124.56(±46.16) | 168.55(±6.26) | 139.74(±32.25) |
| Leaf Dry Matter Content | 0.34(±0.03) | 0.45(±0.03) | 0.42(±0.02) | 0.37(±0.05) | 0.34(±0.01) | 0.39(±0.04) |
| Leaf Thickness | 0.07(±0.02) | 0.04(±0.00) | 0.03(±0.00) | 0.03(±0.01) | 0.02(±0.00) | 0.04(±0.01) |
| **Trait Functional Diversity** | **Salt Spray** | **Rocky Outcrop** | **Dwarf Heath** | **Sphagnum Bog** | **Tall Shrub** | **Tree Island** |
| Plant Height | 0.21(±0.20) | 0.05(±0.03) | 0.11(±0.05) | 0.12(±0.12) | 0.35(±0.19) | 1.40(±0.45) |
| Canopy Width | 0.34(±0.21) | 0.63(±0.12) | 0.90(±0.13) | 0.34(±0.22) | 0.40(±0.14) | 1.07(±0.28) |
| Specific Leaf Area | 0.23(±0.13) | 0.16(±0.02) | 0.30(±0.10) | 0.35(±0.14) | 0.41(±0.12) | 0.75(±0.19) |
| Leaf Dry Matter Content | 1.04(±0.18) | 0.43(±0.24) | 0.56(±0.15) | 0.44(±0.19) | 0.43(±0.10) | 0.72(±0.16) |
| Leaf Thickness | 0.86(±0.19) | 0.11(±0.03) | 0.12(±0.06) | 0.19(±0.11) | 0.08(±0.02) | 0.28(±0.07) |
| **Total Functional Diversity** | **Salt Spray** | **Rocky Outcrop** | **Dwarf Heath** | **Sphagnum Bog** | **Tall Shrub** | **Tree Island** |
| Total | 1.64(±0.15) | 0.87(±0.10) | 1.19(±0.21) | 0.81(±0.38) | 0.92(±0.21) | 2.22(±0.49) |

**Appendix 3.C.** Multiple linear regressions for the 2017, 2011, 2010, 2008, and 2005 (fine scale) datasets and single linear regression for the 2005 dataset (broad scale). The response variables are the community weighted means (plant height, canopy width, specific leaf area, leaf dry matter content, leaf thickness) and the explanatory variables are the stress and heterogeneity variables. A separate linear regression was conducted for each response variable at each spatial scale in each dataset. Both positive (all 95% intervals above 0) and negative associations (all 95% intervals below 0) are italicized. Tukey indicates that a Tukey's ladder of powers transformation was used. Tran = transformation, St = Stress, Het = heterogeneity.

| **2017** | | | | |
|---|---|---|---|---|
| **Community Weighted Mean - Plant Height (cm)** | | | | |
| **Broad (2x25 m Transect)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Leaf Litter Cover (Het) | - | -0.65186533 | -0.24812272 | 0.155619896 |
| Soil Moisture (Het) | log | ***-0.87056299*** | ***-0.4372783*** | ***-0.003993569*** |
| Soil Depth (Het) | - | -0.65422143 | -0.3259428 | 0.002335907 |
| Elevation (Het) | - | -0.13368398 | 0.15783698 | 0.449357945 |
| Leaf Litter Cover (St) | Tukey | -0.09185758 | 0.4546556 | 1.001168814 |
| Soil Moisture (St) | Tukey | ***-1.10432942*** | ***-0.7081030*** | ***-0.311876510*** |
| Soil Depth (St) | - | -0.01416341 | 0.4947885 | 1.003740423 |
| Elevation (St) | Tukey | -0.65230228 | -0.18250007 | 0.287302138 |
| **Fine (1x1 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Leaf Litter Cover (Het) | Tukey | -0.17811746 | -0.05464177 | 0.06883392 |
| Soil Moisture (Het) | Tukey | -0.07374500 | 0.04936599 | 0.17247698 |
| Soil Depth (Het) | Tukey | -0.17414184 | -0.01145912 | 0.15122361 |
| Elevation (Het) | log | ***0.02045309*** | ***0.1388580*** | ***0.25726299*** |
| Leaf Litter Cover (St) | - | ***0.01946904*** | ***0.1797335*** | ***0.33999793*** |
| Soil Moisture (St) | Tukey | -0.11106144 | 0.04452915 | 0.20011975 |
| Soil Depth (St) | - | ***0.05842977*** | ***0.2323992*** | ***0.40636860*** |
| Elevation (St) | Tukey | -0.13014456 | 0.08235257 | 0.29484971 |
| **Very Fine (0.5x0.5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (Het) | sqrt | -0.07512589 | -0.010378118 | 0.05436966 |
| Elevation (Het) | log | -0.04971942 | 0.009648100 | 0.32790515 |
| Soil Depth (St) | Tukey | -0.11978215 | -0.032203811 | 0.05537453 |
| Elevation (St) | - | -0.10107969 | -0.021412668 | 0.05825435 |
| Soil Moisture (St) | - | -0.11613228 | -0.027952357 | 0.06022757 |
| Leaf Litter Cover (St) | - | -0.05823554 | 0.13909287 | 0.07753174 |
| **Community Weighted Mean - Canopy Width (cm)** | | | | |
| **Broad (2x25 m Transect)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Leaf Litter Cover (Het) | - | ***0.4137683954*** | ***0.7220939*** | ***1.03041947*** |
| Soil Moisture (Het) | log | -0.0005309558 | 0.2106321 | 0.42179518 |

| | | | | |
|---|---|---|---|---|
| Soil Depth (Het) | - | ***0.0405054166*** | ***0.20214604*** | ***0.36378666*** |
| Elevation (Het) | - | ***-0.2850368286*** | ***-0.1631098*** | ***-0.04118273*** |
| Leaf Litter Cover (St) | Tukey | -0.3414477460 | 0.11305755 | 0.56756285 |
| Soil Moisture (St) | Tukey | -0.2770506485 | -0.074741330 | 0.12756799 |
| Soil Depth (St) | - | -0.5178421210 | -0.21237118 | 0.09309976 |
| Elevation (St) | Tukey | -0.4563728135 | 0.043806420 | 0.54398565 |
| **Fine (1x1 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Leaf Litter Cover (Het) | Tukey | -0.003802136 | 0.11359460 | 0.230991337 |
| Soil Moisture (Het) | Tukey | ***-0.237755709*** | ***-0.12384726*** | ***-0.009938807*** |
| Soil Depth (Het) | Tukey | ***-0.390758412*** | ***-0.2521039*** | ***-0.113449452*** |
| Elevation (Het) | log | -0.100830463 | 0.008277978 | 0.117386420 |
| Leaf Litter Cover (St) | - | ***-0.287855826*** | ***-0.1450687*** | ***-0.002281603*** |
| Soil Moisture (St) | Tukey | ***-0.319051380*** | ***-0.1758607*** | ***-0.032669965*** |
| Soil Depth (St) | - | -0.254800976 | -0.07819572 | 0.098409545 |
| Elevation (St) | Tukey | ***0.051953783*** | ***0.2166989*** | ***0.381444017*** |
| **Very Fine (0.5x0.5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (Het) | sqrt | -0.11740012 | -0.05652278 | 0.004354564 |
| Elevation (Het) | log | -0.06850848 | -0.005208445 | 0.058091592 |
| Soil Depth (St) | Tukey | -0.05825875 | 0.025672737 | 0.109604225 |
| Elevation (St) | - | -0.10522239 | -0.02865642 | 0.047909544 |
| Soil Moisture (St) | - | -0.12862343 | -0.03743868 | 0.053746065 |
| Leaf Litter Cover (St) | - | -0.49290080 | -0.2405143 | 0.011872256 |
| **Community Weighted Mean - Specific Leaf Area** | | | | |
| **Broad (2x25 m Transect)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Leaf Litter Cover (Het) | - | -0.2915690 | -0.11924367 | 0.05308168 |
| Soil Moisture (Het) | log | -0.2523061 | -0.0138318201 | 0.22464246 |
| Soil Depth (Het) | - | ***-0.4290297*** | ***-0.2288080*** | ***-0.02858630*** |
| Elevation (Het) | - | ***0.1094090*** | ***0.2637744*** | ***0.41813979*** |
| Leaf Litter Cover (St) | Tukey | ***0.1043836*** | ***0.4614270*** | ***0.81847033*** |
| Soil Moisture (St) | Tukey | ***-0.4514071*** | ***-0.2627241*** | ***-0.07404121*** |
| Soil Depth (St) | - | ***0.1901305*** | ***0.5655020*** | ***0.94087359*** |
| Elevation (St) | Tukey | -0.3326033 | -0.1336314 | 0.06534054 |
| **Fine (1x1 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Leaf Litter Cover (Het) | Tukey | -0.16226786 | -0.07383199 | 0.01460388 |
| Soil Moisture (Het) | Tukey | -0.05850282 | 0.029113101 | 0.11672903 |
| Soil Depth (Het) | Tukey | -0.02125099 | 0.09192102 | 0.20509302 |
| Elevation (Het) | log | -0.01175987 | 0.07230596 | 0.15637179 |
| Leaf Litter Cover (St) | - | ***0.23730160*** | ***0.3511873*** | ***0.46507308*** |
| Soil Moisture (St) | Tukey | -0.09277285 | 0.021903502 | 0.13657985 |
| Soil Depth (St) | - | ***0.12012717*** | ***0.260585*** | ***0.40104286*** |
| Elevation (St) | Tukey | ***-0.36897231*** | ***-0.2155850*** | ***-0.06219769*** |

| **Very Fine (0.5x0.5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
|---|---|---|---|---|
| Soil Depth (Het) | sqrt | -0.02702686 | 0.03104488 | 0.08911662 |
| Elevation (Het) | log | -0.05723687 | -0.0023205812 | 0.05259570 |
| Soil Depth (St) | Tukey | -0.03876324 | 0.03388983 | 0.10654290 |
| Elevation (St) | - | -0.06166113 | 0.004024830 | 0.06971079 |
| Soil Moisture (St) | - | ***0.03183113*** | ***0.1063404*** | ***0.18084968*** |
| Leaf Litter Cover (St) | - | ***0.34994404*** | ***0.520082*** | ***0.69022002*** |
| **Community Weighted Mean - Leaf Dry Matter Content** | | | | |
| **Broad (2x25 m Transect)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Leaf Litter Cover (Het) | - | -0.26873943 | -0.036977929 | 0.19478358 |
| Soil Moisture (Het) | log | -0.17670625 | 0.030398819 | 0.23750389 |
| Soil Depth (Het) | - | ***0.05695001*** | ***0.1914659*** | ***0.32598177*** |
| Elevation (Het) | - | ***-0.42735622*** | ***-0.3004412*** | ***-0.17352619*** |
| Leaf Litter Cover (St) | Tukey | -0.31805196 | -0.03581648 | 0.24641900 |
| Soil Moisture (St) | Tukey | -0.24571279 | -0.08681103 | 0.07209074 |
| Soil Depth (St) | - | ***-0.87467749*** | ***-0.6808287*** | ***-0.48698000*** |
| Elevation (St) | Tukey | -0.31343231 | -0.0120971642 | 0.28923798 |
| **Fine (1x1 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Leaf Litter Cover (Het) | Tukey | -0.09177114 | 0.010343401 | 0.112457945 |
| Soil Moisture (Het) | Tukey | -0.16897603 | -0.0700443 | 0.028887436 |
| Soil Depth (Het) | Tukey | ***-0.26524163*** | ***-0.1365955*** | ***-0.007949390*** |
| Elevation (Het) | log | -0.18713220 | -0.09296724 | 0.001197726 |
| Leaf Litter Cover (St) | - | ***-0.47418428*** | ***-0.3485649*** | ***-0.222945583*** |
| Soil Moisture (St) | Tukey | ***-0.24969688*** | ***-0.12744969*** | ***-0.005202508*** |
| Soil Depth (St) | - | ***-0.42884525*** | ***-0.2684946*** | ***-0.108143941*** |
| Elevation (St) | Tukey | -0.11829110 | 0.036419685 | 0.191130468 |
| **Very Fine (0.5x0.5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (Het) | sqrt | -0.0873578976 | -0.020517069 | 0.04632376 |
| Elevation (Het) | log | ***0.0004782047*** | ***0.06274088*** | ***0.12500356*** |
| Soil Depth (St) | Tukey | -0.1142019180 | -0.03121538 | 0.05177116 |
| Elevation (St) | - | -0.0702184000 | 0.004697072 | 0.07961254 |
| Soil Moisture (St) | - | ***-0.1746296770*** | ***-0.09330164*** | ***-0.01197360*** |
| Leaf Litter Cover (St) | - | ***-0.5443953926*** | ***-0.3800392*** | ***-0.21568294*** |
| **Community Weighted Mean - Leaf Thickness (cm)** | | | | |
| **Broad (2x25 m Transect)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Leaf Litter Cover (Het) | - | -0.6198529 | -0.07049504 | 0.14001715 |
| Soil Moisture (Het) | log | -0.1610723 | 0.07514678 | 0.66212455 |
| Soil Depth (Het) | - | -0.5374031 | -0.09040498 | 0.07242919 |
| Elevation (Het) | - | -0.1445340 | 0.03892753 | 0.48065031 |
| Leaf Litter Cover (St) | Tukey | -0.3986341 | 0.0412413 | 0.84311731 |

|  |  |  |  |  |
|---|---|---|---|---|
| Soil Moisture (St) | Tukey | ***-0.7763602*** | ***-0.3536336*** | ***-0.06791003*** |
| Soil Depth (St) | - | -0.7933526 | -0.07759834 | 0.21795912 |
| Elevation (St) | Tukey | ***-1.2562434*** | ***-0.8400868*** | ***-0.42393023*** |
| **Fine (1x1 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Leaf Litter Cover (Het) | Tukey | -0.1492833 | -0.008107105 | 0.086558633 |
| Soil Moisture (Het) | Tukey | -0.1284608 | -0.002591646 | 0.106379396 |
| Soil Depth (Het) | Tukey | -0.2493187 | -0.04476450 | 0.050417206 |
| Elevation (Het) | log | ***-0.2602993*** | ***-0.1370103*** | ***-0.032724280*** |
| Leaf Litter Cover (St) | - | ***-0.3210282*** | ***-0.1284403*** | ***-0.011994952*** |
| Soil Moisture (St) | Tukey | -0.1702444 | -0.005928684 | 0.122272178 |
| Soil Depth (St) | - | -0.3456627 | -0.1193253 | 0.002308803 |
| Elevation (St) | Tukey | ***-0.6192131*** | ***-0.4355727*** | ***-0.251932442*** |
| **Very Fine (0.5x0.5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (Het) | sqrt | -0.07534409 | 0.0002854376 | 0.07742328 |
| Elevation (Het) | log | -0.06888672 | 0.0003813498 | 0.07175780 |
| Soil Depth (St) | Tukey | -0.14931187 | -0.02190620 | 0.04166734 |
| Elevation (St) | - | -0.09187826 | 0.03928018 | 0.29762163 |
| Soil Moisture (St) | - | -0.03751999 | 0.01787200 | 0.12786366 |
| Leaf Litter Cover (St) | - | -0.03112646 | 0.02710863 | 0.15015134 |

| **2011** |  |  |  |  |
|---|---|---|---|---|
| **Community Weighted Mean - Plant Height (cm)** |  |  |  |  |
| **Broad (Site)** | **Tran** | **2.5%** | **Coefficient** | **97.5%** |
| Leaf Litter Thickness (Het) | - | -0.5086339 | -0.008882213 | 0.4908694 |
| Soil Depth (Het) | log | -0.4405790 | 0.065910073 | 0.5723991 |
| Coast Distance (Het) | - | -0.7092489 | 0.10241760 | 0.9140841 |
| Slope (Het) | sqrt | -0.3847018 | 0.26516144 | 0.9150247 |
| Leaf Litter Thickness (St) | - | -0.3331121 | 0.16329233 | 0.6596968 |
| Soil Depth (St) | Tukey | -0.6964682 | -0.12282319 | 0.4508218 |
| Coast Distance (St) | - | -0.8945978 | -0.066769663 | 0.7610585 |
| Slope (St) | - | -0.1206994 | 0.4168797 | 0.9544589 |
| **Fine (1x1 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Elevation (St) | sqrt | -0.1210689 | 0.01556914 | 0.15220715 |
| Slope (St) | - | -0.1486878 | -0.04420534 | 0.06027708 |
| Leaf Litter Thickness (St) | - | -0.1285491 | -0.024537244 | 0.07947462 |
| Soil Depth (St) | .1+log | -0.1053568 | 0.002560383 | 0.11047756 |
| Coast Distance (St) | sqrt | -0.1598119 | -0.03541299 | 0.08898587 |
| **Community Weighted Mean - Canopy Width (cm)** |  |  |  |  |
| **Broad (Site)** | **Tran** | **2.5%** | **Coefficient** | **97.5%** |

|  |  |  |  |  |
|---|---|---|---|---|
| Leaf Litter Thickness (Het) | - | -0.66069906 | -0.20985407 | 0.240990908 |
| Soil Depth (Het) | log | -0.45868331 | 0.019610056 | 0.497903418 |
| Coast Distance (Het) | - | -1.43342857 | -0.3458674 | 0.741693734 |
| Slope (Het) | sqrt | -0.41223578 | 0.2269981 | 0.866231938 |
| Leaf Litter Thickness (St) | - | ***-0.88438191*** | ***-0.4437704*** | ***-0.003158904*** |
| Soil Depth (St) | Tukey | -0.88527761 | -0.3700394 | 0.145198782 |
| Coast Distance (St) | - | -1.14121601 | 0.12054075 | 1.382297509 |
| Slope (St) | - | -0.06924805 | 0.4041461 | 0.877540156 |
| **Fine (1x1 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Elevation (St) | sqrt | -0.20821431 | -0.07217365 | 0.063867016 |
| Slope (St) | - | ***-0.21643731*** | ***-0.10943860*** | ***-0.002439895*** |
| Leaf Litter Thickness (St) | - | -0.16645328 | -0.06084202 | 0.044769245 |
| Soil Depth (St) | .1+log | -0.18986768 | -0.07335930 | 0.043149085 |
| Coast Distance (St) | sqrt | -0.06007778 | 0.08499604 | 0.230069858 |
| **Community Weighted Mean - Specific Leaf Area** |  |  |  |  |
| **Broad (Site)** | **Tran** | **2.5%** | **Coefficient** | **97.5%** |
| Leaf Litter Thickness (Het) | - | -0.5700745 | -0.058020853 | 0.4540328 |
| Soil Depth (Het) | log | -0.6471302 | -0.14034187 | 0.3664465 |
| Coast Distance (Het) | - | -0.8088204 | 1.2647063 | 3.3382330 |
| Slope (Het) | sqrt | -0.7063313 | -0.064505763 | 0.5773198 |
| Leaf Litter Thickness (St) | - | -0.2623064 | 0.27358001 | 0.8094664 |
| Soil Depth (St) | Tukey | -0.5882510 | -0.014361455 | 0.5595281 |
| Coast Distance (St) | - | -3.4520054 | -1.3405958 | 0.7708138 |
| Slope (St) | - | -0.7225774 | -0.16358602 | 0.3954054 |
| **Fine (1x1 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Elevation (St) | sqrt | -0.02727063 | 0.09859296 | 0.2244566 |
| Slope (St) | - | -0.07265281 | 0.03481140 | 0.1422756 |
| Leaf Litter Thickness (St) | - | -0.03723771 | 0.06865402 | 0.1745458 |
| Soil Depth (St) | .1+log | -0.07660213 | 0.03688043 | 0.1503630 |
| Coast Distance (St) | sqrt | -0.12755251 | 0.017394246 | 0.1623410 |
| **Community Weighted Mean - Leaf Dry Matter Content** |  |  |  |  |
| **Broad (Site)** | **Tran** | **2.5%** | **Coefficient** | **97.5%** |
| Leaf Litter Thickness (Het) | - | -0.1949636 | 0.18112812 | 0.5572198 |
| Soil Depth (Het) | log | -0.3773073 | -0.027781209 | 0.3217449 |
| Coast Distance (Het) | - | ***-3.0011364*** | ***-1.798531*** | ***-0.5959250*** |
| Slope (Het) | sqrt | -0.2757232 | 0.112116206 | 0.4999557 |

|  |  |  |  |  |
|---|---|---|---|---|
| Leaf Litter Thickness (St) | - | ***-1.1353281*** | ***-0.7411504*** | ***-0.3469728*** |
| Soil Depth (St) | Tukey | -0.5193851 | -0.09341034 | 0.3325644 |
| Coast Distance (St) | - | ***0.6451548*** | ***1.978781*** | ***3.3124075*** |
| Slope (St) | - | -0.2136654 | 0.14195385 | 0.4975731 |
| **Fine (1x1 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Elevation (St) | sqrt | -0.2425000 | -0.11128884 | 0.01992233 |
| Slope (St) | - | -0.1936147 | -0.08593102 | 0.02175267 |
| Leaf Litter Thickness (St) | - | -0.1031915 | 0.004454919 | 0.11210137 |
| Soil Depth (St) | .1+log | ***-0.2367887*** | ***-0.12384184*** | ***-0.01089500*** |
| Coast Distance (St) | sqrt | -0.1252351 | 0.03448566 | 0.19420645 |
| **Community Weighted Mean - Leaf Thickness (cm)** |  |  |  |  |
| **Broad (Site)** | **Tran** | **2.5%** | **Coefficient** | **97.5%** |
| Leaf Litter Thickness (Het) | - | -0.07534409 | 0.0002854376 | 0.07742328 |
| Soil Depth (Het) | log | -0.06888672 | 0.0003813498 | 0.07175780 |
| Coast Distance (Het) | - | -0.14931187 | -0.02190620 | 0.04166734 |
| Slope (Het) | sqrt | -0.09187826 | 0.03928018 | 0.29762163 |
| Leaf Litter Thickness (St) | - | -0.03751999 | 0.01787200 | 0.12786366 |
| Soil Depth (St) | Tukey | -0.03112646 | 0.02710863 | 0.15015134 |
| Coast Distance (St) | - | -0.07534409 | 0.0002854376 | 0.07742328 |
| Slope (St) | - | -0.06888672 | 0.0003813498 | 0.07175780 |
| **Fine (1x1 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Elevation (St) | sqrt | -0.23594941 | -0.06933461 | 0.01846371 |
| Slope (St) | - | -0.07346231 | 0.006166952 | 0.11706219 |
| Leaf Litter Thickness (St) | - | -0.15987021 | -0.03073025 | 0.02893403 |
| Soil Depth (St) | .1+log | ***-0.56187633*** | ***-0.4605636*** | ***-0.35925078*** |
| Coast Distance (St) | sqrt | -0.08773680 | 0.02097950 | 0.20506346 |

| **2010** |  |  |  |  |
|---|---|---|---|---|
| **Community Weighted Mean - Plant Height (cm)** |  |  |  |  |
| **Fine (5x5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Elevation (St) | Tukey | -0.25275157 | 0.033972668 | 0.3206969 |
| Slope (St) | sqrt | -0.13283971 | 0.08821575 | 0.3092712 |
| Coast Distance (St) | Tukey | -0.16706231 | 0.10063815 | 0.3683386 |
| Soil Moisture (St) | Tukey | -0.04797181 | 0.2002033 | 0.4483783 |
| Soil Depth (St) | Tukey | -0.38913423 | -0.10409931 | 0.1809356 |
| **Community Weighted Mean - Canopy Width (cm)** |  |  |  |  |
| **Fine (5x5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |

| | | | | |
|---|---|---|---|---|
| Elevation (St) | Tukey | -0.2854132 | -0.022924772 | 0.2395637 |
| Slope (St) | sqrt | -0.1051523 | 0.11426743 | 0.3336872 |
| Coast Distance (St) | Tukey | -0.2918137 | -0.029501711 | 0.2328103 |
| Soil Moisture (St) | Tukey | -0.2379412 | 0.007367632 | 0.2526765 |
| Soil Depth (St) | Tukey | -0.3419314 | -0.10450206 | 0.1329273 |
| **Community Weighted Mean - Specific Leaf Area** | | | | |
| **Fine (5x5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Elevation (St) | Tukey | -0.2854132 | -0.022924772 | 0.2395637 |
| Slope (St) | sqrt | -0.1051523 | 0.11426743 | 0.3336872 |
| Coast Distance (St) | Tukey | -0.2918137 | -0.029501711 | 0.2328103 |
| Soil Moisture (St) | Tukey | -0.2379412 | 0.007367632 | 0.2526765 |
| Soil Depth (St) | Tukey | -0.3419314 | -0.10450206 | 0.1329273 |
| **Community Weighted Mean - Leaf Dry Matter Content** | | | | |
| **Fine (5x5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Elevation (St) | Tukey | -0.08371373 | 0.18123565 | 0.44618504 |
| Slope (St) | sqrt | -0.37284908 | -0.15653908 | 0.05977092 |
| Coast Distance (St) | Tukey | -0.21411392 | 0.09835416 | 0.41082224 |
| Soil Moisture (St) | Tukey | -0.23143174 | 0.035860791 | 0.30315333 |
| Soil Depth (St) | Tukey | -0.42392492 | -0.18147466 | 0.06097559 |
| **Community Weighted Mean - Leaf Thickness (cm)** | | | | |
| **Fine (5x5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Elevation (St) | Tukey | -0.671328285 | -0.1513280 | 0.1145398 |
| Slope (St) | sqrt | ***0.007904509*** | ***0.1642597*** | ***0.4322997*** |
| Coast Distance (St) | Tukey | -0.010877506 | 0.3242436 | 0.7639729 |
| Soil Moisture (St) | Tukey | -0.447068615 | -0.1093329 | 0.0557733 |
| Soil Depth (St) | Tukey | -0.135894453 | 0.05399808 | 0.4268664 |

| **2008** | | | | |
|---|---|---|---|---|
| **Community Weighted Mean - Plant Height (cm)** | | | | |
| **Broad (Transect)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (Het) | sqrt | -0.6001723 | -0.002287932 | 0.5567532 |
| Soil Phosphorous (Het) | sqrt | -0.5009015 | 0.02045532 | 0.8151772 |
| Soil Organic Matter (Het) | log | -0.8508504 | -0.0140391 | 0.6351292 |
| Soil Nitrogen (St) | log | -0.5179903 | 0.08118309 | 1.2960237 |
| Soil Depth (St) | Tukey | -0.8237221 | 0.02628883 | 1.1603258 |
| Soil Phosphorous (St) | Tukey | -0.9692815 | -0.09297785 | 0.2659974 |
| Soil Organic Matter (St) | Tukey | -0.8308363 | -0.007072342 | 0.7162695 |
| Soil Nitrogen (St) | Tukey | -1.3348753 | -0.1840078 | 0.3211083 |
| **Fine (2x5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (St) | Tukey | -0.09458489 | 0.06979427 | 0.41715458 |
| Soil Phosphorous (St) | - | -0.32029340 | -0.02451788 | 0.15429849 |

| | | | | |
|---|---|---|---|---|
| Soil Organic Matter (St) | .1+log | -0.44662329 | -0.03336533 | 0.24758537 |
| Soil Nitrogen (St) | .1+log | -0.49079250 | -0.09495383 | 0.09590266 |
| **Community Weighted Mean - Canopy Width (cm)** | | | | |
| **Broad (Transect)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (Het) | sqrt | -0.7765661 | -0.01876524 | 0.3755325 |
| Soil Phosphorous (Het) | sqrt | -0.6167029 | -0.007271775 | 0.4384330 |
| Soil Organic Matter (Het) | log | -0.2177017 | 0.3059529 | 1.5134865 |
| Soil Nitrogen (St) | log | -0.2676518 | 0.04853231 | 0.8729910 |
| Soil Depth (St) | Tukey | -0.5083633 | 0.00109147 | 0.5360886 |
| Soil Phosphorous (St) | Tukey | -0.7615935 | -0.02812748 | 0.3177749 |
| Soil Organic Matter (St) | Tukey | -1.5895585 | -0.06741349 | 0.9538918 |
| Soil Nitrogen (St) | Tukey | -0.5607428 | 0.01104241 | 0.7828710 |
| **Fine (2x5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (St) | Tukey | -0.17305553 | 0.02347077 | 0.3334647 |
| Soil Phosphorous (St) | - | -0.33747526 | -0.03246496 | 0.1357473 |
| Soil Organic Matter (St) | .1+log | -0.09792449 | 0.08883444 | 0.4757039 |
| Soil Nitrogen (St) | .1+log | -0.23725979 | 0.03266227 | 0.4315329 |
| **Community Weighted Mean - Specific Leaf Area** | | | | |
| **Broad (Transect)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (Het) | sqrt | -0.2491941 | 0.04385594 | 0.7805087 |
| Soil Phosphorous (Het) | sqrt | -0.3334557 | 0.01886087 | 0.6981375 |
| Soil Organic Matter (Het) | log | -2.6562170 | -0.8840666 | 2.6173613 |
| Soil Nitrogen (St) | log | -0.8100275 | -0.03096518 | 0.3109496 |
| Soil Depth (St) | Tukey | -0.2534851 | 0.05656081 | 0.8627855 |
| Soil Phosphorous (St) | Tukey | -0.5571447 | 0.0009002872 | 0.5830999 |
| Soil Organic Matter (St) | Tukey | 0.1432288 | 0.9067729 | 2.6846264 |
| Soil Nitrogen (St) | Tukey | -0.6181626 | 0.00167064 | 0.6719449 |
| **Fine (2x5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (St) | Tukey | -0.06289669 | 0.09245625 | 0.4278800 |
| Soil Phosphorous (St) | - | -0.23464734 | 0.0007476085 | 0.2407280 |
| Soil Organic Matter (St) | .1+log | -0.36305262 | -0.01627194 | 0.2425313 |
| Soil Nitrogen (St) | .1+log | -0.32499909 | -0.005609616 | 0.2813009 |
| **Community Weighted Mean - Leaf Dry Matter Content** | | | | |
| **Broad (Transect)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (Het) | sqrt | -1.043544209 | -0.05398213 | 0.2898682 |
| Soil Phosphorous (Het) | sqrt | -0.098385064 | 0.0173814 | 0.5468973 |
| Soil Organic Matter (Het) | log | ***0.705185674*** | ***1.632986*** | ***2.6173613*** |
| Soil Nitrogen (St) | log | -0.525544369 | -0.002774354 | 0.3632226 |
| Soil Depth (St) | Tukey | -0.369697037 | 5.968596e-05 | 0.3734760 |
| Soil Phosphorous (St) | Tukey | -0.001704614 | 0.1096465 | 0.8342867 |

|  |  |  |  |  |
|---|---|---|---|---|
| Soil Organic Matter (St) | Tukey | ***-2.035814782*** | ***-1.134193*** | ***-0.4696020*** |
| Soil Nitrogen (St) | Tukey | -0.947575929 | -0.05666823 | 0.1621147 |
| **Fine (2x5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (St) | Tukey | -0.303376192 | -0.01539869 | 0.1837016 |
| Soil Phosphorous (St) | - | -0.183398468 | 0.0007476085 | 0.2890091 |
| Soil Organic Matter (St) | .1+log | ***0.004910409*** | ***0.1917459*** | ***0.5786736*** |
| Soil Nitrogen (St) | .1+log | -0.140632331 | 0.08790313 | 0.5427668 |
| **Community Weighted Mean - Leaf Thickness (cm)** |  |  |  |  |
| **Broad (Transect)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (Het) | sqrt | ***-1.1588170*** | ***-0.3258033*** | ***-0.07430539*** |
| Soil Phosphorous (Het) | sqrt | -0.2300340 | 0.01413277 | 0.56973086 |
| Soil Organic Matter (Het) | log | -0.1016313 | 0.5402544 | 1.50591341 |
| Soil Nitrogen (St) | log | -0.6548732 | -0.002965229 | 0.57194486 |
| Soil Depth (St) | Tukey | -0.3427120 | 0.006083528 | 0.61340265 |
| Soil Phosphorous (St) | Tukey | -0.2264095 | 0.05888277 | 0.88290294 |
| Soil Organic Matter (St) | Tukey | -1.6039532 | -0.1263540 | 0.59111339 |
| Soil Nitrogen (St) | Tukey | -0.8619295 | -0.01030746 | 0.61340265 |
| **Fine (2x5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (St) | Tukey | -0.16202117 | 0.02865743 | 0.3491679 |
| Soil Phosphorous (St) | - | -0.16499382 | 0.01952360 | 0.3041375 |
| Soil Organic Matter (St) | .1+log | -0.04594494 | 0.1434805 | 0.5274058 |
| Soil Nitrogen (St) | .1+log | -0.18489272 | 0.06391473 | 0.4991868 |

| **2005** |  |  |  |  |
|---|---|---|---|---|
| **Community Weighted Mean - Plant Height (cm)** |  |  |  |  |
| **Fine (1x1 m)** | **Tran** | **2.5%** | **Coefficient** | **97.5%** |
| Soil Moisture (Het) | - | -0.31445950 | -0.10705742 | 0.10034466 |
| Soil Depth (Het) | sqrt | -0.21402087 | -0.01992900 | 0.17416286 |
| Wind Exposure (St) | Tukey | ***-0.44232462*** | ***-0.2391087*** | ***-0.03589284*** |
| Coast Distance (St) | Tukey | -0.33151777 | -0.12888532 | 0.07374712 |
| Soil Depth (St) | Tukey | -0.15300557 | 0.07925940 | 0.31152437 |
| Soil Moisture (St) | sqrt | -0.18969229 | 0.08576892 | 0.36123013 |
| Soil Organic Matter (St) | Tukey | -0.03465678 | 0.17817479 | 0.39100635 |
| Soil Phosphorous (St) | Tukey | -0.11028142 | 0.11549369 | 0.34126880 |
| **Community Weighted Mean - Canopy Width (cm)** |  |  |  |  |
| **Fine (1x1 m)** | **Tran** | **2.5%** | **Coefficient** | **97.5%** |
| Soil Moisture (Het) | - | -0.285529809 | -0.08747962 | 0.110570563 |
| Soil Depth (Het) | sqrt | -0.229515323 | -0.023216420 | 0.183082482 |
| Wind Exposure (St) | Tukey | -0.392213137 | -0.1949594 | 0.002294311 |
| Coast Distance (St) | Tukey | -0.240864509 | -0.034039073 | 0.172786363 |
| Soil Depth (St) | Tukey | ***-0.638891506*** | ***-0.4170691*** | ***-0.195246614*** |

| | | | | |
|---|---|---|---|---|
| Soil Moisture (St) | sqrt | -0.009446981 | 0.2062443 | 0.421935678 |
| Soil Organic Matter (St) | Tukey | -0.013185993 | 0.2072986 | 0.427783215 |
| Soil Phosphorous (St) | Tukey | -0.075712608 | 0.13152439 | 0.338761394 |
| **Community Weighted Mean - Specific Leaf Area** | | | | |
| **Fine (1x1 m)** | **Tran** | **2.5%** | **Coefficient** | **97.5%** |
| Soil Moisture (Het) | - | -0.12728559 | 0.06307876 | 0.25344311 |
| Soil Depth (Het) | sqrt | -0.04002716 | 0.15607451 | 0.35217618 |
| Wind Exposure (St) | Tukey | -0.18074265 | 0.015416177 | 0.21157500 |
| Coast Distance (St) | Tukey | ***-0.42293009*** | ***-0.2205679*** | ***-0.01820577*** |
| Soil Depth (St) | Tukey | ***0.20230331*** | ***0.4174134*** | ***0.63252341*** |
| Soil Moisture (St) | sqrt | -0.38471754 | -0.1809727 | 0.02277217 |
| Soil Organic Matter (St) | Tukey | -0.37389321 | -0.15275033 | 0.06839255 |
| Soil Phosphorous (St) | Tukey | -0.26660621 | -0.04048415 | 0.18563791 |
| **Community Weighted Mean - Leaf Dry Matter Content** | | | | |
| **Fine (1x1 m)** | **Tran** | **2.5%** | **Coefficient** | **97.5%** |
| Soil Moisture (Het) | - | -0.2265966 | -0.035527482 | 0.1555416 |
| Soil Depth (Het) | sqrt | -0.1989490 | -0.024206791 | 0.1505354 |
| Wind Exposure (St) | Tukey | -0.1004966 | 0.08742495 | 0.2753465 |
| Coast Distance (St) | Tukey | ***0.0472536*** | ***0.2336410*** | ***0.4200285*** |
| Soil Depth (St) | Tukey | ***-0.6627552*** | ***-0.4603803*** | ***-0.2580055*** |
| Soil Moisture (St) | sqrt | -0.1362430 | 0.09664485 | 0.3295327 |
| Soil Organic Matter (St) | Tukey | -0.2170448 | -0.0044297803 | 0.2081852 |
| Soil Phosphorous (St) | Tukey | -0.1649888 | 0.05454379 | 0.2740764 |
| **Community Weighted Mean - Leaf Thickness (cm)** | | | | |
| **Fine (1x1 m)** | **Tran** | **2.5%** | **Coefficient** | **97.5%** |
| Soil Moisture (Het) | - | -0.20530090 | 0.0006661751 | 0.211368929 |
| Soil Depth (Het) | sqrt | -0.33524066 | -0.05106949 | 0.080565611 |
| Wind Exposure (St) | Tukey | -0.31495225 | -0.03600838 | 0.106400143 |
| Coast Distance (St) | Tukey | ***-0.49391127*** | ***-0.2368618*** | ***-0.036397988*** |
| Soil Depth (St) | Tukey | -0.14851976 | 0.01558846 | 0.274472688 |
| Soil Moisture (St) | sqrt | -0.03803207 | 0.1012068 | 0.392385582 |
| Soil Organic Matter (St) | Tukey | -0.11788469 | 0.02989021 | 0.312920637 |
| Soil Phosphorous (St) | Tukey | -0.45450643 | -0.1529507 | 0.009648293 |

| **2005 Broad Scale (Site)** | | | | |
|---|---|---|---|---|
| **Height CWM** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Factor 1 (St) | - | -4.150599 | 6.162 | 16.47463 |
| Factor 2 (St) | - | -8.369256 | 3.170 | 14.70997 |
| Factor 3 (St) | - | -7.85499 | 3.572 | 14.99804 |
| Factor 1 (Het) | - | 3.229235 | 10.029 | 16.82781 |
| Factor 2 (Het) | - | -11.20722 | 0.7223 | 12.65190 |
| Factor 3 (Het) | - | -8.297728 | 3.227 | 14.75141 |

| **Canopy CWM** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
|---|---|---|---|---|
| Factor 1 (St) | - | -24.49235 | -10.646 | 3.199908 |
| Factor 2 (St) | - | -11.95867 | 4.743 | 21.44536 |
| Factor 3 (St) | - | -24.72943 | -11.910 | 0.9103835 |
| Factor 1 (Het) | - | -24.36531 | -10.201 | 3.963623 |
| Factor 2 (Het) | - | -9.340826 | 6.703 | 22.74733 |
| Factor 3 (Het) | - | -23.63886 | -8.360 | 6.919114 |
| **Specific Leaf Area CWM** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Factor 1 (St) | **-** | **0.461361** | **7.015** | **13.56791** |
| Factor 2 (St) | - | -10.26345 | -0.7983 | 8.666763 |
| Factor 3 (St) | - | -5.040022 | 3.727 | 12.49399 |
| Factor 1 (Het) | **-** | **1.880539** | **7.677** | **13.47353** |
| Factor 2 (Het) | - | -11.79837 | -2.668 | 6.462454 |
| Factor 3 (Het) | - | -6.638553 | 2.530 | 11.69775 |
| **Leaf Dry Matter Content CWM** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Factor 1 (St) | **-** | **-0.02594115** | **-0.013457** | **-0.000973744** |
| Factor 2 (St) | - | -0.01659379 | 0.001506 | 0.01960513 |
| Factor 3 (St) | - | -0.02414875 | -0.007577 | 0.008995731 |
| Factor 1 (Het) | - | -0.02102694 | -0.003128 | 0.01477087 |
| Factor 2 (Het) | - | -0.009098972 | 0.007505 | 0.02410826 |
| Factor 3 (Het) | - | -0.02102694 | -0.003128 | 0.01477087 |
| **Leaf Thickness CWM** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Factor 1 (St) | - | -0.00516188 | 0.001073 | 0.00730805 |
| Factor 2 (St) | - | -0.006140572 | 0.000180 | 0.006500559 |
| Factor 3 (St) | **-** | **-0.008883203** | **-0.005353** | **-0.001822456** |
| Factor 1 (Het) | - | -0.005314266 | 0.0009411 | 0.007196534 |
| Factor 2 (Het) | - | -0.005239131 | 0.001006 | 0.007252112 |
| Factor 3 (Het) | - | -0.008874198 | -0.003681 | 0.001511381 |

**Appendix 3.D.** Multiple linear regressions for the 2017, 2011, 2010, 2008, and 2005 (fine scale) datasets and single linear regression for the 2005 dataset (broad scale). The response variables are the trait functional diversities (plant height, canopy width, specific leaf area, leaf dry matter content, leaf thickness) and the explanatory variables are the stress and heterogeneity variables. A separate linear regression was conducted for each response variable at each spatial scale in each dataset. Both positive (all 95% intervals above 0) and negative associations (all 95% intervals below 0) are italicized. Tukey indicates that a tukey's ladder of powers transformation was used. Tran = transformation, St = Stress, Het = heterogeneity.

| **2017** | | | | |
|---|---|---|---|---|
| **Trait Functional Diversity - Plant Height (cm)** | | | | |
| **Broad (2x25 m Transect)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Leaf Litter Cover (Het) | | -0.4993376 | -0.01362734 | 0.27687215 |
| Soil Moisture (Het) | log | -0.5272435 | -0.02255402 | 0.23771996 |
| Soil Depth (Het) | | -0.4808971 | -0.04880686 | 0.09066414 |
| Elevation (Het) | | -0.1303721 | 0.01632147 | 0.33212624 |
| Leaf Litter Cover (St) | Tukey | -0.1323967 | 0.07299207 | 0.70416271 |
| Soil Moisture (St) | Tukey | ***-0.9984754*** | ***-0.672636*** | ***-0.34679657*** |
| Soil Depth (St) | | -0.1716416 | 0.04105181 | 0.60570546 |
| Elevation (St) | Tukey | -0.6221280 | -0.01303599 | 0.39464080 |
| **Fine (1x1 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Leaf Litter Cover (Het) | Tukey | -0.14517991 | -0.003340477 | 0.1168821 |
| Soil Moisture (Het) | Tukey | -0.09471524 | 0.009635431 | 0.1670349 |
| Soil Depth (Het) | Tukey | -0.16617743 | -0.002624093 | 0.1448275 |
| Elevation (Het) | log | -0.01365870 | 0.0696882 | 0.2369236 |
| Leaf Litter Cover (St) | | -0.02030171 | -0.02030171 | 0.2976088 |
| Soil Moisture (St) | Tukey | -0.08857249 | 0.01918822 | 0.2132971 |
| Soil Depth (St) | | -0.09976609 | 0.02513903 | 0.2528599 |
| Elevation (St) | Tukey | -0.06117482 | 0.06946879 | 0.3601125 |
| **Very Fine (0.5x0.5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (Het) | sqrt | -0.08168907 | -0.003479813 | 0.05639675 |
| Elevation (Het) | log | -0.05533893 | 0.004241439 | 0.08609078 |
| Soil Depth (St) | Tukey | -0.13360883 | -0.01456274 | 0.04964463 |
| Elevation (St) | | -0.19314844 | 0.003567592 | 0.22058762 |
| Soil Moisture (St) | | -0.10916673 | -0.007788292 | 0.05675380 |
| Leaf Litter Cover (St) | | -0.13116418 | -0.01359978 | 0.05071396 |
| **Trait Functional Diversity - Canopy Width (cm)** | | | | |
| **Broad (2x25 m Transect)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Leaf Litter Cover (Het) | | ***0.25779790*** | ***0.6619069*** | ***1.08943453*** |
| Soil Moisture (Het) | log | ***0.13367036*** | ***0.2297485*** | ***0.49287058*** |

| | | | | |
|---|---|---|---|---|
| Soil Depth (Het) | | ***0.19768705*** | ***0.2352924*** | ***0.47247954*** |
| Elevation (Het) | | ***-0.36048762*** | ***-0.2119578*** | ***-0.10664098*** |
| Leaf Litter Cover (St) | Tukey | -0.65329184 | 0.02053575 | 0.34664801 |
| Soil Moisture (St) | Tukey | -0.03351004 | 0.02181067 | 0.22678561 |
| Soil Depth (St) | | -0.90610910 | -0.1342700 | 0.04068743 |
| Elevation (St) | Tukey | -0.66019124 | -0.01482747 | 0.31379922 |
| **Fine (1x1 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Leaf Litter Cover (Het) | Tukey | ***0.111622651*** | ***0.2340425*** | ***0.35646231*** |
| Soil Moisture (Het) | Tukey | ***0.039942938*** | ***0.1470637*** | ***0.27430412*** |
| Soil Depth (Het) | Tukey | -0.179829952 | -0.004336809 | 0.14308477 |
| Elevation (Het) | log | -0.163240206 | -0.01636589 | 0.06157938 |
| Leaf Litter Cover (St) | | -0.008635732 | 0.09528769 | 0.30128019 |
| Soil Moisture (St) | Tukey | ***0.031467380*** | ***0.1603409*** | ***0.33146863*** |
| Soil Depth (St) | | ***-0.378311928*** | ***-0.1822802*** | ***-0.04025957*** |
| Elevation (St) | Tukey | ***0.075278940*** | ***0.2679446*** | ***0.49183942*** |
| **Very Fine (0.5x0.5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (Het) | sqrt | -0.10655499 | -0.02254987 | 0.01761581 |
| Elevation (Het) | log | -0.07166341 | -0.002805142 | 0.05031272 |
| Soil Depth (St) | Tukey | -0.15684753 | -0.04502476 | 0.01075460 |
| Elevation (St) | | ***-0.49437330*** | ***-0.2426774*** | ***-0.07408069*** |
| Soil Moisture (St) | | -0.08454508 | -0.002892921 | 0.06284084 |
| Leaf Litter Cover (St) | | -0.04205552 | 0.01436693 | 0.12161317 |
| **Trait Functional Diversity - Specific Leaf Area** | | | | |
| **Broad (2x25 m Transect)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Leaf Litter Cover (Het) | | -0.66993300 | -0.05076111 | 0.2214854 |
| Soil Moisture (Het) | log | -0.32374033 | 0.05436001 | 0.8554493 |
| Soil Depth (Het) | | -0.36650330 | 0.006743122 | 0.4683479 |
| Elevation (Het) | | -0.08355405 | 0.1100389 | 0.6110412 |
| Leaf Litter Cover (St) | Tukey | ***0.11752077*** | ***0.5728979*** | ***1.1573988*** |
| Soil Moisture (St) | Tukey | -0.63027241 | -0.04536206 | 0.2238790 |
| Soil Depth (St) | | -0.43456328 | 0.04561609 | 0.9023280 |
| Elevation (St) | Tukey | -0.71948493 | -0.0569641 | 0.2432762 |
| **Fine (1x1 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Leaf Litter Cover (Het) | Tukey | -0.06614947 | 0.01110270 | 0.14158914 |
| Soil Moisture (Het) | Tukey | 0.03018885 | 0.1204411 | 0.23032340 |
| Soil Depth (Het) | Tukey | 0.07120300 | 0.1905045 | 0.30980591 |
| Elevation (Het) | log | -0.06147450 | 0.01077578 | 0.13375715 |
| Leaf Litter Cover (St) | | 0.25907163 | 0.3824351 | 0.50579861 |
| Soil Moisture (St) | Tukey | 0.14884276 | 0.2702091 | 0.39157536 |
| Soil Depth (St) | | -0.19824023 | -0.01098186 | 0.11523757 |
| Elevation (St) | Tukey | -0.21566650 | -0.02682574 | 0.06703914 |

| Very Fine (0.5x0.5 m) | Tran | 2.5 % | Coefficients | 97.5 % |
|---|---|---|---|---|
| Soil Depth (Het) | sqrt | -0.06516093 | 0.003480252 | 0.09011105 |
| Elevation (Het) | log | -0.13038428 | -0.03163683 | 0.01498588 |
| Soil Depth (St) | Tukey | -0.03765436 | 0.02595224 | 0.15610645 |
| Elevation (St) | | ***0.17167929*** | ***0.2866757*** | ***0.40167210*** |
| Soil Moisture (St) | | -0.08485272 | 0.0001471273 | 0.08596832 |
| Leaf Litter Cover (St) | | ***0.03363329*** | ***0.1170021*** | ***0.21534601*** |
| **Trait Functional Diversity - Leaf Dry Matter Content** | | | | |
| **Broad (2x25 m Transect)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Leaf Litter Cover (Het) | | -0.3633984 | 0.01150277 | 0.5240510 |
| Soil Moisture (Het) | log | -0.3005440 | 0.06404979 | 0.8528221 |
| Soil Depth (Het) | | -0.6573061 | -0.08253377 | 0.1482199 |
| Elevation (Het) | | -0.4047806 | -0.006027185 | 0.3093064 |
| Leaf Litter Cover (St) | Tukey | ***0.1536079*** | ***0.7587829*** | ***1.4046523*** |
| Soil Moisture (St) | Tukey | -0.7039761 | -0.1085711 | 0.1271501 |
| Soil Depth (St) | | -1.0290303 | -0.1292852 | 0.2746661 |
| Elevation (St) | Tukey | -0.7173572 | -0.06940516 | 0.2110179 |
| **Fine (1x1 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Leaf Litter Cover (Het) | Tukey | ***0.01235168*** | ***0.09390488*** | ***0.22643354*** |
| Soil Moisture (Het) | Tukey | ***0.04537171*** | ***0.1435802*** | ***0.25083929*** |
| Soil Depth (Het) | Tukey | -0.01482362 | 0.07378825 | 0.24725602 |
| Elevation (Het) | log | -0.09871540 | 0.0002718557 | 0.10097800 |
| Leaf Litter Cover (St) | | ***0.22702972*** | ***0.3575024*** | ***0.48797507*** |
| Soil Moisture (St) | Tukey | ***0.16511727*** | ***0.2979443*** | ***0.43077129*** |
| Soil Depth (St) | | -0.25835312 | -0.02981486 | 0.09090411 |
| Elevation (St) | Tukey | -0.29037625 | -0.06387498 | 0.03540680 |
| **Very Fine (0.5x0.5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (Het) | sqrt | -0.08788352 | -0.004258742 | 0.05688570 |
| Elevation (Het) | log | -0.06382970 | 0.001627508 | 0.07650874 |
| Soil Depth (St) | Tukey | -0.11725727 | -0.006361245 | 0.07234683 |
| Elevation (St) | | ***0.16332721*** | ***0.3071682*** | ***0.45100922*** |
| Soil Moisture (St) | | -0.05384653 | 0.008382731 | 0.10908012 |
| Leaf Litter Cover (St) | | ***0.01131512*** | ***0.08098921*** | ***0.18646000*** |
| **Trait Functional Diversity - Leaf Thickness (cm)** | | | | |
| **Broad (2x25 m Transect)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Leaf Litter Cover (Het) | | -0.66212569 | -0.1662466 | 0.044845213 |
| Soil Moisture (Het) | log | -0.25190315 | 0.04901065 | 0.696562745 |
| Soil Depth (Het) | | -0.50096677 | -0.06948188 | 0.087863677 |
| Elevation (Het) | | -0.20799292 | 0.008360116 | 0.356417549 |

| | | | | |
|---|---|---|---|---|
| Leaf Litter Cover (St) | Tukey | -0.02684375 | 0.2891296 | 0.868008741 |
| Soil Moisture (St) | Tukey | ***-0.63539028*** | ***-0.2210856*** | ***-0.007367942*** |
| Soil Depth (St) | | -0.52743439 | 0.007475821 | 0.613250570 |
| Elevation (St) | Tukey | ***-0.99954411*** | ***-0.5927897*** | ***-0.202257200*** |
| **Fine (1x1 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Leaf Litter Cover (Het) | Tukey | -0.07095506 | 0.008173949 | 0.12823801 |
| Soil Moisture (Het) | Tukey | -0.04120005 | 0.02099730 | 0.14896393 |
| Soil Depth (Het) | Tukey | -0.01335042 | 0.06054818 | 0.21364927 |
| Elevation (Het) | log | -0.10981853 | -0.004531182 | 0.07519676 |
| Leaf Litter Cover (St) | | -0.02154696 | 0.05497997 | 0.22427808 |
| Soil Moisture (St) | Tukey | 0.06488253 | 0.1823902 | 0.30424217 |
| Soil Depth (St) | | -0.10499647 | 0.01522087 | 0.20273472 |
| Elevation (St) | Tukey | -0.69655285 | -0.4924022 | -0.28825157 |
| **Very Fine (0.5x0.5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (Het) | sqrt | -0.08446413 | -0.004036221 | 0.05564122 |
| Elevation (Het) | log | -0.04769440 | 0.004930971 | 0.08257730 |
| Soil Depth (St) | Tukey | -0.11402171 | -0.007606168 | 0.06316375 |
| Elevation (St) | | ***0.06882901*** | ***0.2332233*** | ***0.49370760*** |
| Soil Moisture (St) | | -0.02821251 | 0.02049537 | 0.12236061 |
| Leaf Litter Cover (St) | | -0.03794163 | 0.01725517 | 0.12893534 |

| **2011** | | | | |
|---|---|---|---|---|
| **Trait Functional Diversity - Plant Height (cm)** | | | | |
| **Broad (Site)** | **Tran** | **2.5%** | **Coefficient** | **97.5%** |
| Leaf Litter Thickness (Het) | | -0.33807300 | 0.01516267 | 0.5562567 |
| Soil Depth (Het) | log | -0.35264221 | 0.01241163 | 0.6779904 |
| Coast Distance (Het) | | -0.60489133 | 0.001245591 | 0.6262138 |
| Slope (Het) | sqrt | -0.51734347 | 0.05674905 | 0.9969445 |
| Leaf Litter Thickness (St) | | -0.54807182 | -0.01335650 | 0.3507371 |
| Soil Depth (St) | Tukey | -0.55954323 | -0.003902052 | 0.4978018 |
| Coast Distance (St) | | -0.60827001 | 0.001657338 | 0.6350539 |
| Slope (St) | | ***0.06527513*** | ***0.4479181*** | ***1.0485661*** |
| **Fine (1x1m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Elevation (St) | sqrt | -0.12252316 | 0.006967494 | 0.16967441 |
| Slope (St) | | -0.17974030 | -0.03685841 | 0.02937110 |
| Leaf Litter Thickness (St) | | -0.13753822 | -0.009994594 | 0.07129596 |
| Soil Depth (St) | .1+log | ***0.08844367*** | ***0.1997338*** | ***0.31102401*** |
| Coast Distance (St) | sqrt | -0.04336948 | 0.03741670 | 0.20752035 |
| **Trait Functional Diversity - Canopy Width (cm)** | | | | |
| **Broad (Site)** | **Tran** | **2.5%** | **Coefficient** | **97.5%** |

| | | | | |
|---|---|---|---|---|
| Leaf Litter Thickness (Het) | | -0.62007318 | -0.04222587 | 0.1985845 |
| Soil Depth (Het) | log | -0.46856720 | -0.004334513 | 0.3699745 |
| Coast Distance (Het) | | -1.60801321 | -0.03911277 | 0.9591535 |
| Slope (Het) | sqrt | -0.37236426 | 0.04569685 | 0.8125187 |
| Leaf Litter Thickness (St) | | ***-0.96108658*** | ***-0.5353763*** | ***-0.1432924*** |
| Soil Depth (St) | Tukey | -0.69338772 | -0.02885942 | 0.3031234 |
| Coast Distance (St) | | -0.93968847 | 0.0419372 | 1.6103980 |
| Slope (St) | | -0.01402621 | 0.2391482 | 0.8230901 |
| **Fine (1x1m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Elevation (St) | sqrt | -0.07802378 | 0.07043954 | 0.21890286 |
| Slope (St) | | -0.12269936 | -0.02445496 | 0.07378944 |
| Leaf Litter Thickness (St) | | ***-0.29498430*** | ***-0.1966639*** | ***-0.09834350*** |
| Soil Depth (St) | .1+log | ***0.27566466*** | ***0.3788116*** | ***0.48195849*** |
| Coast Distance (St) | sqrt | -0.20878703 | -0.06909717 | 0.07059270 |
| **Trait Functional Diversity - Specific Leaf Area** | | | | |
| **Broad (Site)** | **Tran** | **2.5%** | **Coefficient** | **97.5%** |
| Leaf Litter Thickness (Het) | | -0.3585750 | 0.02090722 | 0.6469753 |
| Soil Depth (Het) | log | -0.5029474 | 0.002775057 | 0.5484250 |
| Coast Distance (Het) | | -1.2547374 | 0.1244845 | 2.3711473 |
| Slope (Het) | sqrt | -0.4328043 | 0.01703865 | 0.6779904 |
| Leaf Litter Thickness (St) | | -0.5700604 | -0.005383656 | 0.4827564 |
| Soil Depth (St) | Tukey | -0.8001974 | -0.05727308 | 0.2626426 |
| Coast Distance (St) | | -2.3408402 | -0.1976773 | 0.9053659 |
| Slope (St) | | -0.4338111 | 0.01597527 | 0.6696010 |
| **Fine (1x1 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Elevation (St) | sqrt | -0.15778858 | -0.00742918 | 0.10662744 |
| Slope (St) | | -0.09853265 | 0.002626481 | 0.11892706 |
| Leaf Litter Thickness (St) | | -0.13252135 | -0.006933888 | 0.08187020 |
| Soil Depth (St) | .1+log | ***0.02072597*** | ***0.1208938*** | ***0.25512763*** |
| Coast Distance (St) | sqrt | -0.22321204 | -0.05408774 | 0.02720475 |
| **Trait Functional Diversity - Leaf Dry Matter Content** | | | | |
| **Broad (Site)** | **Tran** | **2.5%** | **Coefficient** | **97.5%** |
| Leaf Litter Thickness (Het) | | -0.64999937 | -0.0357977 | 0.2534888 |
| Soil Depth (Het) | log | -0.59719536 | 0.02599822 | 0.2534888 |
| Coast Distance (Het) | | -0.29891680 | 0.004651942 | 0.6751515 |
| Slope (Het) | sqrt | -0.69415075 | 0.02591096 | 0.9589915 |
| Leaf Litter Thickness (St) | | -0.28711683 | 0.02458169 | 0.6106874 |
| Soil Depth (St) | Tukey | -0.31613649 | 0.03374579 | 0.7188131 |
| Coast Distance (St) | | -0.54090840 | 0.01189278 | 0.7333806 |
| Slope (St) | | ***0.07805801*** | ***0.4847865*** | ***1.0845023*** |

| **Fine (1x1 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
|---|---|---|---|---|
| Elevation (St) | sqrt | -0.10675378 | 0.005756219 | 0.14675643 |
| Slope (St) | | -0.12730421 | -0.005710458 | 0.08584831 |
| Leaf Litter Thickness (St) | | -0.08805055 | 0.004630964 | 0.12235942 |
| Soil Depth (St) | .1+log | ***0.06335016*** | ***0.1742033*** | ***0.28868839*** |
| Coast Distance (St) | sqrt | -0.04196012 | 0.03642654 | 0.20260599 |
| **Trait Functional Diversity - Leaf Thickness (cm)** | | | | |
| **Broad (Site)** | **Tran** | **2.5%** | **Coefficient** | **97.5%** |
| Leaf Litter Thickness (Het) | | -0.7681225 | -0.06265662 | 0.2531601 |
| Soil Depth (Het) | log | -0.1863080 | 0.0970332 | 0.8070449 |
| Coast Distance (Het) | | -1.1826973 | -0.1705703 | 0.3352919 |
| Slope (Het) | sqrt | -0.5621487 | -0.002035241 | 0.5299120 |
| Leaf Litter Thickness (St) | | -0.5190483 | 0.003346182 | 0.5694340 |
| Soil Depth (St) | Tukey | -0.4080460 | 0.04152021 | 0.8455533 |
| Coast Distance (St) | | -1.2109922 | -0.1826365 | 0.3283563 |
| Slope (St) | | -0.5449306 | 0.001246949 | 0.5646328 |
| **Fine (1x1 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Elevation (St) | sqrt | -0.1391184 | -0.003763953 | 0.11121900 |
| Slope (St) | - | -0.1416165 | -0.01273017 | 0.06237657 |
| Leaf Litter Thickness (St) | - | ***-0.2888065*** | ***-0.1867046*** | ***-0.08460275*** |
| Soil Depth (St) | .1+log | ***0.2073378*** | ***0.3135177*** | ***0.41969764*** |
| Coast Distance (St) | sqrt | -0.1535318 | -0.009398679 | 0.08887630 |

| **2010** | | | | |
|---|---|---|---|---|
| **Trait Functional Diversity - Plant Height (cm)** | | | | |
| **Fine (5x5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Elevation (St) | Tukey | -0.36781002 | -0.01504361 | 0.2536619 |
| Slope (St) | sqrt | -0.17498525 | 0.01203688 | 0.2673748 |
| Coast Distance (St) | Tukey | -0.20581761 | 0.02673557 | 0.3896722 |
| Soil Moisture (St) | Tukey | -0.03113828 | 0.1424394 | 0.4721390 |
| Soil Depth (St) | Tukey | -0.41366160 | -0.04498355 | 0.1593514 |
| **Canopy Width (cm)** | | | | |
| **Fine (5x5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Elevation (St) | Tukey | -0.28851588 | 0.007525409 | 0.3455540 |
| Slope (St) | sqrt | -0.14872091 | 0.02103564 | 0.2938687 |
| Coast Distance (St) | Tukey | -0.40460622 | -0.03719736 | 0.1730450 |
| Soil Moisture (St) | Tukey | -0.05999826 | 0.09971853 | 0.4329540 |
| Soil Depth (St) | Tukey | -0.37618502 | -0.02884623 | 0.1908415 |
| **Specific Leaf Area** | | | | |
| **Fine (5x5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Elevation (St) | Tukey | -0.2020021 | 0.01694044 | 0.3271167 |

| | | | | |
|---|---|---|---|---|
| Slope (St) | sqrt | -0.2483204 | -0.006753164 | 0.1943827 |
| Coast Distance (St) | Tukey | -0.2315283 | 0.009902922 | 0.3080049 |
| Soil Moisture (St) | Tukey | -0.0383603 | 0.1257279 | 0.4523025 |
| Soil Depth (St) | Tukey | -0.3828366 | -0.03110538 | 0.1880240 |
| **Leaf Dry Matter Content** | | | | |
| **Fine (5x5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Elevation (St) | Tukey | -0.36781002 | -0.01504361 | 0.2536619 |
| Slope (St) | sqrt | -0.17498525 | 0.01203688 | 0.2673748 |
| Coast Distance (St) | Tukey | -0.20581761 | 0.02673557 | 0.3896722 |
| Soil Moisture (St) | Tukey | -0.03113828 | 0.1424394 | 0.4721390 |
| Soil Depth (St) | Tukey | -0.41366160 | -0.04498355 | 0.1593514 |
| **Leaf Thickness (cm)** | | | | |
| **Fine (5x5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Elevation (St) | Tukey | -0.78207808 | -0.2257595 | 0.0615603 |
| Slope (St) | sqrt | -0.10652416 | 0.03973019 | 0.3292546 |
| Coast Distance (St) | Tukey | -0.05580249 | 0.2448958 | 0.7969526 |
| Soil Moisture (St) | Tukey | -0.31322849 | -0.02430256 | 0.1467646 |
| Soil Depth (St) | Tukey | -0.23885823 | 0.001398343 | 0.2503998 |

| **2008** | | | | |
|---|---|---|---|---|
| **Trait Functional Diversity - Plant Height (cm)** | | | | |
| **Broad (Transect)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (Het) | sqrt | -0.6382583 | -0.005097743 | 0.5378179 |
| Soil Phosphorous (Het) | sqrt | -0.4715360 | 0.03374024 | 0.9255477 |
| Soil Organic Matter (Het) | log | -0.8003985 | -0.002839449 | 0.7490778 |
| Soil Nitrogen (St) | log | -0.3158202 | 0.2438244 | 1.6166958 |
| Soil Depth (St) | Tukey | -0.7485551 | 0.09225516 | 1.4972681 |
| Soil Phosphorous (St) | Tukey | -1.0992575 | -0.1881981 | 0.1526423 |
| Soil Organic Matter (St) | Tukey | -0.8124176 | -0.005569484 | 0.7133527 |
| Soil Nitrogen (St) | Tukey | -1.7203980 | -0.1408362 | 0.3224451 |
| **Fine (2x5m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (St) | Tukey | -0.02310202 | 0.1458239 | 0.47863790 |
| Soil Phosphorous (St) | | -0.31802895 | -0.02521150 | 0.14843246 |
| Soil Organic Matter (St) | .1+log | -0.55839108 | -0.1134462 | 0.10610932 |
| Soil Nitrogen (St) | .1+log | -0.55412295 | -0.1328597 | 0.07121296 |
| **Trait Functional Diversity - Canopy Width (cm)** | | | | |
| **Broad (Transect)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (Het) | sqrt | -0.7157652 | -0.01000233 | 0.4617604 |
| Soil Phosphorous (Het) | sqrt | -0.4513621 | 0.01691532 | 0.8166056 |
| Soil Organic Matter (Het) | log | -0.6847391 | -0.003108873 | 0.6079410 |

|  |  |  |  |  |
|---|---|---|---|---|
| Soil Nitrogen (St) | log | -0.3313535 | 0.1189589 | 1.3189182 |
| Soil Depth (St) | Tukey | -0.9062352 | 0.01407776 | 1.0809506 |
| Soil Phosphorous (St) | Tukey | -0.9533634 | -0.1010443 | 0.1749302 |
| Soil Organic Matter (St) | Tukey | -0.7005634 | 0.005900892 | 0.5564852 |
| Soil Nitrogen (St) | Tukey | -1.3708666 | -0.1408362 | 0.3296252 |
| **Fine (2x5m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (St) | Tukey | -0.04242964 | 0.1006585 | 0.4367213 |
| Soil Phosphorous (St) |  | -0.29736967 | -0.01697616 | 0.1691516 |
| Soil Organic Matter (St) | .1+log | -0.22837478 | 0.02641700 | 0.4038915 |
| Soil Nitrogen (St) | .1+log | -0.12579394 | 0.0596071 | 0.4389808 |
| **Trait Functional Diversity - Leaf Dry Matter Content** |  |  |  |  |
| **Broad (Transect)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (Het) | sqrt | -0.2929944 | 0.01782439 | 0.6778463 |
| Soil Phosphorous (Het) | sqrt | -0.6453861 | -0.008562415 | 0.3957446 |
| Soil Organic Matter (Het) | log | -0.3954126 | 0.002895654 | 0.4904259 |
| Soil Nitrogen (St) | log | -0.7409642 | -0.04609615 | 0.1343276 |
| Soil Depth (St) | Tukey | -0.5962957 | -0.02319755 | 0.1825280 |
| Soil Phosphorous (St) | Tukey | ***-0.9441660*** | ***-0.5506896*** | ***-0.2090231*** |
| Soil Organic Matter (St) | Tukey | -0.4062953 | 0.002413218 | 0.4846627 |
| Soil Nitrogen (St) | Tukey | -0.6956038 | -0.03554479 | 0.1961666 |
| **Fine (2x5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (St) | Tukey | -0.42125803 | -0.07868585 | 0.07320633 |
| Soil Phosphorous (St) |  | -0.43256336 | -0.1177723 | 0.02598565 |
| Soil Organic Matter (St) | .1+log | -0.08261043 | 0.1012222 | 0.49632806 |
| Soil Nitrogen (St) | .1+log | -0.18509051 | 0.0496380 | 0.45696159 |
| **Trait Functional Diversity - Specific Leaf Area** |  |  |  |  |
| **Broad (Transect)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (Het) | sqrt | -0.2080395 | 0.1054049 | 0.9271289 |
| Soil Phosphorous (Het) | sqrt | -0.4359578 | 0.02839696 | 0.8459613 |
| Soil Organic Matter (Het) | log | -0.6233962 | 0.05265869 | 1.1630484 |
| Soil Nitrogen (St) | log | -1.0206676 | -0.1085691 | 0.2420234 |
| Soil Depth (St) | Tukey | -0.3663410 | 0.03010599 | 0.7783688 |
| Soil Phosphorous (St) | Tukey | -0.8576160 | -0.02408858 | 0.4783645 |
| Soil Organic Matter (St) | Tukey | -0.2351009 | 0.1696384 | 1.1855634 |
| Soil Nitrogen (St) | Tukey | -0.8519427 | -0.005942689 | 0.7497420 |
| **Fine (2x5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (St) | Tukey | **0.0702271** | **0.2842516** | **0.5415785** |
| Soil Phosphorous (St) | - | -0.2596562 | -0.00749658 | 0.1952379 |
| Soil Organic Matter (St) | .1+log | -0.2539201 | 0.01401733 | 0.3591572 |
| Soil Nitrogen (St) | .1+log | -0.1767772 | 0.03293386 | 0.3923303 |

| **Trait Functional Diversity - Leaf Thickness (cm)** | | | | |
|---|---|---|---|---|
| **Broad (Transect)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (Het) | sqrt | -0.124743489 | 0.023821 | 0.07287313 |
| Soil Phosphorous (Het) | sqrt | -0.083742045 | 0.009700 | 0.10550050 |
| Soil Organic Matter (Het) | log | ***0.001275597*** | ***0.194595*** | ***0.37910473*** |
| Soil Nitrogen (St) | log | -0.194124035 | -0.069728 | 0.07835454 |
| Soil Depth (St) | Tukey | -0.097914190 | 0.020365 | 0.14349001 |
| Soil Phosphorous (St) | Tukey | -0.093577938 | 0.020458 | 0.12790015 |
| Soil Organic Matter (St) | Tukey | -0.303510686 | -0.120875 | 0.05003857 |
| Soil Nitrogen (St) | Tukey | -0.147146322 | 0.004505 | 0.16303335 |
| **Fine (2x5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (St) | Tukey | ***0.207748722*** | ***0.4274439*** | ***0.6471390*** |
| Soil Phosphorous (St) | - | -0.007014691 | 0.1301199 | 0.4172221 |
| Soil Organic Matter (St) | .1+log | -0.178358494 | 0.02820379 | 0.3674893 |
| Soil Nitrogen (St) | .1+log | -0.163786783 | 0.03011973 | 0.3619561 |

| **2005** | | | | |
|---|---|---|---|---|
| **Trait Functional Diversity - Plant Height (cm)** | | | | |
| **Fine (1x1 m)** | **Tran** | **2.5%** | **Coefficient** | **97.5%** |
| Soil Moisture (Het) | | -0.21488388 | -0.001330278 | 0.20305125 |
| Soil Depth (Het) | sqrt | -0.17187620 | 0.01040595 | 0.25579102 |
| Wind Exposure (St) | Tukey | -0.43504278 | -0.1828335 | -0.01614584 |
| Coast Distance (St) | Tukey | -0.35238906 | -0.05298039 | 0.08982526 |
| Soil Depth (St) | Tukey | -0.04185315 | 0.1018364 | 0.40200307 |
| Soil Moisture (St) | sqrt | -0.41147611 | -0.1049830 | 0.03823326 |
| Soil Organic Matter (St) | Tukey | -0.03159537 | 0.1184327 | 0.41861066 |
| Soil Phosphorous (St) | Tukey | -0.34754997 | -0.03814635 | 0.12392825 |
| **Trait Functional Diversity - Canopy Width (cm)** | | | | |
| **Fine (1x1 m)** | **Tran** | **2.5%** | **Coefficient** | **97.5%** |
| Soil Moisture (Het) | | -0.20247094 | -0.001267982 | 0.19145143 |
| Soil Depth (Het) | sqrt | -0.10277832 | 0.02161390 | 0.24751097 |
| Wind Exposure (St) | Tukey | -0.29097990 | -0.03723536 | 0.08149388 |
| Coast Distance (St) | Tukey | -0.05805770 | 0.05457551 | 0.31346653 |
| Soil Depth (St) | Tukey | -0.47185051 | -0.2401288 | -0.05284246 |
| Soil Moisture (St) | sqrt | -0.06353676 | 0.07294015 | 0.41158926 |
| Soil Organic Matter (St) | Tukey | -0.08745953 | 0.0486343 | 0.34390900 |
| Soil Phosphorous (St) | Tukey | -0.22905950 | -0.003795802 | 0.19652494 |
| **Trait Functional Diversity - Specific Leaf Area** | | | | |
| **Fine (1x1 m)** | **Tran** | **2.5%** | **Coefficient** | **97.5%** |
| Soil Moisture (Het) | | -0.07920174 | 0.03957916 | 0.30044303 |
| Soil Depth (Het) | sqrt | -0.05708574 | 0.06083329 | 0.32464494 |

| | | | | |
|---|---|---|---|---|
| Wind Exposure (St) | Tukey | -0.24864798 | -0.01451033 | 0.13405979 |
| Coast Distance (St) | Tukey | -0.26182665 | -0.01246031 | 0.16272928 |
| Soil Depth (St) | Tukey | 0.12428142 | 0.3207733 | 0.52161958 |
| Soil Moisture (St) | sqrt | -0.13757805 | 0.02217024 | 0.29377397 |
| Soil Organic Matter (St) | Tukey | -0.24019358 | -0.003679116 | 0.20808752 |
| Soil Phosphorous (St) | Tukey | -0.32378437 | -0.04508366 | 0.08589969 |
| **Trait Functional Diversity - Leaf Dry Matter Content** | | | | |
| **Fine (1x1 m)** | **Tran** | **2.5%** | **Coefficient** | **97.5%** |
| Soil Moisture (Het) | | -0.1761692 | 0.00728753 | 0.2398781 |
| Soil Depth (Het) | sqrt | -0.1877969 | -0.0003731304 | 0.1844247 |
| Wind Exposure (St) | Tukey | -0.1393084 | 0.01587071 | 0.2629402 |
| Coast Distance (St) | Tukey | -0.3168510 | -0.03999215 | 0.0919417 |
| Soil Depth (St) | Tukey | -0.0256189 | 0.1274983 | 0.4264167 |
| Soil Moisture (St) | sqrt | -0.3500270 | -0.03039016 | 0.1441120 |
| Soil Organic Matter (St) | Tukey | -0.3730978 | -0.05178868 | 0.1003296 |
| Soil Phosphorous (St) | Tukey | -0.3011552 | -0.02028595 | 0.1508965 |
| **Trait Functional Diversity - Leaf Thickness (cm)** | | | | |
| **Fine (1x1 m)** | **Tran** | **2.5%** | **Coefficient** | **97.5%** |
| Soil Moisture (Het) | | -0.13631592 | 0.02005152 | 0.27770029 |
| Soil Depth (Het) | sqrt | -0.24703882 | -0.009806086 | 0.16043711 |
| Wind Exposure (St) | Tukey | -0.32683230 | -0.04900683 | 0.08133221 |
| Coast Distance (St) | Tukey | -0.50060347 | -0.2400540 | -0.03525692 |
| Soil Depth (St) | Tukey | -0.09893226 | 0.03744916 | 0.31771417 |
| Soil Moisture (St) | sqrt | -0.12789156 | 0.02527576 | 0.30318386 |
| Soil Organic Matter (St) | Tukey | -0.16956033 | 0.01084930 | 0.26048454 |
| Soil Phosphorous (St) | Tukey | -0.44638872 | -0.1458711 | 0.01062051 |

| **2005 Broad Scale (Site)** | | | | |
|---|---|---|---|---|
| **Height Fdis** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Factor 1 (St) | | -0.03967287 | 0.06604 | 0.1717465 |
| Factor 2 (St) | | -0.09318692 | 0.02774 | 0.1486684 |
| Factor 3 (St) | | -0.07526829 | 0.04174 | 0.1587383 |
| Factor 1 (Het) | | **0.03785458** | **0.10579** | **0.1737218** |
| Factor 2 (Het) | | -0.1173160 | 0.006468 | 0.1302511 |
| Factor 3 (Het) | | -0.07766769 | 0.03994 | 0.1575413 |
| **Canopy Fdis** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Factor 1 (St) | | -0.3434766 | -0.1167 | 0.1100763 |
| Factor 2 (St) | | -0.2648381 | -0.01109 | 0.2426601 |
| Factor 3 (St) | | -0.3626390 | -0.17849 | 0.005649312 |
| Factor 1 (Het) | | -0.3626862 | -0.17921 | 0.004257155 |
| Factor 2 (Het) | | -0.2347107 | 0.01861 | 0.2719406 |
| Factor 3 (Het) | | -0.3585104 | -0.15484 | 0.04882888 |

| **Specific Leaf Area Fdis** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
|---|---|---|---|---|
| Factor 1 (St) | | -0.01052847 | 0.05178 | 0.1140974 |
| Factor 2 (St) | | -0.05593258 | 0.02159 | 0.09912109 |
| Factor 3 (St) | | -0.08603999 | -0.005884 | 0.07427209 |
| Factor 1 (Het) | | **0.007013863** | **0.06087** | **0.1147213** |
| Factor 2 (Het) | | -0.09249807 | -0.01318 | 0.06613891 |
| Factor 3 (Het) | | -0.09626417 | -0.01782 | 0.06062068 |
| **Leaf Dry Matter Content Fdis** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Factor 1 (St) | | -0.03967287 | 0.06604 | 0.1717465 |
| Factor 2 (St) | | -0.09318692 | 0.02774 | 0.1486684 |
| Factor 3 (St) | | -0.07526829 | 0.04174 | 0.1587383 |
| Factor 1 (Het) | | **0.03785458** | **0.10579** | **0.1737218** |
| Factor 2 (Het) | | -0.1173160 | 0.006468 | 0.1302511 |
| Factor 3 (Het) | | -0.07766769 | 0.03994 | 0.1575413 |
| **Leaf Thickness Fdis** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Factor 1 (St) | | -0.2097826 | -0.10709 | -0.004395282 |
| Factor 2 (St) | | -0.1473476 | -0.0005169 | 0.1463137 |
| Factor 3 (St) | | **-0.2097826** | **-0.10709** | **-0.004395282** |
| Factor 1 (Het) | | -0.07921925 | 0.05669 | 0.1926087 |
| Factor 2 (Het) | | -0.1464601 | 0.000371 | 0.1472020 |
| Factor 3 (Het) | | -0.2048719 | -0.08195 | 0.04097391 |

**Appendix 3.E.** Multiple linear regressions for the 2017, 2011, 2010, 2008, and 2005 (fine scale) datasets and single linear regression for the 2005 dataset (broad scale). The response variable was total functional diversity and the explanatory variables are the stress and heterogeneity variables. A separate linear regression was conducted for each response variable at each spatial scale in each dataset. Both positive (all 95% intervals above 0) and negative associations (all 95% intervals below 0) are Italicized. Tukey indicates that a Tukey's ladder of powers transformation was used. Tran = transformation, St = Stress, Het = heterogeneity.

| **Total Functional Diversity - 2017** | | | | |
|---|---|---|---|---|
| **Broad (2x25 m Transect)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Leaf Litter Cover (Het) | | -0.4548455 | -0.01791128 | 0.1661534 |
| Soil Moisture (Het) | log | -0.3704600 | 0.002093898 | 0.4190046 |
| Soil Depth (Het) | | ***-0.7062019*** | ***-0.4247410*** | ***-0.1853067*** |
| Elevation (Het) | | -0.1975688 | 0.004729722 | 0.3210247 |
| Leaf Litter Cover (St) | Tukey | -0.1084631 | 0.09150087 | 0.6789605 |
| Soil Moisture (St) | Tukey | ***-0.8340032*** | ***-0.5376012*** | ***-0.2411991*** |
| Soil Depth (St) | | -0.4389868 | 0.008516072 | 0.5650870 |
| Elevation (St) | Tukey | ***-0.9752016*** | ***-0.6493132*** | ***-0.3234248*** |
| **Fine (1x1 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Leaf Litter Cover (Het) | Tukey | -0.01767785 | 0.04964758 | 0.19509690 |
| Soil Moisture (Het) | Tukey | ***0.08260665*** | ***0.1847829*** | ***0.28695912*** |
| Soil Depth (Het) | Tukey | -0.02383131 | 0.05908187 | 0.23305459 |
| Elevation (Het) | log | -0.09249001 | 0.001694404 | 0.10585302 |
| Leaf Litter Cover (St) | | ***0.14888523*** | ***0.2826459*** | ***0.41640666*** |
| Soil Moisture (St) | Tukey | ***0.16024122*** | ***0.2906228*** | ***0.42100446*** |
| Soil Depth (St) | | -0.24289954 | -0.02358107 | 0.10262407 |
| Elevation (St) | Tukey | -0.39920221 | -0.08128422 | 0.05413173 |
| **Very Fine (0.5x0.5m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (Het) | sqrt | -0.08347462 | -0.003077964 | 0.06126265 |
| Elevation (Het) | log | -0.05044206 | 0.005241914 | 0.08681809 |
| Soil Depth (St) | Tukey | -0.13759186 | -0.01698676 | 0.04660277 |
| Elevation (St) | | ***0.03706194*** | ***0.1779850*** | ***0.43480768*** |
| Soil Moisture (St) | | -0.06297875 | 0.00493967 | 0.09791375 |
| Leaf Litter Cover (St) | | -0.02326502 | 0.03360550 | 0.15442013 |
| **Total Functional Diversity - 2011** | | | | |
| **Broad (Site)** | **Tran** | **2.5%** | **Coefficient** | **97.5%** |
| Leaf Litter Thickness (Het) | | -0.63952084 | -0.0267334 | 0.288450774 |
| Soil Depth (Het) | log | -0.45867243 | 0.0007472471 | 0.476545582 |
| Coast Distance (Het) | | -1.19475011 | -0.04176575 | 0.619779464 |
| Slope (Het) | sqrt | -0.37630657 | 0.0574845 | 0.880534507 |
| Leaf Litter Thickness (St) | | -0.87514254 | -0.2861486 | 0.004158578 |

|  |  |  |  |  |
|---|---|---|---|---|
| Soil Depth (St) | Tukey | -0.77780781 | -0.03602439 | 0.310372355 |
| Coast Distance (St) |  | -1.05428051 | -0.0003640225 | 1.048521717 |
| Slope (St) |  | -0.03332678 | 0.2372656 | 0.898545959 |
| **Fine (1x1 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Elevation (St) | sqrt | -0.1391184 | -0.003763953 | 0.11121900 |
| Slope (St) | - | -0.1416165 | -0.01273017 | 0.06237657 |
| Leaf Litter Thickness (St) | - | ***-0.2888065*** | ***-0.1867046*** | ***-0.08460275*** |
| Soil Depth (St) | .1+log | ***0.2073378*** | ***0.3135177*** | ***0.41969764*** |
| Coast Distance (St) | sqrt | -0.1535318 | -0.009398679 | 0.08887630 |
| **Total Functional Diversity - 2010** |  |  |  |  |
| **Fine Scale (5x5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (5x5 m) | Tukey | -0.76390990 | -0.2012798 | 0.08929202 |
| Elevation (St) | sqrt | -0.09171587 | 0.04956513 | 0.34404558 |
| Slope (St) | Tukey | -0.08972396 | 0.1966939 | 0.76363545 |
| Coast Distance (St) | Tukey | -0.23997585 | -0.002392614 | 0.21997645 |
| Soil Moisture (St) | Tukey | -0.25558659 | -0.004664804 | 0.21695663 |
| **Total Functional Diversity - 2008** |  |  |  |  |
| **Broad (Transect)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (Het) | sqrt | -0.98088167 | -0.0471278 | 0.30680507 |
| Soil Phosphorous (Het) | sqrt | -0.25797016 | 0.05740546 | 0.93700074 |
| Soil Organic Matter (Het) | log | -0.07762305 | 0.1882763 | 1.09441997 |
| Soil Nitrogen (St) | log | -0.63098007 | -0.002145275 | 0.57302678 |
| Soil Depth (St) | Tukey | -0.34394453 | 0.01889497 | 0.70855878 |
| Soil Phosphorous (St) | Tukey | -1.01611247 | -0.1511373 | 0.08693897 |
| Soil Organic Matter (St) | Tukey | -0.47205823 | 0.04069652 | 0.99744584 |
| Soil Nitrogen (St) | Tukey | -1.03425117 | -0.02328112 | 0.60616511 |
| **Fine (2x5 m)** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Soil Depth (St) | Tukey | ***0.1198476*** | ***0.3421312*** | ***0.5758129*** |
| Soil Phosphorous (St) |  | -0.2028879 | 0.004626949 | 0.2422261 |
| Soil Organic Matter (St) | .1+log | -0.2912436 | -0.001464537 | 0.2787682 |
| Soil Nitrogen (St) | .1+log | -0.2300045 | 0.01140181 | 0.3237571 |
| **Total Functional Diversity - 2005** |  |  |  |  |
| **Fine (1x1 m)** | **Tran** | **2.5%** | **Coefficient** | **97.5%** |
| Soil Moisture (Het) |  | -0.09470402 | 0.03366349 | 0.29407463 |
| Soil Depth (Het) | sqrt | -0.13908114 | 0.01811486 | 0.27438441 |
| Wind Exposure (St) | Tukey | -0.38525901 | -0.09965654 | 0.03781798 |
| Coast Distance (St) | Tukey | -0.38361364 | -0.1056373 | 0.03086195 |
| Soil Depth (St) | Tukey | -0.28898595 | -0.02280985 | 0.13086733 |
| Soil Moisture (St) | sqrt | ***0.04988425*** | ***0.2401020*** | ***0.48137435*** |
| Soil Organic Matter (St) | Tukey | -0.16454777 | 0.01305978 | 0.26686694 |
| Soil Phosphorous (St) | Tukey | -0.31647745 | -0.02342394 | 0.15670968 |

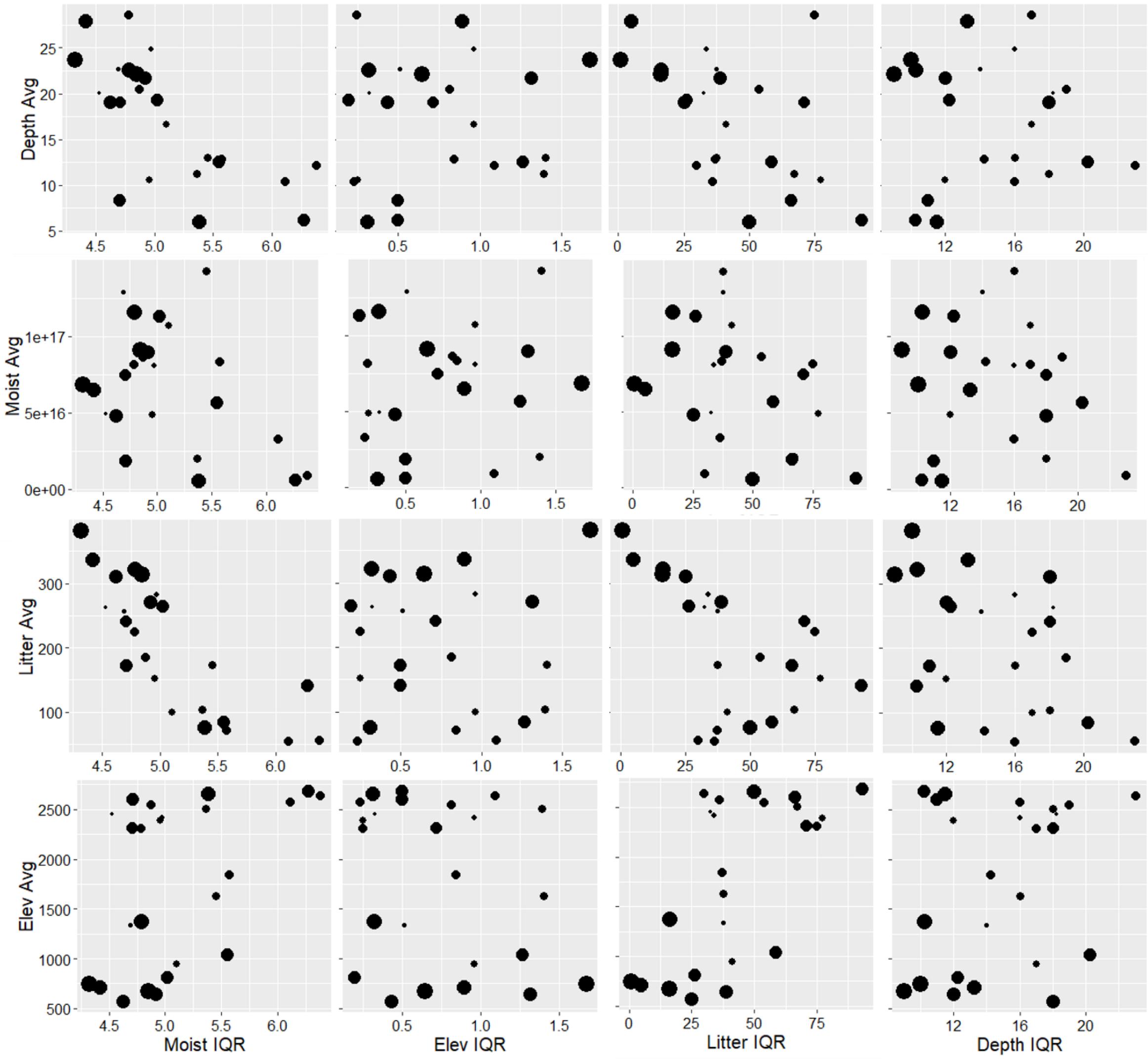
| **2005 Broad Scale (Site)** | | | | |
|---|---|---|---|---|
| **Total Fdis** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Factor 1 (St) | - | -0.1949648 | -0.01110 | 0.1727631 |
| Factor 2 (St) | - | -0.1587001 | 0.02398 | 0.2066602 |
| Factor 3 (St) | - | **-0.2430037** | **-0.17444** | **-0.105877** |
| Factor 1 (Het) | - | -0.212343 | -0.03062 | 0.1511071 |
| Factor 2 (Het) | - | -0.1593579 | 0.02340 | 0.2061481 |
| Factor 3 (Het) | - | **-0.2621375** | **-0.14526** | **-0.0283733** |

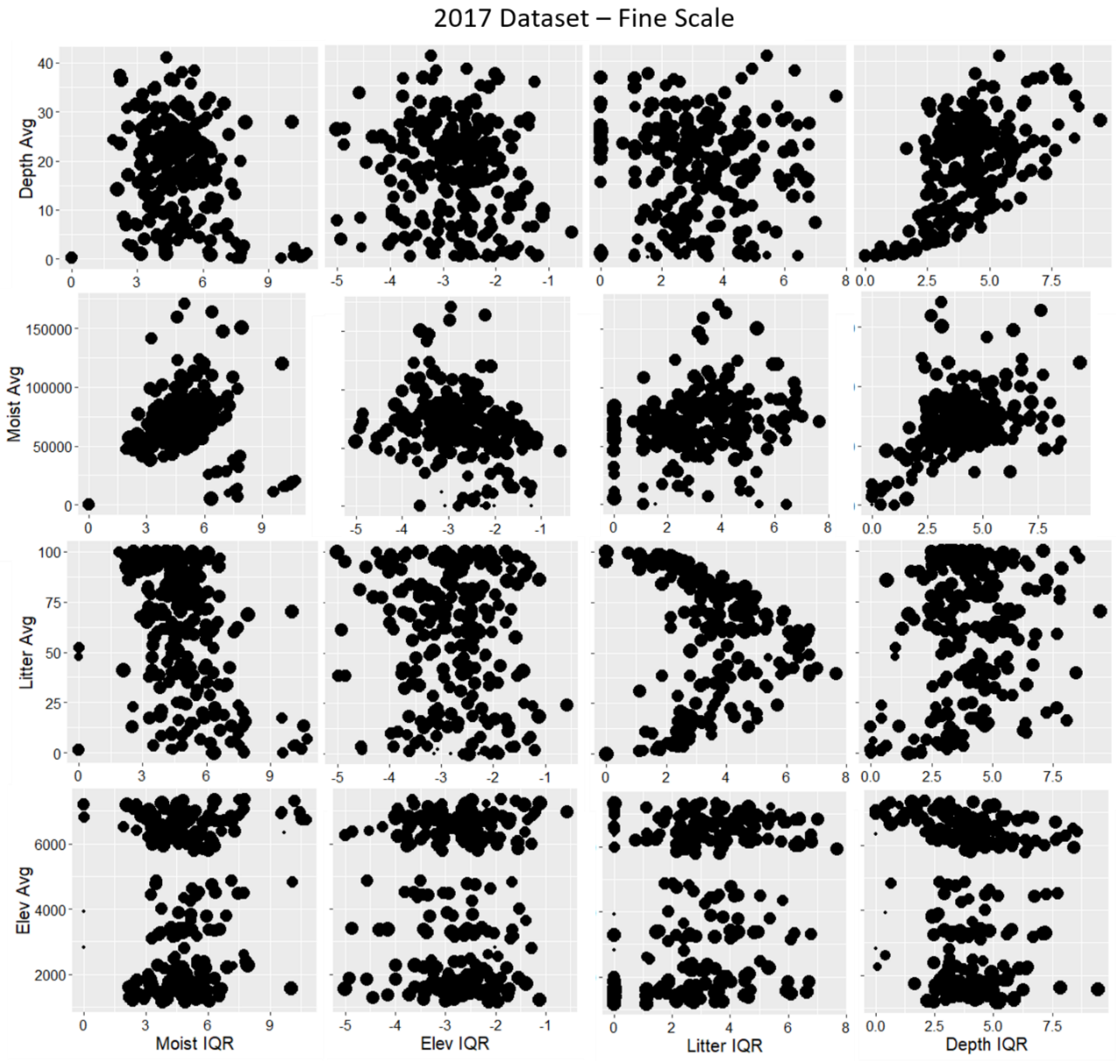
**Appendix 3.F.** Results from the ANOVA conducted on the 2016 dataset which compared functional traits and vegetation types. Tukey indicates that a Tukey's ladder of powers transformation was used.

| Functional Trait | Tran | DF | Sum sq | Mean Sq | F-Value | P-Value |
|---|---|---|---|---|---|---|
| **CWM Height** | Tukey | 5 | 0.06096 | 0.012192 | 38.34 | 6.41e-12 |
| **CWM Canopy** | Tukey | 5 | 41.63 | 8.325 | 22.41 | 3.73e-09 |
| **CWM Specific Leaf Area** | Tukey | 5 | 0.002792 | 0.0005583 | 5.72 | 0.000864 |
| **CWM Leaf Dry Matter Content** |  | 5 | 0.05631 | 0.011262 | 13.3 | 8.87e-07 |
| **CWM Leaf Thickness** |  | 5 | 0.006918 | 0.0013837 | 21.81 | 5.06e-09 |
| **Fdis Leaf Dry Matter Content** |  | 5 | 1.4449 | 0.28898 | 10.08 | 1.14e-05 |
| **Fdis** | Tukey | 5 | 7.555 | 1.5110 | 19.46 | 1.78e-08 |
| **Fdis Leaf Thickness** | Tukey | 5 | 49.48 | 9.896 | 11.43 | 3.73e-06 |
| **Fdis Specific Leaf Area** | Tukey | 5 | 0.05726 | 0.011453 | 8.986 | 3.03e-05 |
| **Fdis Height** | Tukey | 5 | 3.577 | 0.7154 | 16.02 | 1.38e-07 |
| **Fdis Canopy** |  | 5 | 2.836 | 0.5672 | 16.5 | 1.02e-07 |

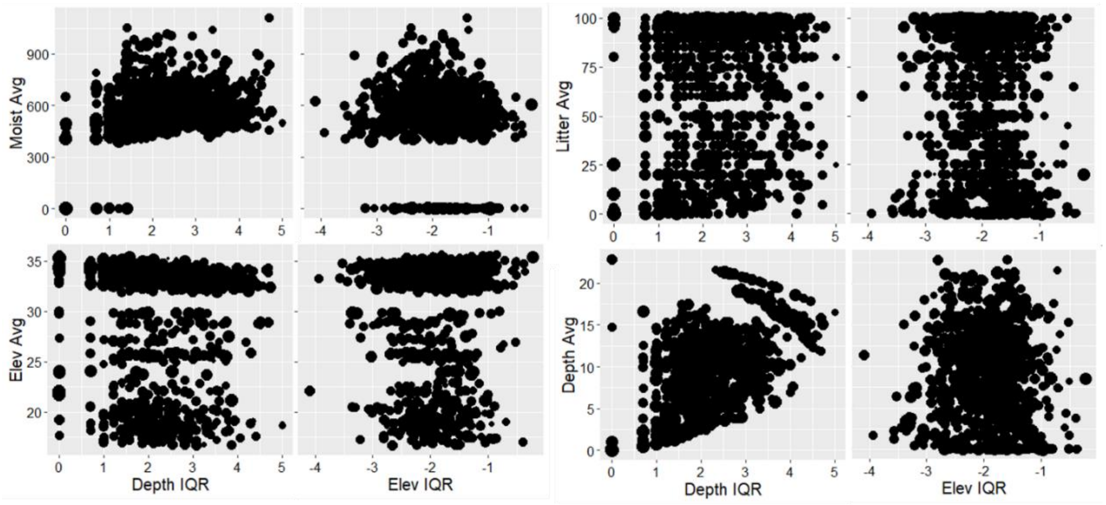
**Appendix 3.G.** Weighted biplot for each dataset and spatial scale. For each dataset and scale that examined both heterogeneity and stress a weighted biplot was used to determine if the stress and heterogeneity variables were interacting. The size of the plots on the biplots was calculated from total functional diversity. Code: IQR = interquartile range

2017 Dataset – Broad Scale

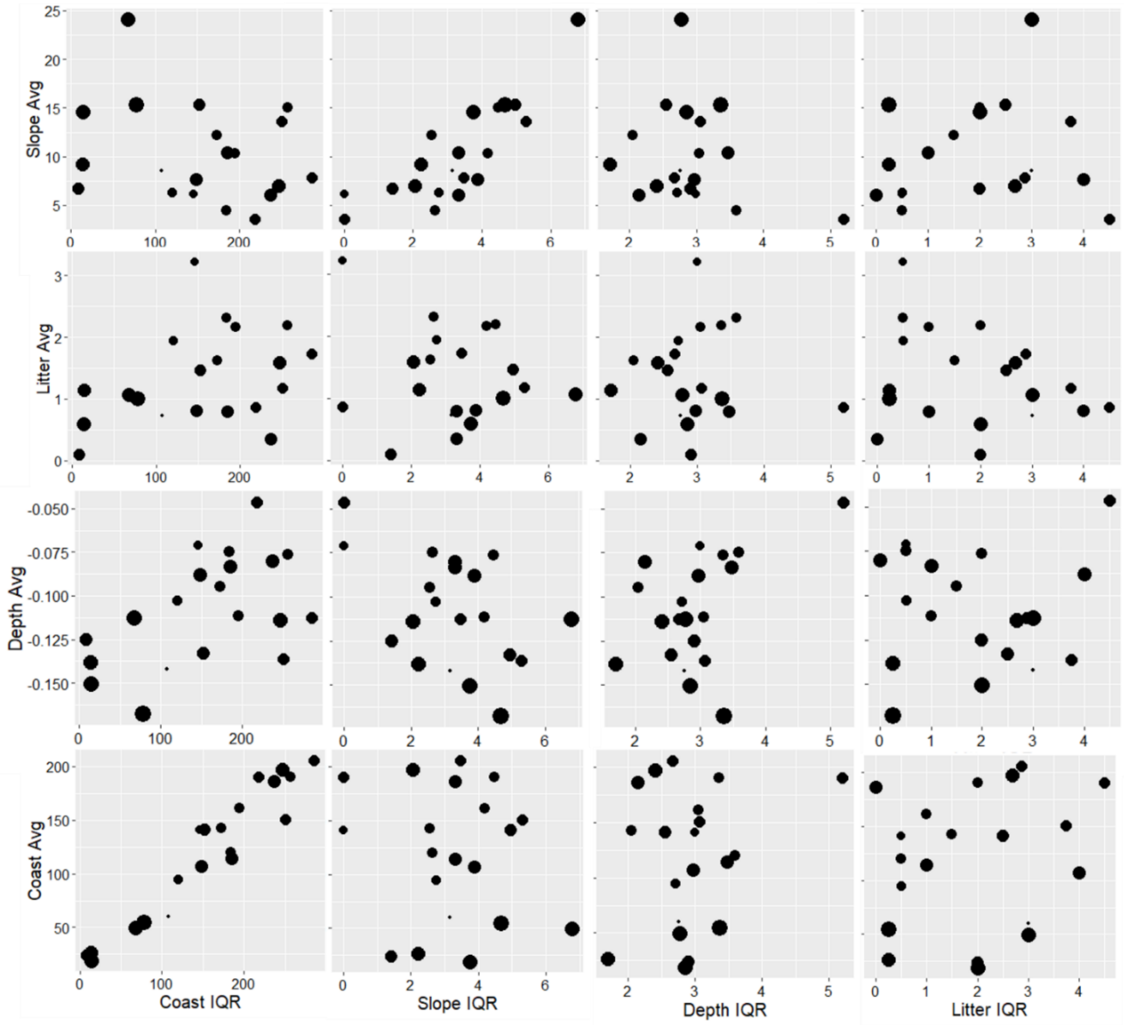


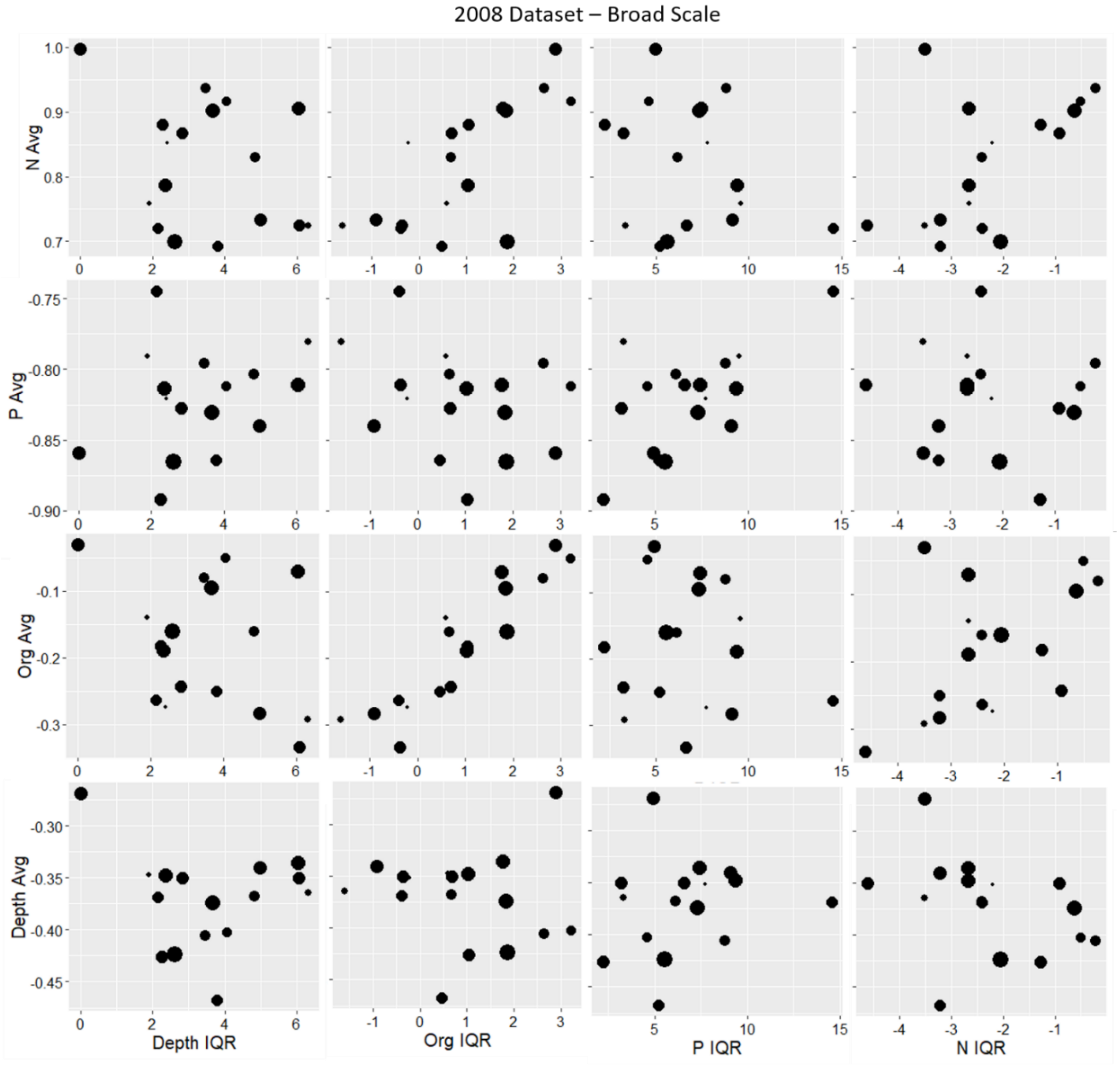

2017 Dataset – Fine Scale
Depth Avg
Moist Avg
Litter Avg
Elev Avg
Moist IQR
Elev IQR
Litter IQR
Depth IQR
0
10
20
30
40
50000
100000
150000
25
50
75
100
2000
4000
6000
3
6
9
-5
-4
-3
-2
-1
2
4
6
8
0.0
2.5
5.0
7.5

2017 Dataset – Very Fine Scale

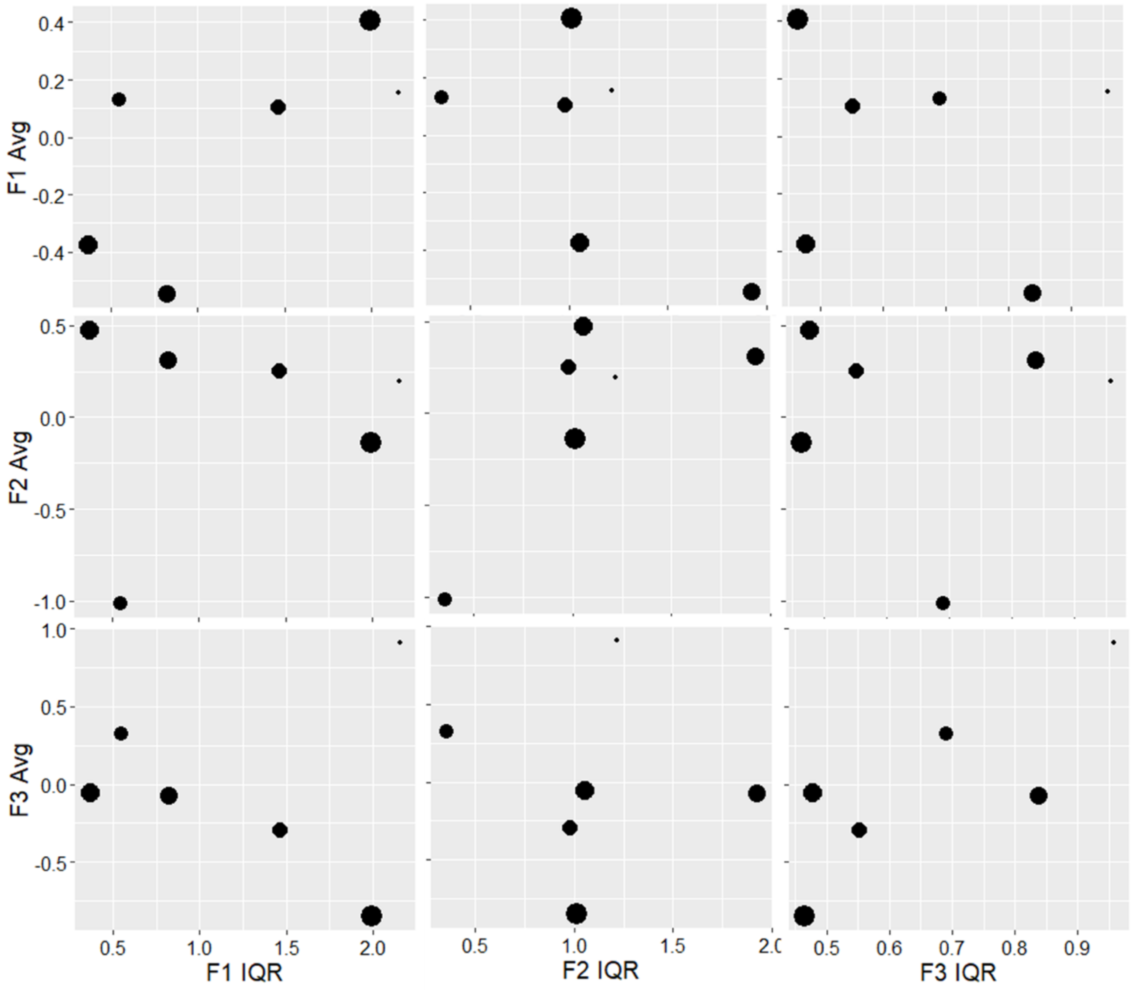


2011 Dataset – Broad Scale

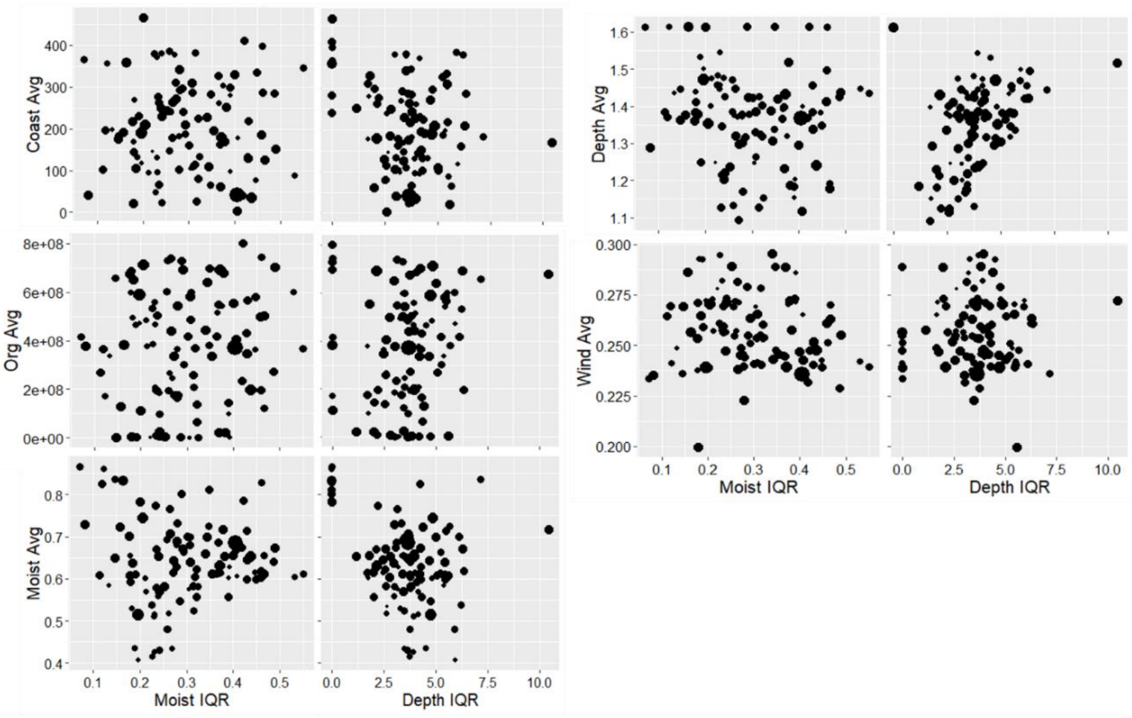



2008 Dataset – Broad Scale
N Avg
P Avg
Org Avg
Depth Avg
Depth IQR
Org IQR
P IQR
N IQR
1.0
0.9
0.8
0.7
-0.75
-0.80
-0.85
-0.90
-0.1
-0.2
-0.3
-0.30
-0.35
-0.40
-0.45
0
2
4
6
-1
0
1
2
3
5
10
15
-4
-3
-2
-1

2005 Dataset – Broad Scale



2005 Dataset – Fine Scale



# Chapter 4

## Changes in plant community composition and functional plant traits over a four-year period on an extensive green roof

### Abstract

A novel area of research concerning plant community dynamics is the application of ecological theory to constructed ecosystems. Unlike natural ecosystems, which form due to a variety of factors, humans control the initial vegetative profile in constructed ecosystems. Since these man-made plant communities have not been subjected to the same checks and balances as vegetation in naturally occurring plant communities, how these constructed ecosystems change over time offers an interesting perspective into plant community dynamics. The goal of this chapter was to determine how green roof plant communities and functional plant traits change over time in response to spatial heterogeneity. I predict that treatments with greater spatial heterogeneity will have higher functional diversity, increasing potential coexistance between co-occurring species. This four-year experiment contained four substrate depth treatments: three treatments with a homogenous substrate depth of 5 cm, 10 cm, and 15 cm, and one treatment with a heterogenous substrate depth that varied between 5 cm and 15 cm (5/15 cm). The quantity of substrate in the 10 cm treatment and 5/15 cm treatment was equal. Data on species abundance was collected for each growing season and a green roof trait database was created using individuals living in plant communities outside the experimental system. Data analysis examined the relationship between functional traits and spatial heterogeneity, as well as patterns concerning species richness/abundance and spatial heterogeneity. By the end of this four-year experiment, variation occurred between treatments for community composition and functional diversity, with the greatest species richness observed in the least stressful treatment (15 cm) and the greatest functional diversity observed in the most stressful treatment (5 cm). Additionally, each treatment varied from its original planting scheme, with all treatments decreasing in functional diversity. When the heterogenous 5/15 cm treatment was compared to the homogenous 10 cm treatment, two distinct plant communities were observed. Furthermore, the 5/15 cm treatment contained species that were taller, a trait value associated with reduced stormwater runoff and substrate temperature. This finding indicates that creating green roofs with a heterogenous substrate depth could improve overall green roof function without increasing roof weight.

## Introduction

One of the goals of community ecology is to understand the factors contributing to the formation of species richness, composition, and abundance within a plant community (Kraft and Ackerly, 2014). One key area of research within community ecology is the investigation into why and how plant communities change over time. In the natural environment, plant communities are dynamic, with community composition influenced by both spatial and temporal heterogeneity (Sousa, 1984; Chesson et al., 2004), leading to variation in the composition of plant communities over time. For example, disturbance can open a habitat to new populations, the introduction of invasive species can lead to competitive exclusion, and demographic stochasticity plays a role in determining which individuals persist in the environment (White, 1979; Pyšek et al., 2012; Martorell and Freckleton, 2014). A novel area of research concerning plant community dynamics is the application of ecological theory to constructed ecosystems (Heim et al., 2021). Plant-based constructed ecosystems are man-made environments usually constructed for a specific function and often designed with a focus on efficiency rather than ecological complexity (Lundholm et al., 2015). Examples include green walls, green roofs, rain gardens, and retention wetlands, which are frequently characterized by low species diversity and a man-made growing medium (Lundholm et al., 2015; Heim et al., 2021). Unlike natural ecosystems, which form due to a variety of factors (species pool, demographic stochasticity, disturbance) (White, 1979; Zobel, 2016; Marteinsdóttir et al., 2018), humans control the initial vegetative profile in constructed ecosystems. Since these man-made plant communities have not been subjected to the same checks and balances as vegetation in naturally occurring plant communities, how these constructed ecosystems change over time offers an interesting perspective into plant community dynamics.

Examining plant communities through the functional trait lens can provide insight into the factors contributing to change over time (Auffret et al., 2017). Furthermore, the use of multiple trait analysis, specifically community weighted means, and functional diversity, allows researchers to examine the multitude of factors contributing to coexistence in a dynamic environment. For example, changes in the community weighted mean of a trait reveals which trait values were preferable for persistence and reproduction (Fried et al., 2019). This was observed in a study by Auffret et al. (2017), who found that, over a 100-year period, taller plant species and those with seeds that could persist in the seed bank were more likely to persist and coexist post-grazing in a Baltic Sea archipelago (Auffret et al., 2017). Changes over time in functional trait diversity can indicate whether a population was influenced by habitat filtering (low functional diversity) or limiting similarity (high functional diversity) (Katabuchi et al., 2012; Cross et al., 2015). In both scenarios, divergence in specific functional traits indicates how coexistence is maintained, with convergence in specific functional traits indicating what trait values are necessary for survival. Maire et al. (2012) used functional diversity analysis to examine community assembly in a grassland plant community. The authors found that the community was complex, with both habitat filtering and limiting similarity active in driving community composition (Maire et al., 2012).

In both natural and constructed ecosystems, changes in species diversity and functional traits are usually due to three factors: immigration, extirpation, and persistence (Auffret et al., 2017). Since urban areas contain a mosaic of diverse urban ecosystems (parks, green walls, green sidewalks, rain gardens, abandoned lots), immigration regularly occurs between these various habitats, with weedy ruderals such as *Taraxacum* spp (dandelion), *Trifolium* spp. (clover), and *Digitaria* spp. (crab grass) commonplace (Dickinson and Royer, 2014). In order to successfully colonize a new environment, a species must be capable of dispersing to a suitable habitat in which they can persist and reproduce (Gallien et al, 2015). Furthermore, incoming species should either occupy an unused niche or be more competitive than the species currently occupying their niche (competitive exclusion) (Gallien et al, 2015). Here, a species niche is defined as all of the biotic and abiotic factors that allow a species to persist and reproduce (Silvertown, 2004). Since the initial plant community in constructed ecosystems is artificially created, there is a need to understand how these unique plant compositions will change over time.

The goal of this chapter was to determine which functional traits and species can coexist in the green roof environment. Specifically I aim to understand how green roof plant communities and, in turn, functional plant traits, change over time in response to environmental stress and heterogeneity. On a green roof, lower substrate depth (in comparison to roofs with a higher substrate depth) is associated with stressful growing conditions, as plants are subjected to higher substrate temperature and desiccation (Chenot et al., 2017). Here, I use substrate depth to manipulate environmental stress and heterogeneity. This four-year experiment contained four substrate depth treatments: three treatments with a homogenous substrate depth of 5 cm, 10 cm, and 15 cm, and one treatment with a heterogenous substrate depth that varied between 5cm and 15 cm (5/15 cm). At the beginning of the study, I established the same suite of 14 species in each treatment. These species represent a range of functional types, allowing me to examine the trait responses to these four treatments.

## Methods

This study took place between May 2014 and September 2018 on the five-story green roof at Saint Mary's University (44°39′N, 63°35′W) in Halifax, Nova Scotia. This experiment lies adjacent to a 24 x 9 m extensive green roof and a modular green roof system. The extensive green roof contains a variety of weedy ruderals (*Erigeron* spp., *Poa compressa*), graminoids (*Festuca rubra*, *Danthonia spicata*), forbs (*Solidago bicolor*, *Symphyotrichum novi-belgii*), and creeping shrubs (*Sibbaldia tridentata*) (Buckland-Nicks et al., 2016; Walker and Lundhom, 2018). The neighboring modular green roof experiment contains 11 vascular species (Chapter 3), four of which (*Sedum album*, *Sedum sexangular, Phedimus spurius*, *Solidago puberula,*) were not included in the suite of 14 species originally established in this experiment. The surrounding ground-level vegetation is primarily managed lawn (Dominant vegetation: *Poa pratensis, Trifolium repens*) (Lundholm and Marlin, 2006) and scattered trees (*Ulmus glabra*, *Acer platanoides*). The region has a yearly average precipitation between 45.1mm – 8.4mm and an average yearly temperature between -27.3°C – 10.9°C (Government of Canada, 2019).

### ***Treatments***

This study consisted of four substrate depth treatments: three homogenous treatments with substrate depths of 5 cm, 10 cm, and 15 cm; and a heterogeneous treatment which had distinct patches of 5 cm and 15 cm depths (5/15 cm). Each treatment was replicated six times and the quantity of substrate in both the 10 cm and 5/15 cm treatments was equal. All treatments were contained in baseless wooden planter boxes (61x61x15 cm) placed atop a nursery-grade weed control fabric (Quest Home & Garden, Mississauga, ON, CA). Substrate depth was manipulated using 5 cm thick concrete slabs, with two concrete slabs (60.96 x 60.96 cm) placed in the 5 cm treatment, one in the 10 cm treatment and none in the 15 cm treatment. For the 5/15 cm treatment, four 5 cm thick concrete slabs (30.48x30.48 cm) were placed two-high diagonally across from each other (creating a depth of 15 cm and 5 cm). A root barrier/water retention fleece was placed in all boxes above the concrete slabs (EnkaRetain and Drain 3111®, Colbond Inc., NC, USA). The boxes were filled to the rim with Sopraflor X substrate (Soprema Inc., Drummondville, QC, CA). The first half of the substrate in each treatment contained substrate from Heim and Lundholm (2014), with boxes filled to the brim with new Sopraflor X substrate (Figure 4.1).

**Figure 4.1.** Experiment before and after planting. The image on the left shows the homogenous 15 cm treatment (left planter box) adjacent to the heterogenous 5/15 cm treatment (right planter box). The image on the right shows the community composition at the end of the first growing season, August 2018.

### *Plant Species*

Between May and September 2014, two individuals each of *Vaccinium angustifolium*, *Maianthemum canadense, Luzula multiflora, Danthonia spicata*, *Solidago bicolor, Vaccinium macrocarpon, Avenella flexuosa,* and *Empetrum nigrum* were transplanted into each replicate. Additionally, 100 seeds each of *Sagina procumbens, Anaphalis margaritacea, Plantago maritima, Sibbaldia tridentata, S. bicolor, D. spicata,* and *A. flexuosa* were also added to each treatment. Transplants were taken from previous green roof experiments conducted at Saint Mary's University. Seeds were collected from the green roof at Saint Mary's University and from the coastal barren site Chebucto Head, Nova Scotia (34°30′ N, 63°31′W). The soil taken from Heim and Lundholm (2014) contained seed and root fragments of *Festuca rubra* and *Sedum acre*. During 2014, treatments were weeded and irrigated once a week (both *F. rubra* and *S. acre* were weeded out at this time). After October 2014, all irrigation occurred through natural precipitation and the treatments were no longer weeded.

### *Data Collection*

Between 2015 and 2018, aboveground biomass for each species, in each treatment, was estimated using the point intercept method (Floyd and Anderson, 1987) in order to provide an estimate of the abundance of each species (canopy density). Biomass data were collected from four sections of each treatment (i.e. each replicate contained four 30.5x30.5 cm subplots) with five interception points per subplot. These data were collected once a month during the growing season (May, June, July, August). At the end of the study (September 2018), all above-ground biomass in each treatment was harvested, separated by species, dried, and weighed.

For every species observed, five traits were measured from representative individuals of each species (i.e., not from the individuals within the treatments): seed weight, specific leaf area, leaf dry matter content, leaf thickness, and plant height (methods: Pérez-Harguindeguy et al., 2016). These traits were chosen due to associations with growth (specific leaf area), resource use (leaf dry matter content), drought tolerance (leaf thickness, specific leaf area, leaf dry matter content, plant height), and reproduction (seed weight) (Poorter and Garnier, 1999; Niinemets, 2001; Wright et al., 2001; Tardy et al., 2015; Vile et al., 2005; Moles et al., 2009; Pérez-Harguindeguy et al., 2016; Wang et al., 2019). The majority of traits were measured from 10 healthy adult individuals, exposed to full sun, from locations around Halifax, NS where these species spontaneously occur: green roofs (Saint Mary's University), dwarf heath (Chebucto Head), and urban green space (Saint Mary's University, Sir Sandford Fleming Park). To reflect the size of colonizing trees observed in this study, functional traits were collected from tree seedlings. Except for *Pinus sylvestris* (only one individual observed in one 10cm treatment during 2015 and 2016), all tree seedlings were less than 8 cm tall. However, due to a lack of *P. sylvestris* seedlings, the average height of this species was determined from seedlings which varied between 4.4 – 25.3 cm.

For four colonizing species, *Aquilegia canadensis*, *Stellaria media*, *Hylotelephium telephium*, and *Hypericum perforatum*, seed traits could not be collected. Therefore, seed traits for these species were calculated from seeds purchased from two different vendors (Salt Spring Seeds, BC, CA - *S. media, H. telephium, H. perforatum;* High Country Gardens, VT, USA – *A. canadensis*). For one colonizing species, *Aquilegia canadensis* (only one individual observed in one 5/15 cm treatment), no native populations were found. For this species, previous research was used to determine specific leaf area (Shipley, 2002) and height (Roland et al., 1998). Leaf thickness was determined from five individuals grown from seed, and leaf dry matter content was calculated as the average leaf dry matter content from all individuals in this study. For four colonizing species, seeds could not be collected from 10 individuals (*Elymus repens* (*n=9*), *Sedum sexangulare* (*n=9*), *Fragaria virginiana* (*n=7*), *S. sempervirens* (n=8).

### ***Statistical Analysis***

Functional diversity, functional evenness, functional richness, and community weighted means (CWM) were calculated using the FD package in R (3.6.0) (Laliberté et al., 2015). Functional richness describes the range in functional traits filled by the community, functional evenness describes how evenly traits are distributed in an n-dimensional trait space, and community weighted mean incorporates abundance to calculate a mean value for each trait (Lavorel et al., 2008). Community weighted mean was calculated for each trait: seed weight, specific leaf area, leaf dry matter content, leaf thickness, and plant height. In this study, functional diversity was determined by calculating functional dispersion, the mean distance from a species' position in multidimensional trait space to the centroid of all species (Laliberté and Legendre, 2010). Functional diversity was calculated from the combination of all traits (total) and for each individual trait: seed weight, specific leaf area, leaf dry matter content, leaf thickness, and plant height.

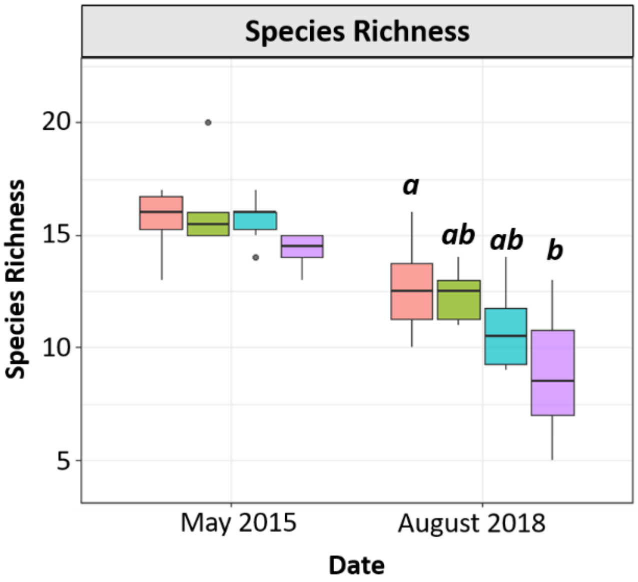
One-way ANOVA and Tukey post-hoc tests were used to determine if treatments differed in functional diversity, functional evenness, functional richness, community weighted means (CWM) and richness/abundance of colonizing species.  Data were checked for normalcy using a Shapiro–Wilk test with data transformed when $P<0.05$. Using the canopy density data, non-metric multidimensional scaling ordination (NMDS) with three dimensions was used to graphically depict variation in community structure by treatment, with permutational multivariate analysis of variance (PERMANOVA) used to test for statistically significant differences between treatments.

## Results

### *Community Composition and Diversity*

In total, 45 vascular plant species were observed: 15 intentionally established species and 30 colonizing species. Species richness was highest in the 15 cm treatment followed by the 5/15 cm, 10 cm, and 5 cm treatments (Figure 4.2). The functional traits of colonizing species were similar to intentionally planted species (Figure 4.3). By the end of the fourth growing season, there was a consistent set of dominant species across the substrate depth treatments: in order of highest biomass; 15 cm: *F. rubra*, *D. spicata*, *Trifolium dubium*, *S. tridentata*, *S. bicolor*; 5/15 cm: *F. rubra*, *D. spicata*, *S. acre*, *S. tridentata*, *T. dubium*; 10 cm: *D. spicata*, *S. acre*, *S. tridentata*, *F. rubra*, *T. dubium*; 5 cm: *S. acre*, *F. rubra*, *R. rosea*, *D. spicata*, *S. tridentata*. Out of these species (in 2018), *F. rubra* had greater biomass in the 5/15 cm treatment and the 15 cm treatment than in the 5 cm and 10 cm treatments. *D. spicata, S. bicolor,* and *S. tridentata* had lower biomass in the 5 cm treatment than in all other treatments. *S. acre* had greater biomass in the 5 cm treatment than in all other treatments, and the 15 cm treatment had less *S. acre* than all other treatments. At the very end of the study, *R. rosea* had more biomass in the 5 cm treatment than in all other treatments. For *T. dubium*, no substantial differences were observed between treatments (Table 4.1). Additionally, by the end of the study (August

2018), the richness (f-value 2.03, p-value 0.142) and abundance (f-value 2.035, p-value 0.141) of colonizing species did not vary between treatments.



**Appendix 4.2.** Boxplot showing species richness for the beginning and end of the study. The letters represent results from Tukey post-hoc tests for which treatment is the independent variable and functional richness/evenness is the dependent variable. Bars that share a letter have a p-value >0.05.

**Table 4.1.** Total species percent biomass (May - August) for 2018 for the five most abundant species in each treatment. For each treatment, those species in bold are the most abundant. Code: intentionally planted species (I) and colonizing species (C).

| **Species** | **I/C** | **15 cm** | **5/15 cm** | **10 cm** | **5 cm** |
|---|---|---|---|---|---|
| *Danthonia spicata* | I | 15.97 | 14.46 | **23.51** | 7.98 |
| *Festuca rubra* | I | **31.86** | **33.17** | 8.72 | 14.83 |
| *Rhodiola rosea* | I | 1.82 | 3.18 | 3.6 | 10.55 |
| *Sedum acre* | I | 2.23 | 9.18 | 15.92 | **31.84** |
| *Sibbaldia tridentata* | I | 7.83 | 7.88 | 11.36 | 5.89 |
| *Solidago bicolor* | I | 7.08 | 6.36 | 6.02 | 3.71 |
| *Trifolium dubium* | C | 8.63 | 7.61 | 7.48 | 5.23 |

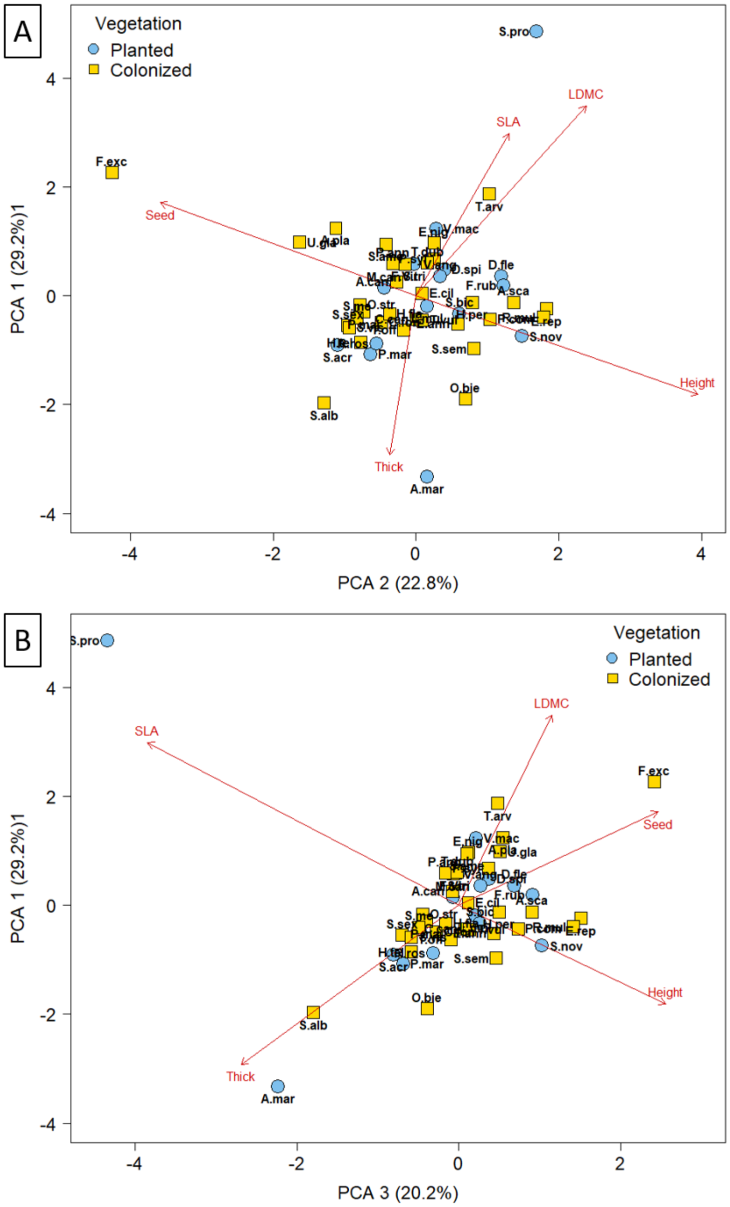


**Figure 4.3.** PCA biplots using functional traits for all species observed in this study: Specific leaf area (SLA), leaf dry matter content (LDMC), leaf thickness (thick), plant height (height), and seed weight (seed). A) shows axes 1 and 2; B) shows axes 1 and 3. The graphs separate species into those intentionally planted (planted) and weedy colonizers (colonized). For this analysis, only axes 1, 2, and 3 had a standard deviation greater than 1. Species code: first letter of genus and first three letters of species (See appendix 4.B for species list).

Overall composition of the communities diverged from 2015 to 2018. The 15 cm and 5 cm treatments diverged most ($R^2$=0.55966, P=0.003996), with the 5/15 cm and 10 cm treatments having intermediate species composition ($R^2$=0.31953, P=0.004995). The 5 cm treatment was dominated by stress-tolerant succulents while the 15 cm treatment was characterized by higher abundances of species associated with more fertile environments, the 5/15 cm treatment had a lot of overlap with the 10 cm treatment but tended to have higher abundances of more competitive species such as *F. rubra* and *S. novi-belgii*, whereas the 10 cm treatment tended to have more biomass of succulents and other stress-tolerant species such as *D. spicata* (Figure 4.4).

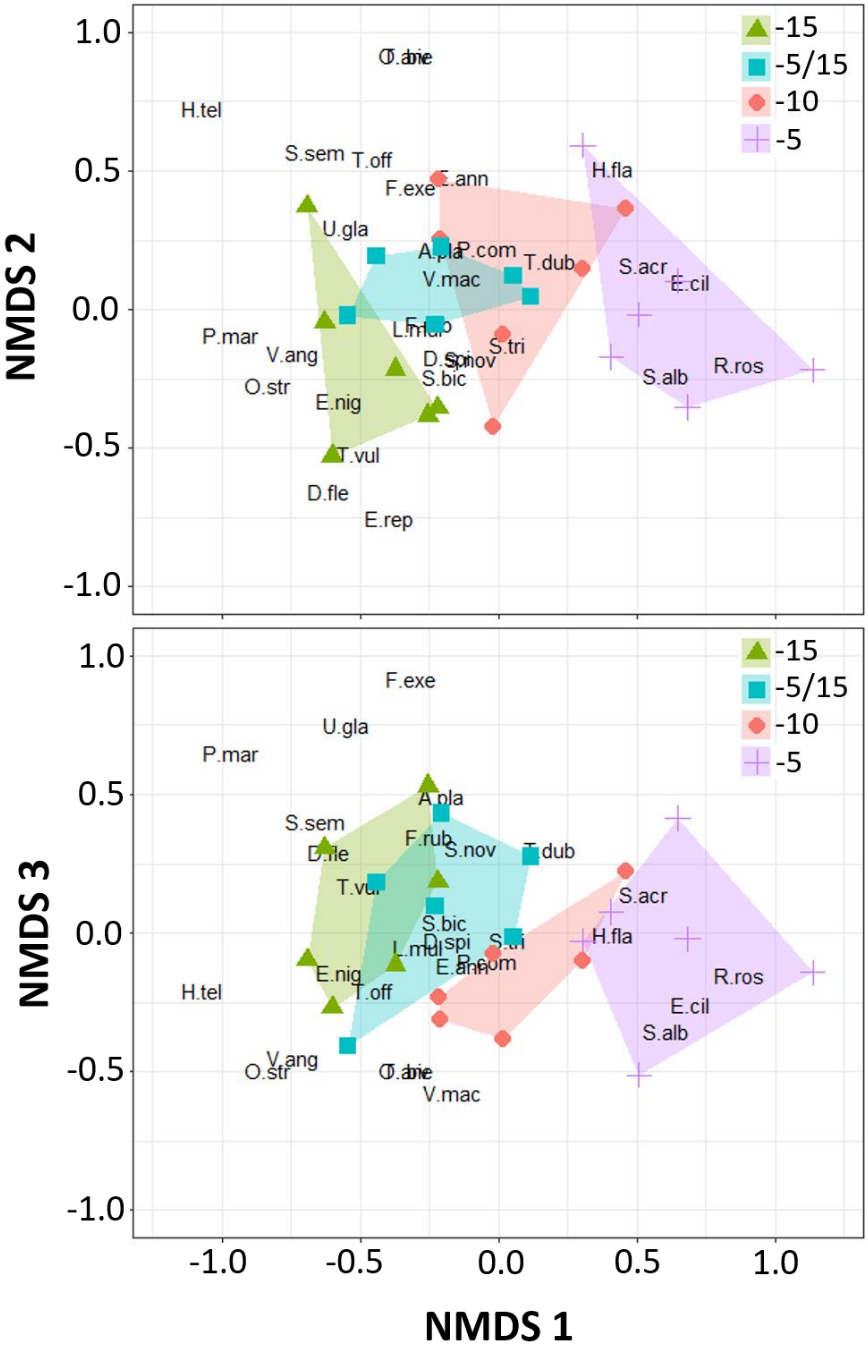


**Figure 4.4.** NMDS calculated from canopy density data taken at the end of the study period (August 2018) for all four treatments (15 cm, 5/15 cm, 10 cm, 5 cm). In this figure $R^2 = 0.488$ and $P = 0.001$. Species code: first letter of the genus and first three letters of the species.

### *Functional Plant Traits*

All trait data discussed in this section are based on trait data from the database created for this study (See Chapter 2).

The 5 cm treatment contained a plant community with a greater abundance of shorter species than all other treatments in July 2017 and 2018. Additionally, the 10 cm treatment contained a plant community with a greater abundance of shorter species than the 15 cm and 5/15 cm treatments in July 2018. Overall, the 5 cm treatment formed a plant community containing species with thicker leaves (July 2017, 2018), lighter seeds (July 2017, 2018), lower leaf dry matter content (July 2016, 2017, 2018), and lower specific leaf area (July 2018) than all other treatments. Finally, the 5 cm treatment formed a plant community that was more functionally diverse then all other treatments in terms of total functional diversity (July 2017, 2018), leaf thickness (July 2017, 2018), and leaf dry matter content (July 2015, 2016, 2017, 2018) in comparison to all other treatments. Additionally, few differences were observed between treatments for the functional diversity of plant height, seed weight, and specific leaf area (Figure 4.5).

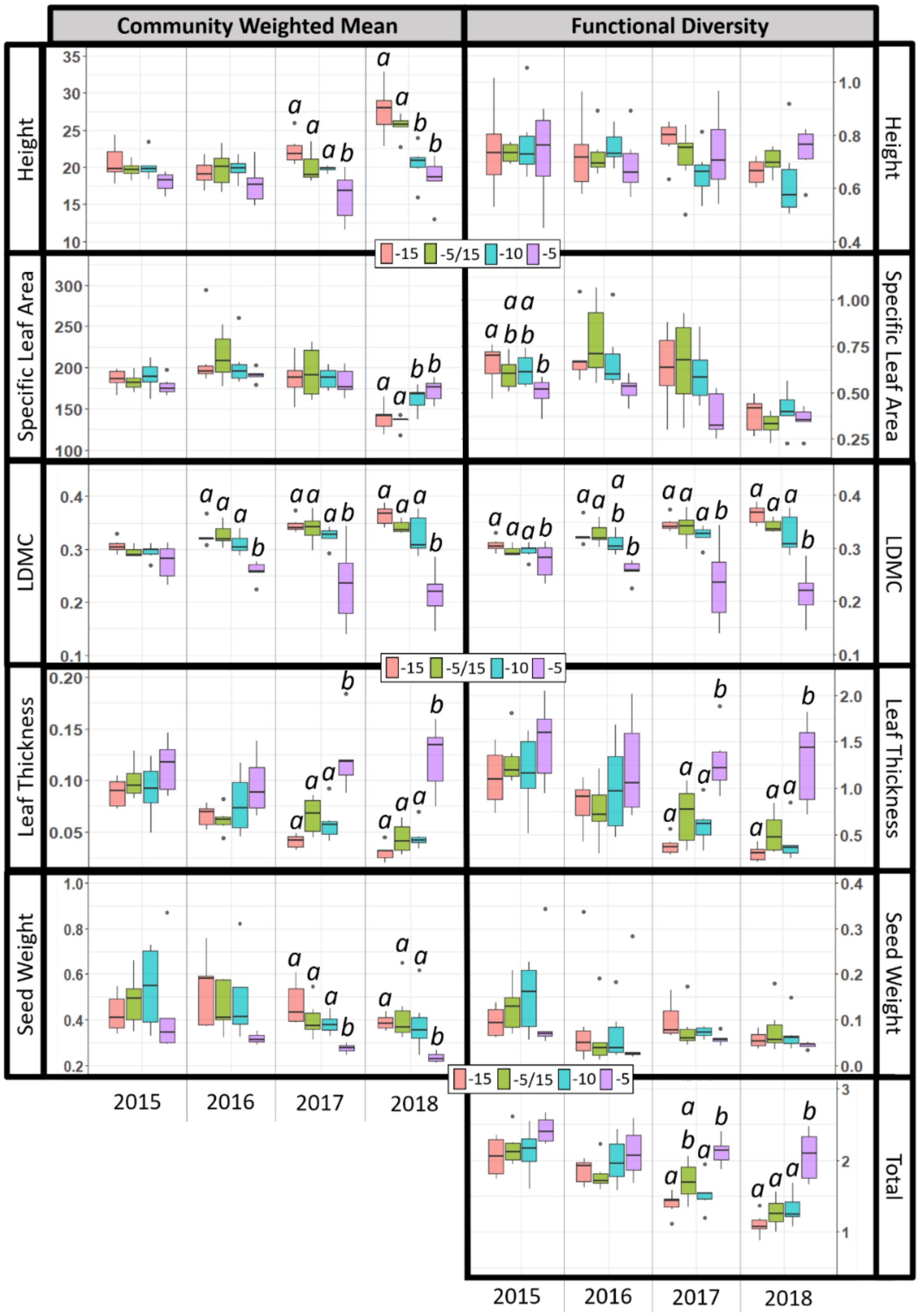


**Figure 4.5.** Comparison between treatments for the community weighted mean and functional diversity of each trait (height, spesific leaf area, leaf dry matter content (LDMC), leaf thickness, seed weight, and the functional diversity of all traits (total) for July 2015-2018. The letters represent results from Tukey post-hoc tests for which functional traits are the independent variables and treatment is the dependent variable. Bars that share a letter have a p-value >0.05.

When community weighted means for July 2018 were analyzed at the subplot scale, diferences were observed between treatments. The subplots containing the tallest species were the 15 cm and 5/15-15 cm subplots. The lowest leaf dry matter content was found in the 5 cm subplots, the lightest seeds were found in the 5/15-5 cm and 5 cm subplots, the lowest specific leaf area was found in the 5/15-5 cm and 5 cm subplots, and the species with the thickest leaves were found in the 5 cm subplots (Figure 4.6).

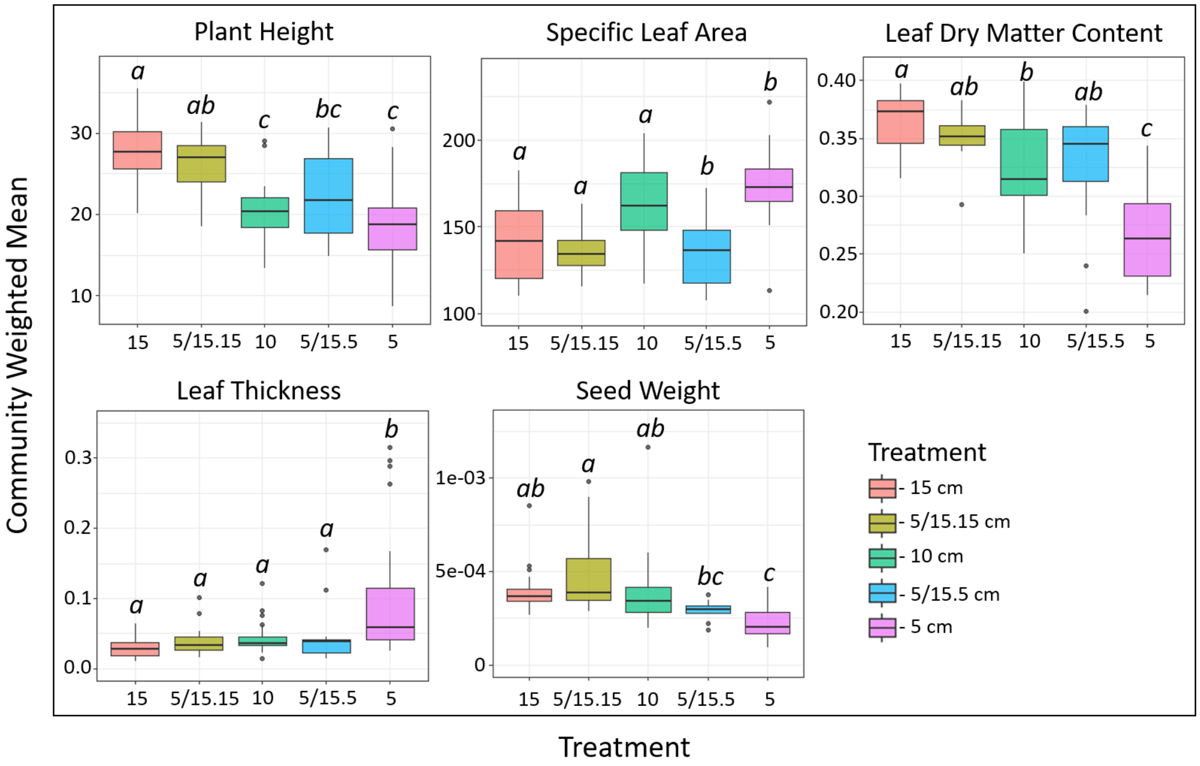


**Figure 4.6.** Comparison between soil depth treatment and community weighted means when treatments were analyzed by subplot for July 2018. The letters represent results from Tukey post-hoc tests for which functional traits are the dependent variables and treatment is the indpendent variable.  Bars that share a letter have a p-value >0.05.

When functional diversity variables were compared between the beginning and end of the study several patterns emerged. All functional diversity variables, except for height in the 5 cm treatment, had higher average values in July 2015 than in July 2018. For community weighted means, plant height was the only variable that was greater for all treatments in 2018 than in 2015 and seed weight was the only variable that was lower for all treatments in 2018 than in 2015. For specific leaf area and leaf thickness, all but the 5 cm treatment, which showed little variation between dates, formed plant communites with higher specific leaf area and leaf thickness in 2015 than in 2018. Finally, only the 5 cm treatment formed a plant community with higher leaf dry matter content in 2015 as opposed to 2018 (Figure 4.7).

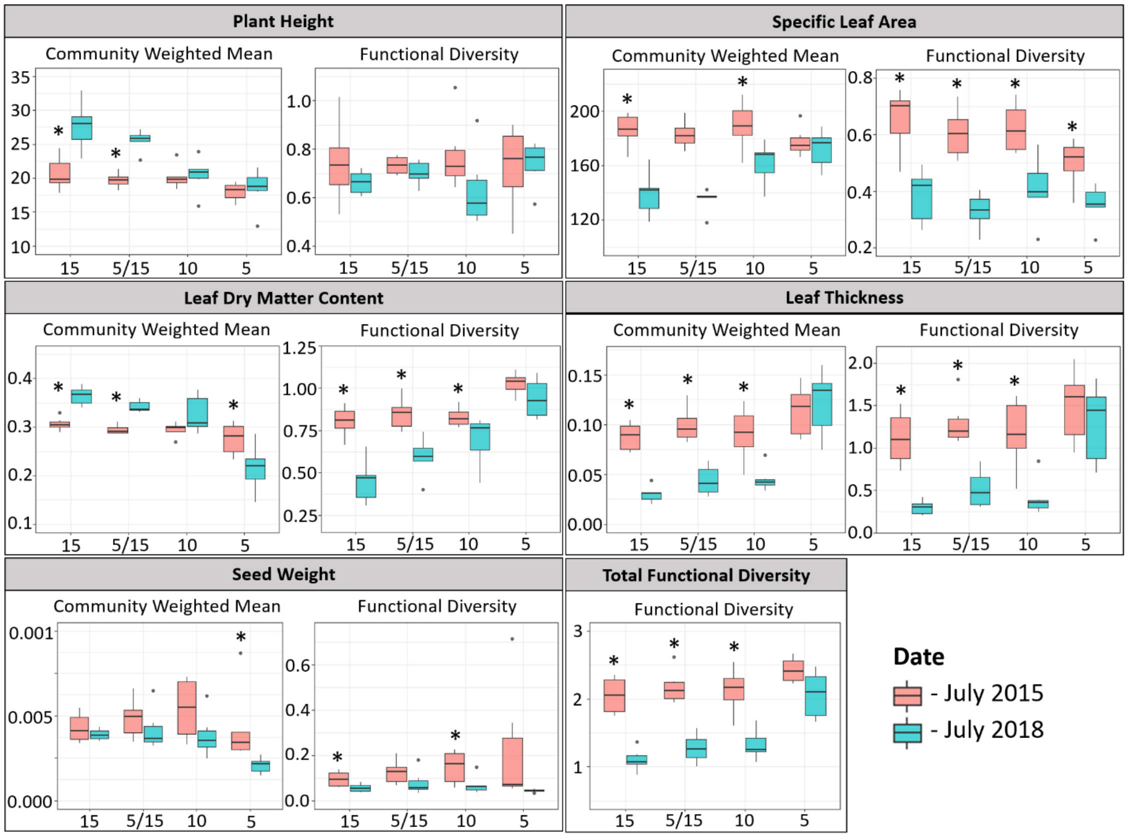


**Figure 4.7.** Comparison between functional diversity and community weighted means for each treatment for the first (July 2015) and last year (July 2018) of the study. Trait data includes specific leaf area, leaf dry matter content, seed weight (g), leaf thickness (cm), and plant height (cm). The * represent results from ANOVA tests for which the p-value is >0.05.

## Discussion

Since variation in plant functional traits can encourage coexistence, the goal of this chapter was to examine how trait diversity changed over time in four soil depth treatments. By the end of the study all treatments had decreased in functional trait diversity and species richness. This result is likely due to a filtering effect with each treatment filtering out specific trait values. Furthermore, little variation in functional diversity or species richness was observed between the homogenous 10 cm treatment and the heterogenous 5/15 cm treatment (containing the same quantity of substrate). This finding indicates that for the majority of species spatial heterogeneity is not the main factor encouraging coexistence in this system.

Overall, all treatments differed from their original community composition, with the largest variation observed along the stress gradient. Specifically, the 5 cm and 15 cm treatments showed minimal overlap in terms of species composition and abundance, with the 5 cm treatment containing a greater abundance of *S. acre* and *R. rosea,* and the 15 cm treatment containing a greater abundance of *T. dubium* and *S. bicolor*. This variation reflects the high stress present in the 5 cm treatment, as the succulents, *R. rosea* and *S. acre,* are stress-tolerant specialists that prefer an exposed, shallow substrate environment. When the heterogeneity gradient is compared, variation in the community composition of the heterogenous 5/15 cm treatment and homogenous 10 cm treatment was less distinct. Even so, the plant communities that emerged from these two treatments contained pronounced differences in specific functional traits and species abundance. Specifically, *F. rubra,* the tallest of the seven most abundant species, had greater abundance in the 5/15 cm treatment than the 10 cm treatment.

### ***Colonizing Species***

Since the majority of the 45 species observed in this study were found in every treatment, many of these species were likely generalists, capable of germinating in a substrate depth of 5-15 cm. Even so, species relative abundance varied between treatments, with succulents dominant in the 5 cm substrate depths and tall herbaceous species dominant in the deeper substrate depths. Furthermore, 67% of the species observed in this study naturally colonized this system. This result is similar to what was observed by Vanstockem et al. (2019), who found that 77% of the species in their green roof survey were not intentionally planted. A 30-year study by Catalano et al. (2016) also observed a high abundance of colonizing species; by the end of their study, the majority of species present on the green roofs had spontaneously colonized. Here, 21 colonizing species were weedy ruderals (forbs and graminoids), six were shrub/tree species, and three were stress-tolerant specialists. The majority of colonizers shared similar functional traits to the intentionally established vegetation, with *Fraxinus excelsior* the only outlier (heaviest seeds in study).

The weedy ruderals observed here are common both at ground level and on the neighboring green roof. The high prevalence of these species is likely due to their ability to disperse via wind and produce seed within one growing season (Dickinson and Royer, 2014). A survey of 129 green roofs in Belgium also found ruderals to be the most common colonizers (Vanstockem et al., 2019). By the end of this study, only a single colonizing species, the ruderal *T. dubium*, recorded high abundance in all treatments. This is particularly interesting because ruderals generally prefer disturbed, but low stress environments (Grime, 2001). The similarity in the abundance of *T. dubium* in the low stress 15 cm treatment and high stress 5 cm treatment may be due to the proximity of these treatments, with the individuals in the more productive treatments ensuring seed would reach the less productive treatments. As with the ruderal species, the large dispersal range and high germination rate of the colonizing trees and shrubs likely resulted in successful initial establishment (Dickinson and Royer, 2014). Local populations of these woody species can be found at ground level, with wind and birds responsible for their access to the green roof (Miller et al., 2014). However, due to the harsh green roof conditions, shallow soil depth and high wind, it is unlikely that these species would have survived to adulthood (Vanstockem et al., 2019). The three specialists, *Sedum sexangulare*, *Sedum album*, and *Solidago sempervirens*, all have populations on the neighboring green roof. Both *Sedum* species have successfully colonized the white rock roof surrounding the green roof. This rock roof contains zero substrate, an indication that, over time, these *Sedum* species could have dominated the 5 cm substrate (Vanstockem et al., 2019). Finally, two species, *Fragaria vesca* and *Aquilegia canadensis*, occurred in only one location through the duration of the study. As these species were originally grown with some of our intentionally planted species, introduction to the roof likely occurred when transplanting took place. Their survival through the first year of weeding was likely due to viable roots within the substrate.

### ***Functional Traits***

The most interesting result from the functional trait analysis was the difference in the community weighted mean of plant height between the 5/15 cm and 10 cm treatments, with the 5/15 cm treatment consisting of a plant community that was around 5 cm taller. Since the 5/15 cm treatment contained the same quantity of substrate as the 10 cm treatment, this finding suggests that differences in heterogeneity led to the development of two distinct plant communities. When the abundance data are examined, the only species that differed between these treatments was *F. rubra*, which had higher abundance in the 5/15 cm treatment. This species is the tallest of the five most abundant species that occurred in these two treatments and was likely the main reason why the community weighted mean of height differed. The success of *F. rubra* in the 5/15 cm treatment was likely due to growth characteristics, with roots accessing resources in the deeper substrate enabling shoots to survive in the shallow substrate. Previous research has also found that *F. rubra* excels in heterogenous substrates (Heim and Lundholm, 2014; Roulston et al., 2020), indicating that soil depth heterogeneity could be one of the components present on the niche axis of this species. Previous research has also found that particular species excel in more heterogeneous environments (Tamme et al., 2010). For example, a study by Pärtel and Helm (2007) in a temperate grassland found that soil depth heterogeneity increased the competitive advantage of woody species (Pärtel and Helm, 2007).

When all four treatments were compared, the greatest differences were observed for the treatment under the greatest environmental stress, the 5 cm treatment, which contained species with thicker leaves, lighter seeds, shorter stature, and lower leaf dry matter content than all other treatments. Since the 5 cm treatment contained the harshest environmental conditions, the thick leaves and short statures possessed by individuals in this treatment are likely an adaptive strategy to deal with environmental stress. Specifically, thick leaves can help reduce water loss and shorter plants have lower water requirements (Niinemets, 2001; Vile et al., 2005; Moles et al., 2009; Wang et al., 2019). The high presence of individuals with lightweight seeds in the 5 cm treatment is likely due to the dominance of *S. acre* (2018 biomass – 31.84%), which had the third-lowest seed weight in this study (0.0308 mg). Contrary to the previous results, trends for leaf dry matter content and specific leaf area do not reflect patterns associated with drought tolerant strategies. For example, low leaf dry matter content and high specific leaf area are usually associated with fast-growing species in productive environments (Poorter and Garnier, 1999; Tardy et al., 2015; Wright, 2001), conditions that do not reflect the 5 cm treatment. This contrary result may be due to the high density of succulents in this treatment that possess thick leaves high in leaf water content (Vendramini et al., 2002). To test this reasoning, the data were re-analyzed with the succulents removed, resulting in no distinct differences between the 5 cm treatment and all other treatments.

In terms of functional diversity, the treatment with the lowest taxonomic diversity, the 5 cm treatment, had greater functional diversity than all other treatments for leaf thickness, leaf dry matter content, and total functional diversity. This trend is likely due to the almost equal distribution of succulents (2018: 44%) and non-succulents (2018: 56%), as succulents possess very different functional traits to both forbs and graminoids (dominant growth forms in the 15 cm, 5/15 cm, and 10 cm treatments).. A study by Wang et al. (2021) along the Yangtze River in China found similar results, with low taxonomic diversity associated with high functional diversity.

### *Community Assembly*

For all treatments, the decrease in functional richness and functional diversity indicates that specific species were filtered out. The environments in the 15 cm, 5/15 cm, and 10 cm treatments resulted in filtering for species with thinner leaves, heavier seeds, taller stature, higher leaf dry matter content, and lower specific leaf area. This finding is particularly evident in the 15 cm treatment, which had the lowest functional evenness. Since this treatment was exposed to the least amount of stress, more competitive fast-growing species had the resources necessary to increase biomass at a faster rate than was possible in the other treatments. The treatment under the greatest environmental stress, the 5 cm treatment, filtered for succulent species and those of a shorter stature. The low abundance of succulent species in the 15 cm (2018: 4%), 5/15 cm (2018: 12%), and 10 cm (2018: 20%) treatments indicates that this growth form is not competitive at deeper substrate depths, with competition for light likely a limiting factor in dense herbaceous canopies. Similar patterns were observed in Heim and Lundholm (2014), where the succulent *S. acre* was less abundant in regions dominated by the graminoid *F. rubra*. Several studies conducted in Europe also recorded the prevalence of stress tolerant species on roofs with a 5-8 cm substrate depth, with ruderals gaining a competitive advantage at deeper substrate depths (Catalano et al., 2016). The high functional diversity observed in the 5 cm treatment for leaf thickness and leaf dry matter content is indicative of limiting similarity, with species using different strategies to access the limiting resources. For example, succulent leaves allow species to store water and persist through dry periods (*Sedum* spp.), dormancy allows species to survive belowground until conditions become favorable (*S. bicolor*, *Symphyotrichum novi-belgii*), an annual growth form allows species to quickly reproduce during favorable conditions (*Trifolium dubium*, *Erigeron annuus*), and hairy leaves allow species to capture more precipitation (*D. spicata*, *Luzula multiflora*) (Grammatikopoulos and Manetas, 1994; Ripley et al., 2013; Dovrat et al., 2019; Volaire and Norton, 2006). Furthermore, the species/individuals in the 5 cm treatment would need to be more stress-tolerant than was necessary in the other treatments. Since slow growth is a characteristic of species in stressful environments, it is possible that these divergent species had not begun to compete for resources. This reasoning reflects the large patches of bare substrate observed in this treatment.

## Conclusion

By the end of this four-year experiment, variation occurred between treatments for community composition and functional diversity, with the greatest species richness observed in the least stressful treatment (15 cm) and the greatest functional diversity observed in the most stressful treatment (5 cm). Additionally, each treatment varied from its original planting scheme, with all treatments decreasing in functional diversity. This trend likely occurred as each treatment filtered for specific species with specific functional traits. A noticeable trend was the prevalence of succulents in the stressful 5 cm substrate depth, with more competitive species observed in the deeper, less stressful, substrate depths. When the heterogenous 5/15 cm treatment was compared to the homogenous 10 cm treatment, which contained the same quantity of substrate, two distinct plant communities were observed. Furthermore, the 5/15 cm treatment contained species that were taller, a trait value associated with reduced stormwater runoff and substrate temperature (Lundholm et al., 2015). This finding indicates that creating green roofs with a heterogenous substrate depth could improve overall green roof function without increasing roof weight.

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# Appendix

**Appendix 4.A.** List of intentionally planted species with information on how they were added to the study. The term fragment indicates fragments of the species roots, and possibly viable seeds, were present in the substrate at the beginning of the study.

| Species | Authority | Transplants # | Seeds # | Fragments |
|---|---|---|---|---|
| *Vaccinium angustifolium* | Aiton | 2 | 0 | Absent |
| *Rhodiola rosea* | Linnaeus | 2 | 0 | Absent |
| *Maianthemum canadense* | Desfontaines | 2 | 0 | Absent |
| *Luzula multiflora* | (Ehrhart) Lejeune | 2 | 0 | Absent |
| *Danthonia spicata* | (Linnaeus) P. Beauvois ex Roemer & Schultes | 2 | 100 | Absent |
| *Solidago bicolor* | Linnaeus | 2 | 100 | Absent |
| *Vaccinium macrocarpon* | Aiton | 2 | 0 | Absent |
| *Avenella flexuosa* | (Linnaeus) Drejer | 2 | 100 | Absent |
| *Empetrum nigrum* | Linnaeus | 2 | 0 | Absent |
| *Sagina procumbens* | Linnaeus | 0 | 100 | Absent |
| *Anaphalis margaritacea* | (Linnaeus) Bentham & Hooker f. | 0 | 100 | Absent |
| *Plantago maritima* | Linnaeus | 0 | 100 | Absent |
| *Sibbaldia tridentata* | (Aiton) Paule & Soják | 2 | 100 | Absent |
| *Festuca rubra* | Linnaeus | 0 | 0 | Present |
| *Sedum acre* | Linnaeus | 0 | 0 | Present |

**Appendix 4.B.** Average functional plant traits for all species in this study (*n=10 individuals*) collected from the field. For one colonizing species, *Aquilegia canadensis*, no native populations were found. Therefore, for this species, specific leaf area and height were determined by referencing previous research (specific leaf area (Shipley, 2002); height (Roland et al., 1998)). Leaf thickness was determined from five individuals grown from seed, and leaf dry matter content was calculated as the average leaf dry matter content from all individuals in this study. For four colonizing species, seeds could not be collected from 10 individuals. Therefore, we collected seeds from as many individuals as could be found (*Elymus repens* (*n=9*), *Sedum sexangulare* (*n=9*), *Fragaria virginiana* (*n=7*), *S. sempervirens* (n=8).

| Species | Seed Weight (g) | Plant Height (cm) | Specific Leaf Area | Leaf Dry Matter Content | Leaf Thickness (cm) |
|---|---|---|---|---|---|
| *Acer platanoides* | 0.013162 | 4.64 | 222.76 | 0.402854 | 0.0274 |
| *Agrostis scabra* | 4.48E-05 | 41.34 | 373.67 | 0.344872 | 0.0109 |
| *Anaphalis margaritacea* | 2.62E-05 | 30.11 | 143.26 | 0.229873 | 0.0643 |
| *Aquilegia canadensis* | 0.000719 | 10 | 342 | 0.282105 | 0.0185 |
| *Cerastium fontanum* | 0.000115 | 13.35 | 364.47 | 0.13696 | 0.032 |
| *Erigeron canadensis* | 4.81E-05 | 21.32 | 287.70 | 0.183718 | 0.0226 |
| *Danthonia spicata* | 0.000697 | 18.83 | 152.131 | 0.385142 | 0.0126 |
| *Avenella flexuosa* | 0.000223 | 33.09 | 612.77 | 0.420471 | 0.0206 |
| *Elymus repens* | 0.003483 | 55.37 | 156.96 | 0.385073 | 0.0286 |
| *Empetrum nigrum* | 0.000595 | 9.3 | 112.88 | 0.492491 | 0.04239 |
| *Epilobium ciliatum* | 8.94E-05 | 17.27 | 218.73 | 0.280349 | 0.0195 |
| *Erigeron annuus* | 3.84E-05 | 31.77 | 188.88 | 0.2253 | 0.0267 |
| *Festuca rubra* | 0.000306 | 35.99 | 97.55 | 0.396002 | 0.00507 |
| *Fragaria virginiana* | 0.000416 | 7.22 | 185.16 | 0.366313 | 0.0266 |
| *Fraxinus excelsior* | 0.052087 | 4.94 | 246.05 | 0.315342 | 0.03 |
| *Hieracium flagellare* | 0.000108 | 13.645 | 211.859 | 0.176452 | 0.0274 |
| *Hylotelephium telephium* | 0.00019 | 10.4 | 150.12 | 0.098357 | 0.0845 |
| *Hypericum perforatum* | 8.78E-05 | 30.42 | 166.33 | 0.327498 | 0.0372 |
| *Luzula multiflora* | 0.000413 | 21.83 | 290.33 | 0.236828 | 0.0168 |
| *Maianthemum canadense* | 0.00165 | 9.62 | 193.14 | 0.25532 | 0.0234 |
| *Oenothera biennis* | 0.00044 | 39.71 | 177.35 | 0.199717 | 0.027 |
| *Oxalis stricta* | 0.000176 | 5.65 | 598.86 | 0.145344 | 0.0121 |
| *Pinus sylvestris* | 0.002461 | 16.12 | 106.23 | 0.429873 | 0.0345 |
| *Plantago major* | 0.000198 | 7.04 | 232.56 | 0.15531 | 0.0309 |
| *Plantago maritima* | 0.000302 | 13.2 | 90.31 | 0.121562 | 0.138 |
| *Poa annua* | 0.000221 | 4.85 | 410.82 | 0.330938 | 0.0098 |
| *Poa compressa* | 0.000197 | 39.34 | 305.94 | 0.266706 | 0.0179 |
| *Rhodiola rosea* | 0.000104 | 15.8 | 172.58 | 0.081811 | 0.5052 |
| *Rosa multiflora* | 0.002829 | 55.35 | 194.21 | 0.352937 | 0.0306 |
| *Sagina procumbens* | 6.13E-06 | 3 | 217.63 | 0.553939 | 0.0229 |
| *Sedum acre* | 3.08E-05 | 5.31 | 204.35 | 0.060388 | 0.08528 |

| | | | | | |
|---|---|---|---|---|---|
| *Sedum album* | 3.95E-05 | 4.17 | 80.86 | 0.061981 | 0.31552 |
| *Sedum sexangulare* | 6.93E-05 | 3.81 | 110.98 | 0.136293 | 0.07827 |
| *Senecio viscosus* | 0.000462 | 6.37 | 298.64 | 0.10274 | 0.055 |
| *Sibbaldia tridentata* | 0.000302 | 9.01 | 98.86 | 0.387593 | 0.033 |
| *Solidago bicolor* | 0.000166 | 28.19 | 110.38 | 0.309268 | 0.0747 |
| *Solidago sempervirens* | 0.000352 | 39.41 | 90.34 | 0.206619 | 0.0743 |
| *Sorbus americana* | 0.003535 | 4.65 | 280.69 | 0.392711 | 0.0099 |
| *Stellaria media* | 0.000229 | 7.7 | 739.95 | 0.094312 | 0.015 |
| *Symphyotrichum novi-belgii* | 0.000228 | 50.39 | 271.49 | 0.2496 | 0.0204 |
| *Tanacetum vulgare* | 0.000113 | 22.89 | 261.06 | 0.189166 | 0.0237 |
| *Taraxacum officinale* | 0.000443 | 19.99 | 278.38 | 0.157542 | 0.0515 |
| *Trifolium arvense* | 0.00043 | 11.7 | 145.33 | 0.725322 | 0.0429 |
| *Trifolium dubium* | 0.000359 | 11.54 | 407.10 | 0.40867 | 0.0462 |
| *Ulmus glabra* | 0.015655 | 3.4 | 281.99 | 0.306275 | 0.0246 |
| *Vaccinium angustifolium* | 0.000249 | 18.2 | 135.63 | 0.36481 | 0.0222 |
| *Vaccinium macropon* | 0.000774 | 7.88 | 90.611 | 0.526168 | 0.0238 |

**Appendix 4.C.** Total species percent canopy density for intentionally planted species (I) and colonizing species (C) for each growing season and each treatment. The species with the highest biomass for each year and treatment is highlighted. A "–" indicates the species was absent from that treatment for that date. canopy density was determined using the point intercept method. Three species, *Sedum sexangulare*,*Senecio viscosus*, and *Stellaria media*, were only observed when final biomass was harvested in September 2018

| | | **2015** | | | | **2016** | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Species** | **I/ C** | **15** | **5/15** | **10** | **5** | **15** | **5/15** | **10** | **5** |
| *Acer platanoides* | C | 0.13 | 0.24 | 0.78 | 0.56 | 0.05 | 0.11 | 0.23 | 0.09 |
| *Agrostis scabra* | C | 0.17 | 0.10 | 0.47 | - | 0.05 | - | 0.17 | - |
| *Anaphalis margaritacea* | I | 0.17 | 0.19 | 0.10 | - | 0.37 | - | 0.46 | - |
| *Aquilegia canadensis* | C | - | 0.10 | - | - | - | 0.17 | - | - |
| *Cerastium fontanum* | C | 0.17 | 0.19 | 0.26 | - | 0.51 | 0.40 | 0.52 | 0.36 |
| *Conyza canadensis* | C | 1.95 | 2.05 | 1.77 | 2.07 | 0.23 | 0.34 | 0.29 | 1.09 |
| *Danthonia spicata* | I | 15.69 | 12.42 | 14.60 | 14.59 | 18.34 | 17.96 | 16.27 | 15.83 |
| *Avenella flexuosa* | I | 5.41 | 3.30 | 4.54 | 3.51 | 3.27 | 4.10 | 4.27 | 1.91 |
| *Elymus repens* | C | - | - | - | - | - | - | - | - |
| *Empetrum nigrum* | C | 3.34 | 2.67 | 3.96 | 4.23 | 2.40 | 1.77 | 3.40 | 1.27 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Epilobium ciliatum* | C | 0.25 | 0.05 | 0.16 | - | 0.37 | 0.17 | 0.29 | - |
| *Erigeron annuus* | C | - | - | - | - | - | - | - | - |
| *Festuca rubra* | I | 5.33 | 4.49 | 4.07 | 5.98 | 8.89 | 10.21 | 5.89 | 7.92 |
| *Fragaria vesca* | C | 0.76 | 1.62 | 2.09 | 1.67 | 0.05 | - | 0.06 | 0.09 |
| *Fraxinus excelsior* | C | - | - | - | - | 0.14 | 0.06 | 0.06 | 0.09 |
| *Pilosella flagellaris* | C | 0.08 | - | - | - | 0.18 | 0.06 | 0.35 | 1.36 |
| *Hypericum perforatum* | C | 0.08 | - | - | - | 0.23 | - | - | - |
| *Hylotelephium telephium* | C | 0.08 | - | - | - | 0.09 | - | - | - |
| *Luzula multiflora* | I | 8.97 | 8.79 | 6.67 | 7.42 | 7.65 | 9.29 | 8.89 | 9.01 |
| *Maianthemum canadense* | I | 1.95 | 2.10 | 2.14 | 1.91 | 2.26 | 1.65 | 1.79 | 2.09 |
| *Oenothera biennis* | C | - | - | - | - | - | - | - | - |
| *Oxalis stricta* | C | 1.14 | 1.10 | 0.89 | 0.56 | 1.29 | 0.63 | 0.52 | 0.64 |
| *Pinus sylvestris* | C | - | - | 0.16 | - | - | - | 0.17 | - |
| *Plantago major* | C | 0.42 | 0.24 | 0.73 | 0.56 | 0.55 | 0.51 | 1.10 | 0.64 |
| *Plantago maritima* | I | 1.95 | 2.01 | 2.14 | 1.91 | 0.97 | 0.97 | 0.87 | 0.27 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Poa annua* | C | - | - | - | - | 0.14 | 0.06 | - | - |
| *Poa compressa* | C | 0.76 | 0.43 | 1.41 | 0.48 | 0.97 | 0.63 | 2.71 | 1.00 |
| *Rhodiola rosea* | I | 10.15 | 13.94 | 11.11 | 14.51 | 6.82 | 7.53 | 9.35 | 10.37 |
| *Rosa multiflora* | C | - | - | - | - | 0.32 | - | - | - |
| *Sagina procumbens* | I | 1.73 | 1.24 | 0.36 | 0.08 | 1.98 | 1.77 | 0.63 | 0.27 |
| *Sedum album* | C | - | - | - | - | - | - | - | - |
| *Sedum acre* | I | 3.64 | 4.63 | 5.21 | 9.25 | 4.06 | 5.36 | 6.46 | 18.02 |
| *Sibbaldia tridentata* | I | 8.80 | 11.41 | 9.85 | 9.17 | 8.29 | 9.75 | 9.98 | 8.28 |
| *Solidago bicolor* | I | 12.27 | 13.61 | 11.99 | 7.58 | 6.45 | 7.87 | 7.79 | 5.46 |
| *Solidago sempervirens* | I | - | - | - | - | - | - | - | - |
| *Sorbus americana* | C | - | - | - | - | 0.18 | 0.11 | 0.29 | - |
| *Symphyotrichum novi-belgii* | I | 5.58 | 4.58 | 5.42 | 4.23 | 6.08 | 5.36 | 5.19 | 2.91 |
| *Taraxacum officinale* | C | 0.25 | 0.33 | 0.63 | 0.16 | 0.51 | 0.63 | 0.46 | 0.36 |
| *Tanacetum vulgare* | C | 0.68 | 0.10 | 0.52 | 0.08 | 0.41 | 0.29 | 0.81 | - |
| *Trifolium arvense* | C | - | - | - | - | 0.09 | 0.17 | 0.12 | - |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Trifolium dubium* | C | 0.25 | 0.72 | 0.16 | 0.24 | 7.88 | 5.59 | 2.60 | 7.73 |
| *Ulmus glabra* | C | 0.21 | 0.38 | 0.21 | 0.48 | 0.46 | 0.34 | 0.35 | 0.36 |
| *Vaccinium angustifolium* | I | 3.09 | 3.30 | 3.55 | 2.87 | 2.53 | 2.51 | 2.71 | 0.18 |
| *Vaccinium macropon* | I | 3.72 | 3.20 | 3.02 | 5.66 | 4.33 | 3.14 | 4.90 | 2.37 |
| *Unknown Graminoid* | C | 0.80 | 0.48 | 1.04 | 0.24 | 0.60 | 0.51 | 0.06 | - |

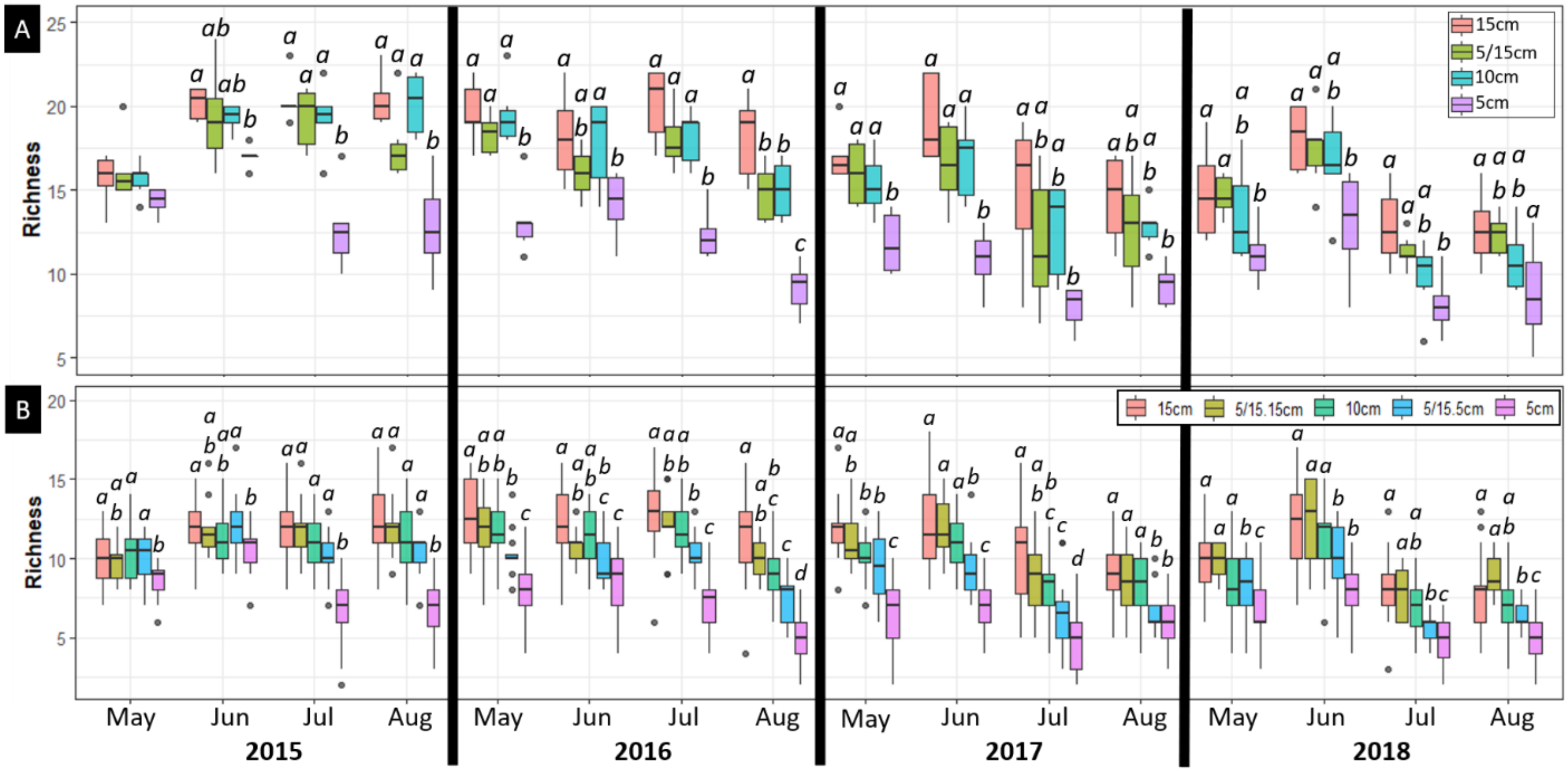
| | | **2017** | | | | **2018** | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Species** | **I/C** | **15** | **5/15** | **10** | **5** | **15** | **5/15** | **10** | **5** |
| *Acer platanoides* | C | - | - | - | - | 0.04 | 0.36 | 0.11 | - |
| *Agrostis scabra* | C | 0.04 | - | 0.05 | - | - | - | - | - |
| *Anaphalis margaritacea* | I | 0.29 | - | 0.21 | 0.09 | 0.15 | - | - | - |
| *Aquilegia canadensis* | C | - | 0.23 | - | - | - | 0.13 | - | - |
| *Cerastium fontanum* | C | 0.37 | 0.56 | 0.64 | 0.71 | 0.15 | 1.70 | 1.41 | 0.76 |
| *Conyza canadensis* | C | - | - | - | 1.07 | - | 0.72 | 0.90 | 3.52 |
| *Danthonia spicata* | I | 15.70 | 14.75 | 23.16 | 10.21 | 15.97 | 14.46 | 23.51 | 7.98 |
| *Avenella flexuosa* | I | 2.26 | 1.97 | 3.36 | 0.36 | 1.29 | 0.58 | 0.79 | - |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Elymus repens* | C | - | - | - | - | 0.61 | - | - | - |
| *Empetrum nigrum* | C | 1.93 | 1.27 | 1.33 | 0.09 | 1.36 | 0.67 | 0.56 | - |
| *Epilobium ciliatum* | C | 0.04 | 0.05 | - | - | 0.08 | 0.13 | 0.51 | 0.19 |
| *Erigeron annuus* | C | 0.25 | 0.14 | - | 0.09 | 0.42 | 1.16 | 1.07 | 1.24 |
| *Festuca rubra* | I | 13.86 | 14.04 | 7.36 | 11.72 | 31.86 | 33.17 | 8.72 | 14.83 |
| *Fragaria vesca* | C | 0.08 | - | - | - | - | - | - | - |
| *Fraxinus excelsior* | C | - | - | 0.21 | - | - | 0.04 | - | - |
| *Pilosella flagellaris* | C | 0.12 | - | 0.16 | 0.36 | 0.08 | 0.49 | 1.18 | 1.81 |
| *Hypericum perforatum* | C | 0.21 | - | - | 0.09 | 0.15 | - | - | - |
| *Hylotelephium telephium* | C | 0.12 | - | 0.16 | - | 0.11 | - | - | - |
| *Luzula multiflora* | I | 4.88 | 3.66 | 4.70 | 2.49 | 3.06 | 3.76 | 3.09 | 1.14 |
| *Maianthemum canadense* | I | 1.31 | 1.13 | 0.69 | - | 1.02 | 0.67 | 0.45 | - |
| *Oenothera biennis* | C | - | - | - | 0.09 | - | - | 0.06 | 0.48 |
| *Oxalis stricta* | C | 0.45 | 0.14 | 0.27 | 0.27 | 0.30 | 0.09 | 0.06 | - |
| *Pinus sylvestris* | C | - | - | - | - | - | - | - | - |

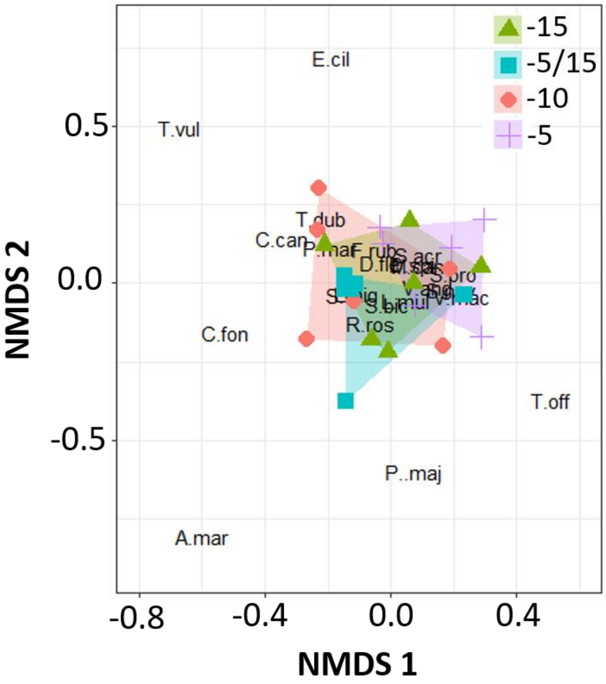
| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Plantago major* | C | 0.04 | 0.38 | 0.21 | 0.27 | - | 0.04 | 0.17 | 0.19 |
| *Plantago maritima* | I | 0.21 | - | 0.11 | - | 0.08 | 0.04 | - | - |
| *Poa annua* | C | 0.12 | 0.09 | 0.11 | 0.18 | - | 0.04 | 0.22 | 0.10 |
| *Poa compressa* | C | 0.94 | 0.94 | 3.31 | 0.80 | 1.82 | 1.75 | 5.34 | 2.66 |
| *Rhodiola rosea* | I | 2.09 | 4.27 | 3.95 | 9.95 | 1.82 | 3.18 | 3.60 | 10.55 |
| *Rosa multiflora* | C | 0.21 | - | - | - | 0.15 | 0.04 | - | - |
| *Sagina procumbens* | I | 0.45 | 0.33 | 0.21 | - | - | - | - | - |
| *Sedum album* | C | - | - | - | - | 0.15 | - | 0.06 | 1.33 |
| *Sedum acre* | I | 2.62 | 4.98 | 6.67 | 25.58 | 2.23 | 9.18 | 15.92 | 31.84 |
| *Sibbaldia tridentata* | I | 6.31 | 6.11 | 8.59 | 5.77 | 7.83 | 7.88 | 11.36 | 5.89 |
| *Solidago bicolor* | I | 7.30 | 6.95 | 8.27 | 3.64 | 7.08 | 6.36 | 6.02 | 3.71 |
| *Solidago sempervirens* | I | - | - | - | - | 0.08 | 0.13 | 0.06 | - |
| *Sorbus americana* | C | 0.04 | 0.05 | 0.05 | 0.09 | - | - | - | - |
| *Symphyotrichum novi-belgii* | I | 4.14 | 3.29 | 2.56 | 2.75 | 6.55 | 2.28 | 2.25 | 3.23 |
| *Taraxacum officinale* | C | 0.21 | 0.56 | 0.16 | 0.18 | 0.19 | 0.27 | 0.17 | 0.76 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Tanacetum vulgare* | C | 0.66 | 0.23 | 0.37 | - | 1.85 | 0.18 | 0.51 | - |
| *Trifolium arvense* | C | 0.29 | 0.70 | 0.64 | 1.42 | 1.78 | 1.12 | 2.59 | 0.95 |
| *Trifolium dubium* | C | 27.63 | 30.67 | 19.32 | 20.78 | 8.63 | 7.61 | 7.48 | 5.23 |
| *Ulmus glabra* | C | 0.29 | 0.19 | 0.16 | 0.09 | 0.26 | 0.94 | 0.39 | 0.57 |
| *Vaccinium angustifolium* | I | 1.15 | 0.80 | 1.01 | - | 0.83 | 0.40 | 0.79 | - |
| *Vaccinium macropon* | I | 2.83 | 1.32 | 1.87 | 0.80 | 1.74 | 0.40 | 0.62 | 0.95 |
| *Unknown Graminoid* | C | 0.57 | 0.19 | 0.11 | 0.09 | 0.30 | - | 0.06 | 0.10 |

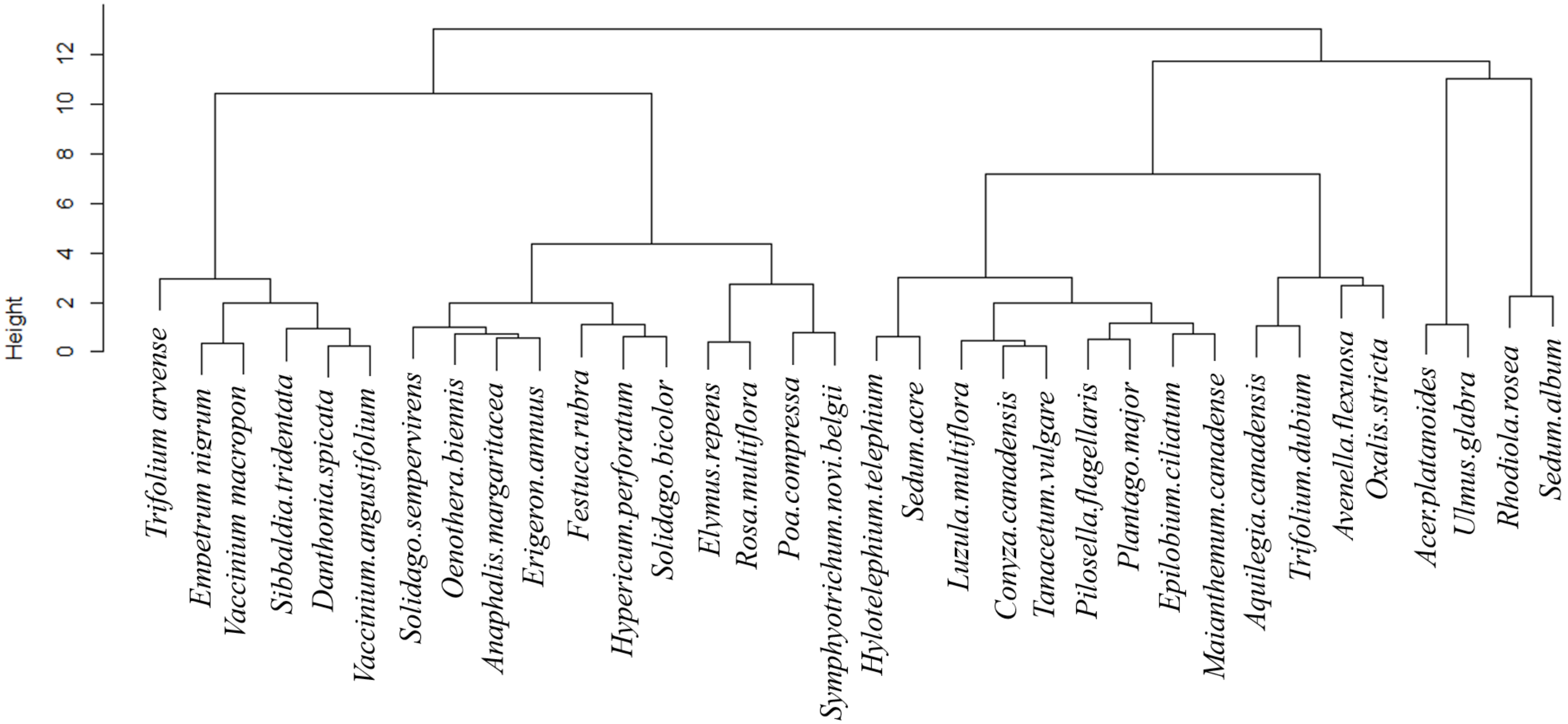
**Appendix 4.D.** A) Average number of species per treatment: 15 cm, 5/15 cm, 10 cm, and 5 cm (plot scale: 0.37 $m^2$); B) Average number of species per subplot (subplots scale: 0.10 $m^2$). For the 5/15 cm treatment, the subplots were separated into two groups, the 15 cm group (5/15-15 cm subplots) and the 5 cm group (5/15-5 cm subplots). The letters represent results from Tukey post-hoc tests for which treatment is the independent variables and richness is the dependent variable. Bars that share a letter are p>0.05.



**Appendix 4.E.** NMDS calculated from biomass data taken at the beginning of the study period (May 2015) for all four treatments (15 cm, 5/15 cm, 10 cm, 5 cm). Species code: first letter of genus and first three letters of species.



**Appendix 4.F.** Cluster diagram for the July 2018 data. This diagram shows how functionally similar species are to each other. Height depicts the distance between clusters.



**Appendix 4.G.** Results of the one-way ANOVA's conducted on the richness data for each date for each treatment by plot (1x1 m) and subplot (0.25x0.25 m). Tran = Transformation, "Tukey" indicates that a Tukey Ladder of Powers transformation was used.

| Whole Plot | | | | Subplot | | |
|---|---|---|---|---|---|---|
| **Richness** | **Tran** | **F-Value** | **Pr(>F)** | **Tran** | **F-Value** | **Pr(>F)** |
| **May 15** | Tukey | 2.07 | 0.136 | Tukey | 12360.545 | <.0001 |
| **June 15** | | 4.331 | 0.0166 | Tukey | 15463.555 | <.0001 |
| **July 15** | Tukey | 10.64 | 0.000215 | Tukey | 1295.2593 | <.0001 |
| **Aug 15** | | 15.56 | 1.86e-05 | | 1304.5092 | <.0001 |
| **May 16** | | 16.94 | 1.34e-05 | | 1959.0768 | <.0001 |
| **June 16** | | 3.997 | 0.0221 | | 1144.7279 | <.0001 |
| **July 16** | | 20.33 | 2.75e-06 | | 1393.5819 | <.0001 |
| **Aug 16** | | 22.59 | 1.24e-06 | | 1173.8797 | <.0001 |
| **May 17** | | 9.433 | 0.000433 | Tukey | 384.8464 | <.0001 |
| **June 17** | | 13.09 | 7.21e-05 | | 328.050 | <.0001 |
| **July 17** | Tukey | 4.868 | 0.0106 | Tukey | 317.2071 | <.0001 |
| **Aug 17** | | 5.354 | 0.00716 | Tukey | 1697.3555 | <.0001 |
| **May 18** | | 3.347 | 0.0397 | Tukey | 1697.3555 | <.0001 |
| **June 18** | | 4.701 | 0.0122 | | 480.7945 | <.0001 |
| **July 18** | | 6.885 | 0.00228 | Tukey | 914.8840 | <.0001 |
| **Aug 18** | | 3.887 | 0.0244 | | 1292.1147 | <.0001 |

**Table H.** ANOVA table for the biomass data for each treatment for dominant species, taken August 2018. Tran = Transformation, "Tukey" indicates that a Tukey Ladder of Powers transformation was used.

| Biomass Dominant Vegetation August 2018 | | | | | |
|---|---|---|---|---|---|
| **Species** | **Tran** | **Sum Sq** | **Mean Sq** | **F-value** | **Pr(>F)** |
| *Festuca rubra* | Tukey | 30.75 | 10.249 | 14.79 | 2.63e-05 |
| *Danthonia spicata* | | 1980 | 660.0 | 8.608 | 0.00072 |
| *Solidago bicolor* | | 142.3 | 47.44 | 7.135 | 0.00192 |
| *Sibbaldia tridentata* | | 227.1 | 75.71 | 7.059 | 0.00202 |
| *Rhodiola rosea* | Tukey | 12.465 | 4.155 | 10.96 | 0.00018 |
| *Trifolium dubium* | Tukey | 2.59 | 0.8621 | 0.346 | 0.792 |
| *Sedum acre* | Tukey | 22.60 | 7.532 | 5.42 | 0.0068 |

**Appendix 4.I.** Results of the permutational multivariate analysis of variance (PERMANOVA) used to test for statistically significant differences between treatments for May 2015 and August 2018.

| **May 2015** | **Df** | **SumsOfSqs** | **MeanSqs** | **F.Model** | **$R^2$** | **Pr(>F)** |
|---|---|---|---|---|---|---|
| All | 3 | 0.28631 | 0.095435 | 2.1341 | 0.24249 | 0.004995 |
| Residuals | 20 | 0.89439 | 0.044720 | 0.75751 | | |
| Total | 23 | 1.18070 | 1.00000 | | | |
| **Aug 2018** | **Df** | **SumsOfSqs** | **MeanSqs** | **F.Model** | **$R^2$** | **Pr(>F)** |
| All | 3 | 1.6818 | 0.56060 | 6.3469 | 0.48771 | 0.000999 |
| Residuals | 20 | 1.7665 | 0.08833 | 0.51229 | | |
| Total | 23 | 3.4483 | 1.00000 | | | |
| **Aug 2018** | **Df** | **SumsOfSqs** | **MeanSqs** | **F.Model** | **$R^2$** | **Pr(>F)** |
| 15:5 | 1 | 1.26060 | 1.26060 | 12.71 | 0.55966 | 0.003996 |
| Residuals | 10 | 0.99182 | 0.09918 | 0.44034 | | |
| Total | 11 | 2.25242 | 1.00000 | | | |
| **Aug 2018** | **Df** | **SumsOfSqs** | **MeanSqs** | **F.Model** | **$R^2$** | **Pr(>F)** |
| 15:10 | 1 | 0.3984 | 0.39840 | 4.4744 | 0.30913 | 0.006993 |
| Residuals | 10 | 0.8904 | 0.08904 | 0.69087 | | |
| Total | 11 | 1.2888 | 1.00000 | | | |
| **Aug 2018** | **Df** | **SumsOfSqs** | **MeanSqs** | **F.Model** | **$R^2$** | **Pr(>F)** |
| 15:515 | 1 | 0.17551 | 0.17551 | 2.7556 | 0.21603 | 0.01898 |
| Residuals | 10 | 0.63690 | 0.06369 | 0.78397 | | |
| Total | 11 | 0.81241 | 1.00000 | | | |
| **Aug 2018** | **Df** | **SumsOfSqs** | **MeanSqs** | **F.Model** | **$R^2$** | **Pr(>F)** |
| 515:10 | 1 | 0.24055 | 0.24055 | 3.1051 | 0.23694 | 0.005994 |
| Residuals | 10 | 0.77470 | 0.07747 | 0.76306 | | |
| Total | 11 | 1.01524 | 1.00000 | | | |
| **Aug 2018** | **Df** | **SumsOfSqs** | **MeanSqs** | **F.Model** | **$R^2$** | **Pr(>F)** |
| 515:5 | 1 | 0.75808 | 0.75808 | 8.6528 | 0.46389 | 0.001998 |
| Residuals | 10 | 0.87611 | 0.08761 | 0.53611 | | |
| Total | 11 | 1.63420 | 1.00000 | | | |
| **Aug 2018** | **Df** | **SumsOfSqs** | **MeanSqs** | **F.Model** | **$R^2$** | **Pr(>F)** |
| 10:5 | 1 | 0.53043 | 0.53043 | 4.6957 | 0.31953 | 0.004995 |
| Residuals | 10 | 1.12962 | 0.11296 | 0.68047 | | |
| Total | 11 | 1.66004 | 1.00000 | | | |

**Appendix 4.J.** Results of the ANOVAs conducted on the trait data for community weighted mean (CWM) and functional diversity (FD) for each treatment for July 2015-2018.

| **July 2015** | **Sum Sq** | **Mean Sq** | **F-value** | **Pr(>F)** |
|---|---|---|---|---|
| Seed Weight CWM | 1.443e-07 | 4.810e-08 | 0.584 | 0.632 |
| Height CWM | 23.67 | 7.889 | 2.599 | 0.0806 |
| Specific Leaf Area CWM | 470 | 156.7 | 0.921 | 0.448 |
| Leaf Dry Matter Content CWM | 0.002868 | 0.0009559 | 2.441 | 0.0941 |
| Leaf Thickness CWM | 0.002463 | 0.0008209 | 1.748 | 0.189 |
| Total FD | 0.07993 | 0.026644 | 3.119 | 0.0491 |
| Height FD | 0.0082 | 0.002735 | 0.137 | 0.937 |
| Leaf Dry Matter Content FD | 0.1835 | 0.06116 | 10.22 | 0.000273 |
| Seed Weight FD | 0.0502 | 0.01672 | 0.825 | 0.495 |
| Specific Leaf Area FD | 0.06987 | 0.02329 | 3.19 | 0.0459 |
| Leaf Thickness FD | 0.5266 | 0.1755 | 1.313 | 0.298 |
| **July 2016** | **Sum Sq** | **Mean Sq** | **F-value** | **Pr(>F)** |
| Seed Weight CWM | 2.000e-07 | 6.665e-08 | 0.289 | 0.833 |
| Height CWM | 18.13 | 6.043 | 1.33 | 0.293 |
| Specific Leaf Area CWM | 1835 | 611.6 | 0.724 | 0.549 |
| Leaf Dry Matter Content CWM | 0.018745 | 0.006248 | 15.59 | 1.83e-05 |
| Leaf Thickness CWM | 0.003984 | 0.0013281 | 2.718 | 0.0719 |
| Total FD | 0.3639 | 0.1213 | 1.553 | 0.232 |
| Height FD | 0.01125 | 0.00375 | 0.336 | 0.8 |
| Leaf Dry Matter Content FD | 0.2256 | 0.07522 | 8.959 | 0.000578 |
| Seed Weight FD | 0.00407 | 0.001355 | 0.158 | 0.924 |
| Specific Leaf Area FD | 0.2140 | 0.07133 | 2.558 | 0.0839 |
| Leaf Thickness FD | 0.746 | 0.2487 | 1.433 | 0.263 |
| **July 2017** | **Sum Sq** | **Mean Sq** | **F-value** | **Pr(>F)** |
| Seed Weight CWM | 1.799e-07 | 5.997e-08 | 10.7 | 0.000207 |
| Height CWM | 121.10 | 40.37 | 8.179 | 0.000949 |
| Specific Leaf Area CWM | 421 | 140.2 | 0.284 | 0.836 |
| Leaf Dry Matter Content CWM | 0.04949 | 0.016497 | 9.418 | 0.000437 |
| Leaf Thickness CWM | 0.021836 | 0.007279 | 16.28 | 1.36e-05 |
| Total FD | 1.8033 | 0.6011 | 12.47 | 8.04e-05 |
| Height FD | 0.04508 | 0.01503 | 1.114 | 0.367 |
| Leaf Dry Matter Content FD | 0.7098 | 0.23659 | 15.59 | 1.84e-05 |
| Seed Weight FD | 0.004956 | 0.001652 | 1.551 | 0.232 |

| | | | | |
|---|---|---|---|---|
| Specific Leaf Area FD | 0.3651 | 0.1217 | 3.307 | 0.0412 |
| Leaf Thickness FD | 2.662 | 0.8873 | 12.77 | 6.92e-05 |
| **July 2018** | **Sum Sq** | **Mean Sq** | **F-value** | **Pr(>F)** |
| Seed Weight CWM | 1.653e-07 | 5.51e-08 | 6.312 | 0.00345 |
| Height CWM | 336.6 | 112.21 | 15.01 | 2.38e-05 |
| Specific Leaf Area CWM | 5878 | 1959.5 | 10.28 | 0.000263 |
| Leaf Dry Matter Content CWM | 0.07871 | 0.026238 | 24.51 | 6.65e-07 |
| Leaf Thickness CWM | 0.031419 | 0.010473 | 27.07 | 3.04e-07 |
| Total FD | 3.266 | 1.0887 | 18.21 | 6.15e-06 |
| Height FD | 0.03987 | 0.01329 | 1.396 | 0.273 |
| Leaf Dry Matter Content FD | 0.7554 | 0.25181 | 15.47 | 1.94e-05 |
| Seed Weight FD | 0.004249 | 0.001416 | 1.17 | 0.346 |
| Specific Leaf Area FD | 0.02179 | 0.007264 | 0.93 | 0.444 |
| Leaf Thickness FD | 3.653 | 1.2178 | 14.95 | 2.44e-05 |

**Appendix 4.K.** Results of the ANOVAs conducted on the trait data for community weighted mean (CWM) for July 2018 at the subplot scale (0.25 x 0.25 m).

| **July 2018** | **F-value** | **p-value** |
|---|---|---|
| Seed Weight CWM | 513.8636 | <.0001 |
| Height CWM | 1802.1928 | <.0001 |
| Specific Leaf Area CWM | 4613.727 | <.0001 |
| Leaf Dry Matter Content CWM | 1529.0880 | <.0001 |
| Leaf Thickness CWM | 111.57123 | <.0001 |

**Appendix 4.L.** Results of the ANOVAs for the community weighted mean (CWM) and functional diversity (FD) for each treatment, comparing data from May 2015 and August 2018. Tran = Transformation, "Tukey" indicates a Tukey Ladder of Powers transformation was used.

| 5 cm | Tran | Df | Sum Sq | Mean Sq | F-value | Pr(>F) |
|---|---|---|---|---|---|---|
| CWM Seed Weight | Tukey | 1 | 14148112 | 14148112 | 15.68 | 0.00269 |
| CWM Height | | 1 | 0.46 | 0.461 | 0.088 | 0.773 |
| CWM Specific Leaf Area | | 1 | 80.8 | 80.79 | 0.512 | 0.491 |
| CWM Leaf Dry Matter Content | | 1 | 0.01085 | 0.010853 | 6.502 | 0.0289 |
| CWM Leaf Thickness | | 1 | 0.000208 | 0.0002081 | 0.238 | 0.636 |
| FD Total | | 1 | 0.3884 | 0.3884 | 4.931 | 0.0506 |
| FD Height | | 1 | 0.0005 | 0.000497 | 0.026 | 0.874 |
| FD Leaf Dry Matter Content | | 1 | 0.02332 | 0.023319 | 2.595 | 0.138 |
| FD Seed Weight | Tukey | 1 | 0.606 | 0.6057 | 1.809 | 0.208 |
| FD Specific Leaf Area | | 1 | 0.06555 | 0.06555 | 11.21 | 0.00738 |
| FD Leaf Thickness | | 1 | 0.1273 | 0.1273 | 0.624 | 0.448 |

| 10 cm | Tran | Df | Sum Sq | Mean Sq | F-value | Pr(>F) |
|---|---|---|---|---|---|---|
| CWM Seed Weight | | 1 | 7.380e-08 | 7.380e-08 | 3.048 | 0.111 |
| CWM Height | | 1 | 0.32 | 0.323 | 0.065 | 0.805 |
| CWM Specific Leaf Area | | 1 | 2251 | 2251.1 | 8.242 | 0.0166 |
| CWM Leaf Dry Matter Content | Tukey | 1 | 633750 | 633750 | 3.091 | 0.109 |
| CWM Leaf Thickness | | 1 | 0.006238 | 0.006238 | 13.94 | 0.00388 |
| FD Total | | 1 | 1.9283 | 1.928 | 25.05 | 0.000534 |
| FD Height | | 1 | 0.06161 | 0.06161 | 2.639 | 0.135 |
| FD Leaf Dry Matter Content | Tukey | 1 | 0.1125 | 0.11254 | 5.646 | 0.0389 |
| FD Seed Weight | Tukey | 1 | 27.85 | 27.855 | 5.218 | 0.0455 |
| FD Specific Leaf Area | | 1 | 0.1389 | 0.13895 | 13.66 | 0.00414 |
| FD Leaf Thickness | | 1 | 1.718 | 1.7175 | 15.52 | 0.00278 |

| 15 cm | Tran | Df | Sum Sq | Mean Sq | F-value | Pr(>F) |
|---|---|---|---|---|---|---|
| CWM Seed Weight | | 1 | 4.720e-09 | 4.723e-09 | 1.139 | 0.311 |
| CWM Height | | 1 | 149.25 | 149.25 | 16.55 | 0.00226 |
| CWM Specific Leaf Area | | 1 | 6651 | 6651 | 32.79 | 0.000191 |

| | | | | | | |
|---|---|---|---|---|---|---|
| CWM Leaf Dry Matter Content | | 1 | 0.010100 | 0.010100 | 39.1 | 9.47e-05 |
| CWM Leaf Thickness | | 1 | 0.009929 | 0.009929 | 73.29 | 6.47e-06 |
| FD Total | | 1 | 2.6851 | 2.6851 | 52.87 | 2.69e-05 |
| FD Height | | 1 | 0.02038 | 0.02038 | 1.362 | 0.27 |
| FD Leaf Dry Matter Content | | 1 | 0.3725 | 0.3725 | 30.56 | 0.000252 |
| FD Seed Weight | | 1 | 0.004684 | 0.004684 | 6.062 | 0.0336 |
| FD Specific Leaf Area | | 1 | 0.2181 | 0.21809 | 20.14 | 0.00117 |
| FD Leaf Thickness | | 1 | 1.9883 | 1.9883 | 36.31 | 0.000128 |

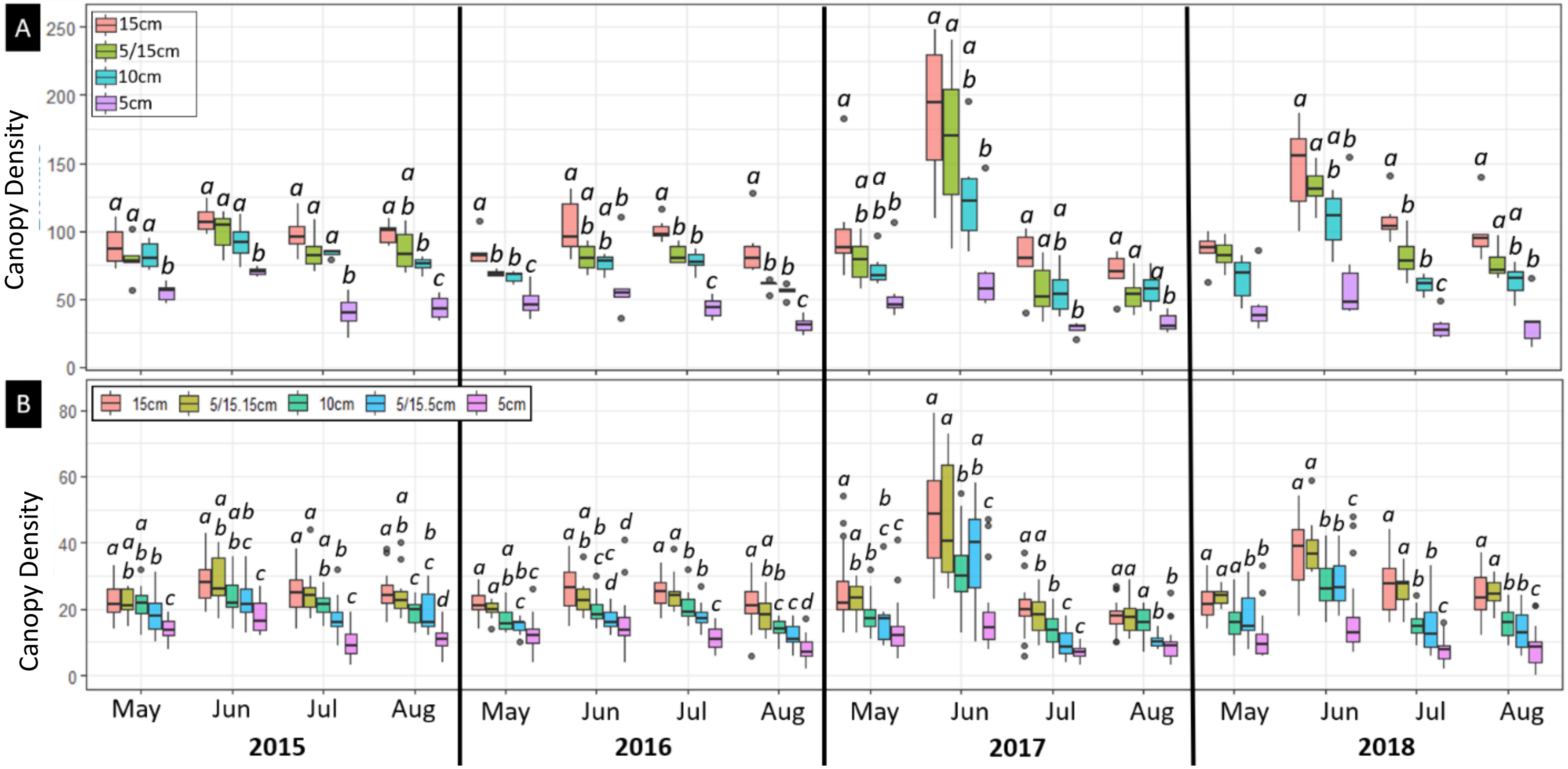
| **5/15 cm** | **Tran** | **Df** | **Sum Sq** | **Mean Sq** | **F-value** | **Pr(>F)** |
|---|---|---|---|---|---|---|
| CWM Seed Weight | | 1 | 1.392e-08 | 1.392e-08 | 0.985 | 0.344 |
| CWM Height | | 1 | 102.41 | 102.41 | 58.06 | 1.8e-05 |
| CWM Specific Leaf Area | | 1 | 6963 | 6963 | 79.59 | 4.48e-06 |
| CWM Leaf Dry Matter Content | | 1 | 0.006762 | 0.006762 | 55.35 | 2.21e-05 |
| CWM Leaf Thickness | | 1 | 0.009292 | 0.009292 | 36.37 | 0.000127 |
| FD Total | | 1 | 2.4472 | 2.4472 | 47.66 | 4.18e-05 |
| FD Height | | 1 | 0.003066 | 0.003067 | 1.646 | 0.228 |
| FD Leaf Dry Matter Content | | 1 | 0.1980 | 0.19798 | 18.28 | 0.00162 |
| FD Seed Weight | | 1 | 0.006861 | 0.006861 | 2.431 | 0.15 |
| FD Specific Leaf Area | | 1 | 0.22941 | 0.22941 | 39.16 | 9.41e-05 |
| FD Leaf Thickness | | 1 | 1.8192 | 1.8192 | 29.96 | 0.000272 |

**Appendix 4.M.** ANOVA tables for functional richness and functional evenness for both date and treatment. Tran = Transformation, "Tukey" indicates a Tukey Ladder of Powers transformation was used.

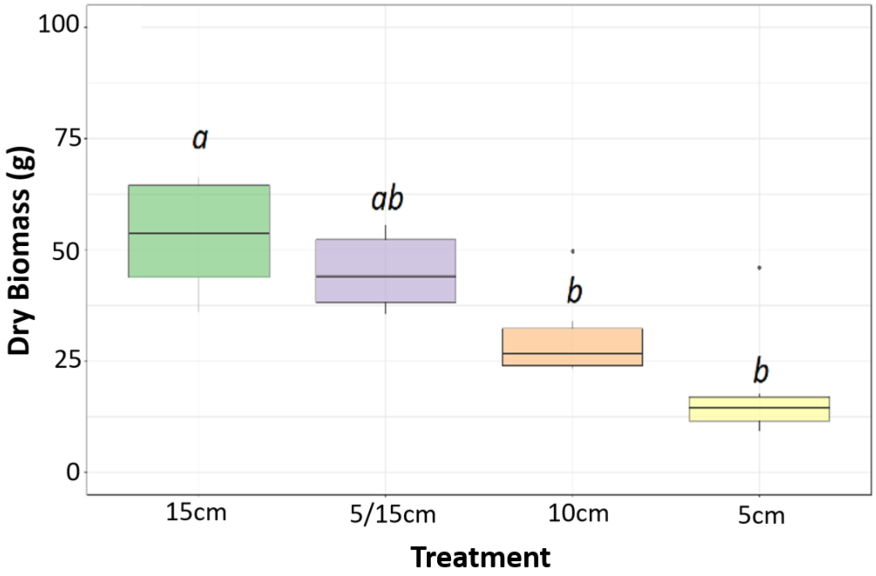
| **Treatment** | | | | | | |
|---|---|---|---|---|---|---|
| **Richness** | **Tran** | **Df** | **Sum Sq** | **Mean Sq** | **F value** | **Pr(>F)** |
| 2015 | - | 3 | 706.3 | 235.4 | 2.313 | 0.107 |
| 2016 | Tukey | 3 | 0.1092 | 0.03641 | 3.163 | 0.047 |
| 2017 | Tukey | 3 | 0.01805 | 0.006018 | 2.955 | 0.0573 |
| 2018 | Tukey | 3 | 0.1272 | 0.04239 | 2.984 | 0.0557 |
| **Evenness** | **Tran** | **Df** | **Sum Sq** | **Mean Sq** | **F value** | **Pr(>F)** |
| 2015 | - | 3 | 0.001161 | 0.0003871 | 0.302 | 0.823 |
| 2016 | - | 3 | 0.01305 | 0.004351 | 0.912 | 0.453 |
| 2017 | - | 3 | 0.1894 | 0.06314 | 12.17 | 9.39e-05 |
| 2018 | - | 3 | 0.26653 | 0.08884 | 25.75 | 4.52e-07 |
| **Date** | | | | | | |
| **Richness** | **Tran** | **Df** | **Sum Sq** | **Mean Sq** | **F value** | **Pr(>F)** |
| 5 cm | Tukey | 3 | 0.0282 | 0.00940 | 6.225 | 0.00368 |
| 10 cm | Tukey | 3 | 0.5886 | 0.1962 | 7.724 | 0.00128 |
| 15 cm | Tukey | 3 | 0.6394 | 0.21312 | 2.714 | 0.0721 |
| 5/15 cm | Tukey | 3 | 34.66 | 11.552 | 5.207 | 0.00805 |
| **Evenness** | **Tran** | **Df** | **Sum Sq** | **Mean Sq** | **F value** | **Pr(>F)** |
| 5 cm | - | 3 | 0.09681 | 0.03227 | 12.15 | 9.5e-05 |
| 10 cm | - | 3 | 0.00800 | 0.002668 | 0.843 | 0.486 |
| 15 cm | - | 3 | 0.12495 | 0.04165 | 12.12 | 9.64e-05 |
| 5/15 cm | - | 3 | 0.00292 | 0.000972 | 0.179 | 0.91 |

## Supplementary Material

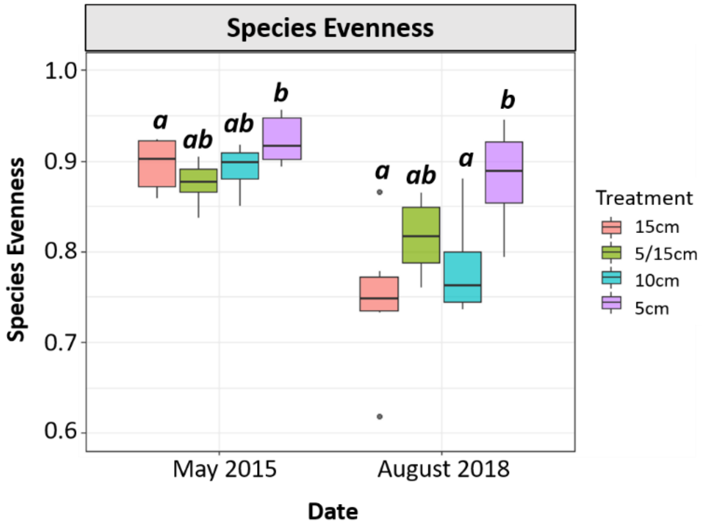
**Appendix 4.1.** A) Average canopy density per treatment: 15 cm, 5/15 cm, 10 cm, and 5 cm (plot scale: 1x1 m) B) Average biomass per treatment (subplots scale: 0.25 x 0.25 m). For the 5/15 cm treatment, the subplots were separated into two groups, the 15 cm group (5/15-15 cm) and the 5 cm group (5/15-5 cm). The letters represent results from Tukey post-hoc tests for which treatment is the independent variable and functional biomass is the dependent variable. Bars that share a letter have a p-value >0.05.



**Appendix 4.2.** Average harvested biomass per treatment: 15 cm, 5/15 cm, 10 cm, and 5 cm (*F=11.54; P=0.000131*). The letters represent results from Tukey post-hoc tests for which treatment is the independent variable and harvested biomass is the dependent variable. Bars that share a letter have a p-value >0.05.



**Appendix 4.3.** Boxplot showing evenness for the beginning and end of the study. Species evenness was calculated using Pielou's Evenness. The letters represent results from Tukey post-hoc tests for which treatment is the independent variable and evenness is the dependent variable. Bars that share a letter have a p-value >0.05.



**Appendix 4.5.** Results of the ANOVAs conducted on the biomass data for each of the seven most common species for each date. Tran = Transformation, “Tukey” indicates that a Tukey Ladder of Powers transformation was used.

| ***Festuca rubra*** | | | | | |
|---|---|---|---|---|---|
| Date | Tran | Sum Sq | Mean Sq | F-value | Pr(>F) |
| May 15 | Tukey | 0.286 | 0.0952 | 0.2 | 0.895 |
| June 15 | Tukey | 0.1221 | 0.04070 | 0.964 | 0.429 |
| July 15 | Tukey | 0.1051 | 0.03502 | 1.469 | 0.253 |
| Aug 15 | Tukey | 2.248 | 0.7492 | 1.617 | 0.217 |
| May 16 | | 29.14 | 9.713 | 1.336 | 0.292 |
| June 16 | Tukey | 0.001550 | 0.0005168 | 1.967 | 0.151 |
| July 16 | Tukey | 0.01377 | 0.004589 | 2.368 | 0.101 |
| Aug 16 | Tukey | 0.09057 | 0.030190 | 5.028 | 0.0093 |
| May 17 | Tukey | 0.01371 | 0.004570 | 3.602 | 0.0314 |
| June 17 | Tukey | 0.03597 | 0.011991 | 2.842 | 0.0652 |
| July 17 | Tukey | 0.3538 | 0.11795 | 4.556 | 0.0137 |
| Aug 17 | Tukey | 0.02030 | 0.006768 | 5.961 | 0.00449 |
| May 18 | Tukey | 20.41 | 6.803 | 7.501 | 0.00149 |
| June 18 | Tukey | 0.10035 | 0.03345 | 8.564 | 0.000741 |
| July 18 | Tukey | 0.24219 | 0.08073 | 21.14 | 2.05e-06 |
| Aug 18 | Tukey | 30.75 | 10.249 | 14.79 | 2.63e-05 |
| ***Danthonia spicata*** | | | | | |
| Date | Tran | Sum Sq | Mean Sq | F-value | Pr(>F) |
| May 15 | | 742.3 | 247.44 | 6.256 | 0.0036 |
| June 15 | | 292.5 | 97.49 | 2.165 | 0.124 |
| July 15 | Tukey | 4.633 | 1.5442 | 6.393 | 0.00325 |
| Aug 15 | Tukey | 0.02690 | 0.008966 | 2.658 | 0.0761 |
| May 16 | | 313.3 | 104.45 | 9.471 | 0.000487 |
| June 16 | Tukey | 0.00754 | 0.002515 | 0.647 | 0.594 |
| July 16 | | 529.5 | 176.49 | 3.986 | 0.0223 |
| Aug 16 | | 401.8 | 133.93 | 3.178 | 0.0464 |
| May 17 | | 373.5 | 124.49 | 6.263 | 0.00358 |
| June 17 | | 882.7 | 294.22 | 3.897 | 0.0251 |
| July 17 | | 889.7 | 296.56 | 8.077 | 0.00101 |
| Aug 17 | | 633.5 | 211.15 | 5.808 | 0.00504 |
| May 18 | Tukey | 15.66 | 5.221 | 4.417 | 0.0154 |
| June 18 | Tukey | 0.1730 | 0.05768 | 4.467 | 0.0148 |
| July 18 | | 742.3 | 247.44 | 6.256 | 0.0036 |
| Aug 18 | | 1980 | 660.0 | 8.608 | 0.00072 |
| ***Solidago bicolor*** | | | | | |

| Date | Tran | Sum Sq | Mean Sq | F-value | Pr(>F) |
|---|---|---|---|---|---|
| May 15 |  | 114.8 | 38.28 | 4.876 | 0.0105 |
| June 15 |  | 236.2 | 78.72 | 4.034 | 0.0214 |
| July 15 | Tukey | 6.971 | 2.3237 | 6.445 | 0.00313 |
| Aug 15 | Tukey | 10.50 | 3.500 | 5.941 | 0.00455 |
| May 16 |  | 24.55 | 8.182 | 3.427 | 0.0381 |
| June 16 | Tukey | 14.46 | 4.820 | 2.384 | 0.0996 |
| July 16 |  | 62.83 | 20.94 | 4.928 | 0.0101 |
| Aug 16 |  | 88.83 | 29.61 | 4.387 | 0.0158 |
| May 17 |  | 99.00 | 33.00 | 11.72 | 0.000119 |
| June 17 |  | 170.6 | 56.87 | 6.554 | 0.00315 |
| July 17 |  | 170.3 | 56.78 | 11.03 | 0.000173 |
| Aug 17 | Tukey | 65.16 | 21.720 | 12.84 | 6.67e-05 |
| May 18 |  | 27.12 | 9.042 | 2.989 | 0.0554 |
| June 18 |  | 153.1 | 51.04 | 6.723 | 0.00256 |
| July 18 |  | 246.5 | 82.15 | 6.212 | 0.00372 |
| Aug 18 |  | 142.3 | 47.44 | 7.135 | 0.00192 |

***Sibbaldia tridentata***

| Date | Tran | Sum Sq | Mean Sq | F-value | Pr(>F) |
|---|---|---|---|---|---|
| May 15 |  | 120.7 | 40.22 | 2.601 | 0.0805 |
| Jun 15 |  | 64.13 | 21.375 | 2.562 | 0.0836 |
| Jul 15 |  | 191 | 63.67 | 3.567 | 0.0325 |
| Aug 15 | Tukey | 0.00836 | 0.002786 | 1.233 | 0.324 |
| May 16 |  | 18.11 | 6.035 | 2.893 | 0.0622 |
| Jun 16 | Tukey | 0.8258 | 0.27527 | 4.061 | 0.0209 |
| Jul 16 | Tukey | 1.227 | 0.4089 | 2.696 | 0.0734 |
| Aug 16 | Tukey | 0.5529 | 0.18431 | 3.142 | 0.048 |
| May 17 | Tukey | 0.07206 | 0.024022 | 4.359 | 0.0162 |
| Jun 17 | Tukey | 0.03517 | 0.011724 | 5.549 | 0.00658 |
| Jul 17 | Tukey | 11.01 | 3.670 | 5.382 | 0.00701 |
| Aug 17 | Tukey | 0.002277 | 0.0007590 | 5.819 | 0.00499 |
| May 18 |  | 58.33 | 19.44 | 5.804 | 0.00505 |
| Jun 18 | Tukey | 0.1474 | 0.04915 | 5.636 | 0.00575 |
| Jul 18 | Tukey | 0.02044 | 0.006815 | 6.28 | 0.00354 |
| Aug 18 |  | 227.1 | 75.71 | 7.059 | 0.00202 |

***Rhodiola rosea***

| Date | Tran | Sum Sq | Mean Sq | F-value | Pr(>F) |
|---|---|---|---|---|---|
| May 15 |  | 136.3 | 45.44 | 1.758 | 0.188 |
| June 15 |  | 38.3 | 12.78 | 0.646 | 0.595 |
| July 15 |  | 82.5 | 27.49 | 1.353 | 0.286 |
| Aug 15 | Tukey | 2.925 | 0.9752 | 1.535 | 0.236 |

| | | | | | |
|---|---|---|---|---|---|
| May 16 | | 2.58 | 0.858 | 0.148 | 0.93 |
| June 16 | | 28.46 | 9.486 | 0.78 | 0.519 |
| July 16 | | 28.33 | 9.444 | 0.804 | 0.506 |
| Aug 16 | Tukey | 0.197 | 0.06565 | 0.306 | 0.821 |
| May 17 | Tukey | 0.0479 | 0.015968 | 3.015 | 0.0541 |
| June 17 | | 21.21 | 7.071 | 1.171 | 0.347 |
| July 17 | Tukey | 0.07611 | 0.025371 | 2.552 | 0.0844 |
| Aug 17 | Tukey | 2.066 | 0.6888 | 1.547 | 0.233 |
| May 18 | Tukey | 0.00365 | 0.001215 | 0.453 | 0.718 |
| June 18 | Tukey | 0.1340 | 0.04466 | 1.258 | 0.316 |
| July 18 | Tukey | 3.829 | 1.276 | 3.976 | 0.0225 |
| Aug 18 | Tukey | 12.465 | 4.155 | 10.96 | 0.00018 |
| ***Trifolium dubium*** | | | | | |
| Date | Tran | Sum Sq | Mean Sq | F-value | Pr(>F) |
| May 15 | Not Present | | | | |
| June 15 | | 0.125 | 0.04167 | 0.333 | 0.801 |
| July 15 | | 1.125 | 0.3750 | 0.474 | 0.704 |
| Aug 15 | Tukey | 0.051 | 0.01687 | 0.066 | 0.977 |
| May 16 | Tukey | 0.169 | 0.0564 | 0.099 | 0.96 |
| June 16 | Tukey | 0.898 | 0.2992 | 0.334 | 0.801 |
| July 16 | Tukey | 2.21 | 0.7367 | 0.835 | 0.491 |
| Aug 16 | Not Present | | | | |
| May 17 | Tukey | 0.63 | 0.2084 | 0.131 | 0.94 |
| June 17 | Tukey | 14.10 | 4.699 | 2.242 | 0.116 |
| July 17 | Tukey | 8.49 | 2.830 | 1.649 | 0.21 |
| Aug 17 | | 5.79 | 1.931 | 0.664 | 0.584 |
| May 18 | Tukey | 3.55 | 1.183 | 0.499 | 0.687 |
| June 18 | Tukey | 5.309 | 1.7696 | 2.714 | 0.0721 |
| July 18 | | 0.1250 | 0.04167 | 1 | 0.413 |
| Aug 18 | Tukey | 2.59 | 0.8621 | 0.346 | 0.792 |
| ***Sedum acre*** | | | | | |
| Date | Tran | Sum Sq | Mean Sq | F-value | Pr(>F) |
| May 15 | Tukey | 0.002049 | 0.000683 | 0.511 | 0.679 |
| June 15 | Tukey | 1.261 | 0.4203 | 0.512 | 0.679 |
| July 15 | Tukey | 1.068 | 0.3561 | 1.036 | 0.398 |
| Aug 15 | Tukey | 0.000317 | 1.057e-04 | 1.483 | 0.25 |
| May 16 | Tukey | 0.01791 | 0.005970 | 5.819 | 0.00537 |
| June 16 | Tukey | 1.568 | 0.5227 | 2.301 | 0.108 |
| July 16 | Tukey | 0.09179 | 0.030598 | 3.829 | 0.0257 |
| Aug 16 | Tukey | 0.01248 | 0.004159 | 5.101 | 0.00877 |
| May 17 | Tukey | 13.462 | 4.487 | 9.774 | 0.000353 |

| | | | | | |
|---|---|---|---|---|---|
| June 17 | Tukey | 20.566 | 6.855 | 19.05 | 5.94e-06 |
| July 17 | Tukey | 10.156 | 3.385 | 7.828 | 0.0012 |
| Aug 17 | Tukey | 12.320 | 4.107 | 9.891 | 0.00033 |
| May 18 | Tukey | 0.005771 | 0.0019235 | 4.246 | 0.0178 |
| June 18 | Tukey | 0.04718 | 0.015727 | 4.758 | 0.0116 |
| July 18 | Tukey | 24.99 | 8.33 | 5.41 | 0.00686 |
| Aug 18 | Tukey | 22.60 | 7.532 | 5.42 | 0.0068 |

**Appendix 4.6.** Results of the one-way ANOVAs conducted on the biomass data for each date for the whole plot (1 x 1 m) and subplot (0.25 x 0.25 m) data. Tran = Transformation, "Tukey" indicates that a Tukey Ladder of Powers transformation was used.

| Whole Plot | | | | Subplot | | |
|---|---|---|---|---|---|---|
| **Date** | **Tran** | **F-value** | **Pr(>F)** | **Tran** | **F-value** | **p-value** |
| **May 15** | | 8.962 | 0.000577 | | 412.5449 | <.0001 |
| **June 15** | | 12.61 | 7.51e-05 | | 1632.7260 | <.0001 |
| **July 15** | | 28.03 | 2.31e-07 | | 1305.8280 | <.0001 |
| **Aug 15** | | 32.08 | 7.74e-08 | | 1457.5565 | <.0001 |
| **May 16** | | 18.95 | 6.17e-06 | | 1423.3330 | <.0001 |
| **June 16** | | 5.714 | 0.00542 | Tukey | 2074.3355 | <.0001 |
| **July 16** | | 54.26 | 8.64e-10 | | 1292.6062 | <.0001 |
| **Aug 16** | | 23.66 | 8.74e-07 | Tukey | 3029.645 | <.0001 |
| **May 17** | Tukey | 5.477 | 0.00651 | Tukey | 1829.0256 | <.0001 |
| **June 17** | | 6.182 | 0.00412 | Tukey | 269.48066 | <.0001 |
| **July 17** | | 8.665 | 0.000695 | Tukey | 3162.0805 | <.0001 |
| **Aug 17** | | 8.864 | 0.000614 | | 586.6489 | <.0001 |
| **May 18** | Tukey | 6.77 | 0.00248 | Tukey | 1238.5896 | <.0001 |
| **June 18** | | 7.622 | 0.00137 | | 258.8129 | <.0001 |
| **July 18** | | 37.31 | 2.2e-08 | Tukey | 2265.3766 | <.0001 |
| **Aug 18** | | 17.45 | 8.34e-06 | | 489.5788 | <.0001 |

**Appendix 4.7.** ANOVA tables for species richness and evenness for May 2015 and August 2018.

| **Richness** | **Df** | **Sum Sq** | **Mean Sq** | **F-value** | **Pr(>F)** |
|---|---|---|---|---|---|
| May 2015 | 3 | 11.13 | 3.708 | 1.91 | 0.161 |
| August 2018 | 3 | 55.00 | 18.333 | 3.887 | 0.0244 |
| **Evenness** | **Df** | **Sum Sq** | **Mean Sq** | **F-value** | **Pr(>F)** |
| May 2015 | 3 | 0.006935 | 0.0023117 | 3.232 | 0.0441 |
| August 2018 | 3 | 0.05806 | 0.019352 | 5.417 | 0.00682 |

**Appendix 4.8.** ANOVA tables for colonizing species richness and evenness for 2018. Tran = Transformation, "Tukey" indicates a Tukey Ladder of Powers transformation was used.

| **August 2018** | **Tran** | **Df** | **Sum Sq** | **Mean Sq** | **F-value** | **Pr(>F)** |
|---|---|---|---|---|---|---|
| Richness | - | 3 | 13.50 | 4.500 | 2.03 | 0.142 |
| Abundance | Tukey | 3 | 4.702 | 1.567 | 2.035 | 0.141 |

**Appendix 4.9.** Results of the ANOVA for the community weighted mean (CWM) and functional diversity (FD) data when succulents were removed. Only includes data which had patterns that differed from expected trends as we believe the presence of succulents led to these unexpected patterns. Tran = Transformation, "Tukey" indicates that a Tukey Ladder of Powers transformation was used.

| **CWM Leaf Dry Matter Content** | **Tran** | **Sum Sq** | **Mean Sq** | **F value** | **Pr(>F)** |
|---|---|---|---|---|---|
| **2016** | | 0.000115 | 0.0001151 | 0.461 | 0.504 |
| **2017** | Tukey | 322975 | 322975 | 1.277 | 0.271 |
| **2018** | | 0.000603 | 0.0006027 | 1.088 | 0.308 |
| **CWM Leaf Thickness** | **Tran** | **Sum Sq** | **Mean Sq** | **F value** | **Pr(>F)** |
| **2017** | | 0.0000066 | 6.561e-06 | 0.297 | 0.591 |
| **2018** | | 0.0000560 | 5.603e-05 | 2.369 | 0.138 |
| **CWM Seed Weight** | **Tran** | **Sum Sq** | **Mean Sq** | **F value** | **Pr(>F)** |
| **2017** | Tukey | 4.919e+29 | 4.919e+29 | 0.035 | 0.853 |
| **2018** | Tukey | 510572 | 510572 | 1.682 | 0.208 |
| **CWM Height** | **Tran** | **Sum Sq** | **Mean Sq** | **F value** | **Pr(>F)** |
| **2017** | | 2.71 | 2.706 | 0.561 | 0.462 |
| **2018** | | 9.93 | 9.927 | 0.858 | 0.364 |
| **CWM Specific Leaf Area** | **Tran** | **Sum Sq** | **Mean Sq** | **F value** | **Pr(>F)** |
| **2018** | | 3226 | 1075.3 | 4.331 | 0.0166 |
| **FD Total** | **Tran** | **Sum Sq** | **Mean Sq** | **F value** | **Pr(>F)** |
| **2017** | Tukey | 32.7 | 10.89 | 0.243 | 0.865 |
| **2018** | | 0.0528 | 0.01761 | 0.503 | 0.684 |
| **FD Leaf Dry Matter Content** | **Tran** | **Sum Sq** | **Mean Sq** | **F value** | **Pr(>F)** |
| **2015** | Tukey | 0.00129 | 0.0004287 | 0.144 | 0.933 |
| **2016** | | 0.01617 | 0.005391 | 0.586 | 0.631 |
| **2017** | Tukey | 0.00606 | 0.002022 | 0.366 | 0.779 |
| **2018** | Tukey | 0.9296 | 0.30986 | 4.384 | 0.0159 |
| **FD Leaf Thickness** | **Tran** | **Sum Sq** | **Mean Sq** | **F value** | **Pr(>F)** |
| **2017** | | 0.0494 | 0.01648 | 0.944 | 0.438 |
| **2018** | | 0.0549 | 0.01831 | 0.417 | 0.743 |

**Appendix 4.10.** Results of the Tukey post hoc test for the community weighted mean (CWM) and functional diversity (FD) data when succulents were removed. Only includes data with an ANOVA p-value above 0.05.

| **CWM Specific Leaf Area 2018** | **diff** | **lwr** | **upr** | **p adj** |
|---:|---:|---:|---:|---:|
| 515:10 | -29.157655 | -54.62058 | -3.6947277 | 0.0212510 |
| 15:10 | -18.974256 | -44.43718 | 6.4886717 | 0.1917684 |
| 5:10 | -4.514243 | -29.97717 | 20.9486842 | 0.9590047 |
| 5:15 | 14.460013 | -11.00291 | 39.9229398 | 0.4066651 |
| 515:15 | -10.183399 | -35.64633 | 15.2795279 | 0.6821551 |
| 515:5 | -24.643412 | -50.10634 | 0.8195154 | 0.0600152 |
| **FD Leaf Dry Matter Content 2018** | **diff** | **lwr** | **upr** | **p adj** |
| 515:10 | -0.5315614 | -0.9611699 | -0.10195288 | 0.0120793 |
| 15-10 | -0.2285949 | -0.6582034 | 0.20101359 | 0.4620419 |
| 5-10 | -0.1230965 | -0.5527050 | 0.30651198 | 0.8526810 |
| 5-15 | 0.1054984 | -0.3241101 | 0.53510688 | 0.9007126 |
| 515-15 | -0.3029665 | -0.7325750 | 0.12664202 | 0.2307753 |
| 515-5 | -0.4084649 | -0.8380734 | 0.02114363 | 0.0660199 |

# Chapter 5

## Functional Trait Divergence Encourages Coexistence

### Abstract

Depending on the plant community, coexistence can be maintained through fluctuation-independent mechanisms, such as resource competition, or through fluctuation-dependent mechanisms, such as temporal variation. In both scenarios, functional trait divergence plays a key role in maintaining species diversity. This is in part due to the fact that functional traits, the morphological, phenological and physiological features of an organism, play an integral role in determining a species' ecological niche. In this study, I created two experiments to determine how trait divergence influences competition and coexistence. Both experiments incorporate species combinations that vary in functional diversity, with combinations including species that are functionally similar, dissimilar, or of intermediate similarity. The first experiment was conducted in a greenhouse and examines how trait divergence influences coexistence in an environment with a dynamic watering regime. Experiment two was conducted on a green roof and incorporates greater species richness than experiment one. Furthermore, experiment two varies species abundance so that I can examine how trait divergence influences a species' potential to persist at low density. In this chapter I use three indices to calculate potential coexistence: (1) I use the relative interaction index to measure facilitative potential, with higher facilitation potential equating lower competition and increased coexistence potential; (2) The ability to increase when rare, an indication the species can persist in the environment and coexist with neighboring species; and (3) I measure Intraspecific competition verses interspecific competition, as modern coexistence theory states that coexistence can only occur if Intraspecific competition is greater than interspecific competition. Overall, co-occurring species with divergent values in height and leaf dry matter content had a less competitive relationship than species with convergent values of the aforementioned traits. Since both height and leaf dry matter content are associated with water uptake and drought tolerance divergent values in these two traits likely encouraged co-existence, as species have different water use requirements. Additionally, there is some support for the storage effect encouraging coexistence between species in the greenhouse study, namely for those treatments containing *S. novi-belgii*. However, since phenological complementarity was low for all treatments, future research examining this possible interaction is necessary.

## Introduction

A species' fundamental niche can be conceived as a hypervolume composed of n-dimensional axes, usually environmental gradients, where the axes contain the boundaries in which a species can maintain their population (Blonder, 2018), and the accumulation of all the axes is a species' niche. For example, the range in soil depth in which a species can persist and reproduce could be one axis. When species possess divergent functional traits, allowing them to occupy different niches, coexistence, co-occurrence for an extended period of time, can occur (Chesson, 2000). However, further research is needed to understand the complex relationship between co-occurring plant species and how trait divergence and convergence influence competition and coexistence (Carmona et al., 2019).

Depending on the plant community, coexistence can be maintained through fluctuation-independent mechanisms, such as resource competition, or through fluctuation-dependent mechanisms, such as temporal variation (Godwin et al., 2020; Hallett et al., 2019). In both scenarios, functional trait divergence plays a key role in maintaining species diversity. This is in part due to the fact that functional traits, the morphological, phenological and physiological features of an organism, play an integral role in determining a species' ecological niche (Kraft 2015). Morphological differences between co-occurring species, such as different plant heights, allow species to differ in the quantity of resources needed, as well as in the physical location resources are acquired from. For example, a study by Wang et al. (2018) found that arctic graminoids possessed deeper roots then co-occurring dwarf shrubs. Due to this trait difference, the graminoids were more efficient at absorbing nutrients from deeper in the soil column and dwarf shrubs were more efficient at absorbing nutrients higher in the soil column (Wang et al., 2018). Phenological differences between co-occurring species, such as differences in peak growth, allow species to acquire resources at different times, reducing competition for the limiting resource. For instance, a study conducted in grassland communities in northern Greece found that $C_3$ annuals and perennials grew from autumn to spring and co-occurring $C_4$ species grew from winter to summer. Since these species grow and use resources at different times, coexistence between them is possible (Mamolos, 2006). Finally, physiological differences between species, such as differences in photosynthesis pathways, allow species to acquire resources in different ways. For example, carnivorous plant species, which can acquire nutrients from prey, are less likely to compete with neighboring species for belowground nutrients (Abbott and Brewer, 2020).

In order to determine how trait divergence contributes to coexistence, researchers can apply modern coexistence theory to ecological systems. The invasibility criterion for species coexistence plays a major role in modern coexistence theory. Here, coexistence is possible if an invading species at low density can persist and increase in growth within the invaded community (Chesson, 2000). Using this principle as a foundation, modern coexistence theory articulates three key principles: intraspecific competition must be greater than interspecific competition, which allows less competitive species to persist as the dominant species are limiting their own growth; species must have niche differences, with a species' niche defined as all the biotic and abiotic factors that allow a species to maintain their population within a community (Hutchinson 1957; Silvertown, 2004); and relative fitness differences must be present. Relative fitness differences lead to variation in a species' competitive ability in space and or time (Godwin et al., 2020; Chesson 2000; Chesson 2018). Although this coexistence framework is robust, more empirical evidence is necessary to understand the role functional trait divergence/convergence plays in the maintenance of species diversity.

Coexistence in dynamic environments also relies on species possessing divergent functional traits. Research into fluctuation-dependent plant communities has led to the development of two dominant models: relative non-linearity, where species respond to the environment in a different nonlinear manner, and the storage effect, in which species store resources from a productive period to survive during an unproductive period (Hallett et al., 2019; Chesson 2000). By far the more complex mechanism, coexistence through the storage effect requires three criteria: species must have divergent traits that lead to different environmental responses (germination temperature, drought-tolerant strategies), species' competitive ability must change as a response to environmental conditions (covariance between species), and species must be capable of surviving unfavorable conditions (Chesson, 2000). For example, if two desert annuals germinate under different temperatures but similar moisture regimes, annual variation in temperature will influence which species has the competitive advantage. So long as both species can survive unfavorable conditions, this annual variation can lead to coexistence (Chesson et al., 2004). Angert et al., (2009) observed the storage effect in winter annuals with divergent traits related to water-use efficiency.  During short but frequent rainfall events, species with low water-use efficacy excelled, and during periods of long but infrequent rainfall events, species with high water-use efficacy excelled. Coexistence between species was possible due to a yearly variation in rainfall supporting the growth of each species in turn (Angert et al., 2009).

Within-year variation can also lead to coexistence via the storage effect. This was observed by Mathias and Chesson (2013), who examined the influence of seasonal temperature variation on the germination and seed set of winter annuals. They found that seasonal temperature variation resulted in disparity in the competitive ability of the winter annuals, leading to coexistence between these species (Mathias and Chesson, 2013). Due to their short life cycles, annual plant communities offer an ideal environment to test coexistence mechanisms. However, there is still a need to empirically test fluctuation-dependent mechanisms in long-lived plant communities.

In this study, I created two experiments to determine how trait divergence influences competition and coexistence. Both experiments incorporate species combinations that vary in functional diversity, with combinations including species that are functionally similar, dissimilar, or of intermediate similarity. I test for coexistence using three indices: (1) I use the relative interaction index to measure facilitative potential, with higher facilitation potential equating lower competition and increased coexistence potential; (2) The ability to increase when rare, an indication the species can persist in the environment and coexist with neighboring species; and (3) I measure Intraspecific competition versus interspecific competition, as modern coexistence theory states that coexistence can only occur if intraspecific competition is greater than interspecific competition. My general expectation was that higher FD communities would have higher values of all the coexistence indices I used. The first experiment was conducted in a controlled greenhouse environment and examines how trait divergence influences coexistence in an environment with a dynamic watering regime. Experiment two is conducted on a green roof and incorporates greater species richness than experiment one. Furthermore, experiment two varies species abundance so that I could examine how trait divergence influences a species' potential to persist at low density.

## Methods

This study consists of two separate experiments conducted at Saint Mary's University in Halifax, Nova Scotia (44°39′N, 63°35′W). The first experiment was conducted in a controlled greenhouse environment between March and August 2019 and the second experiment was conducted on a five-story green roof (see Chapter 2) between June 2019 and September 2020. This region has a yearly average precipitation between 8.4 mm – 45.1 mm and an average yearly temperature between -27.3°C – 10.9°C (Government of Canada, 2019).

All plants used in both experiments were grown in a greenhouse (January-May 2018), harvested from previous green roof experiments at Saint Mary's University or, for *Solidago puberula* and *Avenella flexuosa*, harvested from abandoned lots surrounding the Saint Mary's Campus. For each species in both studies, five different plant traits were collected: specific leaf area, leaf dry matter content, plant height, leaf thickness, and root radius. These traits were chosen due to known associations with plant growth and stress tolerance (Vile et al., 2005; Niinemets 2001; Ogburn et al., 2010; Tardy et al., 2015;

Poorter and Garnier, 1999; Wright et al., 2001; Moles et al., 2009; Wang et al., 2019; Comas 2013). For each species, traits were collected from 10 healthy adult individuals growing in their natural environments (Pérez-Harguindeguy et al., 2016). Aboveground traits for the succulent species were collected from the green roof at Saint Mary's University and aboveground traits for all other species were collected from dwarf heath and salt spray habitats at the Chebucto Head coastal barren site (34°30′ N, 63°31′W). Belowground traits for all but three species were collected from five healthy individuals from the greenhouse experiment at the end of August 2019. Roots were stored in a 70% ethanol 30% water solution at 4ºC until November 2019, at which time traits were calculated. Roots from *Phedimus spurius* and *Festuca rubra* were collected from five healthy adult individuals growing on a green roof adjacent to the green roof experiment, and roots for *Avenella flexuosa* were collected from five individuals grown to adulthood from seed (collected from Chebucto Head). Due to a processing error, only four individuals of *S. album, S. puberula* and *S. sexangular* had roots available to calculate root traits.

### *Greenhouse Experimental Design*

The greenhouse used in this experiment was kept at around 18-30°C and had a light interval set to 16 hours off and 8 hours on (light intensity: 250umol/m$^2$*s, plus natural light). In order to help regulate greenhouse temperatures, a cover was placed over the greenhouse halfway through the experiment, in June 2019.

The species used in this experiment were chosen due to their success in previous experiments (MacIvor and Lundholm, 2011; Heim et al., 2016) and observed trait similarities and differences with the other vegetation in this study. Species included three succulents: *Sedum acre, Sedum album, Sedum sexangulare*; three creeping shrubs: *Empetrum nigrum, Gaultheria procumbens, Vaccinium macrocarpon*; three upright forbs: *Solidago bicolor*, *Solidago puberula*, *Symphyotrichum novi-belgii*; and three species possessing morphological characteristics observed to be of intermediate similarity to the above mentioned species: *Sibbaldia tridentata* (fast growing creeping shrub), *Plantago maritima* (forb with succulent like leaves), and *Danthonia spicata* (thin-leaved, drought-tolerant plant).

All treatments were established in 13 x 13 x 15 cm pots which contained 10 cm of green roof substrate (Sopraflor X: Soprema Inc., Drummondville, QC, Canada). This experiment contained 90 treatments: 12 that contained one individual per pot, 12 monoculture treatments that contained two individuals of the same species per pot, and 66 mixture treatments that contained every possible combination of species with two individuals per pot. However, two *E. nigrum* pairs were excluded due to a lack of *E. nigrum* individuals (*S. bicolor* and *E. nigrum*; *S. album* and *E. nigrum*). Each treatment consisted of five replicates separated into five blocks (Figure 5.1). Treatments were planted and stored outside from June 2019 to February 2020. This was done to allow individuals to establish and undergo one natural dormancy cycle. All treatments were weeded throughout the establishment and experimental periods. Before the experiment began starting in March 2020, treatments were watered weekly either artificially or through natural rain events.

This study subjected all treatments to a fluctuating water regime. This was done to allow for the expression of any phenological differences among species related to wet vs dry conditions. Each water regime lasted four weeks and occurred twice during this six-month experiment. The water regimes included: watering once a week (March, June), watering once every two weeks (April, July), and watering twice a week (May, August). During each watering period, all treatments were watered to saturation (600 ml of water). Between March and August 2020, aboveground biomass was estimated for each treatment once every two weeks using the point intercept method (Floyd and Anderson, 1987), with five intercept points per pot. Each time living aboveground biomass contacted one of the five pins, it was counted. Species that were present in the pot but did not hit the pin were counted as one.

**Figure 5.1.** Greenhouse experimental setup

### ***Green Roof Experimental Design***

Plants were established between May 2018 and 2019 in free-draining green roof modules (36 x 36 x 12 cm) that contained green roof water retention/root barrier fabric (EnkaRetain and Drain 3111®, Colbond Inc., NC, USA) and 10 cm of green roof substrate (Sopraflor X: Soprema Inc., Drummondville, QC, Canada). Modules were weeded monthly during the growing season. Once the experiment began, modules only received moisture from natural precipitation.

As in the greenhouse study, species were chosen due to success in previous experiments (MacIvor and Lundholm, 2011; Heim et al., 2016) and due to observed trait similarities and differences. The species used in this study included: *S. acre, S. album, S. sexangulare*, *S. tridentata, S. bicolor*, *S. puberula*, *S. novi-belgii*, *D. spicata*, *P. spurius, F. rubra,* and *A. flexuosa*. This study consisted of 11 treatments with one individual per module for each species, 11 monoculture treatments with nine individuals of the same species per module for each species, four mixed species combinations containing species with observed trait similarities (*S. acre, S. album, S. sexangular*; *S. bicolor*, *S. puberula, S. novi-belgii*; *D. spicata*, *F. rubra*, *A. flexuosa; D. spicata*, *P. spurius, S. tridentata*), and three mixed species combinations containing species with observed trait dissimilarities (*S. acre, D. spicata, S. bicolor; S. acre, S. tridentata, D. spicata; S. acre, S. tridentata, S. bicolor*) (Table 5.1). In order to further understand how species interactions may change based on functional similarity to neighbors, four species were present in multiple species mixtures: *S. bicolor, D. spicata, S. acre, S. tridentata*.

**Table 5.1.** List of the seven mixture combinations used in this study. Four of these combinations consisted of species with observed trait similarities and three consisted of species with observed trait dissimilarities.

| **Mixture Combinations** | | | | |
|---|---|---|---|---|
| Observed Trait Similarities | | | | |
| 1 | Succulents | *S. album* | *S. sexangulare* | *S. acre* |
| 2 | Tall Forbs | *S. puberula* | *S. novi-belgii* | *S. bicolor* |
| 3 | Graminoids | *F. rubra* | *A. flexuosa* | *D. spicata* |
| 4 | Similar drought tolerance | *P. spurius* | *S. tridentata* | *D. spicata* |
| Observed Trait Dissimilarities | | | | |
| 1 | Mixed Growth Form | *S. acre* | *D. spicata* | *S. bicolor* |
| 2 | Mixed Growth Form | *S. acre* | *S. tridentata* | *D. spicata* |
| 3 | Mixed Growth Form | *S. acre* | *S. tridentata* | *S. bicolor* |

All mixed species combinations were further divided into four density treatments: one equal-density treatment (three randomly distributed individuals of each species per module) and three low-density treatments, one for each species in the mixture (one individual of species A planted in the center of the module surrounded by four randomly distributed individuals of species B and C) (Figure 5.2). All except eight treatments had nine replicates. The eight treatments with five replicates included the monoculture and single individual treatments of the following species:  *S. album*, *S. puberula*, *A. flexuosa*, and *P. spurius*. This experiment was separated into nine blocks.

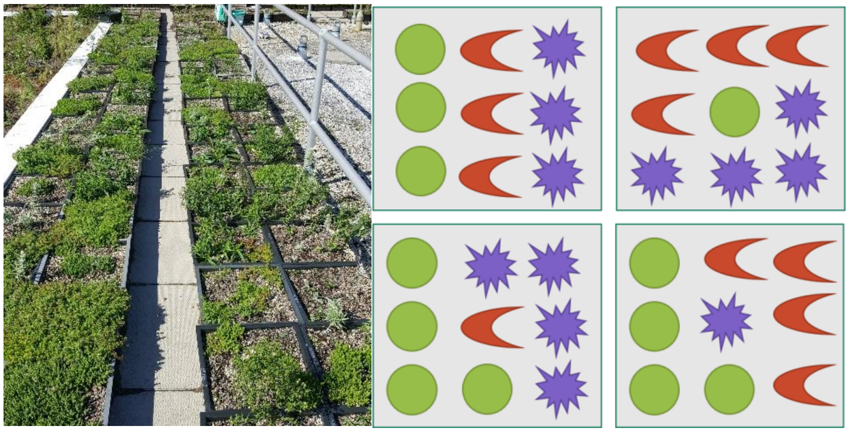


**Figure 5.2.** Photo of modular green roof study and example of the four density treatments for the mixed species combinations.

Using the point intercept method (Floyd and Anderson, 1987), aboveground biomass was estimated once every two weeks during the first growing season (June and August 2019), twice in the fall (September and November 2019), once in the spring (April 2020), and once a month during the second growing season (May-August). Each time living aboveground biomass contacted one of the 12 pins, it was counted. Species that were present in the module but did not hit a pin were counted as one.

### *Phenological complementarity*

Phenological complementarity calculates differences in growth over time. Specifically, it can be used to determine if species increase in biomass at the same point in time. This phenological index was calculated using the following formula (Stevens and Carson 2001):

$$\text{Phenological complementarity} = -log_e\,(Var\{i-1\frac{\Sigma}{n}, S_i\}/Var\{S_i\}i\ -1\frac{\Sigma}{n})$$

$S_i$ is the aboveground biomass for a species on a particular date (i) and Var{} is the sample variance between March and August 2019 for the greenhouse study, and June 2019 and September 2020 for the green roof study. The biomass used in this calculation was collected using the point intercept method. If phenological complementarity < 0 then there was no support for complementarity and species have similar growth patterns (trait convergence/low functional diversity). This index was used as a predictor variable alongside the functional diversity variables as differences the timing of growth indicate differences in resource use which could encourage coexistence. This variable was also included as a way to test for the storage effect, for which differences in growth phenology could encourage coexistence.

*Indicators of coexistence*

The relative interaction index calculates competitive and facilitative interactions between species. In this study it was used to determine how trait dissimilarity influenced species interactions. The relative interaction index was calculated using the following formula (Armas et al., 2004):

$$RII = \frac{Biomass\ with\ multiple\ individuals - Average\ Biomass\ one\ individual}{Biomass\ with\ multiple\ individuals + Average\ Biomass\ one\ individual}$$

Values > 0 indicate a net facilitative effect, values < 0 indicate a net competitive effect, and a value of 0 indicates that the interaction was neutral. RII varies between -1 and 1 with higher values associated with a less competitive interaction and therefore greater potential coexistence. The RII was calculated for each species. Biomass refers to the point intercept data collected in August 2019 for the greenhouse study and in August 2020 for the green roof study. All individuals of the same species in the same treatment were used to calculate the biomass for that species. In the greenhouse study, mixture treatments contained two individuals of two different species. Since biomass was only collected per species and not per individual, monoculture treatments were divided by two so that they could be compared to mixture treatments.

Relative growth rate was calculated for each species per module/pot For both experiments, the relative growth rate was calculated from the point intercept data using the following formula:

$$Relative\ Growth\ Rate = \frac{[Ln(Biomass\ Time\ 2)] - [Ln(Biomass\ Time\ 1)]}{\#\ of\ days}$$

For the greenhouse study, time one refers to March 4, 2019, and time two refers to August 15, 2019. For the green roof study, time one refers to June 12, 2019, and time two refers to August 13, 2020. Relative growth rate was used to calculate two measures of coexistence: (1) intra versus inter competition, with a lower relative growth rate in intraspecific combinations an indication of coexistence; and (2) A positive growth rate when planted at low density an indication of a species' ability to persist and coexist with neighboring species (invasion criterion).

In both greenhouse and green roof experiments, a multiple linear regression was used to understand how functional trait divergence (phenological complementarity and functional diversity) influenced plant growth (relative growth rate and relative interaction index).

Functional diversity was used to determine how similar species’ morphological traits were to each other, with high functional diversity associated with trait divergence. Functional diversity variables were predicted to be positively related to coexistence indicators as variation in functional traits is an indication that species are using resources in a different way (niche differences). Here, functional diversity was determined by calculating functional dispersion, the mean distance from a species' position in multidimensional trait space to the centroid (calculated as the average value of trait(s) across all species), (Laliberté and Legendre, 2010 using the FD package (Laliberté et al., 2015) in R version 3.6.0.). Both individual traits (height, specific leaf area, leaf dry matter content, leaf thickness, root radius) and the combination of all traits (total functional diversity) were used to calculate functional diversity variables. The FD package was also used to create a cluster dendrogram based on the morphological functional traits (phenological complementarity excluded). All explanatory variables were checked for normalcy using a Shapiro–Wilk test and transformed when $P<0.05$.

For the green roof experiment, ANOVA and Tukey post-hoc tests were used to compare the relative growth rate of each species in treatments with an equal distribution of species, and to compare the relative growth rate for each species when planted at low and equal density. The low-density analysis allowed me to assess the invasion criterion, where a species may successfully invade if it has a positive growth rate at low density. Variables were checked for normalcy using a Shapiro–Wilk test and transformed when $P<0.05$. All statistical analysis was calculated using R version 3.6.0.

## Results

### *Greenhouse Experiment*

Halfway through this experiment, at the beginning of month four, one of the greenhouse benches tipped over. The majority of treatments could be saved; however, nine pots from block two were lost. These pots included three pots containing one individual (*E. nigrum, S. acre, G. procumbens*), one pot containing two individuals (*E. nigrum*), and four pots containing two individuals of different species (*G. procumbens*/*V. macrocarpon*, *S. acre/G. procumbens*, *S. album/P. maritima*, and *V. macrocarpon/S. bicolor*).

In the greenhouse experiment, the species pair with the most divergent functional traits was *S. album* and *S. novi-belgii* (total functional diversity: 3.00), and the pairing with the most convergent functional traits was *E. nigrum* and *V. macrocarpon* (total functional diversity: 0.44) (Figure 5.3). Only two functional diversity variables, phenological complementarity (negative correlation) and plant height (positive correlation), were associated with the relative interaction index (Figure 4).

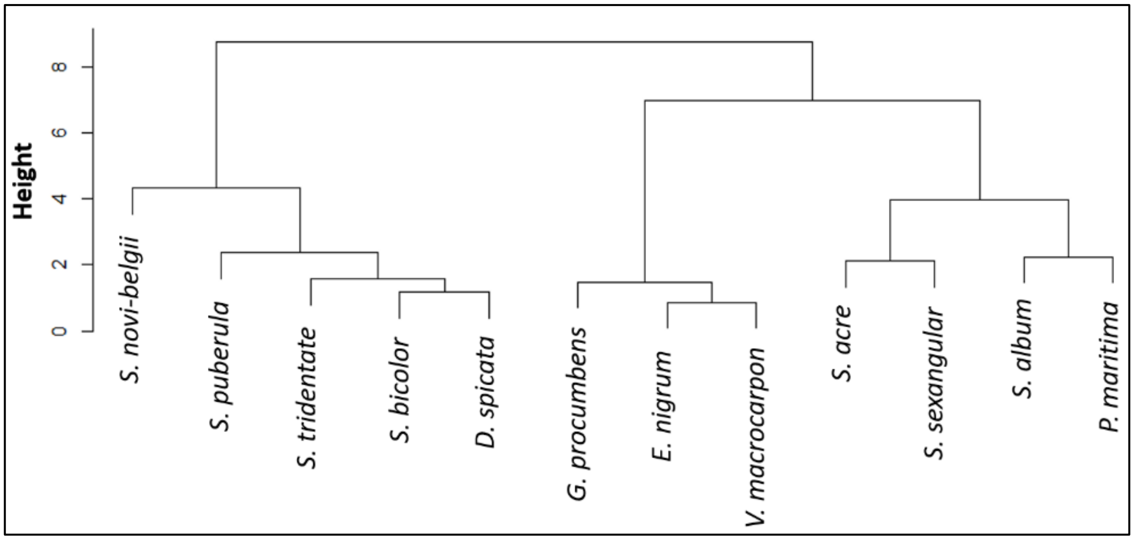


**Figure 5.3.** Cluster dendrogram for the species in the greenhouse experiment. The traits incorporated in this dendrogram include plant height, specific leaf area, leaf dry matter content, root radius, and leaf thickness. Height represents distance between clusters.

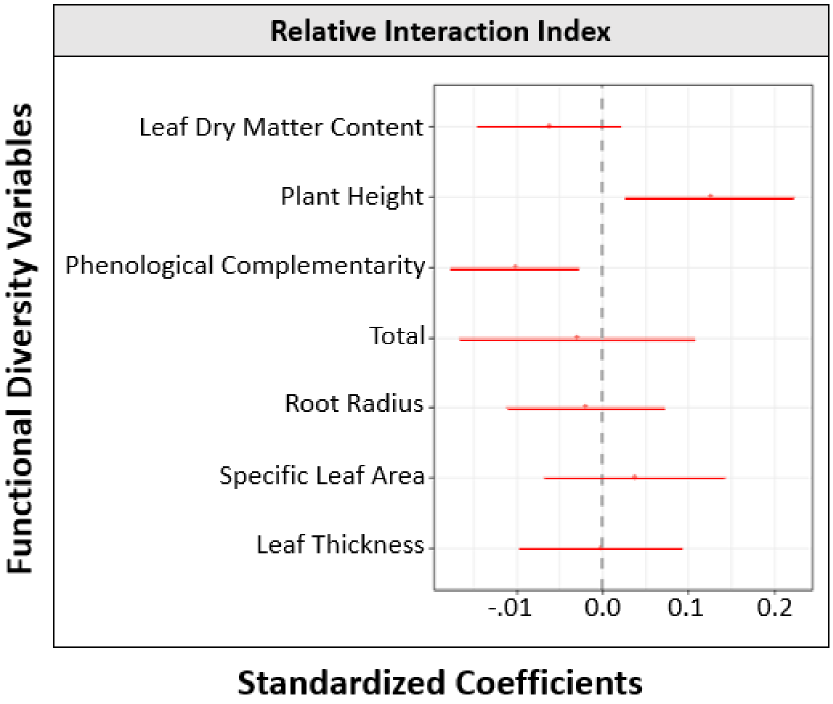


**Figure 5.4.** This graph shows the relationship between the relative interaction index and functional diversity variables for the greenhouse experiment. The lines represent 95% confidence intervals calculated from a multiple linear regression. Legend: functional diversity of all traits (total).

When the relative growth rate was examined, different patterns emerged for each treatment. Species in treatments containing *S. sexangulare, S. acre, S. bicolor, S. novi-belgii, D. spicata, P. maritima, and S. tridentata* generally had a positive growth rate. Species in treatments containing *E. nigrum, P. procumbens, and V. macrocarpon* generally had a negative growth rate or a growth rate of 0 (Figure 5.5).

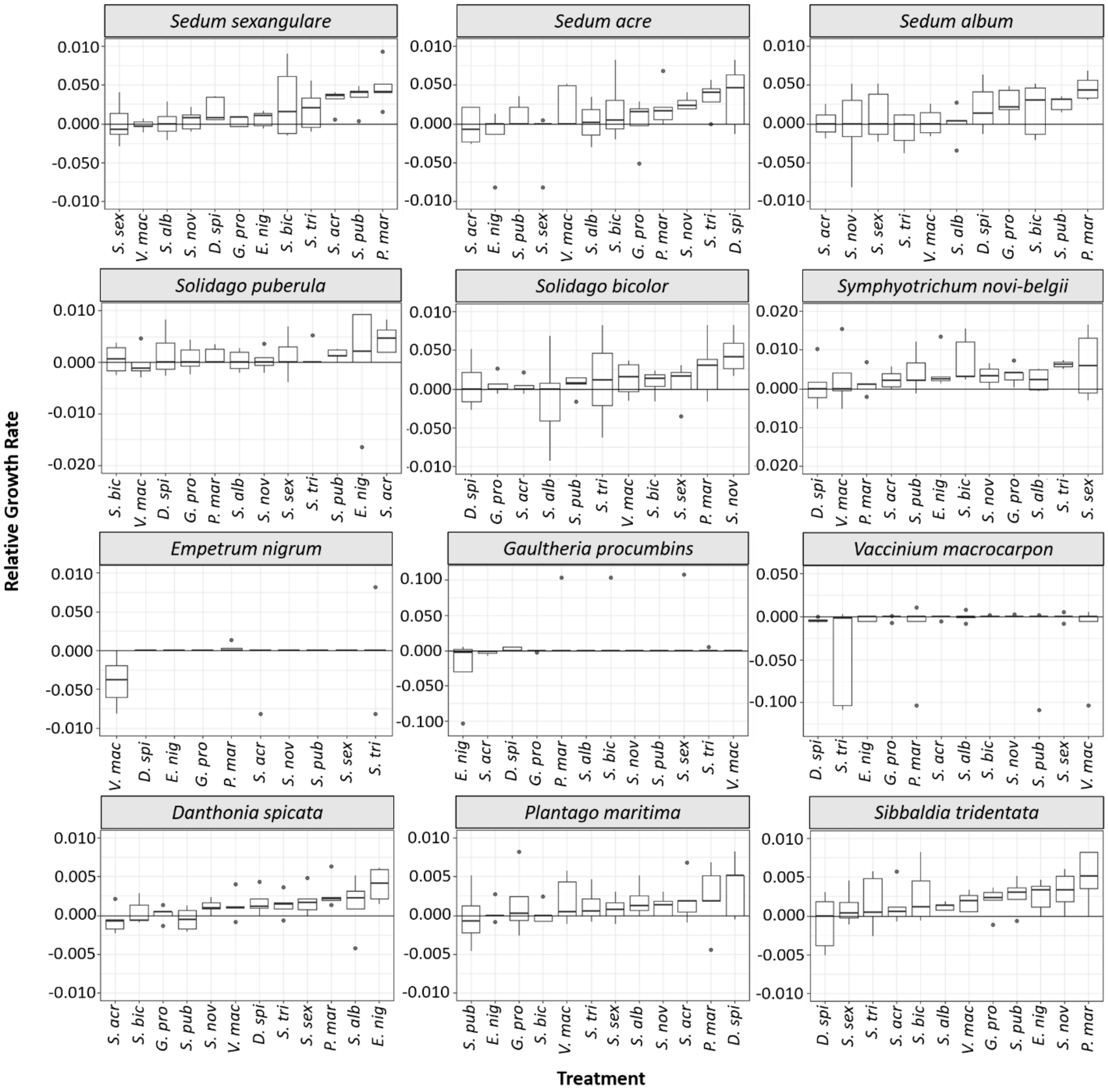


**Figure 5.5.** Average relative growth rate for species in the greenhouse study. Each graph shows the average growth rate for the species specified in the graph title. The x-axis is ordered by the mean and shows the species paired with the species identified in the graph title. X-axis species code: first letter of the genus followed by the first three letters of the species name. See appendix 5.D for a list of the functional diversity variables for each treatment.

### *Green Roof Experiment*

When functional diversity was calculated for each species combination, the combination with the most convergent traits was *S. bicolor/S. novi-belgii/S. puberula* (total functional diversity: 0.89) and the combination with the most divergent traits was *A. flexuosa/D. spicata/F. rubra* (total functional diversity: 2.19) (Table 5.1 and Figure 5.6). For the relative interaction index, species combinations with dissimilar leaf dry matter content had the least competitive relationships (Figure 5.7).

**Table 5.1.** Functional diversity of each plant combination when species abundance is equal. High functional diversity is associated with trait divergence while low functional diversity is associated with trait convergence. Legend: phenological complementarity (PC), functional diversity calculated from all morphological traits (Total), and functional diversity calculated from individual traits: plant height (height), leaf dry matter content (LDMC), root radius (Root), specific leaf area (SLA), leaf thickness (Thick). The species combinations with the highest and lowest functional diversity have been Italicized.

| Species Combination | Total | PC | Height | LDMC | Root | SLA | Thick |
|---|---|---|---|---|---|---|---|
| *S. acre/S. album/S. sexangulare* | 1.55 | 0.51 | ***0.04*** | 0.23 | 0.38 | 0.32 | ***1.17*** |
| *A. flexuosa/D. spicata/F. rubra* | ***2.19*** | ***0.76*** | 0.42 | ***0.09*** | ***0.95*** | ***1.42*** | 0.06 |
| *S. bicolor/S. novi-belgii/S. puberula* | ***0.89*** | 0.65 | 0.5 | 0.17 | 0.38 | 0.41 | ***0.04*** |
| *D. spicata/P. spurius /S. tridentata* | 1.26 | ***-0.07*** | 0.32 | 0.93 | 0.48 | ***0.14*** | 0.37 |
| *D. spicata/ S. bicolor/S. acre* | 1.37 | 0.26 | 0.49 | 0.89 | 0.36 | 0.21 | 0.33 |
| *D. spicata/S. acre/S. tridentata* | 1.35 | 0.24 | 0.31 | ***1.01*** | 0.36 | 0.23 | 0.31 |
| *S. acre/S. bicolor/S. tridentata* | 1.36 | 0.4 | ***0.57*** | 0.9 | ***0.21*** | 0.29 | 0.27 |

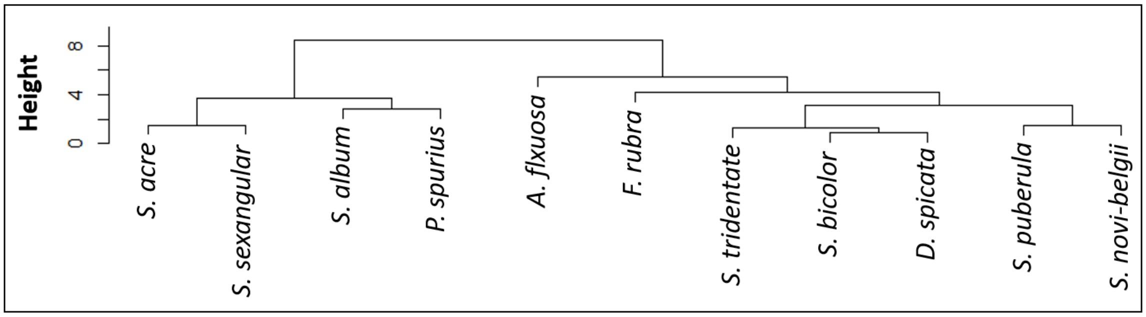


**Figure 5.6.** Cluster dendrogram for the species in the green roof experiment. The traits incorporated in this dendrogram include plant height, specific leaf area, leaf dry matter content, root radius, and leaf thickness. Height on the y-axis represents distance between clusters.

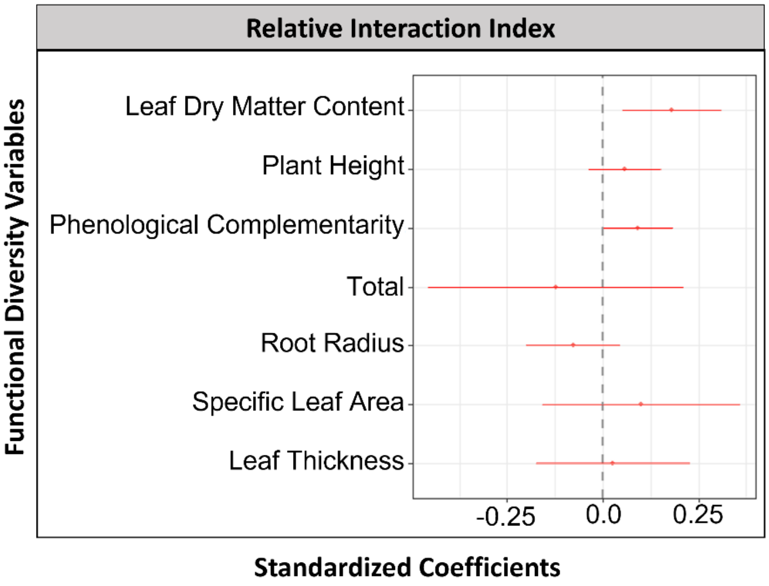


**Figure 5.7.** The relationship between the relative interaction index and functional diversity variables in the green roof experiment. The lines represent the 95% confidence intervals calculated from a multiple linear regression. "Total" represents functional diversity of all traits.

For the four species used in multiple species combinations, two species had a higher growth rate when planted with specific species. For *S. acre*, the relative growth rate was higher in the treatment containing *D. spicata* and *S. tridentata* (total functional diversity: 1.35) and lower in the treatment containing *S. album* and *S. sexangulare* (total functional diversity – 1.55). For *S. tridentata*, growth rate was highest in the treatment containing *S. acre* and *S. bicolor* (total functional diversity: 1.36) (Figure 5.8). For the relative interaction index, all combinations were negative, indicating competitive interactions. Even so, variation did occur between treatments. For *D. spicata*, the relative interaction index was lowest in the treatment containing *S. tridentata* and *P. spurius* (total functional diversity: 1.26) and highest in the treatment containing *S. bicolor* and *S. acre* (total functional diversity: 1.37). For *S. acre*, the relative interaction index was lowest in the treatment containing *S. album* and *S. sexangulare* and highest in the treatment containing *S. tridentaae* and *D. spicata*. For *S. tridentata*, the relative interaction index was lowest in the *S. tridentata* monoculture and highest in the treatment containing *D. spicata* and *P. spurius*. Finally, no variation was observed when the relative interaction index was calculated for *S. bicolor* (Figure 5.9).

For the majority of treatments, there was no difference in the relative growth rate of a species when planted at low or equal density. However, in comparison to the equal density treatment, *A. flexuosa* had a lower relative growth rate at low density when combined with *F. rubra* and *D. spicata*, and *S. acre* had a higher relative growth rate at low density when planted with *D. spicata* and *S. tridentata* (Figure 5.10).

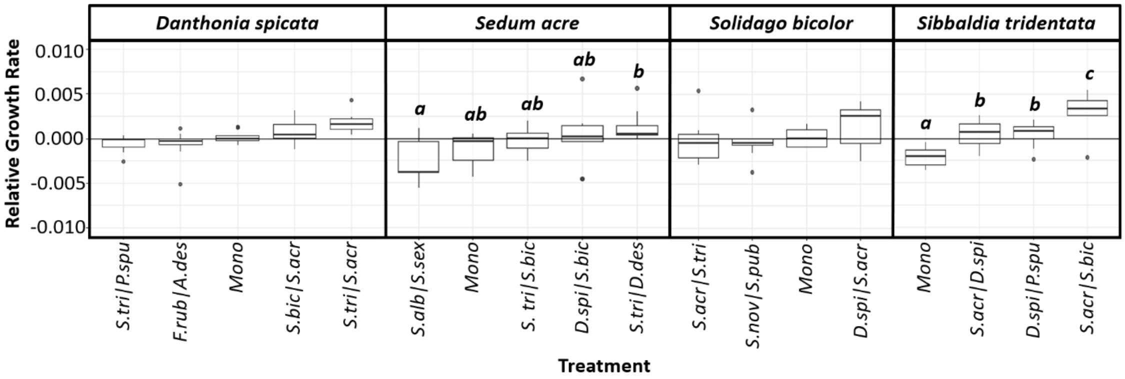


**Figure 5.8.** Boxplots showing the results of ANOVA and Tukey tests used to compare the relative growth rate of the species identified in the title. The x-axis is ordered by the mean and shows which species were planted alongside the species identified in the title and are written as the first letter of the genus name followed by the first three letters of the species name. The letters represent results from Tukey post-hoc tests for which treatment is the independent variable and relative growth rate is the dependent variable. Bars that share a letter have a p-value >0.05. Legend: monoculture containing nine individuals of the same species (Mono), mixture treatment containing three individuals of each species (X.xxx|X.xxx).

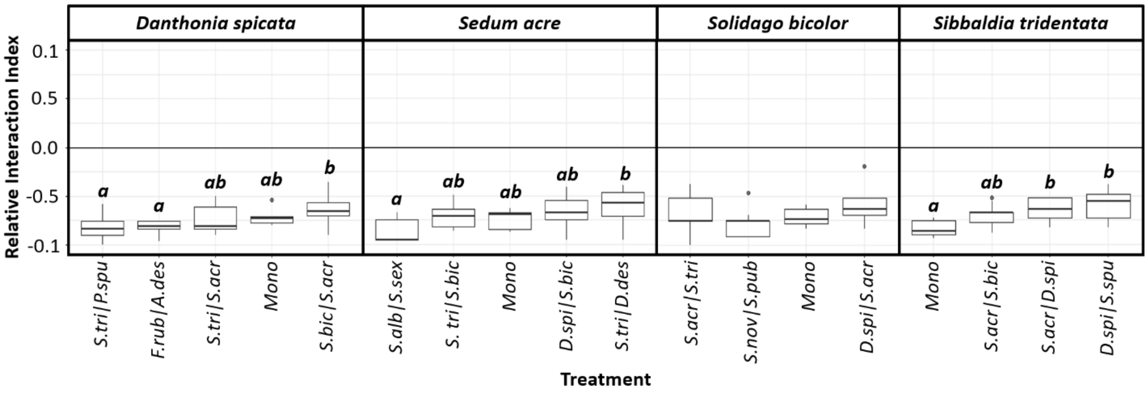


**Figure 5.9.** Boxplots showing the results of Anova and Tukey tests used to compare the relative interaction index of the species identified in the title. The x-axis is ordered by the mean and shows which species were planted alongside the species identified in the title and are written as the first letter of the genus name followed by the first three letters of the species name. The letters represent results from Tukey post-hoc tests for which treatment is the independent variable and relative interaction index is the dependent variable. Bars that share a letter have a p-value >0.05. Legend: monoculture containing nine individuals of the same species (Mono), mixture treatment containing three individuals of each species (X.xxx|X.xxx). See Table 1 for a list of how functional diversity varied between treatments.

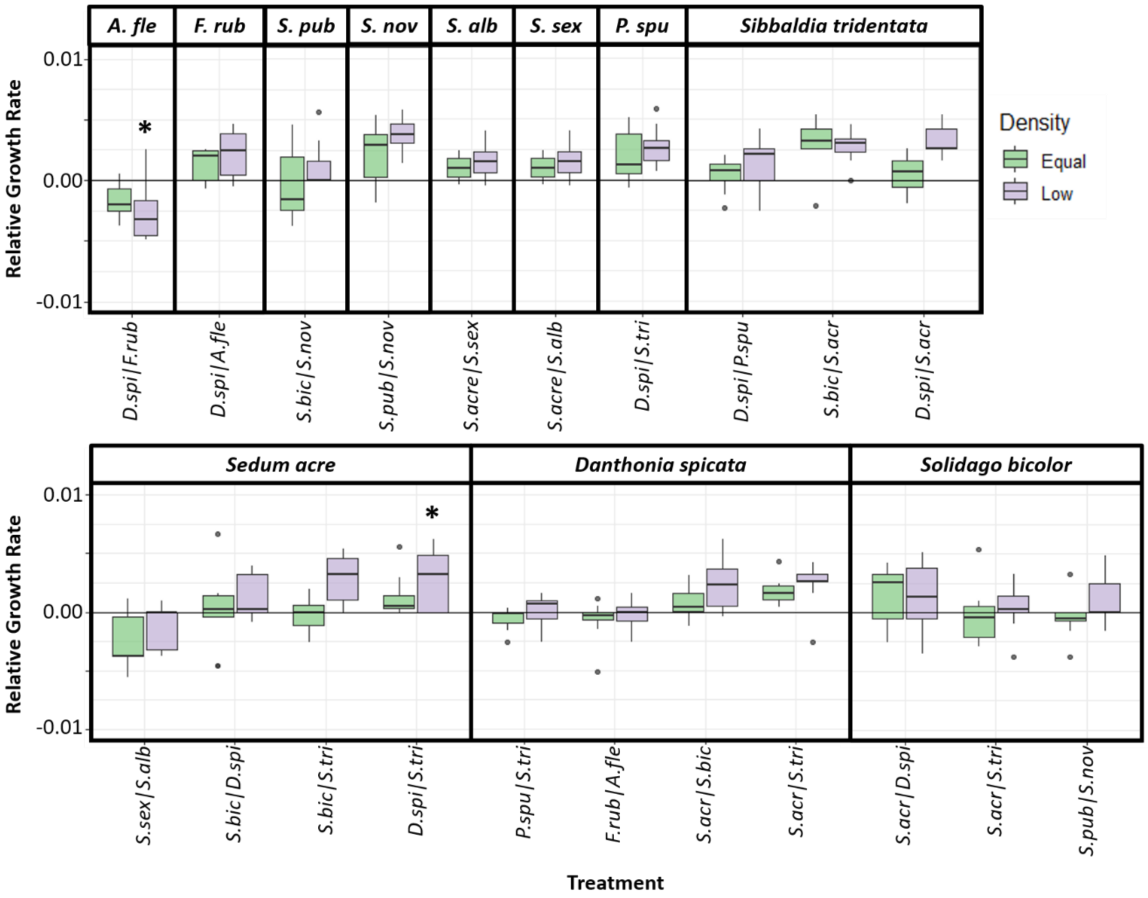


**Figure 5.10**. Boxplots showing the results of Anova and Tukey tests used to compare the relative growth rates of species when planted at low and equal density. The x-axis shows which species were planted alongside the species identified in the title and are written as the first letter of the genus name followed by the first three letters of the species name. The * represent results from Tukey post-hoc tests for which treatment is the independent variable and relative growth rate is the dependent variable. Bars that have a * have a p-value >0.05. Legend: monoculture containing nine individuals of the same species (Mono), mixture treatment containing three individuals of each species (X.xxx|X.xxx). See Table 5.1 for a list of how functional diversity varied between treatments.

## Discussion

The goal of this chapter was to ascertain how trait divergence, determined by functional diversity, influences competition and coexistence. Here the intensity of competition was determined by calculating the relative interaction index and relative growth rate. For the relative interaction index, positive values signify that the species had a higher growth rate in the mixed treatment as opposed to the single individual monoculture treatment, an indication that coexistence between these mixed species is possible. Furthermore, a positive relative growth rate indicates a species can persist in the given treatment, an indication that coexistence is possible.

For RII, no association was observed between competition/coexistence and total functional diversity (calculated from all traits). However, patterns emerged when traits were analyzed individually. Previous research has also found that examining species traits as an aggregate across multiple traits, as opposed to individual traits, neglects potential interactions (Spasojevic et al., 2012; Li et al., 2018). For example, an alpine tundra study by Spasojevic et al. (2012) found no association between variables when functional diversity was calculated using multiple traits together. However, when functional diversity was analyzed separately for height and leaf area wind and cold exposure was found to negatively effect these trait values. Here, co-occurring species with divergent values in height and leaf dry matter content had a less competitive relationship than species with convergent values of the aforementioned traits. Since both height and leaf dry matter content are associated with water uptake and drought tolerance (Tardy et al., 2015; Poorter and Garnier, 1999; Liu et al., 2019), divergent values in these two traits likely encouraged co-existence, as divergent species likely have different water use requirements. A greenhouse study by Matsuoka et al. (2019) found similar results, with increased divergence in growth form and leaf characteristics associated with individuals scoring higher on their health index (Matsuoka et al., 2019).

Interestingly, even though the majority of plant species was shared between experiments, the traits that decreased competitive interactions differed. In the greenhouse study, co-occurring species with divergent heights had the least competitive relationship, whereas divergent values in leaf dry matter content decreased competition in the green roof experiment. These dissimilar results likely occurred due to differences in exposure, with vegetation in the green roof experiment exposed to high winds. Since taller species are more susceptible to desiccation and wind damage (Nagashima and Hikosaka, 2011), coexistence through divergent values of leaf dry matter content rather than plant height makes sense for the green roof environment.

Convergence in only one trait, growth phenology in the greenhouse study, increased coexistence potential. This finding was unexpected as divergent growth patterns are thought to encourage coexistence since peak resource use occurs at different times (Chesson et al., 2004). One possible explanation is that divergent growth could have largely occurred belowground. Since root biomass was only calculated at the end of the study, the overemphasis on aboveground biomass may have misrepresented the phenological complementarity of these treatments. Another possible explanation involves the watering regime incorporated into this experiment. Since convergent growth phenology was observed in 84% of the treatments, the set timeframe watering occurred in likely forced species to grow during favorable moisture conditions. This provides evidence for resource storage, with species growing during favorable conditions and storing resources to survive unfavorable conditions (Chesson, 2000; Angert et al., 2009; Mathias and Chesson, 2013).

Net positive interspecific interactions indicating facilitation were only observed in the greenhouse study, with the growth of *S. novi-belgii* and *P. maritima* facilitated by the majority of species they were paired with. However, facilitation for both these species was one way, with neighboring species scoring a competitive interaction. This finding indicates that *S. novi-belgii* and *P. maritima* prefer to be grown with a neighbor rather than alone in bare substrate. The presence of neighbors may facilitate *S. novi-belgii* and *P. maritima* by sheltering the substrate, leading to reduced water loss and substrate temperature. Facilitation in this manner has been observed in previous green roof experiments. Specifically, both Butler and Orians (2011) and Heim and Lundholm (2014) found that combining upright forbs with dense matted species such as succulents or moss reduced substrate temperature and water loss, encouraging coexistence. Similar interactions also occur in the natural environment. Olofsson (2004) found that, in arctic dwarf shrub communities, shrub canopies facilitate neighbors by creating a warmer, moister microclimate (Olofsson, 2004).

Even if particular species combinations encouraged greater growth, there are indications that the species used in the green roof experiment should be able to coexist for an extended period of time. Two results, requirements for coexistence, support this interpretation: 1) the majority of species had a positive growth rate at low density and 2) interspecific competition was usually lower than intraspecific competition (Chesson, 2000). For the species used in the greenhouse experiment more research is needed to determine potential coexistence. On the plus side, the majority of greenhouse species boasted a positive growth rate in mixed treatments. However, intraspecific competition was not always greater than interspecific competition. This negative result may be due to the short duration of the greenhouse experiment, as previous research observed co-occurrence, for at least four years, between many of these species (Chapter 2; Lundholm et al., 2014).

In the greenhouse study, the treatments with the greatest relative growth rate were often paired with the forb *S. novi-belgii*. This was the tallest species in the study and had one of the strongest reactions to desiccation, with individuals entering dormancy during drought and quickly re-sprouting when conditions became more favorable. These attributes may have made it easier for neighboring species to coexist. However, future research is needed to confirm this reasoning.

Both experiments also contained treatments that were less successful. By the end of the greenhouse experiment three species, the dwarf shrubs *E. nigrum*, *G. procumbens*, and *V. macrocarpon*, had either no change or had declined in aboveground biomass. This result may be due to the short 6-month study period, with the growth of these species too slow to observe, or due to incompatible growing conditions. Previous research concerning these species has found that *E. nigrum* is drought sensitive, with natural populations outcompeted in warmer and drier locations (Hein et al., 2020), *G. procumbens* has a slow intrinsic growth rate, even when conditions are enhanced to promote growth (Donohue et al., 2000), and, for *V. macrocarpon*, research has found that the species prefers a moist environment (Breen, 2021). Previous research by Lundolm et al., (2014) also observed a negative growth rate for these three species when grown on a green roof.

In the green roof experiment, a negative growth rate was observed for two species in treatments containing neighbors with a similar growth form: *A. flexuosa* in the treatment solely containing graminoids (*A. flexuosa*, *F. rubra*, *D. spicata*) and *S. acre* in the treatment solely containing succulents (*S. acre, S. album, S. sexangular*). Out of all treatments, the graminoid combination had the lowest divergence in leaf dry matter content. Since this trait is associated with drought tolerance and nutrient conservation (Tardy et al., 2015; Poorter and Garnier, 1999), the lack of variation may have increased competition between these three species. Out of all treatments, the succulent combination had the lowest divergence in plant height, a trait associated with acquisition of light and soil resources (Moles et al., 2009; Wang et al., 2019). As with the graminoid combination, this lack of variation could have increased competition between these succulent species. Interestingly, both *A. flexuosa* and *S. acre* had specific leaf areas with a higher value then all other species in the similar growth form treatments, a trait for which lower values are usually associated with increased drought tolerance. These findings further support the role trait divergence plays in coexistence. However, since the graminoid treatment had the highest total functional diversity (greatest trait divergence) this finding would have been overlooked had traits not been analyzed individually.

## Conclusion

In this study, both the greenhouse and green roof experiment demonstrate the role trait divergence plays in reducing competition and encouraging coexistence. The traits for which divergent values led to a decrease in competition, plant height and leaf dry matter content, differed between the two experiments. However, both are associated with water uptake and drought tolerance. Therefore, the lack of consistency between these two studies was likely due to a difference in growing conditions, with the high wind on the green roof environment discouraging the growth of tall species. For the greenhouse experiment long term coexistence between species is not assured as intraspecific competition was not always greater than interspecific competition. However, the majority of species used in the greenhouse study were also used on the green roof for which coexistence between many of the species will likely occur. Specifically, the majority of green roof species had a positive growth rate when planted at low density and interspecific competition was usually lower than intraspecific competition. Both experiments emphasize the importance of examining individual trait diversity, as no interactions between total functional diversity and competition/coexistence were observed. Finally, there is some support for the storage effect encouraging coexistence between species in the greenhouse study, namely for those treatments containing *S. novi-belgii*. However, since phenological complementarity was low for all treatments, future research examining this possible interaction is necessary.

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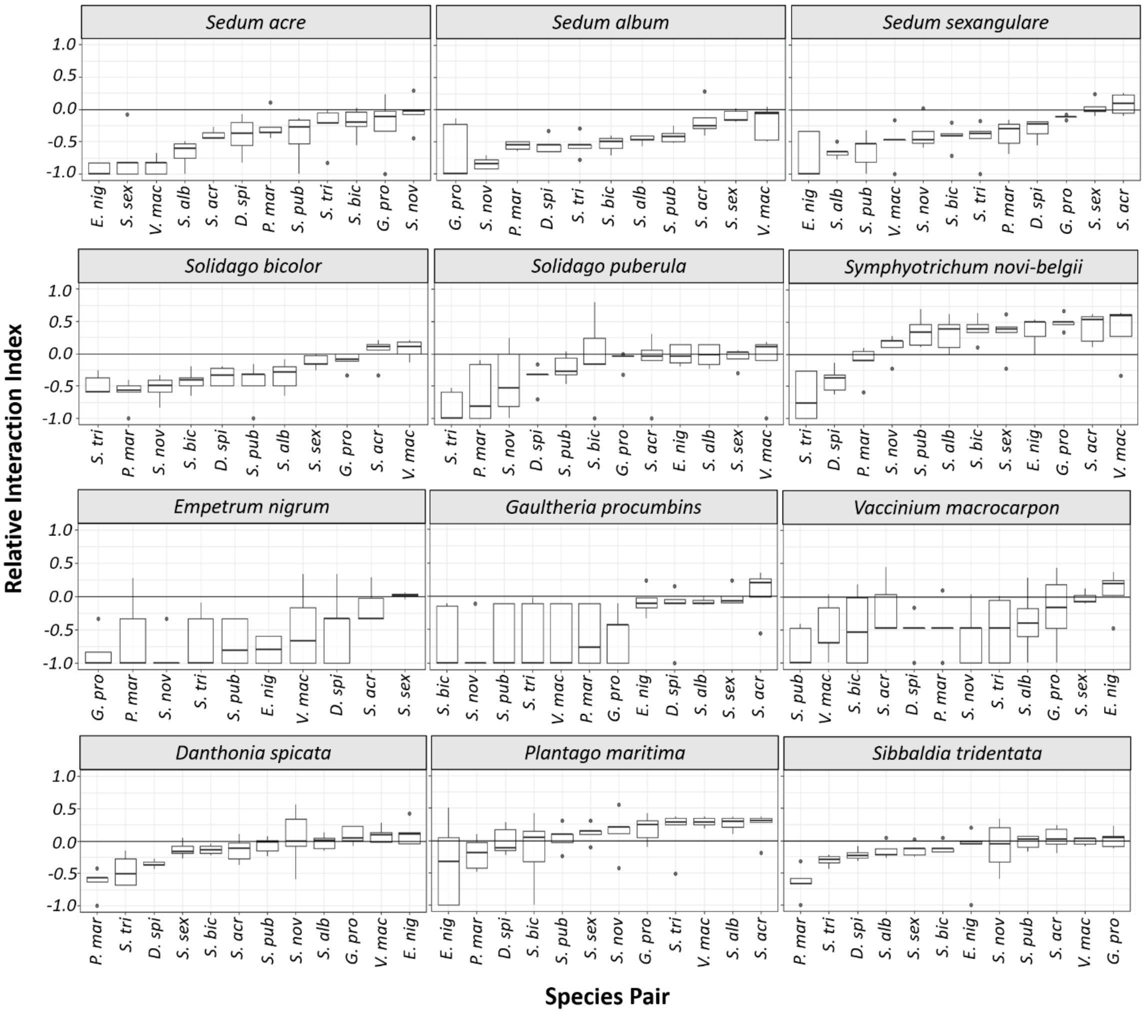
## Appendix - Greenhouse

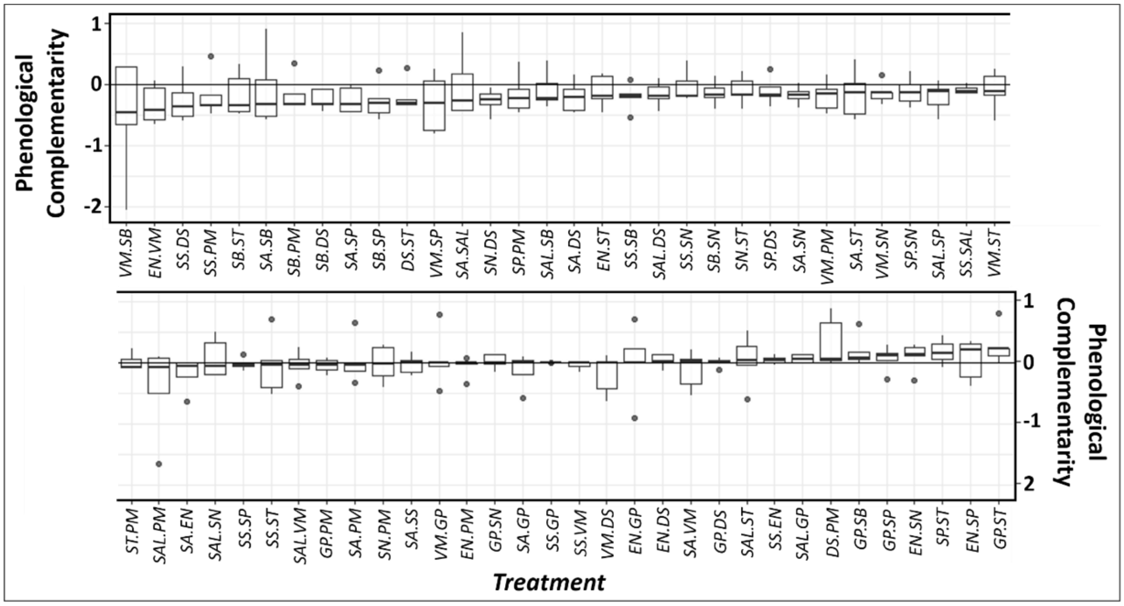
**Appendix 5.A.** Confidence intervals calculated for the relative interaction index and functional diversity variables for the greenhouse study. Intervals were calculated using a multiple linear regression. Tukey indicates that a Tukey's ladder of powers transformation was used. Tran=transformation.

| Relative Interaction Index | | | | |
|---|---|---|---|---|
| | **Tran** | **2.5 %** | **Coefficient** | **97.5 %** |
| **Phenological Complementarity** | **-** | **-0.17611109** | **-0.09688679** | **-0.02658731** |
| **Total Functional Diversity** | Tukey | -0.16695529 | -0.008849247 | 0.10841491 |
| **Specific Leaf Area** | Tukey | -0.06809073 | 0.01236213 | 0.14488960 |
| **Plant Height** | Tukey | **0.02737545** | **0.1167668** | **0.22429061** |
| **Leaf Thickness** | Tukey | -0.09603378 | -0.0002539431 | 0.09407320 |
| **Root Radius** | Tukey | -0.11251654 | -0.005274473 | 0.07326270 |
| **Leaf Dry Matter Content** | Tukey | -0.14530337 | -0.03148153 | 0.02210423 |

**Appendix 5.B** Relative interaction index for the greenhouse study at the end of the study period (August 2019). The x-axis shows the species paired with the species identified in the graph title. X-axis species code: first letter of the genus followed by the first three letters of the species name. See Appendix D for a list of the functional diversity variables for each treatment. For the y-axis, values > 0 indicate a net facilitative effect, values < 0 indicate net competitive effects, and a value of 0 indicates that the interaction was neutral. X-axis species code: first letter of the genus followed by the first three letters of the species name.



**Appendix 5.C.** Phenological complementarity for all heterospecific pairs in the greenhouse experiment. If phenological complementarity < 0 then there was no support for complementarity and species have similar growth patterns. Treatment code: DS.SB, DS and SB indicate which individuals are included in the treatment, D and S are the first letters of the genus name and S and B is the first letter of the species name, so DS.SB means this treatment contains one individual of *D. spicata* and one individual of *S. bicolor*; SAL indicates *Sedum album*; SA indicates *Sedum acre*.



**Appendix 5.D.** Functional diversity variables for each paired treatment in the greenhouse study. Legend: all trait variables used to calculate functional diversity (Total).

| Species One | Species Two | Total | Plant Height | Leaf Dry Matter Content | Root Radius | Specific Leaf Area | Leaf Thickness |
|---|---|---|---|---|---|---|---|
| *S. pub* | *D. spi* | 0.81 | 0.57 | 0.26 | 0.5 | 0 | 0.05 |
| *S. pub* | *E. nig* | 2.05 | 0.9 | 0.6 | 1.44 | 0.35 | 0.13 |
| *S. pub* | *G. pro* | 2.2 | 0.85 | 0.19 | 1.7 | 0.51 | 0.16 |
| *S. pub* | *P. mar* | 1.44 | 0.76 | 0.57 | 0.64 | 0.54 | 0.69 |
| *S. pub* | *S. acr* | 1.85 | 1.03 | 0.76 | 1.1 | 0.46 | 0.38 |
| *S. pub* | *S. alb* | 2.41 | 1.07 | 0.75 | 0.84 | 0.63 | 1.73 |
| *S. pub* | *S. bic* | 0.85 | 0.24 | 0.02 | 0.7 | 0.37 | 0.04 |
| *S. pub* | *S. nov* | 1.26 | 0.52 | 0.17 | 0.37 | 1.05 | 0 |
| *S. pub* | *S. sex* | 2.18 | 1.09 | 0.52 | 1.5 | 0.36 | 0.34 |
| *S. pub* | *S. tri* | 1.39 | 0.91 | 0.27 | 0.9 | 0.47 | 0.07 |
| *S. pub* | *V. mac* | 2 | 0.94 | 0.7 | 1.1 | 0.54 | 0.02 |
| *D. spi* | *E. nig* | 1.54 | 0.33 | 0.34 | 0.94 | 0.35 | 0.17 |
| *D. spi* | *G. pro* | 1.74 | 0.28 | 0.07 | 1.2 | 0.51 | 0.2 |
| *D. spi* | *P. mar* | 1.28 | 0.19 | 0.83 | 0.13 | 0.55 | 0.74 |
| *D. spi* | *S. acr* | 1.53 | 0.47 | 1.02 | 0.6 | 0.46 | 0.43 |
| *D. spi* | *S. alb* | 2.23 | 0.51 | 1.01 | 0.33 | 0.63 | 1.78 |
| *D. spi* | *S. bic* | 0.59 | 0.32 | 0.24 | 0.2 | 0.37 | 0.09 |
| *D. spi* | *S. nov* | 1.58 | 1.09 | 0.43 | 0.13 | 1.05 | 0.05 |
| *D. spi* | *S. sex* | 1.8 | 0.52 | 0.78 | 1 | 0.36 | 0.39 |
| *D. spi* | *S. tri* | 0.72 | 0.34 | 0.01 | 0.4 | 0.47 | 0.12 |
| *D. spi* | *V. mac* | 1.55 | 0.38 | 0.44 | 0.6 | 0.54 | 0.07 |
| *E. nig* | *P. mar* | 1.75 | 0.13 | 1.16 | 0.8 | 0.2 | 0.56 |
| *E. nig* | *S. acr* | 1.71 | 0.14 | 1.36 | 0.33 | 0.81 | 0.25 |
| *E. nig* | *S. nov* | 2.64 | 1.42 | 0.76 | 1.07 | 1.4 | 0.13 |
| *E. nig* | *S. sex* | 1.16 | 0.19 | 1.12 | 0.07 | 0.02 | 0.21 |
| *E. nig* | *S. tri* | 1.17 | 0.01 | 0.33 | 0.53 | 0.12 | 0.06 |
| *E. nig* | *V. mac* | 0.44 | 0.05 | 0.11 | 0.33 | 0.2 | 0.11 |
| *G. pro* | *E. nig* | 0.52 | 0.05 | 0.41 | 0.27 | 0.16 | 0.03 |
| *G. pro* | *P. mar* | 1.65 | 0.09 | 0.76 | 1.07 | 0.04 | 0.53 |
| *G. pro* | *S. acr* | 1.6 | 0.18 | 0.95 | 0.6 | 0.97 | 0.22 |
| *G. pro* | *S. alb* | 2.25 | 0.22 | 0.94 | 0.87 | 0.12 | 1.57 |
| *G. pro* | *S. bic* | 1.65 | 0.61 | 0.17 | 1 | 0.14 | 0.11 |
| *G. pro* | *S. nov* | 2.75 | 1.37 | 0.35 | 1.34 | 1.56 | 0.16 |
| *G. pro* | *S. sex* | 0.81 | 0.24 | 0.71 | 0.2 | 0.15 | 0.18 |
| *G. pro* | *S. tri* | 1.29 | 0.06 | 0.08 | 0.8 | 0.04 | 0.08 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *G. pro* | *V. mac* | 0.82 | 0.1 | 0.51 | 0.6 | 0.03 | 0.14 |
| *P. mar* | *S. acr* | 1.24 | 0.27 | 0.19 | 0.47 | 1.01 | 0.31 |
| *P. mar* | *S. alb* | 1.13 | 0.31 | 0.19 | 0.2 | 0.08 | 1.04 |
| *P. mar* | *S. bic* | 1.07 | 0.52 | 0.59 | 0.07 | 0.18 | 0.65 |
| *P. mar* | *S. nov* | 2.24 | 1.28 | 0.4 | 0.27 | 1.6 | 0.69 |
| *P. mar* | *S. sex* | 1.29 | 0.32 | 0.05 | 0.87 | 0.18 | 0.35 |
| *P. mar* | *S. tri* | 1.1 | 0.14 | 0.84 | 0.27 | 0.08 | 0.62 |
| *P. mar* | *V. mac* | 1.79 | 0.18 | 1.27 | 0.47 | 0 | 0.67 |
| *S. acr* | *S. alb* | 1.8 | 0.04 | 0.01 | 0.27 | 1.09 | 1.35 |
| *S. acr* | *S. bic* | 1.61 | 0.79 | 0.78 | 0.4 | 0.83 | 0.34 |
| *S. acr* | *S. nov* | 2.05 | 1.56 | 0.59 | 0.74 | 0.59 | 0.38 |
| *S. acr* | *S. sex* | 1.06 | 0.05 | 0.24 | 0.4 | 0.82 | 0.04 |
| *S. acr* | *S. tri* | 1.52 | 0.13 | 1.03 | 0.2 | 0.93 | 0.31 |
| *S. acr* | *V. mac* | 1.91 | 0.09 | 1.46 | 0 | 1 | 0.36 |
| *S. alb* | *S. bic* | 2.07 | 0.83 | 0.78 | 0.13 | 0.26 | 1.69 |
| *S. alb* | *S. nov* | 3 | 1.6 | 0.59 | 0.47 | 1.68 | 1.73 |
| *S. alb* | *S. sex* | 1.81 | 0.01 | 0.23 | 0.67 | 0.27 | 1.39 |
| *S. alb* | *S. tri* | 1.96 | 0.17 | 1.02 | 0.07 | 0.16 | 1.66 |
| *S. alb* | *V. mac* | 2.49 | 0.13 | 1.46 | 0.27 | 0.09 | 1.71 |
| *S. bic* | *S. sex* | 1.71 | 0.84 | 0.54 | 0.8 | 0.01 | 0.3 |
| *S. bic* | *V. mac* | 1.63 | 0.7 | 0.68 | 0.4 | 0.17 | 0.02 |
| *S. bic* | *S. nov* | 1.66 | 0.77 | 0.19 | 0.33 | 1.42 | 0.04 |
| *S. bic* | *S. tri* | 0.75 | 0.66 | 0.25 | 0.2 | 0.1 | 0.03 |
| *S. nov* | *S. sex* | 2.71 | 1.61 | 0.36 | 1.14 | 1.42 | 0.34 |
| *S. nov* | *V. mac* | 2.75 | 1.47 | 0.87 | 0.74 | 1.6 | 0.02 |
| *S. nov* | *S. tri* | 2.2 | 1.43 | 0.43 | 0.53 | 1.52 | 0.07 |
| *S. sex* | *S. tri* | 1.42 | 0.18 | 0.79 | 0.6 | 0.11 | 0.27 |
| *S. sex* | *V. mac* | 1.35 | 0.14 | 1.22 | 0.4 | 0.18 | 0.32 |
| *S. tri* | *V. mac* | 1.21 | 0.04 | 0.44 | 0.2 | 0.07 | 0.05 |

## Appendix - Green Roof

**Appendix 5.E.** ANOVA results for the atrium study comparing the relative growth rate between equal and low-density treatments. The species column indicates which species the analysis was conducted for.

| Species Combination | Species | numDF | denDF | F-value | p-value |
|---|---|---|---|---|---|
| *S. acre/S. album/S. sexangulare* | *S. sexangulare* | 1 | 8 | 1.315652 | 0.2845 |
| *S. acre/S. album/S. sexangulare* | *S. album* | 1 | 8 | 0.290769 | 0.6044 |
| *S. bicolor/S. novi-belgii/S. puberula* | *S. puberula* | 1 | 8 | 0.021782 | 0.8863 |
| *S. bicolor/S. novi-belgii/S. puberula* | *S. novi-belgii* | 1 | 8 | 1.8195181 | 0.2143 |
| *A. flexuosa/D. spicata/F. rubra* | *F. rubra* | 1 | 8 | 1.397312 | 0.2711 |
| *A. flexuosa/D. spicata/F. rubra* | *A. flexuosa* | 1 | 8 | 7.154821 | 0.0281 |
| *D. spicata/P. spurius /S. tridentata* | *P. spurius* | 1 | 8 | 2.67603 | 0.1405 |
| *D. spicata/S. acre/S. tridentata* | *S. tridentata* | 1 | 26 | 1.5566584 | 0.2233 |
| *S. acre/S. bicolor/S. tridentata* | *S. tridentata* | 1 | 26 | 0.2433701 | 0.6259 |
| *D. spicata/P. spurius /S. tridentata* | *S. tridentata* | 1 | 26 | 0.5121478 | 0.4806 |
| *A. flexuosa/D. spicata/F. rubra* | *D. spicata* | 1 | 26 | 0.0264558 | 0.8720 |
| *D. spicata/S. acre/S. tridentata* | *D. spicata* | 1 | 26 | 2.853628 | 0.1031 |
| *D. spicata/P. spurius /S. tridentata* | *D. spicata* | 1 | 26 | 0.1909209 | 0.6658 |
| *D. spicata/ S. bicolor/S. acre* | *D. spicata* | 1 | 26 | 2.049792 | 0.1641 |
| *S. acre/S. album/S. sexangulare* | *S. acre* | 1 | 26 | 0.621512 | 0.4376 |
| *S. acre/S. bicolor/S. tridentata* | *S. acre* | 1 | 26 | 1.0046485 | 0.3254 |
| *D. spicata/S. acre/S. tridentata* | *S. acre* | 1 | 26 | 4.850212 | 0.0367 |

|  |  |  |  |  |  |
|---|---|---|---|---|---|
| *D. spicata/ S. bicolor/S. acre* | *S. acre* | 1 | 26 | 0.299480 | 0.5889 |
| *D. spicata/ S. bicolor/S. acre* | *S. bicolor* | 1 | 26 | 2.7606874 | 0.1086 |
| *S. acre/S. bicolor/S. tridentata* | *S. bicolor* | 1 | 26 | 0.1696203 | 0.6838 |
| *S. bicolor/S. novi-belgii/S. puberula* | *S. bicolor* | 1 | 26 | 0.0606781 | 0.8074 |

**Appendix 5.F.** ANOVA results for the atrium study for *S. tridentata*, *D. spicata*, *S. acre*, and *S. bicolor*. The analysis compared the relative interaction index between treatments.

| Species | DF | Sum Sq | Mean Sq | F-value | p-value |
|---|---|---|---|---|---|
| *S. tridentata* | 3 | 0.2745 | 0.0915 | 5.792 | 0.00279 |
| *D. spicata* | 4 | 0.221 | 0.05525 | 3.653 | 0.0125 |
| *S. acre* | 4 | 0.3333 | 0.08332 | 3.885 | 0.00929 |
| *S. bicolor* | 3 | 0.1622 | 0.05406 | 2.068 | 0.124 |

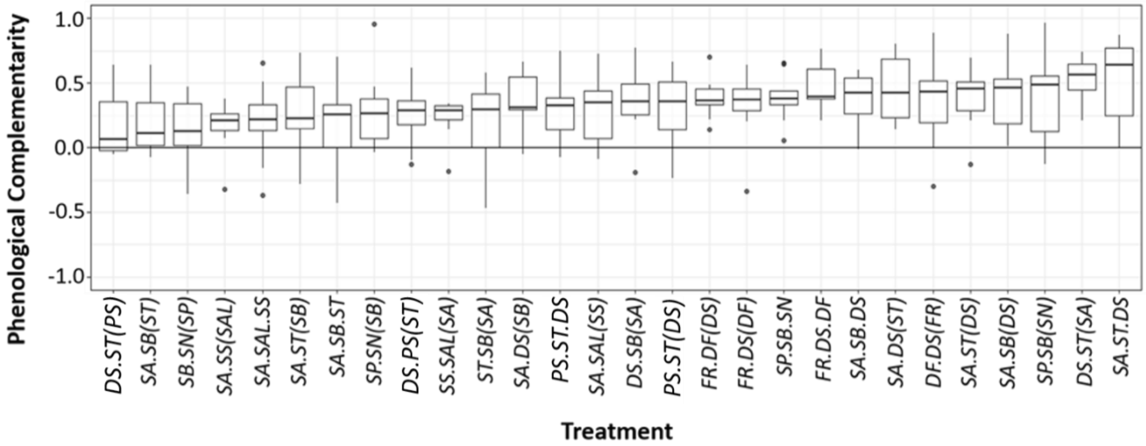
**Appendix 5.G.** ANOVA results for the atrium study for S. tridentata, D. spicata, S. acre, and S. bicolor. The analysis compared the relative growth rate between treatments.

| Species | Num DF | Den DF | F-value | p-value |
|---|---|---|---|---|
| *D. spicata* | 4 | 32 | 1.3854239 | 0.2611 |
| *S. bicolor* | 3 | 24 | 1.1874579 | 0.3355 |
| *S. acre* | 4 | 32 | 3.863264 | 0.0114 |
| *S. tridentata* | 3 | 24 | 19.496258 | <.0001 |

**Appendix 5.H.** Confidence intervals from the multiple linear regression examining the relationship between the relative interaction index and functional diversity variables for the green roof study. Legend: all trait variables used to calculate functional diversity (Total).

| | 2.5 % | Coefficients | 97.5 % |
|---|---|---|---|
| Phenological Complementarity | -0.002206479 | 0.06503931 | 0.18430801 |
| Total | -0.455524381 | -0.0540806 | 0.21017813 |
| Plant Height | -0.038109307 | 0.02648424 | 0.15389646 |
| Specific Leaf Area | -0.157193485 | 0.04137993 | 0.35962463 |
| Leaf Dry Matter Content | **0.050521643** | **0.1802806** | **0.31089327** |
| Leaf Thickness | -0.175081187 | 0.009863729 | 0.22897776 |
| Root Radius | -0.200487850 | -0.04282241 | 0.04601994 |

**Appendix 5.J.** Phenological complementarity for all heterospecific treatments and densities in the green roof experiment. If phenological complementarity < 0 then there was no support for complementarity and species have similar growth patterns. Treatment code: the first letter is the genus name followed by the first letter of the species name (DS.SB.SA = *D. spicata, S. bicolor, S. acre*); Density is indicated by punctuation, XX.YY.ZZ = three individuals of each species and XX.YY(ZZ) = four individuals of XX and YY and one individual of ZZ; SAL indicates *Sedum album*; SSP indicates *Phedimus spurius*.



# Chapter 6

# Research Application: Extensive Green Roofs

## Introduction

Green roofs are a novel environment incorporated into the urban landscape as a way to increase green space and provide ecosystem services, such as stormwater retention, thermal benefits, reduced air pollution, and habitat for local fauna (Niachou et al., 2001; VanWoert et al., 2005; Mentens et al., 2006; Currie and Bass, 2008; Yang et al., 2008; Castleton et al., 2010; Stovin, 2010; Cook-Patton and Bauerle, 2012;). Green roofs are generally broken down into two distinct categories: intensive green roofs with a substrate depth greater than 20 cm and extensive green roofs with a substrate depth less than or equal to 15 cm (Oberndorfer et al., 2007). Due to weight restrictions, the majority of green roofs fall into the extensive category, which is associated with harsh growing conditions such as shallow substrate, drought, and high winds (Oberndorfer et al., 2007; Castleton et al., 2010; Olly et al., 2011). Due to these conditions, the majority of green roofs are planted with succulents, mainly from the genus *Sedum* (Dunnett and Kingsbury, 2004; MacIvor and Lundholm, 2011). Additional growth forms, including forbs, graminoids, and creeping shrubs, can also succeed in the green roof environment. These various growth forms are known to excel at different ecosystem services, leading to a growing demand for biodiverse green roofs (MacIvor and Lundholm, 2011; Cook-Patton and Bauerle, 2012; Lundholm et al., 2015). However, research is needed to understand how biodiversity can be maintained over time and to determine which species combinations will excel at a given ecosystem service.

Through the incorporation of functional plant traits, each chapter of this dissertation provides insights that can be directly applied to green roof construction. The functional trait database created for Chapter 3 can be used to determine which additional native species can be used on green roofs in Nova Scotia. The experiment in Chapter 4 provides empirical evidence in support of heterogenous green roofs, which can influence community composition and the provision of ecosystem services. Finally, the insights gained from the experiments described in Chapter 5 can be used determine which functional trait combinations are likely to coexist and excel at desired ecosystem services.

## Chapter 2 and Chapter 3

In Nova Scotia, extensive green roofs are exposed to similar environmental conditions (high winds, desiccation, extreme temperatures) to coastal barren rocky outcrops, dwarf heath, and the salt spray zone (MacIvor and Lundholm, 2011). Previous green roof research conducted in the region relied on this similarity to determine which native species could survive the green roof environment (MacIvor and Lundholm, 2011). In order to expand the list of native green roof vegetation, I searched my functional trait database for native species that share similar functional trait values with successful green roof vegetation (Chapter 2). Furthermore, when choosing the limits of my threshold, I chose to exclude succulent species as these growth forms do not follow the conventional trait patterns observed for non-succulent vegetation (Vendramini et al., 2002). To address this exclusion, my list includes all coastal barren succulents not yet used on green roofs in

Nova Scotia. My trait threshold was based off of the trait values of the following Nova Scotian green roof vegetation: the species with the highest specific leaf area (*Symphyotrichum novi-belgii* (275.2±18)), the species with the lowest leaf dry matter content (*Mononeuria groenlandica* (0.1717±0.0105)), and the tallest species (*Symphyotrichum novi-belgii* (50.39±5.72)) (Table 6.1). According to the data, there are 44 species that naturally occur on coastal barren dwarf heath, exposed outcrop, or salt spray habitat that possess an average specific leaf area below 300, a leaf dry matter content greater than 0.2, and/or are shorter than 60 cm. This list of potential green roof vegetation contains 23 shrubs, 15 forbs, three graminoids, one succulent, and one vine (Table 6.2). Future research should test these species to determine if they are capable of surviving the harsh green roof environment.

**Table 6.1.** Table of plant species native to Nova Scotia that have survived multiple years on extensive green roofs. The table includes information on the growth form of each species and mean (n=10) trait values ± the standard error.

| Species | Growth Form | Specific Leaf Area mm$^2$mg$^{-1}$ | Leaf Dry Matter Content (g) | Plant Height (cm) |
|---|---|---:|---:|---:|
| *Coremi conradii* | Shrub | 74±9 | 0.5558±0.0863 | 9.89±1.38 |
| *Campanula rotundifolia* | Forb | 208.2±17 | 0.2651±0.0151 | 23.06±2.57 |
| *Carex nigra* | Graminoid | 218.6±17.9 | 0.3492±0.0111 | 39.99±3.02 |
| *Cornus canadensis* | Shrub | 181.9±12.1 | 0.3234±0.0232 | 13.5±0.91 |
| *Danthonia spicata* | Graminoid | 152.1±13.5 | 0.3851±0.0083 | 18.83±3.96 |
| *Empetrum nigrum* | Shrub | 112.9±17.8 | 0.4925±0.0567 | 9.3±1.21 |
| *Festuca rubra* | Graminoid | 97.5±6.8 | 0.396±0.0287 | 35.99±3.22 |
| *Gaultheria procumbens* | Shrub | 94.4±17.9 | 0.3626±0.0367 | 10.64±1 |
| *Hylotelephium telephium* | Succulent | 150.1±6.6 | 0.0984±0.0031 | 10.4±1.51 |
| *Juniperus communis* | Shrub | 88.5±7.4 | 0.4688±0.036 | 10.1±0.6 |
| *Linnaea borealis* | Forb | 201.1±9.9 | 0.2919±0.007 | 7.8±0.66 |
| *Maianthemum canadense* | Forb | 193.1±12.2 | 0.2553±0.0101 | 9.62±0.89 |
| *Mononeuria groenlandica* | Annual, Forb | 247.4±20.6 | 0.1717±0.0105 | 7±0.49 |
| *Morella pensylvanica* | Shrub | 186.2±15.9 | 0.3022±0.014 | 25.37±1.7 |
| *Phedimus spurius* | Succulent | 142.9±8.4 | 0.0878±0.0036 | 4.88±0.46 |
| *Plantago maritima* | Forb, Leaves Succulent-Like | 90.3±9.5 | 0.1216±0.009 | 7.04±0.63 |
| *Rhodiola rosea* | Succulent | 172.6±9 | 0.0818±0.0098 | 15.8±3.3 |
| *Sedum acre* | Succulent | 204.3±14.7 | 0.0604±0.0064 | 5.31±0.41 |
| *Sedum album* | Succulent | 80.9±6 | 0.062±0.0032 | 4.17±1.27 |
| *Sedum sexangulare* | Succulent | 111±7.9 | 0.1363±0.018 | 3.81±0.55 |
| *Sibbaldia tridentata* | Shrub | 89.2±3 | 0.3952±0.0052 | 9.01±1.52 |
| *Solidago bicolor* | Forb | 110.4±6.8 | 0.3093±0.03 | 28.19±1.81 |
| *Symphyotrichum novi-belgii* | Forb | 275.2±18 | 0.251±0.006 | 50.39±5.72 |
| *Vaccinium angustifolium* | Shrub | 135.6±7.9 | 0.3648±0.0116 | 18.2±2.32 |
| *Vaccinium macrocarpon* | Shrub | 90.6±5.6 | 0.5262±0.0215 | 7.88±0.69 |

**Table 6.2.** Table of plant species native to Nova Scotia that have mean trait values similar to species that have survived for multiple years on extensive green roofs. The table includes information on the growth form of each species and mean (n=10) trait values ± the standard error.

| Species | Growth Form | Specific Leaf Area | Leaf Dry Matter Content | Plant Height (cm) |
|---|---|---|---|---|
| *Agalinis neoscotica* | Forb | 188±20.1 | 0.2467±0.0084 | 9.26±0.87 |
| *Agrostis stolonifera* | Graminoid | 652.2±25.7 | 0.2442±0.0119 | 17.4±3.31 |
| *Andromeda polifolia* | Shrub | 49±3.3 | 0.488±0.0229 | 16.25±1.74 |
| *Aralia nudicaulis* | Forb | 191.4±19.6 | 0.6936±0.2963 | 25.6±3.46 |
| *Arctostaphylos uva-ursi* | Shrub | 45.6±3.3 | 0.4771±0.0116 | 5.7±0.67 |
| *Aronia arbutifolia* | Shrub | 133.8±3 | 0.3015±0.006 | 53.85±5.11 |
| *Aronia melanocarpa* | Shrub | 101.6±2.9 | 0.3758±0.009 | 18.9±3.91 |
| *Artemisia stelleriana* | Forb | 140±9.5 | 0.2678±0.0113 | 11.68±0.8 |
| *Cakile edentula* | Succulent | 172.6±14.1 | 0.1071±0.0044 | 19.39±4.31 |
| *Calamagrostis pickeringii* | Graminoid | 182.9±11.6 | 0.3645±0.0136 | 34.73±1.22 |
| *Clintonia borealis* | Forb | 241.8±10.1 | 0.119±0.0059 | 13.02±1.07 |
| *Convolvulus arvensis* | Vine | 214.5±13.9 | 0.22±0.0089 | 33.26±5.46 |
| *Coptis trifolia* | Forb | 259±9.2 | 0.3128±0.0132 | 3.75±0.45 |
| *Empetrum eamesii* | Shrub | 81.6±8.6 | 0.4929±0.0201 | 8.24±1.95 |
| *Gaultheria hispidula* | Shrub | 153.9±16 | 0.3851±0.0418 | 1.5±0.2 |
| *Gaylussacia baccata* | Shrub | 205.9±15.8 | 0.2924±0.0232 | 49.1±4.99 |
| *Gaylussacia bigeloviana* | Shrub | 152.4±12.3 | 0.2985±0.0131 | 24.35±2.61 |
| *Hudsonia ericoides* | Shrub | 328.6±39 | 0.4836±0.0669 | 4.4±0.67 |
| *Ilex glabra* | Shrub | 72.7±2.2 | 0.4924±0.0285 | 56±6.1 |
| *Iris setosa* | Forb | 133.3±9.6 | 0.2219±0.0103 | 28.25±1.16 |
| *Iris versicolor* | Forb | 124.6±6.6 | 0.1617±0.0103 | 45.4±2.03 |
| *Juncus arcticus* | Graminoid | 31.5±2 | 0.47±0.0124 | 46.8±2.16 |
| *Juniperus horizontalis* | Shrub | 108.1±10.5 | 0.3471±0.0704 | 13.5±2.72 |
| *Kalmia angustifolia* | Shrub | 95.4±2.8 | 0.4232±0.0113 | 24.27±2.1 |
| *Kalmia polifolia* | Shrub | 102.1±11.1 | 0.4214±0.0122 | 16.74±1.29 |
| *Ligusticum scoticum* | Forb | 199.1±6.3 | 0.2123±0.0069 | 9.53±0.52 |
| *Lysimachia borealis* | Forb | 223.7±15.9 | 0.248±0.0126 | 19.2±1.62 |
| *Maianthemum stellatum* | Forb | 159.4±6.6 | 0.2413±0.0039 | 24.7±2.29 |
| *Mitchella repens* | Shrub | 78.1±23.3 | 4.4511±1.915 | 3±0.77 |
| *Oclemena acuminata* | Forb | 371.1±21.4 | 0.196±0.0062 | 32.5±2.19 |
| *Oclemena nemoralis* | Forb | 152.3±17.8 | 0.0005±0.0001 | 27.7±2.94 |

| | | | | |
|---|---|---|---|---|
| *Oclemena x blakei* | Forb | 190.3±7 | 0.3002±0.006 | 25.67±1.36 |
| *Rhinanthus minor* | Forb | 227.1±9.4 | 0.1819±0.0062 | 47.52±2.95 |
| *Rhododendron canadense* | Shrub | 152.8±23.3 | 0.4089±0.0118 | 58.37±4.74 |
| *Rhododendron groenlandicum* | Shrub | 73±4.8 | 0.3793±0.0088 | 11.15±2.17 |
| *rosa nitida* | Shrub | 200.1±11.1 | 0.3536±0.007 | 55.35±4.09 |
| *Rosa virginiana* | Shrub | 180±17.6 | 0.499±0.1401 | 36.01±3.25 |
| *Rubus allegheniensis* | Shrub | 221.8±16.4 | 0.3523±0.0132 | 42±5.17 |
| *Rubus idaeus* | Shrub | 281.8±23.6 | 0.3151±0.0079 | 9±1.06 |
| *Rubus pubescens* | Shrub | 242.6±6.4 | 0.3226±0.0044 | 13.03±0.9 |
| *Solidago nemoralis* | Forb | 142.9±8.5 | 0.3574±0.0131 | 35.46±4.09 |
| *Vaccinium myrtilloides* | Shrub | 365.3±28.6 | 0.2575±0.0161 | 32.1±3.28 |
| *Vaccinium vitis-idaea* | Shrub | 64.9±3.9 | 0.4832±0.0369 | 7.33±1.14 |

## Chapter 4

From a green roof perspective, the objective of Chapter 4 was to determine if substrate heterogeneity can increase the provision of ecosystem services and species richness. To address these goals, I collected data on substrate temperature and analyzed final species richness using a species accumulation curve. Data for substrate temperature were collected once in July 2018 and twice in August 2018 by inserting a thermometer (Taylor 9878 Slim-Line Pocket Thermometer Probe, Commercial Solutions Inc., Edmonton, Alberta, Canada) 5 cm deep into the center of each of the four subplots found in each treatment during full sun at solar noon.

Since species richness in Chapter 4 did not vary between the two treatments containing the same quantity of substrate, the homogenous 10 cm treatment and the heterogenous 5/15 cm treatment, I created a species accumulation curve to determine if species richness would vary given more time. The species accumulation curve was estimated for each treatment (15 cm, 5/15 cm, 10 cm, 5 cm) using plot-level data. Additionally, I created a new "combined" treatment incorporating data from both the 5 cm and 15 cm homogeneous treatments. This was done to estimate how heterogenous plots larger than the ones used in my study (My study plots 1 x 1 m, combined plots 2 x 2 m) would influence species richness.

The most interesting result from the functional trait analysis was the difference in the community weighted mean of plant height between the 5/15 cm and 10 cm treatments, with the 5/15 cm treatment containing, on average, a greater abundance of taller species. Since the 5/15 cm treatment contained the same quantity of soil as the 10 cm treatment, this finding suggests that differences in heterogeneity led to the development of two distinct plant communities. Furthermore, as taller species are associated with increased storm water retention and substrate cooling (Lundholm et al., 2015), the use of heterogeneity may improve the provision of green roof ecosystem services without increasing the weight of the green roof system. This finding is supported by measurements of substrate temperature, with the 5/15 cm treatment containing a substrate temperature similar to the coolest treatment, the 15 cm treatment, and the 10 cm treatment containing a substrate temperature similar to the warmest treatment, the 5 cm treatment (Figure 6.1). However, more research is needed to test how soil depth heterogeneity will influence ecosystem services, as only substrate temperature was measured in this experiment.

When species richness is examined, the slopes of the species accumulation curves suggest that species richness will be highest on a roof with a homogenous 15 cm substrate depth. However, due to weight restrictions, a green roof containing this quantity of substrate is not always possible. In cases where soil depth is limited, incorporating soil depth heterogeneity can increase species richness, with heterogeneous patches $\geq 0.37$ $m^2$ preferred (Figure 6.2).

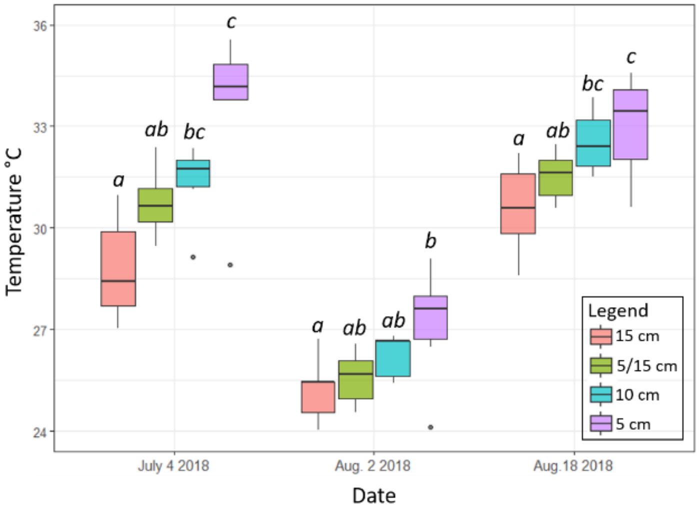


**Figure 6.1.** Boxplots depicting results from the ANOVA and Tukey post-hoc tests for substrate temperature for each treatment for July 4th, August 2nd, and August 18th 2018. The letters represent results from Tukey post-hoc tests for which treatment is the independent variable and temperature is the dependent variable. Bars that share a letter have a p-value>0.05.

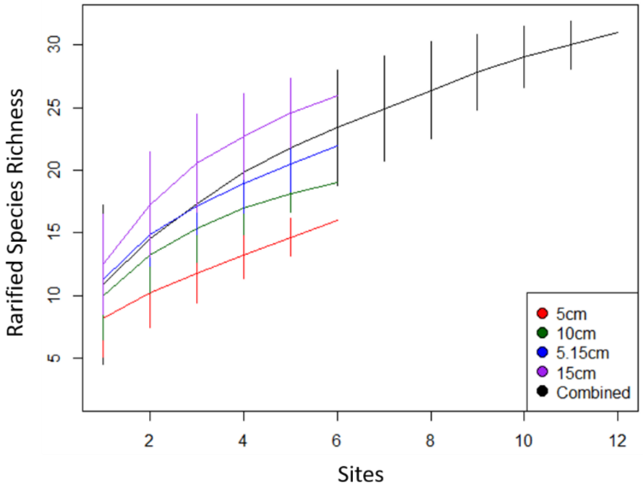


**Figure 6.2.** Species accumulation curves conducted on the subplot data for each treatment, as well as the combined plot data for the homogenous 5 cm and 15 cm plots (Combined). The 5 cm and 15 cm homogenous plots were combined to see how a larger-scale heterogenous treatment would compare to a homogenous treatment containing the same quantity of substrate (10 cm). Error bars are 95% confidence intervals.

## Chapter 5

The combination of species with distinct functional trait profiles may improve overall green roof function, as different traits are associated with different ecosystem services (Lundholm et al., 2015). In these two experiments I tested this idea. I examined the association between the functional diversity of functional plant traits and stormwater retention, substrate temperature, and biomass. I then analyzed associations between the community weighted mean of the measured functional traits and these three ecosystem services.

At the end of the greenhouse study, above and belowground biomass was harvested, separated by species, dried, and weighed. Additionally, at the end of each month, stormwater retention was calculated for each treatment by weighing each pot, watering, then weighing each pot again. Stormwater retention was calculated as wet pot weight – dry pot weight.

Atrium substrate temperature was collected using a Taylor 9878 slim-line pocket thermometer probe (Commercial Solutions Inc., Edmonton, Alberta, Canada) inserted into the center of the module, down to the base, around solar noon on July 9th and 30th 2019, and on June 23rd, July 21st, August 6th, and September 16th, 2020. Stormwater retention (% VWC) was calculated with a ProCheck by inserting a GS3 soil moisture sensor approximately 2 cm below the soil surface into the center of the module one day before and the day after a rain event, with retention calculated as the difference between wet and dry soil. Stormwater retention was collected July (8th and 10th), August (24th and 26th), and September (21st and 24th) 2020.

Based on results from the greenhouse experiment, increased stormwater retention can be achieved from species combinations with convergent root radiuses, convergent leaf thicknesses, and divergent heights. Although no preference was observed for root radius, species combinations with thinner leaves, taller statures, and lower specific leaf areas were the most efficient at reducing stormwater runoff (Figure 3). This trend likely occurred because species with thinner leaves are more susceptible to evapotranspiration, while taller species have greater water requirements (Niinemets 2001; Vile et al., 2005; Wang et al., 2019). Previous research has found that low specific leaf area is usually associated with lower stormwater retention (Lundholm et al., 2015). The contrary result observed here may be due to the periodic drought incorporated into the study, with species possessing lower specific leaf areas, a drought-tolerant strategy, quicker at absorbing water post-drought. For the green roof experiment, high specific leaf area was the only variable associated with an increase in stormwater retention (Figure 6.4). The lack of similarity in stormwater retention results between the greenhouse and green roof experiment may be due to the difference in how stormwater was collected. The method used in the greenhouse experiment is based on weight change and involves a set addition of stormwater, making it better suited to detecting minor differences between treatments.

In the green roof experiment, species combinations containing individuals with divergent total traits and convergent leaf dry matter contents, specific leaf areas, and root radiuses were the most efficient at reducing substrate temperature. The most efficient treatments were those containing individuals with a tall stature, low leaf dry matter content, and low specific leaf area. The pattern observed for plant height and leaf dry matter content reflects what has been observed in previous research, with functional traits associated with faster growth, and taller statures associated with reduced substrate temperature (Lundholm et al., 2015). However, the finding for specific leaf area was unexpected, as a low specific leaf area is associated with water conservative individuals, which tend to have lower rates of evapotranspiration (Lundholm et al., 2015; Wright et al., 2001). This finding likely reflects the dense canopy produced by the two species with the lowest specific leaf area, *F. rubra* and *S. album*. Previous research has also found that species with a dense canopy are efficient at reducing substrate temperature (Lundholm et al., 2015).

On green roofs, high vegetative biomass is associated with reduced stormwater runoff and lower substrate temperature (Lundholm et al., 2015), with both biomass patterns reflected in the greenhouse and green roof experiment. Because of this, architects are interested in establishing plant combinations that create high vegetative biomass and cover the substrate throughout the growing season. Based on the biomass results from the greenhouse and green roof experiments, plant combinations containing individuals with convergent root radiuses and leaf dry matter contents and divergent statures, leaf thicknesses, and total traits will produce the greatest biomass (Figure 6.5 and 6.6).

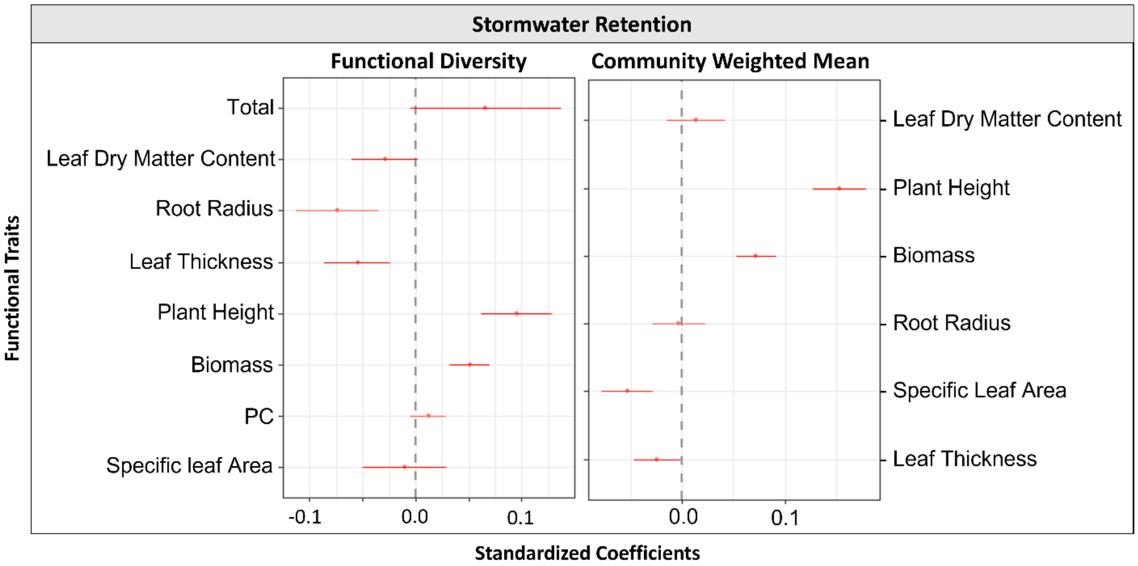


**Figure 6.3.** Results from the multiple linear regression conducted on greenhouse data for stormwater retention. The bars indicate 95% confidence intervals. Legend: PC (phenological complementarity), Total (functional diversity calculated from all 5 traits).

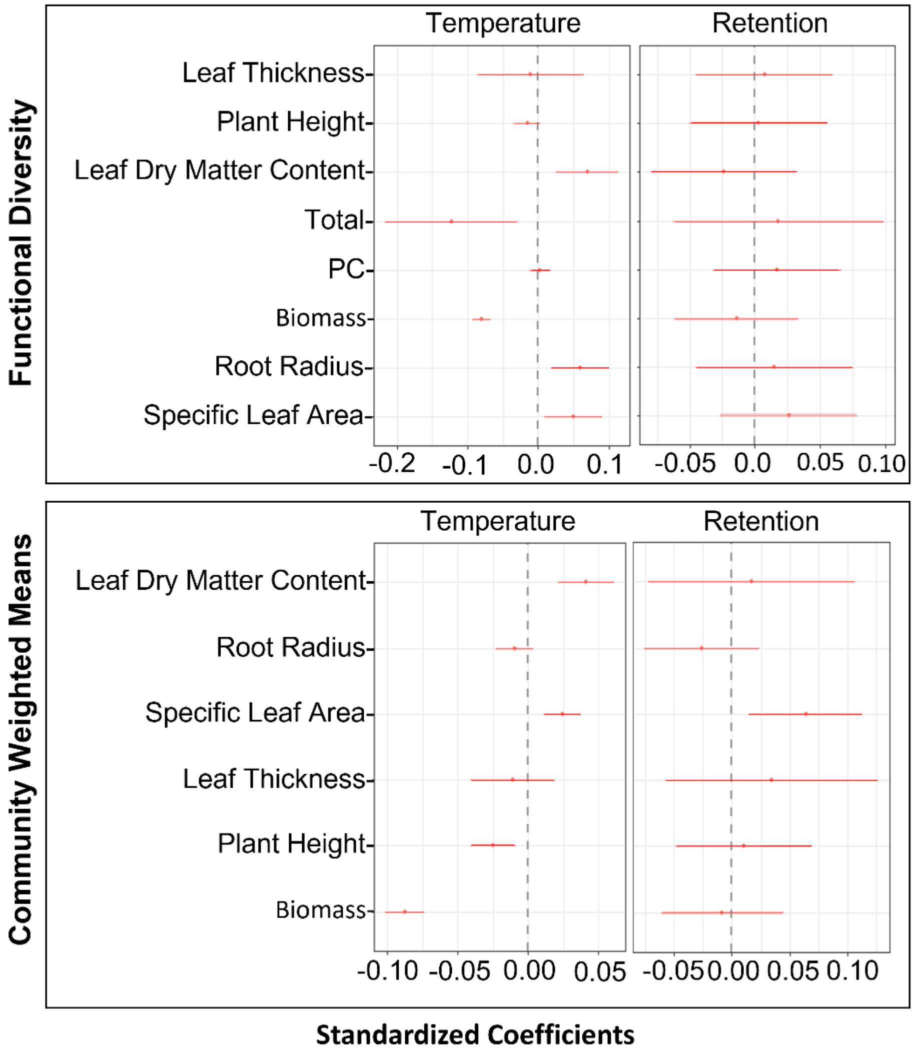


**Figure 6.4.** Results from the multiple linear regression conducted on green roof data for stormwater retention and substrate temperature. The bars indicate 95% confidence intervals. Legend: PC (phenological complementarity), Total (functional diversity calculated from all 5 traits).

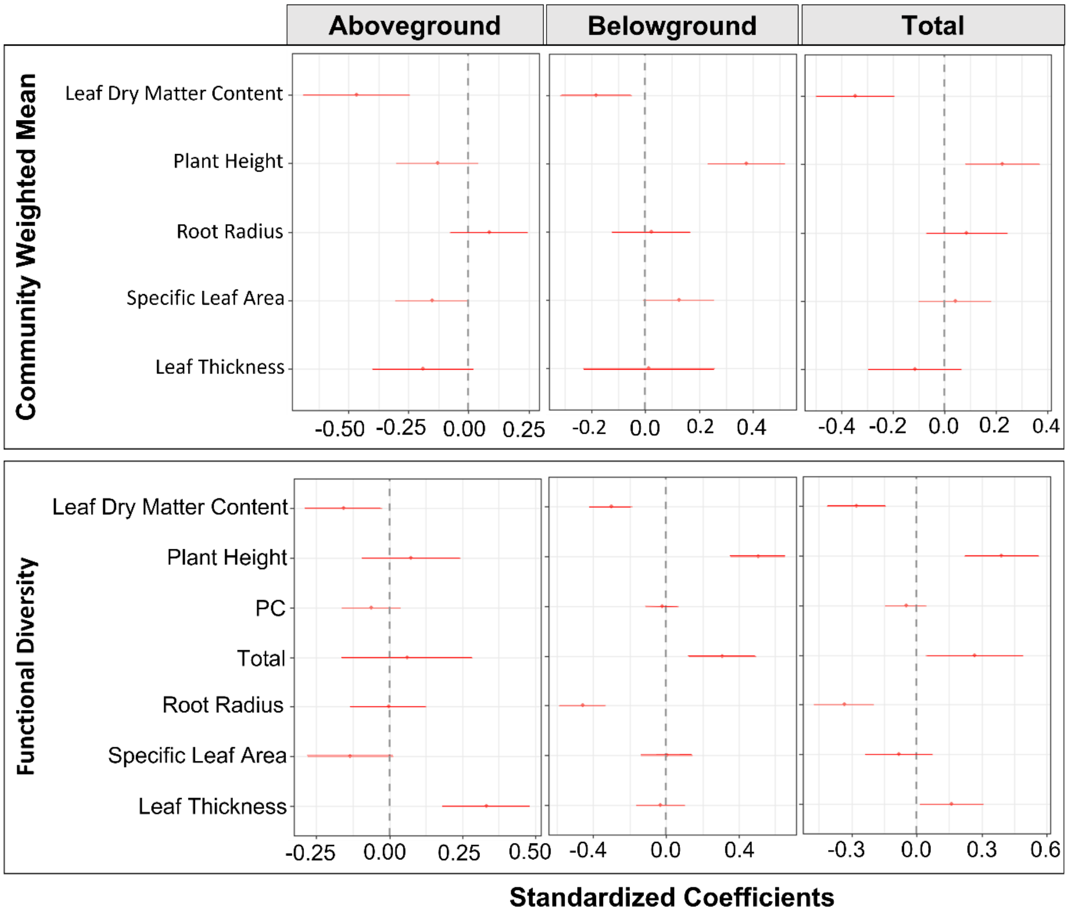


**Figure 6.5.** Results from the multiple linear regression conducted on greenhouse data for aboveground, belowground, and total biomass harvested from each individual in each treatment at the end of the greenhouse study. The bars indicate 95% confidence intervals. Legend: PC (phenological complementarity), Total (functional diversity calculated from all 5 traits).

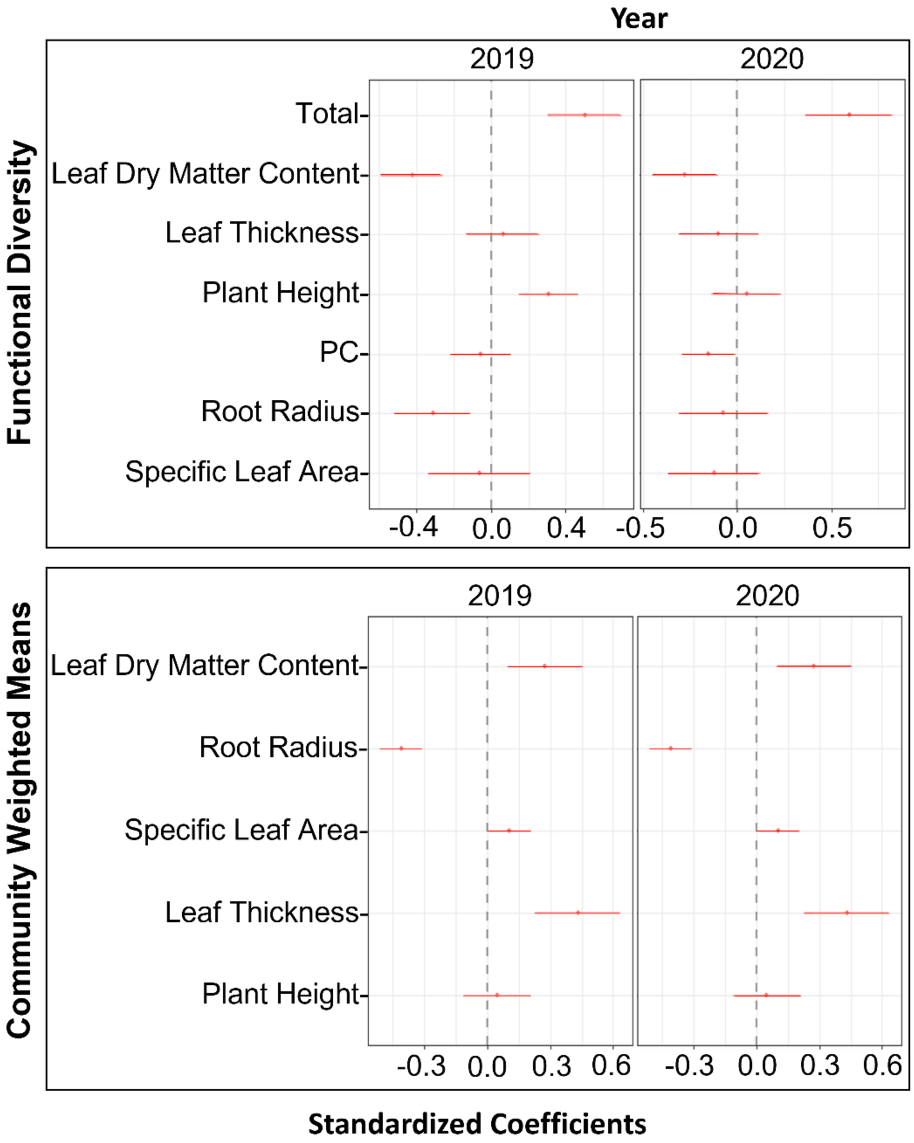


**Figure 6.6.** Results from the multiple linear regression conducted on green roof data for aboveground biomass measured August 2019 and 2020. The bars indicate 95% confidence intervals. Legend: PC (phenological complementarity), Total (functional diversity calculated from all 5 traits).

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## Appendix

**Appendix 6.A.** Results of the ANOVA conducted on the temperature data from Chapter 4.

| Date | Sum Sq | Mean Sq | F-value | Pr(>F) |
|---|---|---|---|---|
| July 2, 2018 | 70.58 | 23.526 | 11.928 | 0.000128 |
| August 2, 2018 | 14.843 | 4.948 | 4.649 | 0.01337 |
| August 18, 2018 | 20.79 | 6.93 | 10.19 | 0.000323 |

**Appendix 6.B**. Confidence intervals from the multiple linear regressions conducted on the biomass and stormwater retention data from the Greenhouse study in Chapter 5. Tukey indicates that a Tukey's ladder of powers transformation was used. Tran=transformation.

| Green House Harvested Biomass: Community Weighted Mean | | | | |
|---|---|---|---|---|
| **Belowground** | **Tran** | **2.5 %** | **Coefficient** | **97.5 %** |
| Plant Height | Tukey | **0.23332078** | **0.3766682** | **0.52001571** |
| Specific Leaf Area | Tukey | -0.00669175 | 0.08623345 | 0.25684463 |
| Leaf Dry Matter Content | Tukey | **-0.31522922** | **-0.1651090** | **-0.04747993** |
| Leaf Thickness | Tukey | -0.22943496 | 0.005141941 | 0.25799024 |
| Root Radius | | -0.12305040 | 0.006326994 | 0.16875112 |
| **Aboveground** | **Tran** | **2.5 %** | **Coefficient** | **97.5 %** |
| Plant Height | Tukey | **-0.30073041** | **-0.07623713** | **-0.040274754** |
| Specific Leaf Area | Tukey | -0.30386650 | -0.1130822 | 0.002090264 |
| Leaf Dry Matter Content | Tukey | **-0.68841323** | **-0.4660988** | **-0.243784462** |
| Leaf Thickness | Tukey | **0.40186126** | **-0.1239289** | **0.021666604** |
| Root Radius | | -0.07784945 | 0.03556334 | 0.247983127 |
| **Total Biomass** | **Tran** | **2.5 %** | **Coefficient** | **97.5 %** |
| Plant Height | Tukey | **0.07968707** | **0.2113013** | **0.37020773** |
| Specific Leaf Area | Tukey | -0.10041579 | 0.01264342 | 0.18021729 |
| Leaf Dry Matter Content | Tukey | **-0.50027201** | **-0.3470132** | **-0.19375448** |
| Leaf Thickness | Tukey | -0.29811151 | -0.05152531 | 0.06634991 |
| Root Radius | | -0.07355429 | 0.03350543 | 0.24366612 |

| Green House Biomass: Functional Diversity | | | | |
|---|---|---|---|---|
| **Aboveground** | **Tran** | **2.5 %** | **Coefficient** | **97.5 %** |
| Phenological Complementarity | | -0.16310635 | -0.02604699 | 0.03871083 |
| Total | Tukey | -0.16296995 | 0.01923883 | 0.28389961 |
| Specific Leaf Area | Tukey | -0.28056487 | -0.09107248 | 0.01411686 |
| Plant Height | Tukey | -0.09489903 | 0.02728488 | 0.24477324 |
| Leaf Thickness | Tukey | **0.18255775** | **0.331678** | **0.48079816** |
| Root Radius | Tukey | -0.13237801 | -0.0008016047 | 0.12623347 |
| Leaf Dry Matter Content | Tukey | **-0.28821616** | **-0.1309104** | **-0.02244832** |
| **Belowground** | **Tran** | **2.5 %** | **Coefficient** | **97.5 %** |

| | | | | |
|---|---|---|---|---|
| Phenological Complementarity | | -0.1119039 | -0.00580794 | 0.07028118 |
| Total | Tukey | **0.1258085** | **0.31162** | **0.49743139** |
| Specific Leaf Area | Tukey | -0.1378665 | 0.001315424 | 0.14799113 |
| Plant Height | Tukey | **0.3549795** | **0.5046377** | **0.65429585** |
| Leaf Thickness | Tukey | -0.1633428 | -0.00802098 | 0.10543163 |
| Root Radius | Tukey | **-0.5831573** | **-0.4567024** | **-0.33024755** |
| Leaf Dry Matter Content | Tukey | **-0.4208922** | **-0.3025356** | **-0.18417903** |
| **Total Biomass** | **Tran** | **2.5 %** | **Coefficient** | **97.5 %** |
| Phenological Complementarity | | -0.14556696 | -0.01772424 | 0.04811702 |
| Total | Tukey | **0.04339046** | **0.2315200** | **0.49408449** |
| Specific Leaf Area | Tukey | -0.23478765 | -0.03063010 | 0.07460315 |
| Plant Height | Tukey | **0.21848794** | **0.3916674** | **0.56484680** |
| Leaf Thickness | Tukey | **0.01504233** | **0.1290373** | **0.31004402** |
| Root Radius | Tukey | **-0.47143643** | **-0.3335825** | **-0.19572854** |
| Leaf Dry Matter Content | Tukey | **-0.41424016** | **-0.2774594** | **-0.14067866** |

| Green House: Functional Diversity | | | | |
|---|---|---|---|---|
| Stormwater retention | Tran | 2.5 % | Coefficient | 97.5 % |
| Biomass | Tukey | **0.031923648** | **0.05087135** | **0.069819053** |
| Phenological Complementarity | | -0.005111620 | 0.005825398 | 0.029168034 |
| Total | | -0.005514393 | 0.05031400 | 0.137482644 |
| Specific Leaf Area | | -0.049773848 | -0.003823787 | 0.029485366 |
| Plant Height | | **0.062086602** | **0.09550809** | **0.128929580** |
| Leaf Thickness | | **-0.085724558** | **-0.05463563** | **-0.023546694** |
| Root Radius | | **-0.112493477** | **-0.07385651** | **-0.035219541** |
| Leaf Dry Matter Content | | -0.059974139 | -0.02062552 | 0.002065364 |

| Green House: Community Weighted Mean | | | | |
|---|---|---|---|---|
| Stormwater Retention | Tran | 2.5 % | Coefficient | 97.5 % |
| Biomass | Tukey | **0.05272627** | **0.07209042** | **0.091454570** |
| Specific Leaf Area | | **-0.07792531** | **-0.05249127** | **-0.027057222** |
| Plant Height | | **0.12602537** | **0.152652** | **0.179278657** |
| Leaf Thickness | | **-0.04626111** | **-0.01775062** | **-0.001539775** |

|  |  |  |  |  |
|---|---|---|---|---|
| **Root Radius** |  | -0.02877009 | -0.0007614302 | 0.023238579 |
| **Leaf Dry Matter Content** |  | -0.01504276 | 0.005744819 | 0.042391389 |

**Appendix 6.C.** Confidence intervals from the multiple linear regressions conducted on the biomass, temperature, and stormwater retention data from the green roof study in Chapter 5. Tukey indicates that a Tukey's ladder of powers transformation was used. Tran=transformation.

| **Green Roof: Biomass August 2019** | | | | |
|---|---|---|---|---|
| **Functional Diversity** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Phenological Complementarity | - | **-0.5133106** | **-0.3019779** | **-0.1092055** |
| Total | Tukey | **0.3040997** | **0.5014163** | **0.6987328** |
| Plant Height | - | -0.2183186 | -0.01735684 | 0.1056048 |
| Specific Leaf Area | log | -0.3354496 | -0.01806324 | 0.2113298 |
| Leaf Dry Matter Content | sqrt | **-0.5882077** | **-0.4213384** | **-0.2544690** |
| Leaf Thickness | Tukey | **0.1504536** | **0.3080375** | **0.4656214** |
| Root Radius | Tukey | -0.1309915 | 0.01911602 | 0.2615527 |
| **Community Weighted Means** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Plant Height | sqrt | -0.11156202 | 0.01482014 | 0.2090559 |
| Specific Leaf Area | Tukey | **0.00238063** | **0.07574384** | **0.2069820** |
| Leaf Dry Matter Content | Tukey | **0.09431613** | **0.2756285** | **0.4569410** |
| Leaf Thickness | log | **0.22712547** | **0.4312242** | **0.6353229** |
| Root Radius | Tukey | **-0.50841611** | **-0.4079174** | **-0.3074187** |

| **Green Roof: Biomass August 2020** | | | | |
|---|---|---|---|---|
| **Functional Diversity** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Phenological Complementarity | | -0.3122526 | -0.02296189 | 0.165528086 |
| Total | Tukey | **0.3626883** | **0.5950748** | **0.827461374** |
| Plant Height | | **-0.2980740** | **-0.1103289** | **-0.006634076** |
| Specific Leaf Area | log | -0.3709786 | -0.04577137 | 0.125733675 |
| Leaf Dry Matter Content | sqrt | **-0.4520421** | **-0.2778189** | **-0.103595824** |
| Leaf Thickness | Tukey | -0.1376167 | 0.01470541 | 0.234681940 |
| Root Radius | Tukey | -0.3138332 | -0.03540702 | 0.113689130 |
| **Community Weighted Means** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Plant Height | sqrt | -0.1455115 | 0.002996537 | 0.1671366 |
| Specific Leaf Area | Tukey | **0.1194481** | **0.2235494** | **0.3276507** |
| Leaf Dry Matter Content | Tukey | -0.0275739 | 0.1166969 | 0.3849581 |
| Leaf Thickness | log | -0.0191948 | 0.1518100 | 0.4406414 |
| Root Radius | Tukey | **-0.6480752** | **-0.5432822** | **-0.4384892** |

| **Green Roof: Substrate Temperature** | | | | |
|---|---|---|---|---|
| **Functional Diversity** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Phenological Complementarity | | -0.012918608 | 0.0007284767 | 0.018116669 |
| Biomass | Tukey | **-0.093407188** | **-0.08029959** | **-0.067192000** |
| Total | | **-0.216232551** | **-0.1044413** | **-0.028479339** |
| Plant Height | | -0.035233054 | -0.009509545 | 0.003695881 |
| Specific Leaf Area | | **0.008984189** | **0.04251797** | **0.090968361** |
| Leaf Dry Matter Content | | **0.025060538** | **0.06917694** | **0.113293342** |
| Leaf Thickness | | -0.086954443 | -0.005123207 | 0.064626236 |
| Root Radius | | **0.017416491** | **0.05873571** | **0.100054925** |
| **Community Weighted Means** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Plant Height | | **-0.04092339** | **-0.02474540** | **-0.009098301** |
| Specific Leaf Area | Tukey | **0.01081871** | **0.02437024** | **0.037921768** |
| Leaf Dry Matter Content | | **0.02166719** | **0.04135907** | **0.061050941** |
| Leaf Thickness | log | -0.04050959 | -0.003297539 | 0.019426002 |
| Root Radius | Tukey | -0.02305091 | -0.004685069 | 0.003962328 |
| Biomass | Tukey | **-0.10115316** | **-0.08721997** | **-0.073286785** |

| **Green Roof: Stormwater Retention** | | | | |
|---|---|---|---|---|
| **Functional Diversity** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Phenological Complementarity | | -0.03160493 | 0.005169793 | 0.06624986 |
| Biomass | Tukey | -0.06160702 | -0.003979676 | 0.03340420 |
| Total | | -0.06275200 | 0.005276681 | 0.09853432 |
| Plant Height | | -0.05069790 | 0.0006243162 | 0.05574809 |
| Specific Leaf Area | | -0.02687026 | 0.009267406 | 0.07888659 |
| Leaf Dry Matter Content | | -0.07942500 | -0.00781590 | 0.03206071 |
| Leaf Thickness | | -0.04552103 | 0.001872119 | 0.06025161 |
| Root Radius | | -0.04547413 | 0.004250825 | 0.07530999 |
| **Community Weighted Means** | **Tran** | **2.5 %** | **Coefficients** | **97.5 %** |
| Plant Height | | -0.04854405 | 0.002937576 | 0.06924409 |
| Specific Leaf Area | Tukey | **0.01450965** | **0.06234375** | **0.11382543** |
| Leaf Dry Matter Content | | -0.07266712 | 0.004918091 | 0.10646627 |
| Leaf Thickness | log | -0.05779912 | 0.01167502 | 0.12680826 |
| Root Radius | Tukey | -0.07583475 | -0.009823181 | 0.02348303 |

| | | | | |
|---|---|---|---|---|
| Biomass | Tukey | -0.06109817 | -0.002311119 | 0.04442265 |

# Chapter 7

# Synthesis

According to modern coexistence theory, species coexistence can only occur if three conditions are met: (1) intraspecific competition must be greater than interspecific competition, (2) species must have niche differences, and (3) relative fitness differences must be present. A species' traits play an important role in coexistence theory, as co-occurring species with more divergent traits should differ in resource acquisition strategies, encouraging coexistence. Additionally, spatial heterogeneity should result in an increase in trait diversity as different traits are known to excel in different environmental conditions. However, research to determine the degree to which trait divergence/convergence encourages coexistence, and the role spatial heterogeneity plays in structuring the functional trait profile of plant communities was lacking. For this reason, I designed one observational and three experimental studies. In each study I examined variation in functional plant traits to determine how plant communities within the study system coexist.

## Observational Study: Chapter 3. Multiple Assembly Processes Form Coastal Barren Plant Communities

***Question One:*** How do spatial heterogeneity and environmental stress influence functional trait diversity?

***Hypothesis One:*** Increased spatial heterogeneity leads to increased functional trait diversity and coexistence in more productive environments.

***Findings:*** Multiple assembly processes are active on Nova Scotia's coastal barrens. Both high (limiting similarity) and low (habitat filtering) functional diversity were observed in environments with higher values of environmental heterogeneity and stress. Nevertheless, environmental stress had far more associations with functional diversity than environmental heterogeneity, an indication that, on Nova Scotia's coastal barrens, environmental stress is the main driver of plant community diversity. Even so, multiple species can coexist in this extreme environment if they vary in specific trait values.

## Experimental Study 1: Chapter 4. Changes in Plant Community Composition and Functional Plant Traits Over a Four-Year Period on an Extensive Green Roof

***Question:*** How does spatial heterogeneity influence functional trait diversity and coexistence over time?

***Hypothesis One:*** Increased niche space, due to substrate depth heterogeneity, results in greater functional diversity and coexistence.

***Findings:*** This hypothesis was not supported, with little variation observed between the homogenous 10 cm treatment and the heterogenous 5/15 cm treatment. This result may be due to spatial scale, with heterogeneity smaller than the size of individuals. Specifically, the roots of individuals in the heterogenous treatment could access resources in both the 5 cm and 15 cm substrate depths.

## Experimental studies 2 and 3: Chapter 5. Functional Trait Divergence Encourages Coexistence

***Question:*** How do trait convergence and divergence influence coexistence?

***Hypothesis One:*** Species pairs that differ in growth due to the fluctuating environment will be more likely to coexist, with coexistence possible due to the storage effect.

***Findings:*** For both experiments, divergent growth patterns were not associated with coexistence. However, there is some support for the storage effect encouraging coexistence in the greenhouse study, namely for those treatments containing *S. novi-belgii*, as treatments paired with this species frequently had the greatest relative growth rate. *S. novi-belgii* was the tallest species in the study and had one of the strongest reactions to desiccation, with individuals entering dormancy during drought and quickly re-sprouting when conditions became more favorable. These attributes may have made it easier for neighboring species to coexist. Specifically, competition between the dormant *S. novi-belgii* and neighbors would be negligible during drought. Although *S. novi-belgii* grows back quickly during favorable conditions, the frequent desiccation incorporated into this experiment may have helped less competitive neighbors survive. However, future research is needed to confirm this reasoning.

***Hypothesis Two:*** Species with divergent traits will be the least antagonistically competitive, increasing the potential for them to coexist.

***Findings:*** No association was observed between competition/coexistence and total functional diversity (calculated from all traits). However, patterns emerged when traits were analyzed individually. Here, co-occurring species with divergent values in height and leaf dry matter content had a less competitive relationship than species with convergent values of the aforementioned traits. Since both height and leaf dry matter content are associated with water uptake and drought tolerance, divergent values in these two traits likely encouraged co-existence, as species have different water use requirements.

## Discussion

The insights gained from each research chapter are applicable across the various studies conducted in this dissertation. In Chapter 3, high stress due to low soil moisture was associated with an increase in the functional diversity of plant height and leaf thickness. Chapters 4 and 5 also found that divergent heights encourage coexistence between species in a drought-prone environment. This trend likely occurred as species with divergent heights tend to differ in water-use requirements (Moles et al., 2009; Wang et al., 2019). For leaf thickness, high functional diversity was also observed in Chapter 4’s 6 cm treatment. In Chapters 2 and 3, this trend was possible due to the nearly 50/50 split between species with succulent and non-succulent leaves. This finding is particularly interesting because high stress is usually associated with low functional diversity as species require specific traits to survive (Chesson et al., 2004; Katabuchi et al., 2012; Spasojevic et al., 2012; Cross et al., 2015). Here, I demonstrated that high functional diversity is possible, and perhaps common, in stressful environments containing a species pool with diverse stress strategies.

The results of Chapters 3, 4, and 5 demonstrate the importance of analysing the functional diversity of individual traits. This analysis allows researchers to understand which specific strategies encourage coexistence and co-occurrence. In Chapters 3 and 4, the analysis of individual traits allowed me to determine which functional trait values were necessary for survival, and which traits allowed species to coexist. In Chapter 4, total functional diversity was not associated with potential coexistence. It was only when traits were analyzed individually that I learned that divergent heights and specific leaf areas can encourage coexistence in a green roof environment. Previous research has also found that examining species traits as a whole, as opposed to individual traits, neglects potential interactions (Spasojevic et al., 2012; Li et al., 2018).

## Conclusion

Environmental stress, rather then spatial heterogeneity, led to an increase in functional trait diversity. Since species with more divergent traits are less likely to compete for limiting resources, this finding indicates the presence of a filter, encouraging coexistence between species that differ in stress tolerant strategies. This finding is further emphasised when specific functional traits are examined. Specifically, coexistence in water limiting environments is possible when species differ in plant height and leaf dry matter content. Coexistence between species under high stress was more likely if they possessed divergent heights and leaf thicknesses. This dissertation also demonstrates the importance of analysing the functional diversity of individual traits. This analysis allows researchers to understand which specific strategies encourage coexistence and co-occurrence.

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