INVESTIGATING TRADE-OFFS USING ECOLOGICAL STOICHIOMETRY IN THE BOREAL FOREST

By

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ABSTRACT

Studying trade-offs allows for the investigation of complex ecosystem interactions and processes. Ecological stoichiometry measures the elemental ratios and the balance of ratios in organisms and allows for comparisons across species, populations, and ecosystems. I tested two questions regarding ecological trade-offs. First, I tested whether there is interannual variation in the stoichiometric traits of boreal plant species and, if so, what is driving the variation. Second, I tested how herbivore space use is influenced by perceived predation risk and food quality. I found that interannual variation occurs in percent carbon for all species and that the evergreen conifer was the only species that experienced interannual variation in other elements. I found temperature, moisture, and productivity to be drivers of interannual variation. For the second question, I found that snowshoe hare space use is influenced by perceived predation risk and food quality. These factors interact and produce an effect at the individual level, where hares increase space use in high risk areas if there is high-quality food and vice versa. Predation risk and plant stoichiometry are connected through their shared impact on foraging behaviour, which influences herbivore life cycles. This work establishes ecological stoichiometry as an exciting framework to investigate biological trade-offs and contributes to our understanding of the temporal variation of resources and herbivore space use.

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List of Abbreviations and Symbols

ΔAIC – Delta (Change) in Akaike’s Information Criterion

AFL – Agriculture & Food Lab

AIC – Akaike Information Criterion

C – Carbon

EVI – Enhanced Vegetation Index

GDD – Growing Degree Days

KUD – Kernel Utilization Distribution

N – Nitrogen

NDMI – Normalized Difference Moisture Index

OFT – Optimal Foraging Theory

P – Phosphorus

RAH – Risk Allocation Hypothesis

StDM – Stoichiometric distribution model

TERG – Terrestrial Ecology Research Group

Chapter 1 – Introduction and Overview

In this thesis, I investigate two questions regarding ecological trade-offs in the boreal forest. In chapter 2, I quantify the interannual variation in the elemental composition of four boreal plant species and determine the mechanisms behind the variation. Second, in chapter 3, I investigate the trade-offs made by snowshoe hare (*Lepus americanus*) regarding their space use in relation to perceived predation risk and food quality. Finally, in chapter 4, I highlight the key points of my work and outline how my research has contributed to the broader field of ecology.

1.1 Perspective & Positionality

The land that I have worked and lived on while completing this thesis is the unceded and stolen land of the Beothuk people. As a descendant of the white, settler-colonial Europeans who grew up on the traditional homelands of the Haudenosaunee, Anishinaabe, and Attiwonderonk Peoples, my approach to science will always be influenced by my heritage. Through the intentional and cruel work of my European ancestors, the Beothuk people in Newfoundland were driven to extinction. The original people of this place are no longer present to collaborate with and ask meaningful and interesting scientific questions, a fact that I have tried to remind myself of throughout my thesis work. Although some may argue that my background as a cisgender, white, settler-colonial is not relevant to my pursuit of research in the "objective" natural sciences, I believe that the privilege that one holds directly informs the science that they produce. By outlining my biases, I give context and credibility to the work I have done, much like a well-crafted introduction or detailed methods section would.

The systems in which I worked to produce this thesis are ones of implicit oppression that have been intentionally designed by colonialism, patriarchy, and capitalism. My training and approach to the biological sciences have been informed by a Eurocentric worldview, which is but one of many possible approaches – a fact I learned during my Master's due to the generous and intensely important work of peers, mentors, and teachers. My perspective and biases impact the way I ask questions and approach science – my privilege is intertwined with my research in a way that can only be addressed by acknowledging and discussing it. The Eurocentric worldview that I hold views humans and nature as distinct entities and takes a reductionist approach to the sciences, which is the approach that I brought to my research questions. I investigate the different aspects of the boreal forest as distinct pieces, which then fit together to form an ecosystem. In addition, I view the boreal forest and the plants and animals within it as inherently distinct from humans and anthropogenic influence, as opposed to other worldviews such as the "All My Relations" worldview held by many groups of Indigenous peoples. My approach is not wrong, but it is tied to my biases and fundamentally affects how I ask questions, which is something that I believe all scientists should consider when approaching their research.

1.2 Key Ecological Concepts

1.2.1 Trade-Offs

All organisms make trade-offs. Trade-offs occur when life-history traits are negatively associated with each other, creating the need for an individual to balance their investment (Zera and Harshman 2001). Trade-offs can occur at different scales, starting at the individual level and building to population and communities (Kneitel and Chase 2004). For example, trade-offs for individual Alaskan porcupines require choosing a habitat that provides thermal cover while also providing enough foraging resources to survive the winter season (Coltrane and Sinnott 2013). However, at the community level, porcupines that prioritize feeding can damage preferred forage species, such as Sitka spruce (Eglitis and Hennon 1997). The different prioritization that individuals employ shapes individual and population fitness (Werner and Hall 1988; Watson et al. 2007). In addition to shaping fitness, trade-offs impact the community composition of both plants and animals, which in turn, shapes ecosystems (Kneitel and Chase 2004).

In terrestrial ecosystems, plants are often co-limited by nitrogen and phosphorus (Elser et al. 2000; Güsewell 2004; Marleau et al. 2015). Nitrogen and phosphorus both contribute to key physiological processes in plants, and depending on a plant's life stage and surrounding ecosystem, its allocation of limited elements to specific physiological processes changes (i.e., growth, reproduction, or defense; refer to Fig. 1-1). Element allocation, uptake, and recycling by plants are further shaped by biotic and abiotic processes (González et al. 2011, 2014; Sardans et al. 2011; Sardans and Peñuelas 2013). Climate, the surrounding plant community, and herbivory all have direct impacts on the elements of plants (Sardans and Peñuelas 2013; Borer et al. 2015; Moorhead et al. 2017). For example, higher mean annual precipitation in Mediterranean forests led to higher nitrogen and phosphorus contents in tree leaves, resulting in more growth and increased biomass (Sardans and Peñuelas 2013). In turn, changes in how plants use elements impacts the entire ecosystem (Sinclair et al. 2000; Mcarthur et al. 2012; Kurze et al. 2017). If investment is focused on defense and increased toxin levels, for instance, species reduce foraging levels, therefore affecting the success of the plant as well as the success and fitness of the herbivore and its predators (McArthur et al. 2012).

Trade-offs drive animal behaviour, whether they are between fecundity and recruitment ability (Amarasekare 2003), displacement ability and resource exploitation (Amarasekare 2003), or foraging and predation risk (Lima and Dill 1990; Verdolin 2006). Prey species often must trade safety from predation for foraging opportunities (Figure 1b, Lima and Dill 1990; Wilson et al. 2012), and predators trade energy for hunting opportunities (Michel and Adams 2009; Laundré 2010). The balance between safety from predation and foraging opportunities often results in prey species exhibiting trade-off tactics between one or the other, shaping their spatial distributions (Lima and Dill 1990; Wilson et al. 2012). For example, moose that selected habitat based on forage and habitat quality and areas with unproductive habitat types had larger home ranges than moose in areas with higher proportions of productive habitat types (Bjørneraas et al. 2012). Given that herbivore space use and their distribution on the landscape has implications across trophic levels (Brown et al. 1999), determining what is driving herbivore space use can provide insight into the structure of the ecosystem.

1.2.2 Habitat Selection & Home Ranges

Animal habitat selection occurs on several scales. As Johnson (1980) describes, habitat selection works first at the geographical and physical range of a species, secondly at the home ranges of individuals or groups, then describes the usage of space within the home range, and lastly the selection of food within a used patch. Animal space use has been studied at each of these scales, with each scale facilitating very different questions and inferences. Studying moose from 10 populations reveals how landscape-scale variables such as plant productivity impact the space use and distribution of these large ungulates (Allen et al. 2016). Conversely, looking at the fine-scale movements of moose, reveals that they select for patches of higher digestibility of forage within their home range (Van Beest et al. 2010). Habitat selection occurs on many scales, but the scale at which it is studied determines the questions that can be asked and the inferences that should be made.

The concept of a home range of an animal is fundamental to ecology. The first definition of a home range in the scientific literature described it as the area that is traversed by the individual when it is doing its normal activities of foraging and reproduction (Burt 1943). Although home ranges capture an animal’s normal activities, the areas are not used homogenously, with core areas of use arising within an individual’s home range (Samuel et al. 1985). Understanding the mechanistic drivers of use by individuals within their home range can reveal interactions between individuals and their environment, which can help inform how individuals make trade-offs (Samuel et al. 1985).

1.3 Tools & Study System

1.3.1 Ecological Stoichiometry

Organisms’ trade-offs and the mechanisms driving those trade-offs can be investigated using ecological stoichiometry. Ecological stoichiometry measures the ratios of elemental components that make up living things and the balance of those ratios (Sterner and Elser 2002). Understanding the stoichiometry of an ecosystem and how stoichiometric composition varies spatially and temporally provides knowledge on ecosystem functioning and improves our ability to predict how changes to an ecosystem will affect individuals and populations (Asner et al. 2015; Kaspari and Powers 2016).

Measuring the stoichiometry of plants provides a foundation for studying the entire ecosystem. Carbon, nitrogen, and phosphorus are three of the main elements that govern organic life (Elser et al. 2000; Sterner and Elser 2002). Most plants, with the exception of nitrogen-fixing and carnivorous species, obtain nitrogen and phosphorus from the abiotic environment, lifting it from the substrate they are growing in (Vitousek et al. 2010). In contrast, plants produce carbon through the biotic process of photosynthesis, which is dependent on a host of other factors, including light and water availability as well as temperature (Welp et al. 2007; Wu et al. 2012). These three elements can be used to facilitate plant growth and improve physical and chemical defenses while also determining if the plant is high- or low-quality forage for animals (Sterner and Elser 2002). The availability of elements determines which plant species will succeed in an environment. Some plants are better at fixing limiting elements such as nitrogen, giving them an advantage in low nutrient systems (Macedo et al. 2008), whereas other plants use elements to outgrow their competition (Boerner 1984; Zhao and Zeng 2019). Indeed, element availability and use are important factors in determining plant community composition. In turn, the plant community determines the quality of the habitat for prey and predator species. Plant community is a large factor in the physical structure of the community, impacting how much cover prey species have from predation and how easily a predator can hunt (Jones et al. 1994; Michel and Adams 2009). The stoichiometry of plants determines their food quality for herbivores, influencing space use of both herbivores and their predators (Hebblewhite and Haydon 2010; Laundré 2010; Leroux et al. 2017). By measuring the ecological stoichiometry of plants, we can uncover how many ecological processes work together to shape ecosystems and their functioning.

1.3.2 Boreal Forest

The boreal forest offers a system uniquely suited to investigate ecological trade-offs. The boreal is a low-nutrient system, limited by low levels of phosphorus and nitrogen as well as extreme temperatures, low plant growth rates, and low diversity (Price et al. 2013). The limited nature of the boreal creates a scenario where trade-offs are highly prevalent. For plants, suboptimal conditions result in slow growth rates, with the plants investing in more chemical defenses to ward off herbivory (Bryant et al. 1983) and adjusting their biomass allocation to their roots (Aerts 1999). Because the plants are slow-growing, have high levels of chemical defenses, and are nutritionally limited, there is intense pressure on herbivores to find patches of high-quality food or devise a way to consume large quantities of low-quality food (Van der Wal et al. 2000;

Van Beest et al. 2010). In addition, the risk of predation for herbivores is always present in the boreal, creating a trade-off between predation risk and food quality (Lima and Dill 1990; Krebs et al. 1995).

The study system that I conducted my research in specifically includes four 25 ha study areas in the boreal forest of eastern Newfoundland, Canada, in and around Terra Nova National Park. The study sites are second-growth forests varying in age from 20-40 up to 80-100 years old. They consist mainly of white spruce and black spruce (*Picea mariana*) trees, with white birch (*Betula papyrifera*), and red maple (*Acer rubrum*) as well. There are large patches of speckled alder (*Alnus incana*) throughout the study sites, and the understory is dominated by sheep laurel (*Kalmia angustifolium*), lowbush blueberry (*Vaccinium angustifolium*), Labrador tea (*Rhododendron groenlandicum*), and bunchberry (*Cornus canadensis*). The study system has an unusually low diversity of terrestrial mammals, with 13 native mammals and 14 non-native mammals inhabiting the boreal forest of Newfoundland (Strong and Leroux 2014). The snowshoe hare, a focal species in this study, is a non-native mammal in this system and was introduced to the island of Newfoundland in 1864 (Strong and Leroux 2014).

1.4 Terrestrial Ecology Research Group

The study areas used in this thesis are part of a research project that is run by the Terrestrial Ecology Research Group (TERG). TERG is composed of three Principal Investigators, Dr. Yolanda Wiersma, Dr. Shawn Leroux, and Dr. Eric Vander Wal, along with their graduate students. Four graduate students overlapped with my tenure on the team; Travis Heckford, Matteo Rizzuto, Juliana Balluffi-Fry, and Joanie Kennah. Each student had their own individual thesis project, and we collaborated closely by meeting fortnightly to discuss research ideas, collecting field data together, providing code and analysis to each other when relevant, and providing critical feedback on written documents. We are all co-authors on various pieces of the others' work, resulting in my co-authorship on six manuscripts by the end of my degree. Together, we investigate how elements, mainly carbon, nitrogen, and phosphorus, act as an ecological currency across space, time, and food chains (see the co-author statement in section 1.6). My first chapter investigates how elements vary over time in our study plant species, which is work that supports the use of our interannual elemental data by my colleagues and draws on data collected by students before I joined the team. My second chapter, which looks at how snowshoe hare use space and why is part of a larger investigation into herbivore space use using ecological stoichiometry as a measure of food quality.

1.5 Thesis Overview

I investigate trade-offs made in the boreal forest by several plant species (chapter 2) and one animal (chapter 3). In chapter 2, using multiple measures of ecological stoichiometry – ratios and percentages of three elements (C, N, P) – I quantify the interannual variation in the ecological stoichiometry of four commonly occurring boreal plant species. After determining if year is a relevant factor in the variation of stoichiometry for each species, I then test four potential mechanisms for the variation, covering both abiotic and biotic drivers. The quantity and ratio of elements within a plant determine what physiological processes they can invest in, which has a direct impact on the trade-offs that occur.

In chapter 3, I tested how a keystone boreal herbivore, the snowshoe hare, uses space with respect to food quality and perceived predation risk. At the home range scale, I quantified the intensity of space use by a population of snowshoe hares and tested how the intensity of space use varies with habitat complexity and food quality of one of their preferred forage species. Herbivores have top-down and bottom-up effects on an ecosystem, influencing both plant and predator distributions. Determining what drives prey species space use provides important insight for ecosystem functioning.

Overall, my thesis seeks to investigate trade-offs for both plants and herbivores using ecological stoichiometry as the tool. Ecosystems are complex, with many interactions occurring all the time within and between organisms. To determine the drivers behind complex ecological processes, such as the intensity of space use by an individual, it requires research into many different variables. Trade-offs provide a framework to quantify and explain ecological interactions. By reducing organisms to their elemental components, ecological stoichiometry allows comparisons across species, trophic levels, and ecosystems (Sterner and Elser 2002). In addition, carbon, nitrogen, and phosphorus are three of the main building blocks of life (Sterner and Elser 2002). For these reasons, ecological stoichiometry is a novel and appropriate tool to study variation in plants and to use as a proxy for food quality with respect to herbivores.

1.6 Co-Authorship Statement

Chapter 2 and Chapter 3 of this thesis were co-authored with Eric Vander Wal, Shawn J. Leroux, Juliana Balluffi-Fry, Matteo Rizzuto, Travis R. Heckford, Joanie L. Kennah, and Yolanda F. Wiersma. I led the study designs, data analyses, and writing for all chapters in this thesis. E. Vander Wal, S.J. Leroux, and Y.F. Wiersma provided guidance and funding. All co-authors provided critical feedback on research design and written documents. In addition, Juliana Balluffi-Fry trained me in the field, trapped and collared the hares used in chapter 3, and collected telemetry data in 2018. Matteo Rizzuto set up the study sites, collected field data used to produce the stoichiometric data used in chapters 2 and 3, collected telemetry data in 2017, and provided assistance with code and analysis for chapter 3. Travis R. Heckford set up the study sites, collected field data used to produce the stoichiometric data used in chapters 2 and 3, produced the elemental stoichiometry layers used in chapters 2 and 3, and assisted with code and analysis in chapter 2. Chapter 2 has been accepted at the *Journal of Plant Ecology* and is formatted for that journal. Chapter 3 will be submitted for review at *Canadian Journal of Zoology* and is formatted for that journal.

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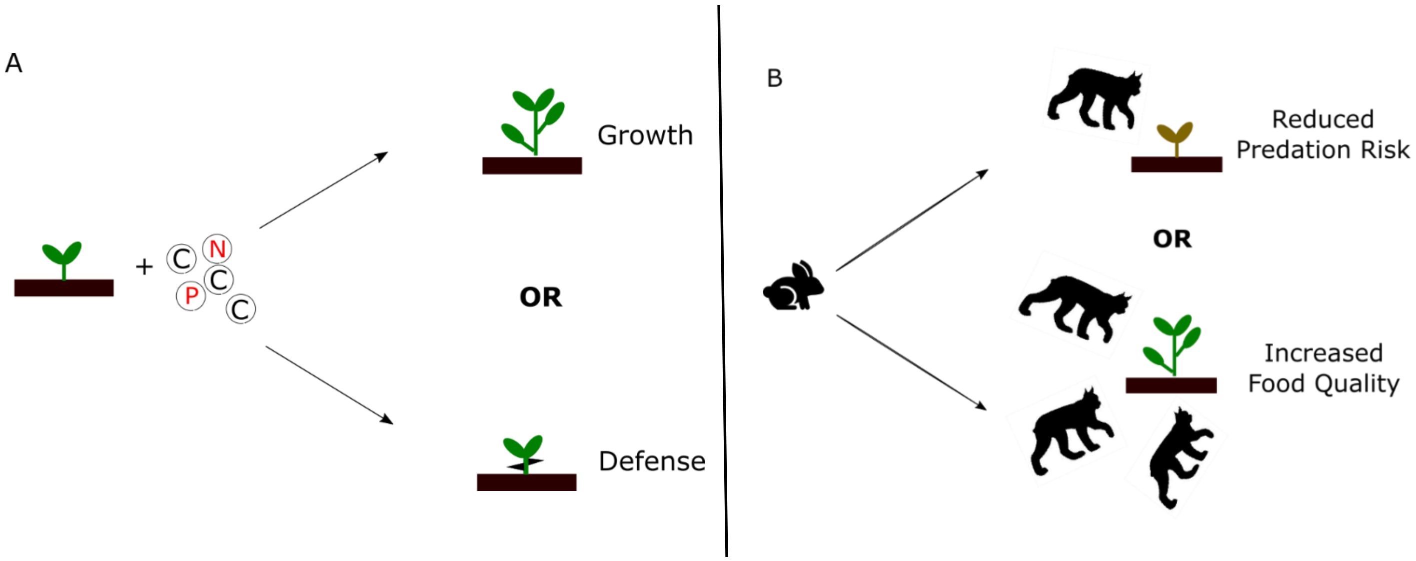

Figure 1-1. Common examples of ecological trade-offs a) Juvenile plant receives limited N and P and makes a trade-off between physiological processes of growth and defense. Trade-offs depend on life history and environmental surroundings b) Snowshoe hare must forage to survive and make a trade-off between food quality and predation risk based on life history and environmental surroundings.

Chapter 2 – Temporal variation and its drivers in the elemental traits of four boreal plant species[†]

[†] This chapter has been revised and resubmitted to the Journal of Plant Ecology

2.1 Abstract

Aims

Intraspecific variation in plant traits has important consequences for individual fitness and herbivore foraging. For plants, trait variability across spatial dimensions is well documented. However, temporal dimensions of trait variability are less well known but may be influenced by seasonal differences in growing degree days, temperature, and precipitation. Here, we aim to quantify the intraspecific temporal variation of traits and the drivers of that variation for four commonly occurring boreal plant species.

Methods

We sampled the elemental and stoichiometric traits (%C, %N, %P, C:N, C:P, N:P) of four common browse species' foliage across two years. Using a two-step approach, we first fit generalized linear models (GzLM, n = 24) to our study species' elemental and stoichiometric traits to test if they varied across years. When we observed evidence for temporal variability, we fit a second set of GzLMs (n = 8) with temperature, productivity, and moisture as explanatory variables.

Important Findings

We found no evidence of temporal variation for most of the elemental and stoichiometric traits of our four boreal plants, with two exceptions. Year was an important predictor for percent carbon across all four species (R^2 = 0.47 to 0.67) and for multiple elemental and stoichiometric traits in balsam fir (5/8 models, R^2 = 0.29 to 0.67). Thus, variation in percent carbon is related to interannual differences, more so than nitrogen and phosphorus, which are limiting nutrients in the boreal forest. These results also indicate that year may explain more variation in conifers' stoichiometry than for deciduous plants due to life history differences. Growing degree days (GDD) was the most frequently occurring variable in the second round of models (8/8 times, $R^2 = 0.21$ to 0.41), suggesting that temperature is an important driver of temporal variation in these traits.

Keywords: biogeochemistry, boreal forest, elemental phenotype**,** ecological stoichiometry, environmental drivers, plant traits, plant variation

2.2 Introduction

Variation in plants can be described in terms of different traits, e.g., physiological, elemental, morphological, and in different ways, e.g., across time, space, species. Variation in traits allows individuals, and therefore populations, to adapt to their dynamic environments. For example, leaf size, leaf area, and leaf nitrogen concentration were found to be highly plastic within yellow birch (*Betula alleghaniensis*), varying with light availability, a factor that is controlled by other individuals in the ecosystem (Delagrange et al. 2004; Williams et al. 2020). Wood characteristics, i.e., wood density and phosphorus levels, in tropical species are variable and dependent on soil nutrient availability (Heineman et al. 2016). Morphological plasticity, i.e., changes in pitcher size, was observed in the northern pitcher plant (*Sarracenia purpurea* subsp. *purpurea*) following transplantation between two different wetland environments and is posited to be a strategy for improving fitness in a nutrient-limited environment (Bott et al. 2008). Plant traits influence species distributions and nutrient dynamics for the whole ecosystem (Borer et al. 2015; Heineman et al. 2016). Therefore, uncovering the mechanisms and levels of variation in different traits within a plant species, such as elemental composition within a plant species, provides knowledge on how ecosystem-level changes occur. Disentangling the presence and causes of interannual variation in elemental traits provides the opportunity to see if and why ecosystems are changing across years. Interannual variation or lack thereof in plant elemental traits impacts individual fitness as well as population and ecosystem dynamics.

Elemental variation happens within and across species due to many mechanisms and has effects reaching over landscapes and throughout trophic levels. The large-scale effects are part of the reason elemental variation is of ecological interest to quantify and explain. In addition to the ecosystem-level effects of variation in elemental composition, such as changes in nutrient cycling and community composition, the universal nature of elements allows the use of elemental and stoichiometric traits as an effective tool to facilitate comparisons across populations and species. Ecological stoichiometry describes elemental ratios (e.g., Nitrogen:Phosphorus, hereafter N:P) and their balance found within living organisms (Sterner and Elser 2002). In contrast, elemental composition is the quantification of the fundamental elements of an individual. Both elemental and stoichiometric traits are important because they measure the flow of energy/nutrients within and between individuals and trophic levels (Jeyasingh et al. 2014; Leal et al. 2017). For instance, several studies have shown that stoichiometric traits vary both inter- and intra-specifically across different spatial scales (Tsoi et al. 2011; Martiny et al. 2013; Kaspari and Powers 2016). Examples of variation in the elemental and stoichiometric traits of different plants include changes in nutrient allocation and growth between evergreen gymnosperm, broadleaved evergreen angiosperm, and deciduous angiosperm forest types across moisture and temperature gradients (Sardans and Peñuelas 2013), and variation in percent C, N, and P among young white birch trees growing in different plots across a boreal landscape (Leroux et al. 2017). Further, plant elemental traits, which are associated with available nutrients and uptake, have ecosystem-level impacts such as plant community species richness and primary productivity levels (Bracken et al. 2015; Li et al. 2017). Describing the variation in stoichiometric and elemental traits of plants will deepen our understanding of the species that we measure, as well as the ecosystem level processes associated with them.

Plants allocate elements differently depending on their age (Güsewell 2004); however, the magnitude and direction of the variation in elemental traits from one year to another are still unclear. In contrast, the spatial variation of elemental and stoichiometric traits in plants can be driven by local conditions as well as large-scale patterns such as latitudinal trends (Elser et al. 2010; Martiny et al. 2013; Bracken et al. 2015). If plant stoichiometric and/or elemental traits vary between years, then the resources they provide for consumers also vary (González et al. 2014). Variation in resources effectively changes the landscape for consumers, which could impact their survival and distribution. For example, risk-averse daphnia change their diel vertical migration to capitalize on nutrient-rich algae (Moe et al. 2005). In addition, when plant traits vary temporally, ecosystem processes such as nutrient cycling are affected because of the variation in elemental inputs and uptake (Sterner and Elser 2002; Welti et al. 2017). Variation in a process as fundamental as nutrient cycling has implications that scale up and across the ecosystem. In addition, understanding how and why temporal variation occurs is essential for accurately modelling the elemental resources of an ecosystem.

Plant elemental and stoichiometric traits in the boreal forest system are driven by a variety of factors, including temperature, productivity, and moisture. The boreal forest is a nutrient-limited system that experiences distinct seasonal and interannual changes in abiotic conditions. Mean annual temperature has a significant relationship with foliar N and P and available soil N across climactic gradients, including in North America (Sardans et al. 2016; Sardans et al. 2015; Yin 1992). Productivity in the boreal forest is a nitrogen limited process and is therefore connected to elemental and stoichiometric traits of plants. More specifically, higher productivity is caused by higher N availability/uptake and results in more Carbon (hereafter C) production in plants (Vitousek and Howarth 1991; LeBauer and Treseder 2008). Higher moisture increases the uptake of N and causes a shift in P allocation, increasing P concentration in foliage and decreasing overall uptake (Cramer, Hawkins, and Verboom 2009; Pastor and Post 1986; Sardans and Peñuelas 2007).

In this study, we address two questions: 1) what is the extent of interannual variation in the elemental and stoichiometric traits of four common boreal plants? 2) what mechanisms are driving the variation? We replicated our study across four study sites and four plant species to strengthen our inferences. Because the interannual variation of plant elemental composition has impacts on the entire ecosystem, our study is designed with an emphasis on browsing and herbivory. We hypothesized that 1) year would be an important factor in explaining the variation in the elemental and stoichiometric traits of plants (C, N, P, C:N, C:P, N:P) for all four species due to yearly environmental changes and plant growth influencing nutrient allocation and uptake and 2) if there was in fact interannual variation in the elemental composition of our four study species, this ecological variation is driven by temperature, moisture, and productivity differences between years. We predicted that plants experiencing higher i) temperature, ii) moisture, and iii) productivity will have higher concentrations and quantities of C, N, P.

2.3 Materials and Methods

2.3.1 Study Region

Our four study sites are in the central-eastern region of the island of Newfoundland, Canada, within and around Terra Nova National Park. The maximum distance between any two sites is 32 km (Fig. 2-1). The sites were chosen using forest cover and stand age variables derived from datasets provided by the Provincial Government of Newfoundland and Labrador and Parks Canada (Fig. 2-1). Study sites are black spruce (*Picea mariana*) dominated forest stands that differ in age and follow a chronosequence, belonging to the following age classes; 20-40, 41-60, 61-80, and 81-100 years old. The sampling grids are approximately 500 m x 500 m and are composed of 50 sample locations distributed along six meandering transect lines (Fig. A-1, found in Appendix A). Throughout the stands, there is varying forest growth consisting mainly of black spruce, white spruce (*Picea glauca*), paper birch (*Betula papyrifera*), balsam fir (*Abies balsamea*), and red maple (*Acer rubrum*). The understorey shrub layer is dominated by sheep laurel (*Kalmia angustifolia*), Labrador tea (*Rhododendron groenlandicum*), and lowbush blueberry (*Vaccinium angustifolium*). At each sampling location (n = 50/stand) within the stands (n = 4), we established an 11.3 m radius plot (see Fig. A-2 in Appendix A for layout), used to measure shrub density and collect plant samples for each of our four study species (*Abies balsamea* hereafter balsam fir, *Acer rubrum* hereafter red maple*, Betula papyrifera* hereafter white birch, and *Vaccinium angustifolium* hereafter lowbush blueberry).

2.3.2 Response Variables

We sampled plants once per year at the end of the growing season, between July-August, for all four sites in 2016 and 2017, following the procedure summarized below (see Heckford et al. in review for further details on sampling procedure). At each of the 11.3 m radius plots (n = 50/stand), we collected shrub density and vegetation samples for each of our study species. The four study species were chosen due to their dominance in the plant community as well as prominence as common browsing plants for primary mammalian herbivores within the boreal forest on the Island of Newfoundland (Dodds 1960).

Plant Elemental Composition

Each sampling plot was divided into four primary intercardinal directions (NE, NW, SE, SW, Fig. A-2). Beginning in the NE corner, we collected the new growth leaf and stem of one individual per study species per intercardinal direction. Both leaf and stems were combined for elemental analysis. These portions were collected as they represent what is typically consumed by herbivores. We sampled moving clockwise through each intercardinal direction until there was an approximate weight of 20 g collected total. After collection, the samples were frozen until they were ready for processing. In the lab, we combined individual plant samples to obtain 10 grams of sample per plot for elemental analysis. These samples were grouped by sampling plot and sent to the Agriculture and Food Lab (AFL) at the University of Guelph, Ontario, Canada, for elemental analysis. Samples were dried to remove water content and then ground to homogenize plot-level samples at the AFL. Percent carbon (C) and nitrogen (N) were determined using an Elementar Vario Macro Cube. Percent phosphorus (P) was determined using a microwave acid digestion CEM MARSxpress microwave system and brought to volume using Nanopure water. The solution was then diluted by ten and entered into the inductively coupled plasma mass spectrometry detector (ICP-MS, Poitevin, 2016).

Shrub Belt

Each sampling plot had a 22.6 m long and 1 m wide transect that went through the centre of the plot and was used to collect density estimates for each of the four study species in 2016 (Fig. A-2). We walked along the transects in a south-north direction, measuring the height, basal diameter, and distance along the transect of an individual of every species for a maximum of five individuals per species. We did this for four height categories: 0-50 cm, 51-100 cm, 101-150 cm, and 151-200 cm. Sampling was restricted to individuals with heights between 0-2 m, as this is the height that is available to the main herbivores in the region, moose (*Alces alces*) and snowshoe hare (*Lepus americanus*).

Biomass

Biomass was estimated by collecting all new growth foliar material and measuring the height and basal diameter for approximately 50 individuals of each of our study species at all four study sites in 2017. Sampling occurred in randomly chosen locations on the periphery of the study grids as to not disturb long-term monitoring sites inside the grid and to avoid destructive sampling. By doing so, we assume that individuals outside the grid are representative of those inside the grid. Biomass data collected in 2017 was used for both 2016 and 2017 allometric models. The samples were distributed across four height categories: 0-50 cm, 51-100 cm, 101-150 cm, and 151-200 cm.

Stoichiometric Distribution Models

We built stoichiometric distribution models at each of our study sites using the elemental composition data, shrub belt data, and biomass estimates for each of our study species. First, biomass dry weights were used to construct allometric models of biomass based on height and basal diameter collected for each species in 2017. The allometric models allowed us to estimate the density of study species by height class based on the shrub belt data and we used these estimates to predict plant biomass by height class at the plot density level. We used this information to sum biomass estimates at the plot level for each height class. We then divided the plot level biomass by the plot area and multiplied the 2017 biomass value by the 2016 and 2017 elemental compositions of C, N, and P obtained from lab analysis to produce a quantity value (g/m^2) of each element for both years. Then, to obtain the stoichiometric ratios, we divided the 2016 and 2017 quantities of C, N, and P by their respective molar masses and divided the resulting values to get ratios of C:N, C:P, and N:P for both years (as reported in Heckford et al. in review).

2.3.3 Explanatory Variables

Weather

We evaluated weather across seasons using the number of growing degree days (GDD) that each site experienced from January 1 of each year to the date of sampling. We calculated GDD as per Sirois (2000):

$$GDD = \sum\nolimits_{i=1}^{n} \left(\frac{(T_{max} - T_{\min})}{2} \right) - T_{base}$$

Where *GDD* represents the number of growing degree days, *i* represents each day of the growing season where the mean daily temperature was >5°C, T_{max} represents the maximum recorded temperature for a day, T_{min} represents the minimum recorded temperature for a day, and T_{base} represents the base temperature where growth can occur. We calculated GDD using 5°C as the base temperature (Brown et al. 2019). We collected temperature data from Environment and Climate Change Canada's historical weather dataset from the weather station closest to each study site (n = 2). Three of the four study sites shared the closest weather station. However, because sampling occurred on different days of the year for each site, the number of GDD varied even when the same weather station was used. If the closest weather station had missing data, we supplemented the data from the next closest weather station (Fig. A-3).

Moisture

We used Normalized Difference Moisture Index (NDMI) as a proxy to measure vegetation moisture at every sampling point. We obtained Landsat 8 satellite imagery from the Earth Resources Observation (EROS) and Science Centre Science Processing Architecture (ESPA). We selected Landsat 8 imagery (30 m resolution) that coincided with our study species' growing season, May to August, for both years. This resulted in three dates with imagery for both 2016 and 2017. Landsat 8 imagery is provided with a preprocessed NDMI surface reflectance scene. Using the Landsat Quality Assurance ArcGIS toolbox, publicly accessible software from the U.S. Geological Survey, we extracted the following cloud coded bits from the pixel QA band: cloud shadow, snow, cloud, high cloud confidence, and high cirrus confidence (Jones *et al.* 2013; U.S. Geological Survey 2017). Using the 'Extract by Mask' ArcGIS function, we removed cloudy pixels from our NDMI scenes. In R, we rescaled NDMI scenes by dividing by 0.0001. Using the 'approxNA' function from the *raster* R package (Hijmans *et al.* 2020), we computed a linear interpolation across our temporal scenes to fill cloud removed pixels (please see Fig. A-4 for before and after interpolation maps and pixel histograms). We average our temporal NDMI scene to obtain an estimated seasonal measure of moisture. Using the ‘raster.transformation’ function from the *spatialEco* R package (Evans *et al.* 2020), we standardized the NDMI annual moisture scene by subtracting the scene mean from each pixel and dividing by the scene standard deviation. NDMI values range from 0-1, with higher values representing more moisture. We selected Landsat 8 imagery as our measure of moisture and productivity instead of precipitation and temperature data from local weather stations due to the increased spatial resolution of Landsat data. Specifically, Landsat 8 imagery allowed us to have a distinct measurement for each of the 50 sampling points within all four grids for each date measured.

Seasonal Productivity

We used Enhanced Vegetation Index (EVI) extracted from Landsat 8 imagery as a proxy for seasonal productivity and measured it using the same protocol as for NDMI. EVI has been shown to be less sensitive to saturation when compared to the Normalized Difference Vegetation Index (NDVI), which allows for a better measure of productivity in wet boreal forest conditions (Vermote *et al.* 2016). We selected Landsat 8 imagery that coincided with the growing period of our study species, May to August, for both years, resulting in three images in 2016 and four images in 2017. We calculated EVI for both years by taking the average EVI value for each pixel across the multiple images for both 2016 and 2017 (see Fig. A-5). EVI values range from 0-1, with higher values representing more moisture.

2.3.4 Statistical Analyses

We conducted our statistical analyses in two steps. In all steps, we ran general linear models with Gaussian error distributions and a nested structure. Our response variables pooled all samples collected at all four sites across both years (Table 2-1, n = 114 balsam fir, n = 120 red maple, n = 99 white birch, n = 191 lowbush blueberry). In the first step, we had elemental compositions and stoichiometric ratios as response variables and year and site as explanatory variables for each of the four study species (Table 2-2, 24 groups of models total). All model groups for all analyses included an intercept-only model. Competing models were compared with AICc (Burnham and Anderson 1998), using the 'aictab' function from the *AICcmodavg* package (Mazerolle 2019). Four models were compared per response variable, including the intercept-only model. Then, for response variables where year was in the top-ranked model, we ran a second step of generalized linear models (Table 2-4, 8 models total). To test our predictions i-iii, we used GDD, NDMI, and EVI as our explanatory variables. These model sets were then evaluated, including an intercept-only model, and ranked with AICc only considering univariate and two-way interactions using the *MumIn* package (Barton 2020). Elemental composition data were standardized to control for differences in magnitude across elements. The data were standardized by subtracting the mean from the values and dividing by the standard deviation. In all modelling, pretending variables were omitted from top models where applicable, and then models were re-ranked (Leroux 2019). All statistical analysis was done using R 4.0.0 (R Core Team, 2020).

2.4 Results

2.4.1 Overview

Plot-level percent C across all study species varied between 45.10 to 55.50% (mean = 51.05%) across 2016 and 2017. Plot-level percent C for balsam fir, red maple, white birch, and lowbush blueberry varied between 49.00 to 53.60% (mean = 52.15%), 45.70 to 51.08% (mean = 49.83%), 45.90 to 55.50% (mean = 50.02%), 45.10 to 53.16% (mean = 51.68%) respectively, across 2016 and 2017. In contrast, percent N and P varied between 0.48 to 2.87% (mean = 1.34%) and 0.02 to 0.35% (mean = 0.11%), respectively, across 2016 and 2017. Growing degree days (GDD) varied between 456.75 to 892.75 (mean = 725.58) in 2016 and 439.75 to 754.80 (mean = 566.34) in 2017. EVI varied between 0.31 to 0.59 (mean = 0.43) in 2016 and 0.27 to 0.45 (mean = 0.36) in 2017 and NDMI varied between 0.21 to 0.60 (mean = 0.43) in 2016 and 0.18 to 0.62 (mean = 0.41) in 2017.

2.4.2 Interannual Variation

Of the 24 model sets with percent C/N/P and C:N/C:P/N:P as response variables, year appeared in the top-ranked model 8 times (Table 2-3). Year was always accompanied by site and their interaction term if it was in the top model. Balsam fir had the most interannual variation of any species, with year appearing in the top model for 5 out of the 6 models (Table 2-3). Specifically, for balsam fir, year was in the top models for percent C, N, P, C:N, and C:P (mean $R^2 = 0.38$, Table 2-4, for full AIC results see Tables A-1 and A-2). For balsam fir, stoichiometric ratios and %C were lower in 2017 than in 2016. By contrast, for red maple, white birch, and lowbush blueberry, year only appeared once as a top-ranked model, and it was in the models with percent C as the response variable (mean $R^2 = 0.62$, Table 2-3, for full AIC results see Tables A-4 to A-8). For percent elemental C across all species, elemental traits were lower in 2017 than in 2016 (Fig 2-2). Year and site appeared in the top model for percent C for all four species (Table 2-3).

2.4.3 Mechanisms of Variation

For the eight response variables that showed evidence of temporal variation (Table 2-3), we fit additional models to explore potential drivers of this variation (Table 2-4). Based on our predictions i-iii, our explanatory variables for these models included GDD, NDMI, and EVI. Prediction i anticipated a positive relationship between GDD and elemental and stoichiometric traits. GDD was found in the top model of all variables tested (8/8) and had a positive relationship with all elemental and stoichiometric traits except percent N and C:P in balsam fir (mean $R^2 = 0.30$, Table 2-5, Fig. 2-3; for full AIC results see Tables A-9 to A-12).

We predicted (ii) that moisture would have a positive relationship with elemental and stoichiometric traits. NDMI was present in the top model for lowbush blueberry percent C and had a negative relationship ($R^2 = 0.32$, Table 2-5; for full AIC results, see Table A-12). NDMI appeared in the top-ranked model for all balsam fir elemental and stoichiometric traits (5/5). NDMI had a positive relationship with balsam fir percent C, C:N, and C:P (mean $R^2 = 0.34$, Table 2-5; for full AIC results, see Table A-9). Accordingly, NDMI had a negative relationship with balsam fir percent N and P (mean $R^2 = 0.32$, Table 2-5; for full AIC results, see Table A-9).

Our last prediction (iii) stated that productivity would have a positive relationship with elemental and stoichiometric traits. EVI was present in the top-ranked percent C models for red maple and lowbush blueberry and was found to have a positive relationship (2/4, mean $R^2 = 0.28$, Table 2-5; for full AIC results, see Tables A-10 and A-12). In addition, EVI was present in the top model of every elemental and stoichiometric trait of balsam fir except percent C (4/5). EVI had a negative relationship with percent N and P of balsam fir (mean $R^2 = 0.32$, Table 2-5; for full AIC results, see Table A-9). Accordingly, EVI had a positive relationship with balsam fir C:N and C:P (mean $R^2 = 0.31$, Table 2-5; for full AIC results, see Table A-9). Interaction terms appeared in the top models less frequently than individual terms. The EVI*NDMI interaction term was the most prevalent in the top-ranked model, appearing 5/8 times (mean $R^2 = 0.32$, Table 5, for full AIC results, see Tables A-9 and A-12). GDD*NDMI appeared in the top model 4/8 times (mean $R^2 = 0.34$), and GDD*EVI appeared in the top model only 2/8 times (mean $R^2 = 0.28$, Table 2-5, for full AIC results see Tables A-10 to A-12).

2.5 Discussion

Interannual variation in elemental and stoichiometric traits of plants impacts individual fitness as well as higher trophic levels such as herbivores. Quantifying how and why these traits vary in common boreal plant species provides us with a deeper understanding of the entire ecosystem. Our first hypothesis, that year is an important factor in accounting for the variation in elemental composition of boreal plants, was partially supported. Percent C in all study species and several elemental and stoichiometric traits of the evergreen conifer in this study (balsam fir), varied across years. However, we found little evidence to support interannual variation of most elemental and stoichiometric traits in plants. Other than for the evergreen conifer and percent C, our study demonstrates elemental and stoichiometric traits of boreal plants experience limited interannual variation.

The interannual variation in percent C we observed in our boreal study species supports patterns observed in other ecosystems. Specifically, variation in seasonal and interannual C has been reported in temperate grasslands, evergreen forests across climates, and in temperate forests (Flanagan et al. 2002; Sierra et al. 2009; Wu et al. 2012). Our results indicate that the unique way that C is produced by the plant (i.e., via photosynthesis), instead of only being assimilated from abiotic resources, may result in percent C showing more variation between years. There is evidence that C is robust to substantial variation in the long-term (Wu et al. 2012), however, this study shows that we should be careful in the study of boreal plant C dynamics over short-term studies given the large interannual variation observed.

The assimilation and production of C in plants depends on a variety of factors. C assimilation is closely tied to N and P (Tang et al. 2018), but unlike N and P assimilation, it also depends on weather conditions that in turn affect rates of photosynthesis (Flanagan et al. 2002; Sierra et al. 2009). Weather conditions that control photosynthesis, such as temperature and light availability, are highly variable in and across the boreal forest, which could explain the variation in percent C found across species. Consistent with prediction (i), we observed that temperature was an important factor driving interannual variation in plant elemental and stoichiometric traits. GDD appeared in the top model and had a positive relationship with percent C across all species. Temperature is known to have a relationship with plant growth, and therefore elemental composition (Welp et al. 2007). Higher ambient and soil temperatures in the boreal forest are tightly coupled with higher uptake rates of N and P and higher rates of photosynthesis translating to growth, all of which leads to variation in elemental composition, especially higher levels of C (Melillo et al., 2011; Sardans et al., 2016). As plants grow and mature, they decrease in digestibility for consumers (Renecker and Hudson 1988). The prevalence of GDD in top-ranked models from our dataset could be capturing this trend, as GDD is calculated at the time of sampling.

As for prediction (ii), moisture also appeared as a variable driving interannual variation in percent C. NDMI was in the top model for percent C for two out of four species. However, inconsistent with our prediction, NDMI had a positive relationship with balsam fir percent C but a negative relationship with lowbush blueberry percent C. The relationship between moisture and nutrient uptake is dependent on system, species, and moisture levels (Pastor and Post 1986;

Reichstein et al. 2002; Kljun et al. 2007; Mariotte et al. 2017). Lower moisture, more specifically drought, has been linked to decreased primary productivity and therefore C uptake (Ciais et al. 2005; Kljun et al. 2007; Welp et al. 2007). However, there have been instances where decreased moisture has led to an increase in C levels due to respiration being more sensitive to moisture changes than primary production, causing C to accumulate (Goulden et al. 1998). The complex relationship between moisture and C uptake and differences in life-history between balsam fir and lowbush blueberry may explain why the direction between NDMI and percent C was inconsistent.

In support of our prediction (iii), we found productivity to be an important variable driving interannual variation in plant elemental and stoichiometric traits. EVI was in the top model and had a positive relationship with percent C for two out of four species. Primary productivity is known to correlate with plant elemental compositions (Vitousek and Howarth 1991; Yin 1992; LeBauer and Treseder 2008). Higher nitrogen levels in the soil and plant tissues lead to increased net primary productivity, which in turn leads to carbon sequestration by the plant (Tang et al. 2018).

Our evidence of weak interannual variation of N and P for most species is a key finding which may contribute to our understanding of ecosystem functioning in the boreal. N and P and their limited supply play a crucial role in the composition and biological processes that occur in the boreal forest (Walker and Syers 1976; Vitousek et al. 2010). Regulation of primary productivity and C sequestration in terrestrial ecosystems is influenced by N and P availability in the soil and resulting allocation within the plant (Tang et al. 2018). In addition, N and P are considered indicators of food quality for consumers due to their roles in building proteins and nucleic acids (Sterner and Elser 2002). The weak evidence of temporal variation that we saw in our study indicates that much of the interannual variation in forage quality can be attributed to changes in C, rather than N and P. Considering that N and P are assimilated from the environment, their uptake by boreal plants is mostly tied to N and P availability within the soil, which is influenced by leaf litter quality and decomposition rate (Huang and Schoenau 1997). The boreal forest is limited by both N and P, and plant communities are constantly competing for this resource (Tamm 1991; Giesler et al. 2002; Vitousek et al. 2010; Hedwall et al. 2017). Therefore, the weak evidence for high levels of variation in N and P we observed in this study is most likely due to limited opportunity for uptake and intense competition.

Our study suggests that evergreen conifer trees have more interannual variation in their elemental composition than broadleaved deciduous trees. There is evidence of plant-specific responses to herbivory (Karban and Myers 1989), and balsam fir is a favourite winter forage for moose in the Eastern North American boreal forest (Thompson and Mallik 1988; Brandner et al. 1990). Balsam fir suppresses its growth in response to heavy grazing and to resume growth at a later time (McLaren 1996), which inevitably has impacts on N and P uptake and C production and could account for some of the variations across years seen in our study. In addition, evergreen conifers have a fundamentally different physical make-up than deciduous trees (Lamlom and Savidge 2003). The management of elements by evergreen conifer trees is unlike deciduous trees, with conifers experiencing significantly higher leaf:wood C ratios and having lower N requirements for growth (Sardans and Peñuelas, 2013). Such interspecific differences in nutrient levels could explain why evergreen conifers differ in elemental traits more between years than deciduous plants of the boreal forest. It is important to note, however, that due to the heavy herbivory of balsam fir by moose in Newfoundland, there was one site with very few balsam fir individuals present (Bloomfield, Fig. 2-2). In addition, the disparity in sample size in species across evergreen conifers and deciduous species in our sample (i.e., n = 1 for evergreen conifers and n = 3 for broadleaved deciduous) may be masking some key trends between groups.

Assessing temporal variation in plants is an important but challenging task. We believe that by comprehensively sampling our sites that exist on a chronosequence, we have strengthened our inference regarding interannual variation even with only two years of data collected. We reduced our sampling in 2017 to a subset of what we had done in 2016 due to budget constraints. This reduction in sample numbers led to higher variation in measurements in 2017 when compared to 2016 (Fig. 2-2). However, even with higher variation, we did not find evidence of interannual variation for most of our response variables, indicating that subsetting the data were a valid method of data collection. We designed this study to try to capture the variation that is relevant across trophic levels on a biological time scale. Herbivores in the boreal forest are limited by nitrogen and phosphorus, causing them to seek these nutrients out in their forage (Sterner and Elser 2002). However, they are also limited by predation and often have short lifespans (Keith and Windberg 1978), meaning that measuring interannual variation across two years has important ecosystem implications even if it is a short time span with respect to the plant’s lifecycle. Our sampling design of collecting biomass data in only one year of the study means that we are assessing variation due to changes in percent C, N, P, not due to both biomass and percent change. Annual variation in elemental composition has been shown to be much more variable than changes in biomass in Canadian trees, supporting our decision to minimize the destructive sampling of biomass estimates (Paré et al. 2013). However, studies of intraspecific variation on elemental traits over longer time periods should also measure biomass changes over time. Lastly, there is evidence that plants experience a time-lag when responding to changes in environmental factors, such as climate change (Wu et al. 2015). It is possible that there is a time-lag effect occurring within our system, where changes in moisture or temperature could impact the variation in elemental composition in stoichiometry years from now. Our models do not account for this time-lag, and it is possible that if incorporated, it could explain some of the remaining variation. We believe that this is an interesting opportunity for future research.

The weak evidence for important interannual variation in key limiting elements, N and P, as well as stoichiometric ratios for three of the four study species indicate that these measures are robust to environmental changes on a short-time scale. Our findings, especially with regards to percent C, N, and P, highlight the potential strength of elemental composition and ecological stoichiometry as a tool to investigate ecosystems and their processes. There are several studies that use elemental composition and ecological stoichiometry in an effective and scientifically sound manner across years (e.g., González et al. 2011; Jobbágy and Jackson 2004; Tsoi et al. 2011). We recommend being mindful of the potential for interannual variation if measuring elemental and stoichiometric traits across years that experienced different weather conditions (e.g., one of the sampling years experienced a drought or cold snap), to try and sample individuals at the same time in the growing season across years to minimize variation, and to check temporal variation when possible. However, most elemental and stoichiometric traits appeared robust to temporal variation in the boreal forest at the scale we measured. We found growing degree days were a prominent variable in driving interannual variation. Because of this close relationship, there is potential for the development of a correction factor that takes into account weather conditions and incorporates them into modelling, much like what we see today in productivity analyses for agriculture (Njuki et al. 2018). Using elemental and stoichiometric traits is a potentially powerful approach to investigate ecosystem-level processes across species, trophic levels, and populations as C, N, and P are universal elements in the biotic world that govern all ecosystem processes. Our findings show that using elemental and stoichiometric traits across years and studies is a valid and exciting way to create opportunities for novel inquiry.

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Table 2-1. Life history differences between the four study species. Sampling numbers refer to total samples taken across both years (2016 and 2017). Sampling points were distributed equally across the four study sites, resulting in 200 total. The distribution of sampling points represents the number of sampling points where the respective species were found. C = Carbon, N = Nitrogen, P = Phosphorus.

Species	Life Form	Sampling Numbers	Distribution		Mean %C ± Std. Dev.	Mean %N ± Std. Dev.	Mean %P ± Std. Dev.	Mean C:N ± Std. Dev.	Mean C:P ± Std. Dev.	Mean N:P ± Std. Dev.
			Large-Scale	Sampling points (50/site)						
Balsam Fir	Evergreen conifer tree	114	Central-Eastern Canada & Northeastern US	95/200	52.15 ± 0.88	0.90 ± 0.19	0.08 ± 0.03	70.42 ± 14.16	1948.93 ± 752.99	27.42 ± 8.20
Red Maple	Deciduous broad-leaved tree	120	Eastern North America	91/200	49.83 ± 0.95	1.59 ± 0.24	0.14 ± 0.06	37.48 ± 5.82	1092.92 ± 379.81	29.50 ± 9.57
White Birch	Deciduous broad-leaved tree	99	Trans-Canadian & Northern US	71/200	50.02 ± 1.38	1.66 ± 0.45	0.16 ± 0.06	38.63 ± 14.79	1027.26 ± 756.61	25.66 ± 8.12
Lowbush Blueberry	Deciduous broad-leaved shrub	191	Eastern Canada & Northeastern US	160/200	51.68 ± 1.21	1.27 ± 0.21	0.09 ± 0.02	48.64 ± 8.04	1668.22 ± 501.92	34.54 ± 9.53

Table 2-2. The structure for the first step of analysis. Models were grouped by species, and then each measure of elemental composition (6 total) was used in a model with site, year, and their interaction term as the response variables. All model groups included an intercept-only model. This resulted in 24 groups of models tested for the first round of analysis. Models were then ranked using AICc.

Variable	Variable Type	Factor Type	Levels		Model Type
Species	Response	-	4	Balsam fir Red maple White birch Lowbush Blueberry	
Elemental Composition	Nested response	-	6	C/N/P (%) C:N/C:P/N:P	GLM with standardized data GLM
Year	Explanatory	Fixed	2	2016 2017	
Site	Explanatory	Fixed	4	Bloomfield Dunphy’s Pond Terra Nova North Unicorn	

Table 2-3. Summary table of the first round of models, showing those models that had year appear as one of the variables in the top-ranked model (for full AIC tables see Tables S1-S8). In all top-ranked models, there were no models within 2 ΔAICc. Nagelkerke Pseudo-R^2 is displayed.

Species	Response Variable	Top Model	Pseudo-R^2
Balsam Fir	C (%)	Year + Site + Year*Site	0.67
	N (%)	Year + Site + Year*Site	0.32
	P (%)	Year + Site + Year*Site	0.30
	C:N	Year + Site + Year*Site	0.31
	C:P	Year + Site + Year*Site	0.29
Red Maple	C (%)	Year + Site + Year*Site	0.68
White Birch	C (%)	Year + Site + Year*Site	0.47
Lowbush Blueberry	C (%)	Year + Site + Year*Site	0.70

Table 2-4. Structure for the second step of analysis testing the mechanisms of interannual variation based on our predictions i-iii. Only response variables that had year in the top model in the first round of analysis were evaluated in the second round (see Table 2). Models used growing degree days (GDD), normalized difference moisture index (NDMI), and enhanced vegetation index (EVI) as explanatory variables. This resulted in 8 model sets total for the second round of analysis. Models were then ranked using AICc.

Variable	Variable Type	Levels		Model Type	Data Source
Species	Response	4	Balsam fir Red maple White birch Lowbush Blueberry		Field collection
Elemental Composition	Nested response	5	C/N/P (%) C:N/C:P	GLM with standardized data GLM	Field collection
GDD	Explanatory (Fixed)	1	Continuous		Environment & Climate Change Canada
NDMI	Explanatory (Fixed)	1	Continuous		Landsat Imagery
EVI	Explanatory (Fixed)	1	Continuous		Landsat imagery

Table 2-5. Summary table of the models testing the mechanisms of interannual variation, showing only models that had year appear as one of the variables in the top model of the first round (full AIC results presented in Tables S9-S12). Lowbush blueberry had four models within 2 ΔAICc of the top model. Nagelkerke Pseudo-R^2 presented in the table. GDD: Growing degree days; NDMI: normalized difference moisture index; EVI: enhanced vegetation index. * indicates an interaction.

Species	Response Variable	Top Model	Pseudo-R^2
Balsam Fir	C (%)	GDD+NDMI+GDD*NDMI	0.41
	N (%)	EVI + GDD +NDMI + EVI*NDMI	0.33
	P (%)	EVI+GDD+NDMI+EVI*NDMI+GDD*NDMI	0.32
	C:N	EVI+GDD+NDMI+EVI*NDMI	0.33
	C:P	EVI+GDD+NDMI+EVI*NDMI+GDD*NDMI	0.29
Red Maple	C (%)	EVI+GDD+EVI*GDD	0.23
White Birch	C (%)	GDD	0.21
Lowbush Blueberry	C (%)	Global (EVI+GDD+NDMI+EVI*GDD+ EVI*NDMI+GDD*NDMI)	0.32

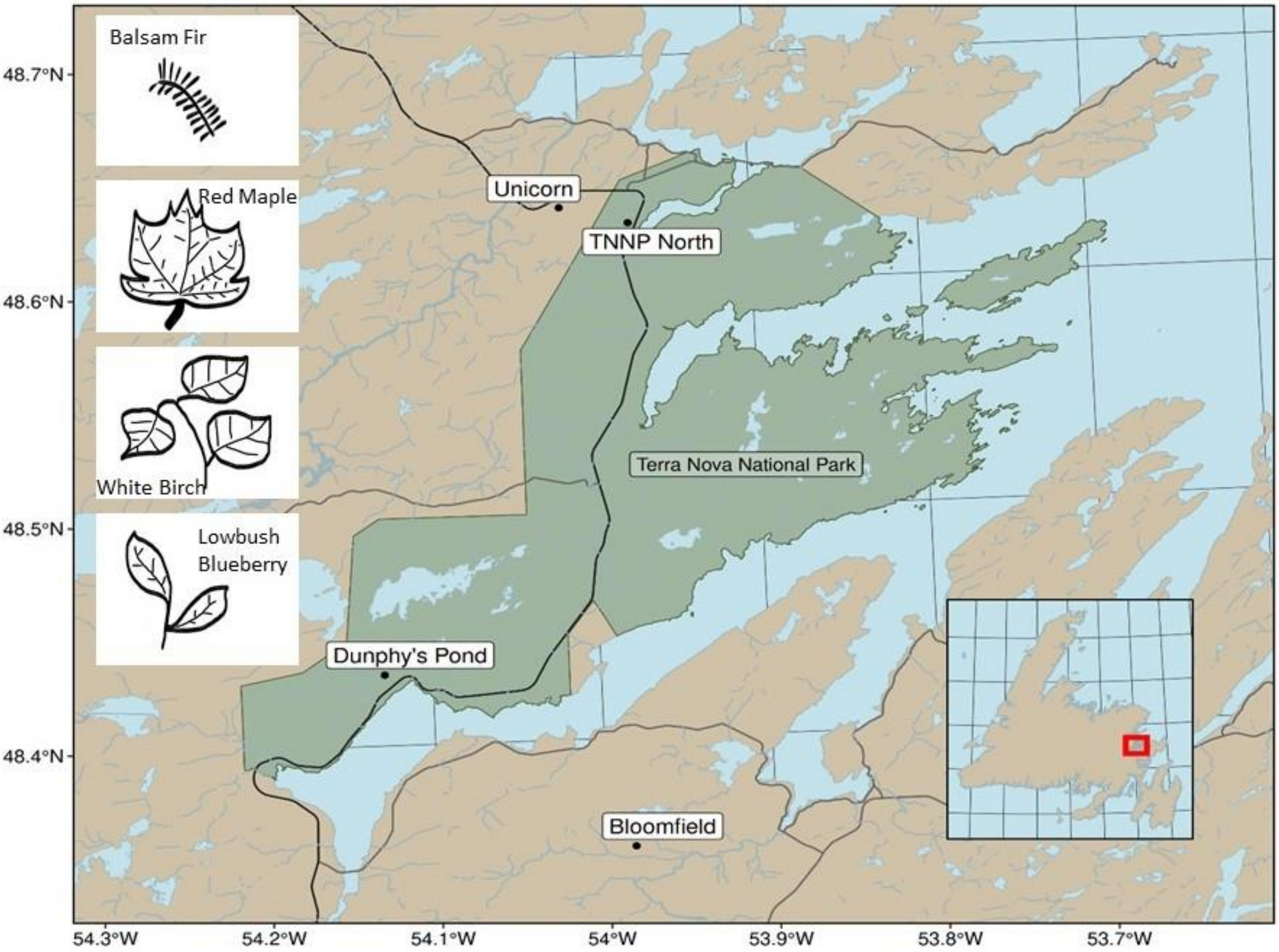

Figure 2-1. Map showing the four study sites in Central Newfoundland with four study species represented. Terra Nova National Park boundary obtained from Open Canada and roads from Open Street Map.

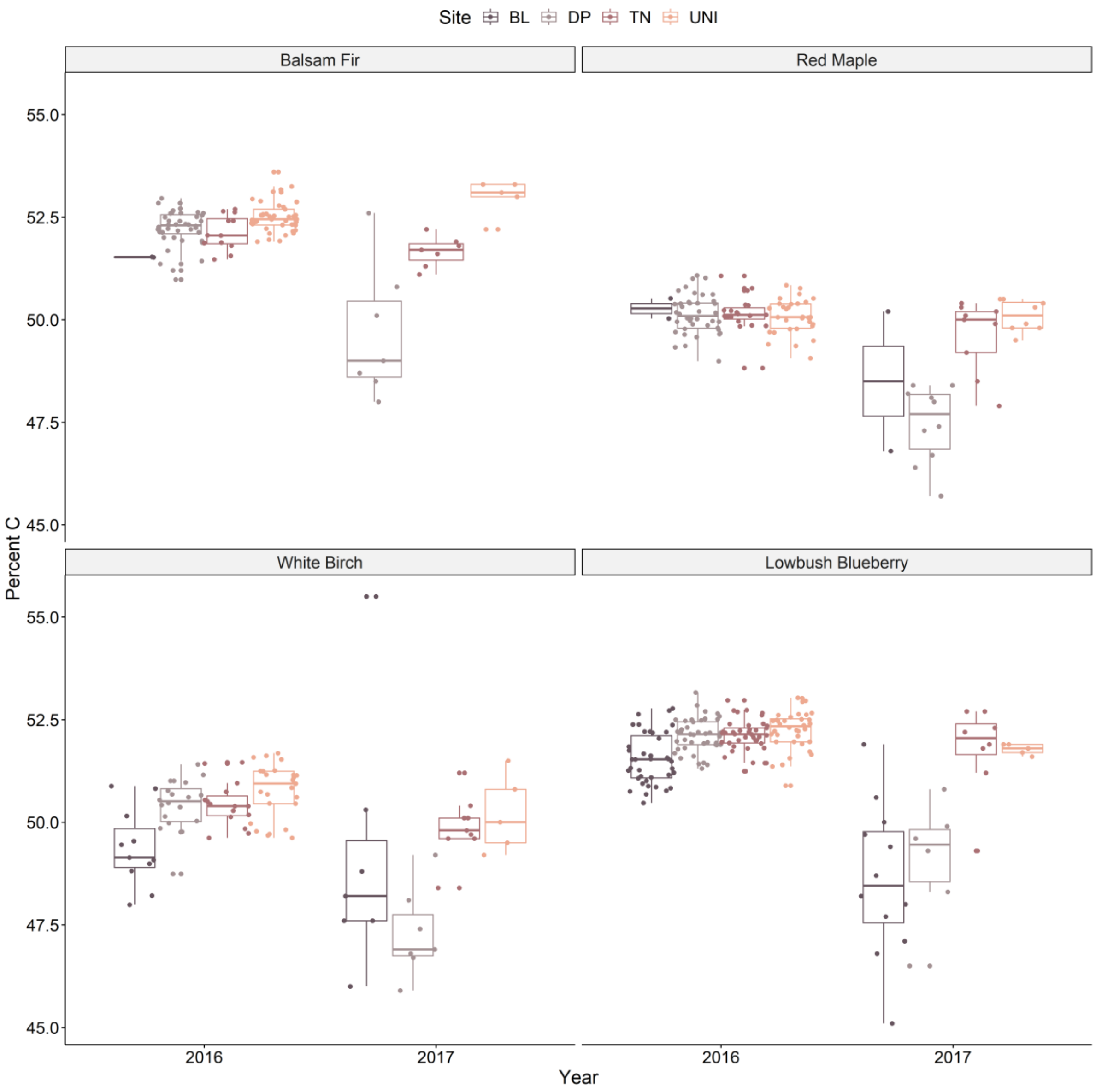

Figure 2-2. Boxplots comparing annual percent C for each of the four study species at each study site. Each point in a boxplot represents a sampling plot level measurement at that site for the respective species (n = 524 points total). The four study sites (BL=Bloomfield, DP=Dunphy's Pond, TN=Terra Nova, UNI=Unicorn) are represented by different colours. The points are distributed across the x-axis to improve visibility. Percent C was consistently higher in 2016 for all four study species.

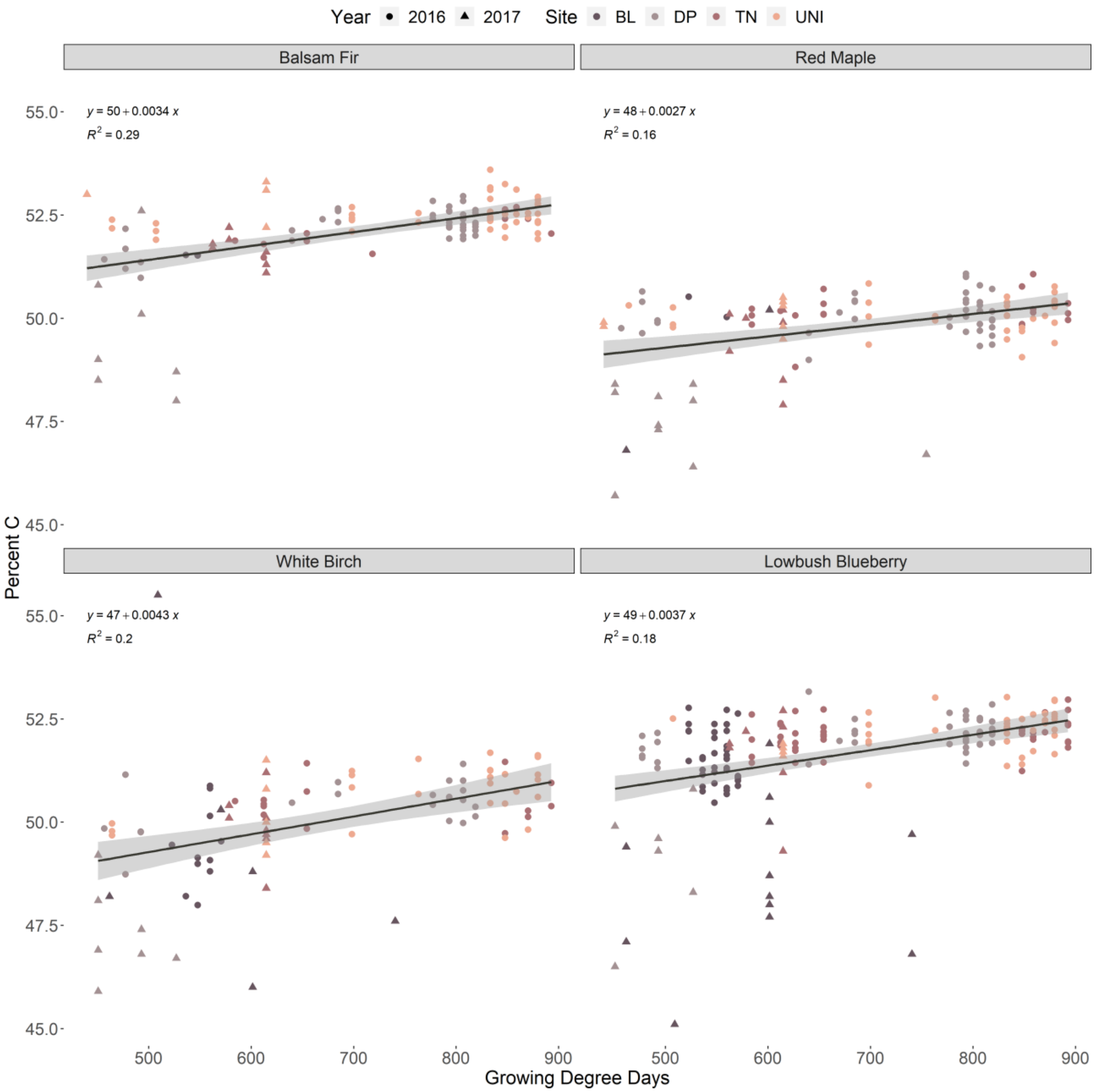

Figure 2-3. Relationship between percent C and growing degree days (GDD) for each of the study species. The four sites (BL=Bloomfield, DP=Dunphy's Pond, TN=Terra Nova, UNI=Unicorn) are represented by different colours. Each point represents a plot-level sample value (n = 524 total).

Chapter 3 – Individual herbivores take risks based on resource quality: stoichiometric distribution models with snowshoe hares

3.1 Abstract

Herbivores should adjust their space use to moderate predation risk so it is proportional to the profitability of their available resources. Here, we apply a spatially explicit ecological stoichiometry framework to evaluate resource quality, which we use to test predictions that intersect the Risk Allocation Hypothesis (RAH) and Optimal Foraging Theory (OFT). Our model system uses population and individual estimates of snowshoe hares (*Lepus americanus*, n = 30) space use derived from biotelemetry across three summer seasons. We evaluate resource forage quality for favoured lowbush blueberry (*Vaccinium angustifolium*) using carbon:nitrogen and carbon:phosphorus ratios. We use habitat complexity to proxy perceived predation risk and intersect that with forage quality. We analyzed how food quality, perceived predation risk, and their interaction impacted the intensity of herbivore space use using linear mixed-effects models structured to enable us to make inferences at the population and individual home range level. We failed to find support for RAH and OFT at the population level ($R^2 = 0.01$). However, when viewed at the individual level, we found that individual hares spend more time in areas of high perceived predation risk only when food quality was high and vice versa, thus supporting an interaction between the RAH and OFT. Overall, we illustrate spatially explicit empirical support for the interaction between two important foraging theories using two novel prisms: application of ecological stoichiometry to foraging ecology and partitioning individual behavioural responses.

Keywords: *Lepus americanus,* snowshoe hare, ecological stoichiometry, trade-offs, foraging, habitat complexity

3.2 Introduction

Animals make trade-offs that shape ecosystems, and one of the most ecologically relevant decisions made by herbivores is the trade-off between food acquisition and danger (Lima and Dill 1990; Verdolin 2006). Herbivores optimize their space use to obtain food with adequate levels of nutrients (Charnov 1976; Bjørneraas et al. 2012) and minimize predation risk (Lima and Bednekoff 1999; Graham and Nash 2013; Liu et al. 2014). Often, the parts of the landscape that provide enough nutrients to herbivores do not provide enough safety, forcing a balance in space use (Lima and Dill 1990; Wilson et al. 2012). Across studies, the space use of herbivores has been shown to be influenced by both food quality and predation risk (Brown and Alkon 1990; Brown et al. 1999; Bakker et al. 2005). The result of these space use decisions by herbivores can influence the surrounding ecosystem through processes such as nutrient cycling and plant growth rates (Molvar et al. 1993; Moorhead et al. 2017). The purpose of this study is to investigate the spatially explicit relationship between food quality and predation risk using two novel prisms.

Optimal Foraging Theory predicts that animals make fine-scale foraging decisions to maximize their energy gain (Charnov 1976). For example, Bigeye tuna alter their space use in the water column according to prey availability, individual body size, and water temperature to maximize energy gains (Thygesen et al. 2016). Herbivores specifically deal with the energy-intensive process of transforming carbon-rich plant material into their nitrogen (N)- and phosphorus(P)-rich bodies (Sterner and Elser 2002). Because of this energy-intensive process, we would expect herbivores to spend time in areas that have either high quality or high quantity of forage. In order to increase consumption of high-quality forage, we would expect herbivores to spend time in areas where plants have a higher nitrogen and phosphorus content to maximize the return on their foraging efforts. Indeed, desert insect herbivores shift their space use according to P availability in plants (Schade et al. 2003), and European rabbits visit N-enhanced feeding sites up to four times more frequently (Bakker et al. 2005). Herbivores modify their space use to select forage that maximizes their investment, and this is one half of the foraging and predation risk trade-off.

Understanding plant stoichiometry can be an excellent framework for assessing Optimal Foraging Theory for herbivores as they Have to convert C-rich plants into N- and P-rich animal tissue. Plant stoichiometry, and more broadly ecological stoichiometry, refers to the measure of elemental ratios and their balance within living organisms (Sterner and Elser 2002). For herbivores, studies have shown that carbon:nitrogen and carbon:phosphorus ratios of forage (hereafter C:N and C:P) are most important because they control individual body growth rates and defense abilities, as well as ontogeny (Meunier et al. 2017). For example, increased nitrogen levels, and therefore lower C:N, in forage plants led to higher survival rates of nettle-feeding butterflies (Kurze et al. 2017). Plant C:N and C:P ratios are determined by environmental factors such as temperature, precipitation, and soil nutrient availability (Sardans et al. 2011; Heineman et al. 2016). They are also influenced by biological factors such as biomass, growth rates, and the surrounding biological community (Güsewell 2004; González et al. 2011; Borer et al. 2015). Therefore, the quality of forage across a landscape is dynamic and elicits a dynamic response from herbivores (Branco et al. 2010).

Within landscapes shaped by elemental nutrients, herbivores also need to perceive and avoid predation risk, impacting which habitats they occupy (Morris 2005; Bleicher 2017). The Risk Allocation Hypothesis anticipates that prey species will change their behaviour, including space use, based on the level of predation risk present in their habitat (Lima and Bednekoff 1999). For example, crested porcupines spend less time foraging in areas that are riskier (Brown and Alkon

1990). Animals assess their environment for predation risk even when a predator is not present, resulting in energetic costs to the individual (Bleicher 2017). The stress from predation risk triggers a physiological change in the herbivore (Hawlena and Schmitz 2010). Grasshoppers experiencing stress caused by predation risk had increased metabolisms, resulting in an increased demand for C-rich carbohydrates (Hawlena and Schmitz 2010). Accordingly, the grasshoppers shifted their diet to increase C:N content to meet these changed physiological demands (Hawlena and Schmitz 2010). Thus, perceived predation risk impacts both the space use and physiology of herbivores.

Perceived predation risk can have detrimental impacts on the behavioural and survival of prey species. Indeed, when direct predation risk was eliminated, and only predator cues were evaluated, perceived predation risk decreased song sparrow offspring productivity by 40% (Zanette et al. 2011). Complex habitats, such as forest understorey with dense trees and high visual obstruction, are preferred by prey species when they perceive an elevated risk of predation (Litvaitis et al. 1985) because habitat complexity can act as refuge from predation (Brooker et al. 2013; Catano et al. 2015; Loke and Todd 2016). Snowshoe hares exhibit trade-off behaviour when in complex habitats, decreasing vigilance in more complex habitats due to decreased predation risk (Morris 2019). The use of complex habitats by prey to minimize perceived predation risk means that habitat complexity should influence space use by prey species and act as a proxy for perceived predation risk. Perceived predation risk gives us insight into what aspects of habitat provide shelter from predation for prey. As the second half of the foraging and predation risk trade-off, evaluating the effects of perceived predation risk on prey species by quantifying habitat complexity gives us insight into the distribution and space use of prey.

The Risk Allocation Hypothesis and Optimal Foraging Theory interact to create complementary predictions for animal space use. The Risk Allocation Hypothesis states that herbivores should use times of low predation risk to forage, and times of high risk should be allocated to avoiding predators (Ferrari et al. 2009). Therefore, when assessing perceived predation risk, we would expect herbivores to forage in areas with low risk, and therefore more habitat complexity, and thus use that habitat more. Optimal Foraging Theory explicitly includes forage quality to explain herbivore space use and implicitly includes predation risk in its framework (Charnov 1976). Under Optimal Foraging, we would expect an herbivore to use the area with the highest forage quality and lowest perceived predation risk to maximize energy gain. Because herbivores are constantly balancing predation risk and forage quality, the trade-off between these two requirements produces a dynamic landscape of herbivore space use at population and individual scales. If an area with low perceived predation risk and high forage quality exists, that is where we would expect to see the most space use by herbivores. However, often habitats do not offer both, and animals are forced to choose between predation risk and forage quality (Liu et al. 2014). When choosing between predation risk and forage quality, Risk Allocation and Optimal Foraging interact to create a continuum of habitat quality across a landscape and forcing trade-offs.

In this study, we use an ecological stoichiometry framework to ask how food quality and perceived predation risk interact to impact the space use of a boreal herbivore, the snowshoe hare (*Lepus americanus*), at a population and individual level. Optimal Foraging Theory predicts that animals will allocate more time feeding in profitable patches. Similarly, the Risk Allocation Hypothesis predicts that animals will attenuate their risk by spending less time in risky places. Within our ecological stoichiometry framework, we, therefore, predict 1) intensity of use will increase in areas of high food quality, low C:N and C:P, and low perceived predation risk, high habitat complexity. We also predict 2) that when habitat with high food quality and low perceived predation risk is not available, that a trade-off will occur, and intensity of use will be higher in areas where there is low food quality only when there is low perceived predation risk and vice versa. Lastly, we predict 3) that at the population and individual level, we will see an overall trend of higher intensity of use in areas with high food quality and low perceived predation risk, but at the individual level, if the preferred habitat is not available individual hares will make trade-offs.

3.3 Methods

3.3.1 Trapping grid

We set up a 25 ha trapping area in the boreal forest of eastern Newfoundland, Canada, approximately 30 km south of Terra Nova National Park. We deployed 50 Tomahawk live traps (Tomahawk Live Trap Company, Hazelhurst, WI) approximately 75 m apart in a snaking formation throughout the study area (Fig. 3-1). We baited traps with apple slices, Timothy adult rabbit food, and alfalfa to attract snowshoe hare (*Lepus americanus*). We set traps at sunset and checked at sunrise the next morning. We set traps on seven nights in 2016, five nights in 2017, 13 nights in 2018, and four nights in 2019. At the point of capture, we marked hares with unique ear tags, weighed them, sexed them, and equipped them with 25 g Very High Frequency (VHF) radio collars (M1555, Advanced Telemetry Systems, Isanti, MN) before release. We captured 111 unique individuals between June 2016 and June 2019, only individuals where the VHF collar was $\leq$5% of the hare's body weight were fitted with a collar. Of the 111 individuals captured, 76 had a VHF collar deployed. VHF collars were monitored every other day from mid-June to late August in 2017, daily from mid-June to early August in 2018, and daily in May, June, and late August with weekly checks in July to early August in 2019. All details of animal handling were approved by Memorial University's animal use ethics committee (AUP 18-02-EV).

3.3.2 Telemetry & Kernel Utilization Distributions

We used the VHF collars to locate hares and assess intensity of snowshoe hare space use. We applied a data screening criterion that included individuals that had been located more than 15 times per summer and used those individuals for analysis (Börger et al. 2006), resulting in a total of 30 individuals (n = 4 from 2017, n = 6 from 2018, and n = 20 from 2019), including four who were sampled over two years. To assure independence between samples, we chose to include these individuals in only one year of their sampling, and we used the year with the most data. We triangulated the VHF collars to obtain individuals' locations using radio-telemetry techniques in the summer from 2017-2019. We took a minimum of three bearings to triangulate a hare once per day, and the average window of time taken to achieve triangulation was 38 mins. We rotated the time of day hares were relocated to maximize independence between samples. The mean number of relocations per collar was 31 (range: 15-46).

Location coordinates and error estimates were calculated using an Azimuthal Telemetry Model from the *razimuth* package in R 4.0.0 (Gerber et al. 2018; R Core Team 2020). We took the relocations and their error estimates and used them to estimate the kernel utilization distributions (KUDs) for each individual hare to assess the intensity of snowshoe hare space use (Fig. 3-1). First, telemetry locations and their error estimates were visualized using variograms to assess the autocorrelation structure of the data. Next, we fit models with different parameters to the variograms for each individual. We selected a continuous-time movement model for our telemetry animal tracking data for each individual by performing model selection on our different model parameters, using a perturbative Hybrid Residual Maximum Likelihood approach (pHREML, Fleming *et al.* 2019). Once each individual had a movement model, we calculated the debiased kernel utilization distribution for that individual. We extracted the 95% home range area and a raster containing the probability density function of the space use from the KUDs for each snowshoe hare individual. Probability density functions were normalized using the *spatialEco* package to be bound by 0,1 so that they could be compared across individuals (Evans et al. 2020). Much of the code used for this analysis was adapted from an existing GitHub repository (Droghini 2020). All KUD and home range calculations were carried out using the *ctmm* package in R 4.0.0 (Fleming et al. 2015; Fleming and Calabrese 2017; R Core Team 2020).

3.3.3 Food quality

We define food quality as the carbon:nitrogen (C:N) and carbon:phosphorus (C:P) ratios of lowbush blueberry. Mammals such as the snowshoe hare are nitrogen and phosphorus limited, meaning that lower C:N and C:P ratios indicate a higher food quality (Sterner and Elser 2002). Lowbush blueberry, which is widespread in our study area, is a preferred forage for snowshoe hare and has been shown to influence their home range size (Dodds 1960; Rizzuto et al. 2020). In the summer of 2016, we set up an 11.3 m radius plot to collect lowbush blueberry samples at each of the 50 traps on the grid. Beginning in the NE corner of the plot, we collected the new growth leaf and stem of one individual per intercardinal direction. We sampled moving clockwise until we collected approximately 20 g of sample. We froze and grouped the samples by intercardinal direction and sent them to the Agriculture and Food Lab (AFL) at the University of Guelph, Ontario, Canada, for elemental analysis. Samples were dried to remove water content and then ground to homogenize plot-level samples at the AFL. Percent carbon and nitrogen were determined using an Elementar Vario Macro Cube. Percent phosphorus was determined using a microwave acid digestion (CEM MARSxpress microwave system) and brought to volume using Nanopure water. The solution was then diluted by ten and entered into the inductively coupled plasma mass spectrometry detector (ICP-MS, Poitevin 2016). Next, we estimated biomass by collecting new growth foliar material and measuring the height and basal diameter for 50 lowbush blueberry individuals located in random locations outside of the study site in 2017. We constructed allometric models from the dry weights and used the estimates from the models to parameterize shrub belt density and predict biomass at the plot level. We divided the plot level biomass by the plot area and multiplied the biomass value by the elemental composition of C, N, and P to produce quantities (g/m^2) of each element. Then, we divided the quantity value by their respective molar masses and used these numbers to calculate the molar ratios of C:N and C:P of lowbush blueberry (see Heckford et al. in review for further details on sampling procedure).

3.3.4 Habitat complexity

To assess perceived predation risk, we measured habitat complexity across the sampling grid. Hares are known to hide when threatened, so an area with high habitat complexity can be interpreted as an area with lower perceived predation risk (Murray 2003). We sampled habitat complexity, i.e., vegetation characteristics such as coarse woody debris and shrub density, at 72 evenly distributed plots throughout the trapping grid (Fig. 3-1). We evaluated the habitat complexity plots in July 2019, after green-up, to capture full foliage. Each plot had a 10 m radius with a transect running the radius of the circle in each cardinal direction and was used to measure 15 variables that affect the complexity of the area (Table 3-1, as per protocol in Rodgers et al. 2008). After collection, these variables were split as overstory or understory measurements. This separation was done because snowshoe hare in Newfoundland experience two types of predation, terrestrial predation from coyote (*Canis latrans*) and lynx (*Lynx canadensis*), which could be influenced by forest understory traits, and aerial predation from predatory birds, which could be influenced by forest overstory traits.

3.3.5 Statistical Analysis

Following the classification of habitat complexity variables into understory and overstory (Table 3-1), we analyzed each group of variables with a principal component analysis (PCA, Figs. B-1 and B-2). Then, for each habitat complexity sampling point (n = 72), we extracted the points' value on the first axis of the understory and overstory PCA. To determine the direction of the relationship between the respective PCA axis and habitat complexity, we took the values of the axes at each sampling point and plotted them against the variables used in the PCA. If the axis had a negative relationship with habitat complexity (e.g., a lower value associated with a higher density of shrubs), the values of the axis were multiplied by -1 to reverse the relationship and simplify the interpretation. The values of the extracted axes at each sampling point were then used as a measure of overstory and understory habitat complexity moving forward.

We extracted the normalized probability density function of the 95% KUD, a measure of the intensity of space use, at each habitat complexity sampling point for every individual hare. No hare home ranges overlapped all habitat complexity sampling points. Therefore, when a snowshoe hare home range did not overlap with one of the 72 habitat complexity sampling points and the extracted value was, therefore, zero, we changed the value for that point to NA. In addition, we extracted lowbush blueberry C:N, C:P, understory complexity, and overstory complexity at each of the habitat complexity sampling points. Before analysis, we centered and scaled all explanatory variables by subtracting the variable mean from each value and then dividing the subtracted value by the variable's standard deviation. After extracting and scaling the data, we ran four linear mixed-effects models with the KUD values as our response variable. For all models, we did not meet the assumptions of Gaussian error distribution, and therefore we log-transformed our response variable and re-ran the models. The models were designed to test the effect of the predation risk food quality trade-off at the population level using the fixed effects and at the individual level using the random effects. Fixed effects result in a single slope for the entire population, which is why we use them as our population-level measure. Random variables result in a unique slope for each individual hare, which is why we use them as our individual-level measure. Our fixed effect explanatory variables were lowbush blueberry C:N and C:P, and the overstory and understory complexity. Our random effect explanatory variables were lowbush blueberry C:N and understory complexity with varying slopes and intercepts across individuals. We evaluated the four competing models them using Akaike's Information Criterion corrected for small sample size (Table 3-2, AIC_c, Burnham and Anderson 1998).

We compared three models plus a null model with AIC_c. Our first model was the global model, which included lowbush blueberry C:N and C:P, overstory and understory complexity, all 2-way interaction terms of fixed effects, and individuals as a random effect. Our second model was a perceived predation risk model, with overstory complexity, understory complexity, their interaction term, and individuals as a random effect. Our third model was a food quality model, with lowbush blueberry C:N and C:P, their interaction term, and individuals as a random effect. Finally, our last model was a null model, which included the intercept as well as individuals as a random effect. To determine which variable would have random slopes across individuals for the random effects, linear regressions between explanatory and response variables were investigated for each individual hare. Because there was variation in the linear regression for all explanatory variables across individuals, we ran models with multiple random effects with their slopes varying across all explanatory variables. This approach resulted in overfitted models and non-convergence, so we prioritized the explanatory variables that had the most variation in slope across individuals; lowbush blueberry C:N and understory complexity (Table 3-2, Fig. 3-2). When building our null model, we tested all variations of random variables but allowing the slopes to vary did not improve the overall fit of the model, which we evaluated using ANOVA. For that reason, our null model includes the random variables with varying intercepts but not varying slopes. Lastly, for illustrative purposes, we regressed the random slopes to test for individual-based trade-offs between perceived predation risk and food quality (Fig 3-3). We extracted the slope value of lowbush blueberry C:N and understory complexity for each individual hare and regressed them against each other to visualize the trade-offs occurring at the individual level. We calculated all linear mixed-effects models using the *lme4* package and completed all AICc using the *AICcmodavg* package. We performed all statistical analyses in R 4.0.0 (Mazerolle 2019; Bates et al. 2020; R Core Team 2020).

3.4 Results

In addition to the analysis done for this thesis, post-exam I completed a Bayesian analysis for this chapter. The methods and results from the Bayesian analysis can be found in Appendix C and are intended to be used for publication.

3.4.1 Overview

Values of lowbush blueberry C:N ranged from 45.41 to 48.64 (mean = 46.96, Fig. B-3), and variation in C:P ranged from 1205.04 to 1899.04 (mean = 1349.83, Fig. B-3) at the points sampled for analysis. Understory complexity at each sampling point as measured using values from the first PCA axis of the understory variable PCA ranged from -7.34 to 2.55, with a mean very close to zero ($1.03\text{x}10^{-16}$, Fig. B-3) and overstory complexity at each sampling point measured using the values from the first PCA axis of the overstory variable PCA ranged from -3.37 to 2.61 with a mean very close to zero ($-4.52\text{x}10^{-16}$, Fig. B-3). KUD values were bound by 0 and 1, so they could be compared across individuals, with a mean of 0.13 at the points sampled for analysis (Fig. 3-1).

3.4.2 Model Comparison

We used AICc to compare four models that explored our hypotheses and predictions for the effect of the perceived predation risk food quality trade-off (Table 3-2). The third model, which included food quality only, ranked highest in our AIC_c (marginal $R^2 = 0.01$, conditional $R^2 = 0.06$, Table 3-2). All other models had greater than 2 ΔAIC_c. All models had marginal R^2 values ranging from 0.0 to 0.02 (Table 3-3).

Food quality was our top model and included lowbush blueberry C:N, lowbush blueberry C:P, and the interaction term as its fixed explanatory variables. Fixed explanatory variables were designed to indicate the population-level effect. We found no evidence for a relationship between KUD and lowbush blueberry C:P and the interaction term at the population level (Table B-1). However, lowbush blueberry C:N had a positive relationship with intensity of use at the population level (Estimate = 0.19, SE = 0.11, Table B-1). None of the fixed effects were highly correlated in our model.

Our top model had one random effect, indicating the individual-level effect of the predation risk food quality trade-off. Lowbush blueberry C:N had variable slopes across individuals and, as a random effect, explained 6.76% of the variance.

3.4.4 Food Quality-Predation Risk Interaction

Individual hares exhibited different strategies of space use depending on food quality (Fig. 3-2). When C:N slope varies across individuals, the direction and magnitude of the effect are dependent on the individual (-0.47 to 0.80, Fig. 3-2). Furthermore, although not a statistical test, Figure 3-3 depicts a positive correlation between safety and food quality (R = 0.44). Therefore, individuals optimize their behaviour and energy intake in response to the quality of food resources and predation risk.

3.5 Discussion

We used an ecological stoichiometry framework in conjunction with habitat complexity to evaluate food quality and perceived predation risk across a range of space use intensities. The interaction of the Risk Allocation Hypothesis (Lima and Bednekoff 1999) and Optimal Foraging Theory (Charnov 1976) creates a continuum of habitat quality across a landscape. We did not find support for prediction 1), which expected intensity of use to increase in areas with high food quality and low perceived predation risk. We saw no evidence of a relationship between snowshoe hare space use and perceived predation risk in our models, and there was evidence of a positive relationship between space use and C:N in our food quality models at the population level, the opposite of what we predicted. We found mixed support for prediction 2), which expected to see trade-offs occur when habitat with high food quality and low perceived predation risk was unavailable. Our results show that trade-offs do occur between food quality and perceived predation risk but only at the individual level. Individual hares make trade-offs in space use, favouring high-risk areas when there are high food quality and low-risk areas in patches of low food quality. We predicted, 3) that the preference for high food quality and low perceived predation risk to increase intensity of use in those areas at both the population and individual level. In addition, prediction 3) anticipated trade-offs between food quality and perceived predation risk to happen at the individual level. We found mixed support for this prediction, with no support found at the population level but evidence of trade-offs occurring at the individual level.

Foraging fulfills a basic need of prey species. Prey, regardless of size or taxa, have been shown to make space use decisions based on forage quality, supporting the Optimal Foraging Theory (Bjørneraas et al. 2012; Catano et al. 2015; Leroux et al. 2017). Indeed, our study found food quality as the highest-ranking model at both the individual and population-scale (Table 3-3). Both our population and individual models found a positive relationship between space use and lowbush blueberry C:N (Tables B-1 and B-2), the opposite of what we predicted. However, the Risk Allocation Hypothesis can be extended to explain prey spending more time in safe places (Ferrari et al. 2009). When individuals are exposed to short periods of high risk, the tenets of the Risk Allocation Hypothesis dictate that those individuals can obtain their energy by foraging in suboptimal areas that are safe (Ferrari et al. 2009; Ferrari and Chivers 2011). Our results show that there is a positive correlation for individual hares between risk and reward; hares select habitat with low food quality when it is also low risk, which explains the positive relationship observed in our model between C:N and space use (Fig. 3-3). Selecting for poorer food quality to avoid risk of predation has been observed in other species. For example, elk in Banff National Park migrated in order to reduce risk of predation, leading to an overall decrease in food quality when compared to their stationary counterparts (Hebblewhite and Merrill 2009). At the population level, the fine-scale trade-off between predation risk and food quality is lost in our sample of snowshoe hare, with no major trends observed (Fig. 3-4), further emphasizing the importance of trade-offs occurring at the individual level. The positive relationship between C:N and space use at the population level is likely due to the nature of systems with heterogeneously distributed resources, where there are large patches with similar food quality and high habitat complexity and few patches of very high quality food. Consistent with findings in similar studies (Marin et al. 2003; Prokopenko et al. 2017), our results show that herbivores are making fine-scale decisions regarding the predation risk food quality trade-off at the individual level.

Generalist herbivores need to consume several species to meet their nutritional demands (Provenza et al. 2003). Our study found food quality to be the highest-ranking model, however, it explained little variation in space use by snowshoe hares (Table 3-3, Fig. 3-4). We chose to use one preferred forage species, lowbush blueberry, to assess the food quality of the landscape because of the correlation between site and overall stoichiometry. Often, a site or patch with high levels of N and P has relatively high levels across species, indicating low C:N and C:P ratios overall (McClain et al. 2003; Schade et al. 2005). This is most likely due to the highly correlated relationship between element concentration in soils and nutrient uptake in plants (Huang and Schoenau 1997; Jobbágy and Jackson 2004). However, different plant species use N and P differently, producing a variety of toxic plant secondary compounds (Karban and Myers 1989; Branco et al. 2010). Generalist herbivores, such as snowshoe hares, deal with this toxicity by consuming multiple preferred forage species, balancing toxicity while also meeting nutritional demands (Dodds 1960; Provenza et al. 2003). Therefore, future studies investigating a broader forage plant community may explain the residual variation in snowshoe hare space use.

A tenet of Optimal Foraging Theory that was not examined in this chapter is the dependency on travel time between patches. The marginal value theorem states that foraging and space use will be dependent on the travel time required to move between patches (Charnov 1976). The spatial distribution of forage patches across the landscape impacts the likelihood of an herbivore moving from one patch to another, thus impacting their space use. Future studies would benefit from considering where the patches that individual hares are using are located and how they are situated compared to surrounding patches. An isolated patch may cause an individual to use space in that area more intensely due to the high cost of travelling, even if the resource quality is low. The effect of travel time between patches impacts patterns of space use and could be a confounding effect not considered in this study.

Perceived predation risk has been shown to impact the space use of several prey species (Orrock et al. 2003; Schirmer et al. 2019; Studd et al. 2019). For example, black-tailed jackrabbits increased space use in safer habitats even when they had lower forage resources to avoid risk of predation (Marin et al. 2003). Habitat complexity determines a prey's ability to hide and their ability to be vigilant. When habitat complexity is too high, it reduces visibility for vigilance by hares, resulting in improved conditions for terrestrial predators such as coyotes and increased perceived predation risk (Arias-Del Razo et al. 2012; Morris 2019). However, being completely exposed with high visibility also increases hare perceived predation risk for aerial and terrestrial predators (Morris 2019). Our perceived predation risk models did not show any evidence of relationships at the population or individual level. However, individual hare space use is dictated by the interaction between predation risk and food quality (Fig. 3-3). Individuals in our study optimize their decision making, selecting risky habitats if the reward is high enough (Fig. 3-2). Trading high risk for high forage reward has been observed in other herbivores, such as the pygmy rabbit, which will use burrows in areas with relatively high predation risk if their understory food resources are high (Wilson et al. 2012). This is consistent with Optimal Foraging Theory, the value of a patch decreases when risk is higher, meaning that forage quality should increase in order for the patch to still be viable to an individual (Brown et al. 1999). Similar to the effect of food quality, the effect of perceived predation risk at the population level is washed out due to the nature of the fine-scale decisions being made.

Space use of an animal can only be studied after selecting which scale is of ecological relevance. Our study looked at the intensity of space use within the home range of snowshoe hares, or second-order spatial selection (Johnson 1980). We chose to investigate at the home range scale because snowshoe hare home range size is partially dependent on forage quality and variation (Rizzuto et al. 2020). Although we predicted a population-level effect, it is possible that the population effect is happening at a larger spatial extent than what we measured. Landscape-scale selection has been shown in mule deer, which selected for higher nutritional quality on the landscape, suggesting that they choose an area based on its high food quality and then exhibit limited selection for home range placement within the larger habitat (Merems et al. 2020). Our hare population is situated in a patch of relatively high nutrient concentration relative to the surrounding landscape (Fig. B-3) and is of a preferred stand age for snowshoe hare (20-40 years old, Thornton et al. 2012). Further, the trade-offs that an herbivore makes are a function of its life-history. Migratory herbivores, such as elk, make large scale decisions to reduce overall predation risk, thus allowing them to make fine-scale foraging decisions once they have successfully migrated into refuge (Hebblewhite and Merrill 2009). However, herbivores such as snowshoe hare that do not migrate are forced to make fine-scale trade-offs between both predation risk and food quality, eliminating a population-level effect.

Using an ecological stoichiometry framework allowed us to highlight trade-offs being made between food quality and perceived predation risk. Our study investigates the influence of perceived predation risk and food quality throughout the same season, with measurements taken a maximum of once per day. The data resolution we used in this study provided information on coarse trade-off patterns. However, the fine-scale decisions regarding herbivore space use and the predation risk food quality trade-off could benefit from fine-scale data collection across both spatial and temporal scales to improve inference. For example, a study examining snowshoe hares on an hourly temporal scale showed that hares move between habitats with varying levels of food quality and cover on a daily basis to improve foraging but return to safety to rest in dense cover (Feierabend and Kielland 2014). Our work broadly touches on this, demonstrating a negative relationship between intensity of space use and food quality, indicating that most of the time, individuals are in low quality, safe habitat. Our study may have oversampled risk-averse behaviours due to the nature of data collection, revealing a trade-off between food quality and predation risk that has implications for snowshoe hare space use and thus the ecosystem as a whole, but excluding intricacies that occur on a finer scale.

Herbivore space use and distribution on the landscape have cascading effects across trophic levels (Brown et al. 1999). How herbivores use space determines the elemental composition of themselves, plants, and predators (Leroux et al. 2020) as well as shapes nutrient cycling (Moorhead et al. 2017). Within a spatially explicit ecological stoichiometry framework, we showed support for the interaction between the Risk Allocation Hypothesis and Optimal Foraging Theory, with individual herbivores making trade-offs in intensity of space use depending on the perceived predation risk and food quality of their habitat. In addition, our result showing a negative relationship between food quality and intensity of space use in our highest-ranking model provides support for Risk Allocation Hypothesis by showing that herbivores spend more time foraging in a safe habitat. The decisions that herbivores make when using space have implications for trophic levels below and above them. Quantifying and understanding those decisions contribute to a more holistic understanding of the ecosystems we are studying.

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3.7 References

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Table 3-1. Variables included in habitat complexity sampling. Group refers to the group they were in for the PCA analysis. Refer to Rodgers *et al.* (2008) for a complete description of the sampling protocol. Horizontal complexity was measured as per Nudds (1977).

Variable	Group	Description
Shrub Count	Understory	Total shrub count across all species on transects
Shrub Height	Understory	Average shrub height (m) for first 5 shrubs on transects across species
Shrub Diameter	Understory	Average basal diameter for first 5 shrubs on transects across species
Stump Count	Understory	Sum of all tree stumps in plot
Fallen Log Count	Understory	Sum of fallen logs on transects
Fallen Log Distance	Understory	Average distance to closest fallen log
Horizontal Complexity	Understory	Average visibility score at 10 m distance and 0-1 m height
Leaf Litter Depth	Understory	Average depth in cm
Canopy Closure	Overstory	Calculated with densiometer and averaged for 4 cardinal directions
Dead Tree Count	Overstory	Sum of all dead trees in plot
Canopy Intersections	Overstory	Total intersections of all species on transects
Understory Distance	Overstory	Average distance (m) to the closest understory tree
Overstory Distance	Overstory	Average distance (m) to the closest overstory tree
Understory DBH	Overstory	Average DBH (m) of the closest understory tree
Overstory DBH	Overstory	Average DBH (m) of the closest overstory tree

Table 3-2. Model construction of our models. Fixed effects test the predation risk food quality trade-off at the population level, and random effects test the trade-off at the individual level. All models had a Gaussian error distribution. The response variable, kUD (kernel utilization distribution) was log-transformed to meet assumptions of normality. The explanatory variables were scaled before analysis. C:N = Lowbush blueberry Carbon:Nitrogen, C:P = Lowbush blueberry Carbon:Phosphorus, understory = understory habitat complexity, overstory = overstory habitat complexity

Model Name	Model Parameters
1 – Global	kUD ~ overstory + understory + C:N + C:P + overstory*understory + C:N*C:P + overstory*C:N + overstory*C:P + understory*C:N + understory*C:P + (1+C:N|Individual) + (1 + understory|Individual)
2 – Habitat Complexity	kUD ~ overstory + understory + overstory*understory + (1+understory|Individual)
3 – Food Quality	kUD ~ C:N + C:P + C:N*C:P + (1+C:N|Individual)
4 – Intercept	kUD ~ 1 + (1|Individual)

Table 3-3. AIC table showing the model comparison for the four competing models. Habitat complexity was used as a proxy for perceived predation risk, and the intercept model refers to our null model. K = number of estimated parameters; Δ AICc = difference in AICc value from next highest model; AICc Weight = normalized relative likelihood of a model; Log Likelihood = relative likelihood of the model or relative strength of evidence; Mar. R^2 = marginal R^2 and Con. R^2 = conditional R^2. Models are linear mixed-effects models with a Gaussian error distribution.

Model name	K	Δ AICc	AICc Weight	Log Likelihood	Mar. R^2	Con. R^2
3 – Food Quality	8	0.00	0.99	-1945.32	0.01	0.06
1 – Global	16	18.84	$8.12\text{x}10^{-5}$	-1946.52	0.02	0.07
4 – Intercept	3	21.49	$2.15\text{x}10^{-5}$	-1961.13	0.00	0.02
2 – Habitat Complexity	8	31.86	$1.20\text{x}10^{-7}$	-1961.25	0.01	0.02

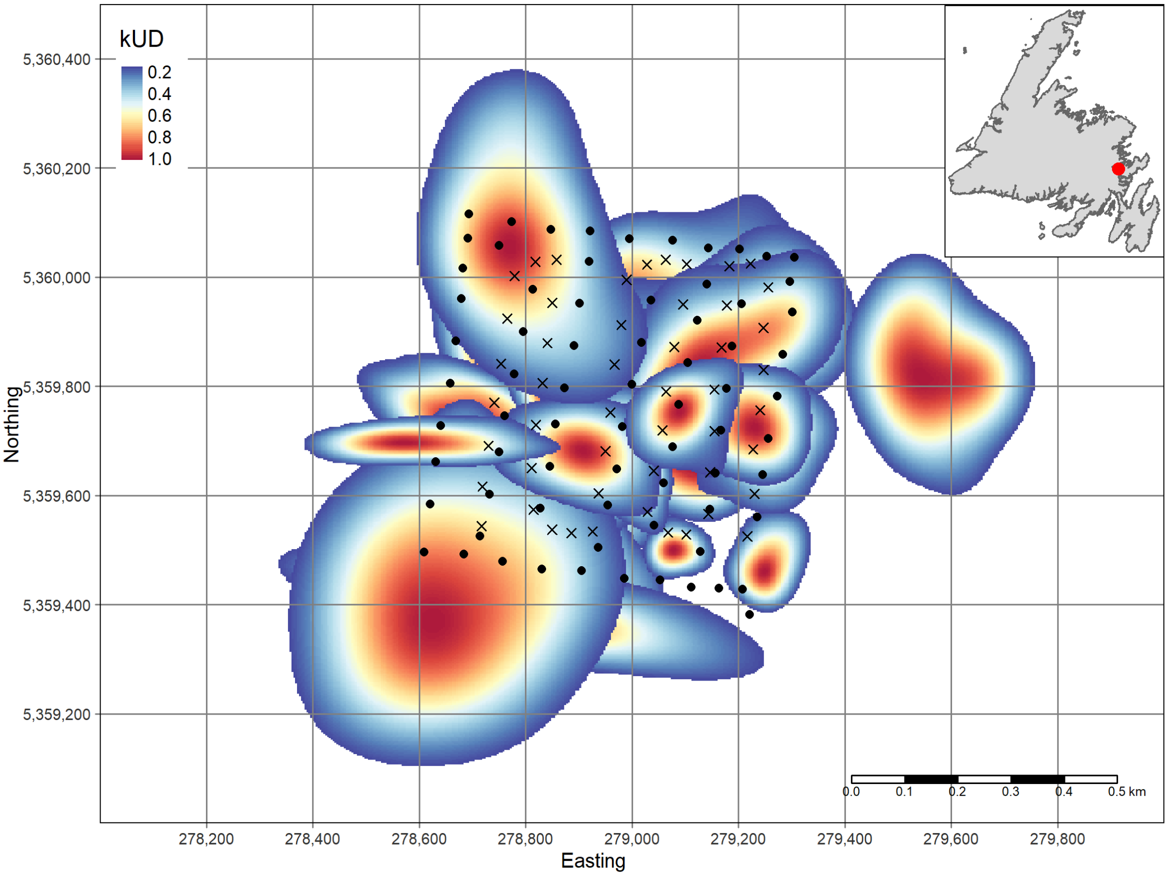

Figure 3-1. Kernel utilization distributions of all individual snowshoe hares included in the analysis (n = 30). kUD represents the normalized probability distribution function from the kernel utilization distribution, with low values (blue) depicting a low probability of space use and high values (red) depicting areas with a high probability of space use. Closed black circles represent the locations where habitat complexity was sampled, X's represent the locations of Tomahawk traps and where plant samples for stoichiometric analysis were taken. Inset shows study area location on the island of Newfoundland, Canada, as a red dot. Map projection is in WGS 84 UTM 22N (epsg: 32622).

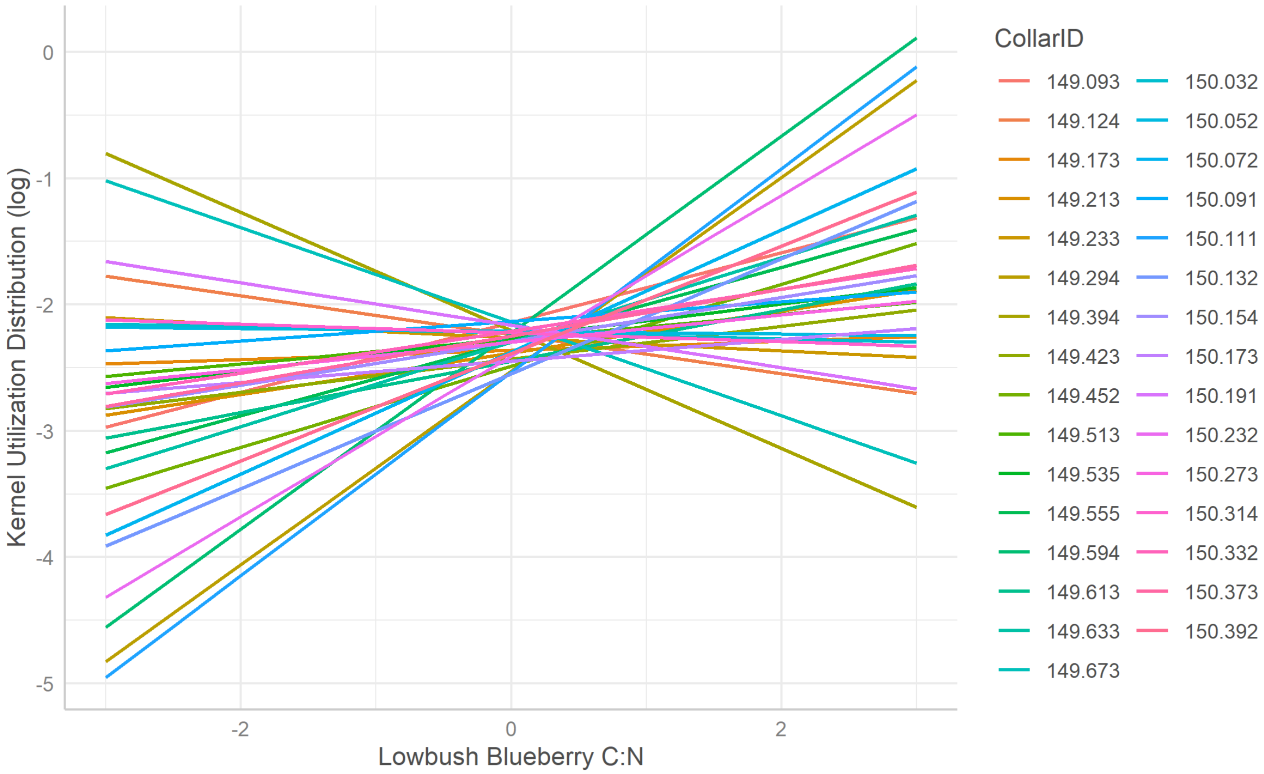

Figure 3-2. Varying slopes of lowbush blueberry C:N across each individual (n = 30). This variable was used in the second group of models, designed to analyze the individual-level effect of the predation risk food quality trade-off.

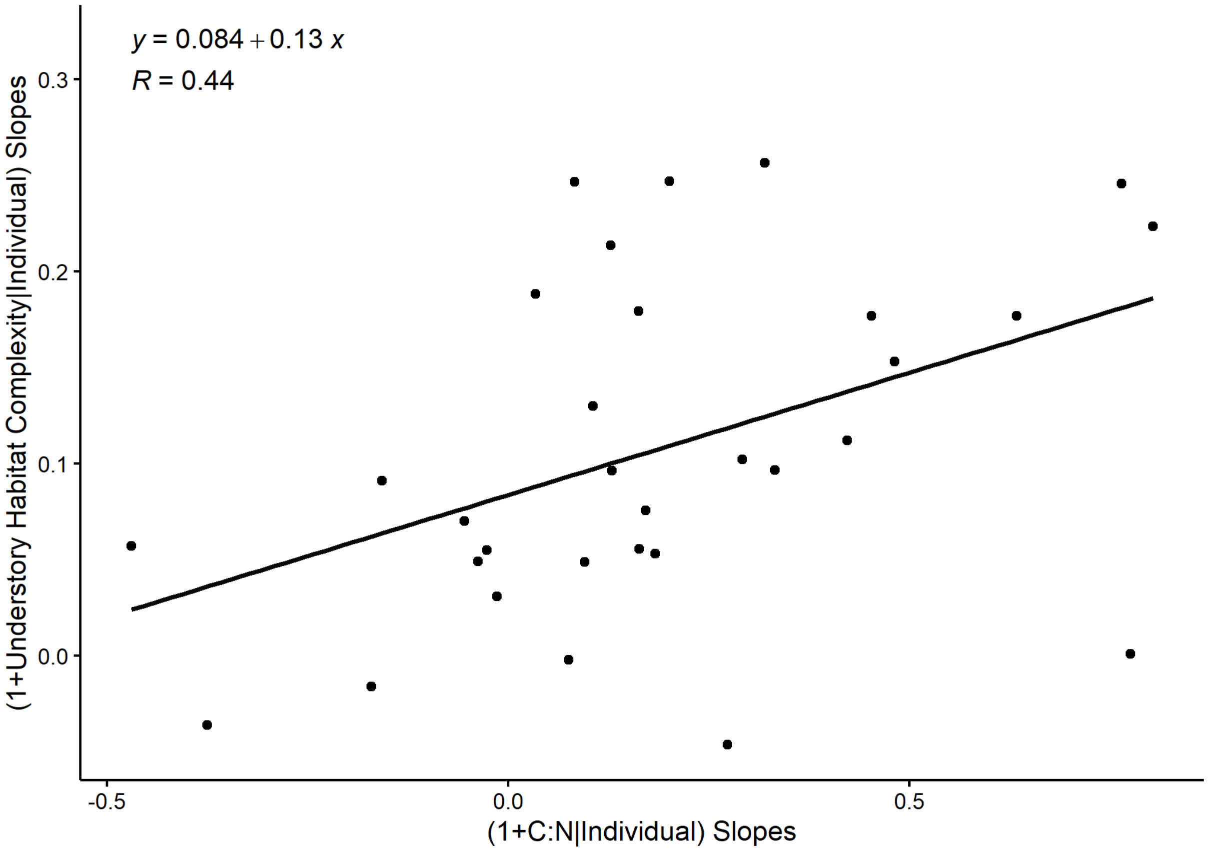

Figure 3-3. Relationship between the lowbush blueberry carbon:nitrogen (C:N) slopes and understory habitat complexity slopes for each individual hare. Slopes were extracted from the food quality and predation risk models from the second group of models. The line represents a linear regression line. Each point represents one individual hare in the study (n = 30). R indicates the correlation coefficient, and the equation represents the linear regression.

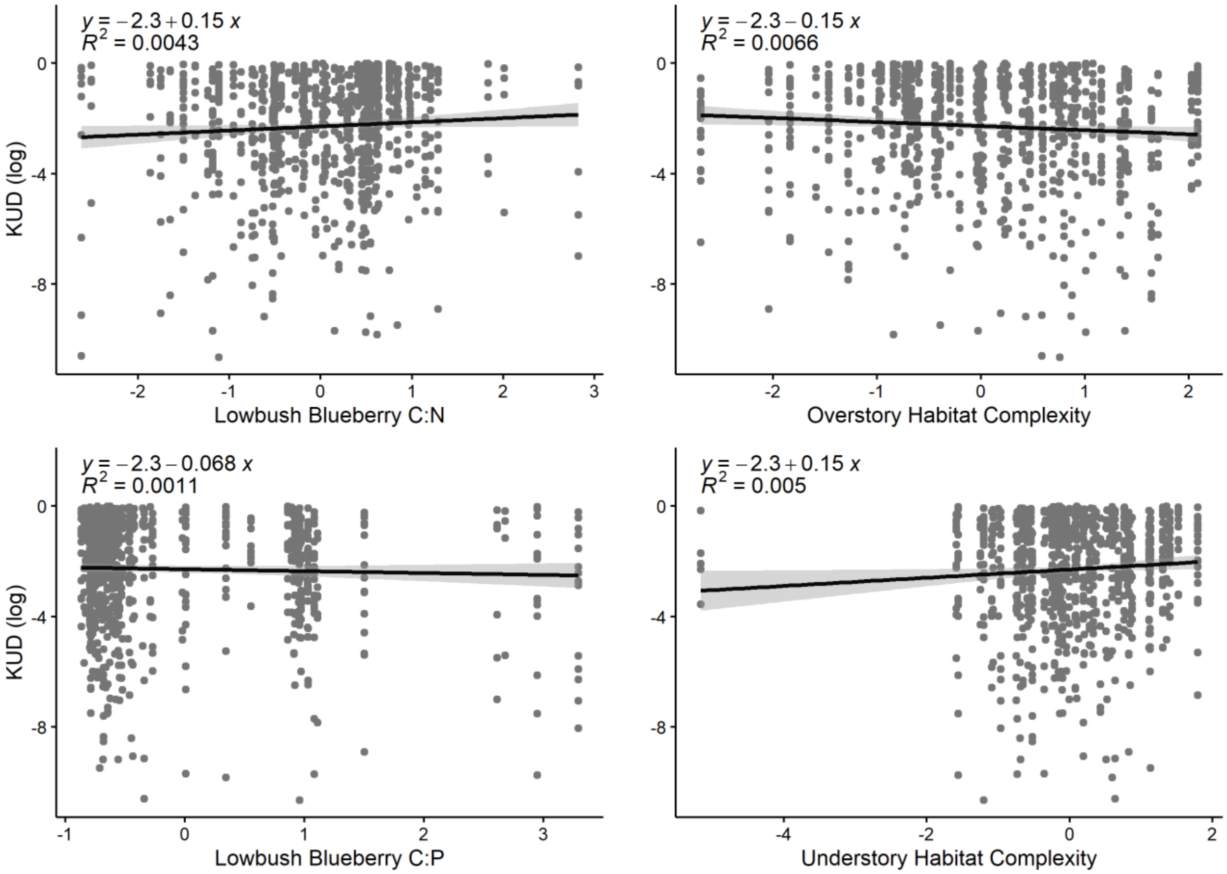

Figure 3-4. Relationship between intensity of space use (measured using the log-transformed kernel utilization distribution, KUD, of snowshoe hare) and each of the explanatory variables at the population level. C:N = carbon:nitrogen, C:P = carbon:phosphorus. The line represents a linear regression line, and the ribbon depicts the 95% confidence intervals. Each point represents a sampled value (n = 938).

Chapter 4 – Summary

4.1 Thesis Summary

The competing nature of many life-history traits, such as reproduction and growth, mean that ecological trade-offs are an important part of daily life for most organisms (Zera and Harshman 2001). By investigating how trade-offs influence animal and plant traits, we can obtain a holistic understanding of the individual. In this thesis, I investigated the ecological trade-offs of four boreal plant species and one keystone herbivore using ecological stoichiometry. My work quantifying the temporal changes in plant traits and their mechanisms has led to a deeper understanding of the distribution of resources across the boreal forest landscape, as well as the factors that drive this distribution. My work investigating snowshoe hare space use has contributed to the greater field of prey behaviour, demonstrating the fine-scale decisions that individual snowshoe hare make, which inevitably shape the ecosystem around them. My findings on hare space use in conjunction with my findings on temporal variation in primary producers add to the evidence demonstrating dynamic foraging behaviour by herbivores. We did not find any strong effect of food quality, indicating that there is variation in foraging behaviour. Changes in resource quality over time and space would cause changes in foraging and thus space use, resulting in weak or no patterns.

In chapter 2, I quantified the interannual variation in the elemental composition of four dominant boreal plant species and determined the mechanisms behind this variation. Variation in plant traits is well documented; there is variation in many leaf and wood traits based on climactic and soil changes (Wang et al. 2015; Heineman et al. 2016). Further, the spatial variation in plant elemental composition between species has been documented in both aquatic and terrestrial systems (Tsoi et al. 2011; Martiny et al. 2013; Leroux et al. 2017). Conversely, intraspecific temporal variation in plant elemental traits is not well documented and has important consequences for individual fitness and herbivore foraging. I measured the % Carbon (C), % Nitrogen (N), % Phosphorus (P), C:N, C:P, and N:P for all four species in the summers of 2016 and 2017. I found there was no interannual variation in the elemental composition, with two exceptions. First, %C had significant interannual variation for all four species measured (R^2 = 0.47 to 0.67). Second, balsam fir (*Abies balsamea*), our only evergreen conifer species, had more interannual variation than all other plants (5/6 variables tested, % C, N, P, C:N, and C:P, R^2 = 0.29 to 0.67). The remaining three species, red maple (*Acer rubrum*), white birch (*Betula papyrifera*), and lowbush blueberry (*Vaccinium angustifolium*), did not show any evidence of interannual variation except for %C. These results suggest that % C is affected by interannual differences, more so than N and P, which are limiting nutrients in the boreal forest. Higher interannual variation in C compared to N and P is reasonable since C assimilation is dependent on weather conditions and occurs on short time scales (Flanagan et al. 2002), whereas N and P assimilation is dependent on availability in soil and is unlikely to differ over a time scale such as two years (Huang and Schoenau 1997). In addition, N and P are limiting nutrients in the boreal, and so fluctuations in their uptake are less likely (Walker and Syers 1976; Vitousek et al. 2010). My results also indicate that year may explain more variation in evergreen conifers' stoichiometry than broadleaved deciduous' stoichiometry. Evergreen conifers have very different life-history strategies than broadleaved deciduous trees, which could lead to increased interannual variation. Balsam fir is known to suppress its growth when exposed to herbivory and resumes growth at a later date (McLaren 1996), inevitably impacting elemental uptake and assimilation. Evergreen conifers also require significantly different levels of elements for growth than deciduous trees and distribute them within the plant differently (Lamlom and Savidge 2003;

Sardans and Peñuelas 2013). With respect to the mechanisms driving interannual variation, we tested three well-known drivers of variation in plant elemental composition: temperature, moisture, and productivity (Sardans and Peñuelas 2013; Bracken et al. 2015; Li et al. 2017). For the species and elements that had evidence of interannual variation, temperature, measured using growing degree days, was the most frequently occurring driver (8/8 times, $R^2 = 0.21$ to 0.41). Moisture measured using the Normalized Moisture Difference Index, and productivity, measured using the Enhanced Vegetation Index, also correlated with interannual variation (6/8 times each). My results suggest that temperature, moisture, and productivity are all important drivers of the temporal variation of plant elemental composition. My results are consistent with the literature; temperature, moisture, and productivity have each respectively been shown to cause variation in plant traits (Pastor and Post 1986; Yin 1992; Welp et al. 2007; Sardans et al. 2016). Although our study shows that all three are important mechanisms explaining interannual variation, the strength and consistency of the relationship between temperature and interannual variation suggests that the effects of temperature are the strongest driver of the three measured.

In chapter 3, I investigated snowshoe hare space use and how space use relates to the trade-off between perceived predation risk and food quality using a framework based on the Risk Allocation Hypothesis and Optimal Foraging Theory. Herbivores balance their nutritional needs with the risk of predation (Liu et al. 2014). When choosing between predation risk and forage quality, the Risk Allocation Hypothesis and Optimal Foraging Theory interact, creating a continuum of habitat quality across a landscape and forcing trade-offs by herbivores. To assess the predation risk food quality trade-off, I measured perceived predation risk by sampling the habitat complexity across 30 hares' home ranges. Perceived predation risk has been demonstrated to impact herbivore behaviour through the use of giving-up-densities, home range placement, and foraging decisions (Brown and Alkon 1990; Bakker et al. 2005; Bjørneraas et al. 2012). I measured food quality by sampling the C:N and C:P ratios of a common browse species, lowbush blueberry, across the same home ranges. Similar to perceived predation risk, food quality is a factor that impacts herbivore behaviour and physiology (Sinclair et al. 1982; González et al. 2014). At the individual level, we found support for the interaction between the Risk Allocation Hypothesis and Optimal Foraging Theory, with individual hares spending time in areas of high perceived predation risk only when food quality was high and vice versa. Our findings build on previous findings of herbivores selecting for poorer food quality to avoid risk of predation (Hebblewhite and Merrill 2009) and that herbivores make fine-scale decisions regarding space use at the individual level (Marin et al. 2003; Prokopenko et al. 2017). We found support for the importance of food quality at both the population level and individual level, where food quality was consistently the top-ranked model. Food quality as the top-ranking model supports previous research showing the importance of forage quality in herbivore space use decisions (Catano et al. 2015; Leroux et al. 2017). Herbivore space use may impact plant communities (Poe et al. 2019), ecosystem carbon cycling (Leroux et al. 2020), and predator distribution (Laundré 2010). This chapter demonstrates that the space use of herbivores is dependent on both perceived predation risk and food quality and varies across individuals.

4.2 Thesis Limitations

It is important to acknowledge the limitations within this thesis so that future work can consider these gaps. In chapter 2, elemental data collection occurred over two years, whereas biomass collection occurred in only one. Collecting biomass data in only one year meant that my allometric modelling of the biomass density of each plot was based on the same value for both years, thus assuming negligible growth in biomass across years. Biomass has been shown to vary interannually and is impacted by abiotic factors such as temperature, moisture, and productivity (Delagrange et al. 2004; Sardans and Peñuelas 2007). However, due to the destructive nature of biomass sampling, I was only able to use one year of data. If biomass data were to be collected across both years of sampling, we might expect to see more evidence of interannual variation. In addition, collecting elemental data over only two years could be considered a limitation when assessing interannual variation. The study was designed to consider interannual variation at a scale relevant to higher trophic levels, such as the snowshoe hare. Snowshoe hares often have short lifespans due to predation (Keith and Windberg 1978), and thus changes in forage species across two years are a relevant time scale. However, due to the established "time-lag" of plants adjusting to environmental variation (Wu et al. 2015), this approach may be missing how environmental factors from several years prior are impacting interannual variation. If we increased our elemental data collection over a larger span of years, we might be able to determine stronger signals of the drivers behind interannual variation and explain more of the interannual variation that does occur. There is evidence that interannual variation in C balances out over time (Wu et al. 2012), so extending our data collection to a larger subset of years may actually reduce the effect of the interannual variation in percent C that we found in our study.

In chapter 3, I used a multimodel approach to my statistical analysis (Burnham and Anderson 1998), a common method in my research group (Leroux et al. 2017; Rizzuto et al. 2019; Balluffi-Fry et al. 2020). While not necessarily a limitation, there are many possible ways to do this analysis, i.e., Bayesian statistics, that should be considered for future directions of this research. In addition, the coarse resolution of radio-telemetry location data was a limitation when assessing the fine-scale space use of the snowshoe hares. With only one location per day, I was unable to assess the more fine-scale space use of hares, limiting the inference of the study to broader spatial patterns. A similar research project using GPS collars providing multiple locations per day would provide a more fine-scale perspective on space use, for example, differentiating in the perceived predation risk (for example, as a function of different levels of predator activity at different times of day) and food quality between a core area versus a home range.

4.3 Management Implications

I believe that the work I did in chapters 2 and 3 demonstrates the usefulness of ecological stoichiometry as a framework for assessing a variety of ecosystem processes and functions. The forestry industry focuses on carbon pools and fluxes as part of their management strategy (Kurz and Apps 1999; Paula et al. 2015). Carbon storage and the functioning of forests are not just limited to trees. Herbivores have significant impacts on carbon cycling within forests (Leroux et al. 2020). The universal nature of elements allows for the comparison across systems, trophic levels, and species and reduces the landscape into a common unit. The flow of elements has implications for both forestry and wildlife management and can explain relevant ecological processes such as nutrient cycling and species distribution.

In chapter 2, I demonstrated that there is minimal interannual variation in N, P, C:N, C:P, and N:P for broadleaved deciduous trees in the boreal forest. This finding has important implications for future sampling and data usage. Because there was limited evidence for interannual variation in ecological stoichiometry, we can assume patterns of stoichiometry are consistent through space and time. Essentially, a patch that was of high forage quality for an herbivore several years ago will continue to be high quality for several years if the system stays undisturbed. This allows efforts in successive sampling years to be focused elsewhere, instead of requiring annual sampling of the same location, thus increasing the scope of research overall.

This also decreases the associated costs of stoichiometric research, which is a relevant management implication. In addition, the variation demonstrated in percent C is an important finding for forestry management. Variation on the amount of C varying interannually based on temperature, moisture, and productivity has implications for management practices and costs of management (Winjum et al. 1993; Brown et al. 1996). Considering how unique weather years could impact the amount of C in a forest across years is an important management implication of this research.

In chapter 3, I demonstrate that space use by a keystone herbivore in the boreal forest is driven by both habitat complexity and food quality. Current wildlife management practices do not consider elemental composition as much as forestry management does (but see Rizzuto et al. 2019 for an example of an investigation of the elemental composition of a mammal). However, the predation risk food/quality trade-off made by herbivores has implications for forestry and wildlife management. Herbivore space use has implications for plant communities and predator space use (Arias-Del Razo et al. 2012; Moorhead et al. 2017). Therefore, understanding the broad drivers behind herbivore space use allows managers to make informed conservation or management decisions for multiple trophic levels at once. In addition, herbivore space use can have direct and indirect effects on C cycling in forests (Leroux et al. 2020), thus making herbivore space use an important factor in forestry management in addition to wildlife management.

Lastly, how carbon and other nutrients move through ecosystems has important implications for climate change. The boreal forest is the largest forested biome on Earth and is responsible for a large proportion of terrestrial C sequestration (Gauthier et al. 2015). Nitrogen and phosphorus levels within plants influence plant growth rates, therefore impacting C production and sequestration (Melillo et al. 2011; Sardans et al. 2016). Understanding how and why C changes interannually in dominant boreal plant species provides knowledge on a process that has implications for global C cycling.

4.4 Future Research Directions

There is huge potential for future research in the field of ecological trade-offs using a stoichiometry lens. Interannual variation of plant composition should be investigated at different levels of plants, from understory plants to juvenile and adult trees. Element uptake and allocation vary across species, functional groups, and plant age (Güsewell 2004; Borer et al. 2015; Sardans et al. 2016). Therefore, I would hypothesize that investigating the interannual variation of elemental composition across different plant groups and ages would reveal interesting nuances in elemental cycling and use. Differences in elemental uptake have interesting implications for herbivory, plant growth, and nutrient cycling (Molvar et al. 1993; González et al. 2011; Borer et al. 2015). Differences in elemental allocation across ages of plants, such as juvenile trees investing in growth over chemical defenses while young (Bryant et al. 1983), add an interesting lens to the investigation of interannual variation. Although the uptake of elements may be the same across years for a certain tree, investigating how those elements are used when a tree is transitioning from juvenile to adult impacts the quality of that resource for herbivores (Bryant et al. 1983; Hébert and Weladji 2013; Liang et al. 2018). Travis Heckford, a member of TERG, has begun to produce the distribution of phytochemicals across a chrono-sequenced boreal landscape, which will result in another lens added to the trade-offs made by boreal plants experiencing a nutrient-limited system.

Quantifying the interannual variation in elemental composition of the different organs of the plants measured, i.e., roots, stems, trunks, leaves, would give a holistic view of interannual variation and would allow us to see if the variation is occurring within the plant. In addition, measuring how different mechanisms, such as weather or nutrient input, drive interannual variation differently would provide a way to predict both fine and large-scale changes in plant elemental composition. Elemental variation may occur within the plant, shifting elements from organ to organ, or conversely, within the ecosystem, shifting from organism to organism. I hypothesize that both interannual variation within plant organs and across plants occurs, depending on the different drivers such as nutrient input and temperature shifts (Yao et al. 2015; Liang et al. 2018; Tang et al. 2018). I would also hypothesize that variation in the elemental composition of plant organs as well as plant species would impact herbivory strategies, resulting in interannual variation in larger ecosystem processes, such as herbivore space use.

Assessing the stoichiometry of the soil in the same places where plant stoichiometry is assessed would open a whole new perspective on interannual variation. Element concentration in soils is directly related to the uptake of nutrients in plants (Huang and Schoenau 1997; Jobbágy and Jackson 2004). In addition, element concentration and availability within the soils are dependent on a variety of factors, such as weather, soil type, and surrounding plant community (Pastor and Post 1986; Macedo et al. 2008). I hypothesize that when there is evidence of interannual variation in the elemental composition of plants, there is also evidence of interannual variation in the elemental composition of the surrounding soil. Improving our understanding of soil stoichiometry would provide a holistic understanding of interannual variation in elemental composition across trophic levels and would improve our knowledge of interannual variation in nutrient cycling, a key ecosystem process.

When looking at the ecological trade-offs made by herbivores, future research should consider the different scales at which decisions are made. There are several scales of selection order that can be categorized for animal space use, each one providing different inferences (Johnson 1980). Assessing the predation risk food quality trade-off at the home range scale provided important insight on the fine-scale decisions of herbivore space use but assessing the same trade-off at the landscape scale could provide an interesting insight into population and species range distributions. By evaluating how food quality and predation risk vary across a landscape and assessing how the population of an herbivore is distributed, it allows you to see what the drivers of space use are on a large scale. I hypothesize that perceived predation risk, based on the structure of the habitat, determines the distribution of snowshoe hare on the landscape scale, whereas food quality is impacting space use on a finer scale, once the population distribution has been established. The pattern of large-scale decisions being driven by predation risk and fine-scale decisions being driven by food quality has been shown for other herbivores, such as moose (Balluffi-Fry et al. 2020). Incorporating spatial distribution of patches, annual variations in productivity due to nutrient cycling, and density-dependent interactions of herbivores would greatly influence the outcomes of trade-off research.

In addition, using experimental trials that assess herbivores' reactions to perceived predation risk and food quality in a controlled environment could provide more information on the behaviour and tendencies of specific herbivore species. A member of TERG, Joanie Kennah has started work on this. By placing snowshoe hares in enclosures with high and low-quality food options and manipulating the perceived predation risk by adding and removing cover, we will tease out how changes in perceived predation risk impact vigilance and feeding behaviour.

To conclude, my thesis has used ecological stoichiometry to assess trade-offs in a variety of boreal species. I quantified the interannual variation in four plant species and identified the drivers behind the variation. In addition, I demonstrated a perceived predation risk/food quality trade-off occurring at the individual level for snowshoe hare. I worked as part of a larger research group to contribute to the investigation of elemental flows within the boreal forest ecosystem. More specifically, contributing to the understanding of how elements vary and are used at the primary producer and herbivore levels.

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Appendices

Appendix A. Chapter 2 Supplementary Figures and Tables

Additional Methods

Below, I provide additional details on data collection and analysis methods from chapter 2. Figure A-1 is a detailed schematic of the field sampling that was replicated in each of the four sites. In Figure A-2, I illustrate the specific sampling strategy that was implemented at each point in Figure A-1. Figure A-3 depicts the correlation analysis done between two weather stations before I supplemented missing data from the Lethbridge station with data from the Clarenville station. Figure A-4 shows the results of the interpolation done of the Landsat 8 imagery for our ecoregion prior to the extraction of the Normalized Moisture Difference Index. Figure A-5 shows the results of the interpolation done of the Landsat 8 imagery for our ecoregion prior to the extraction of the Enhanced Vegetation Index.

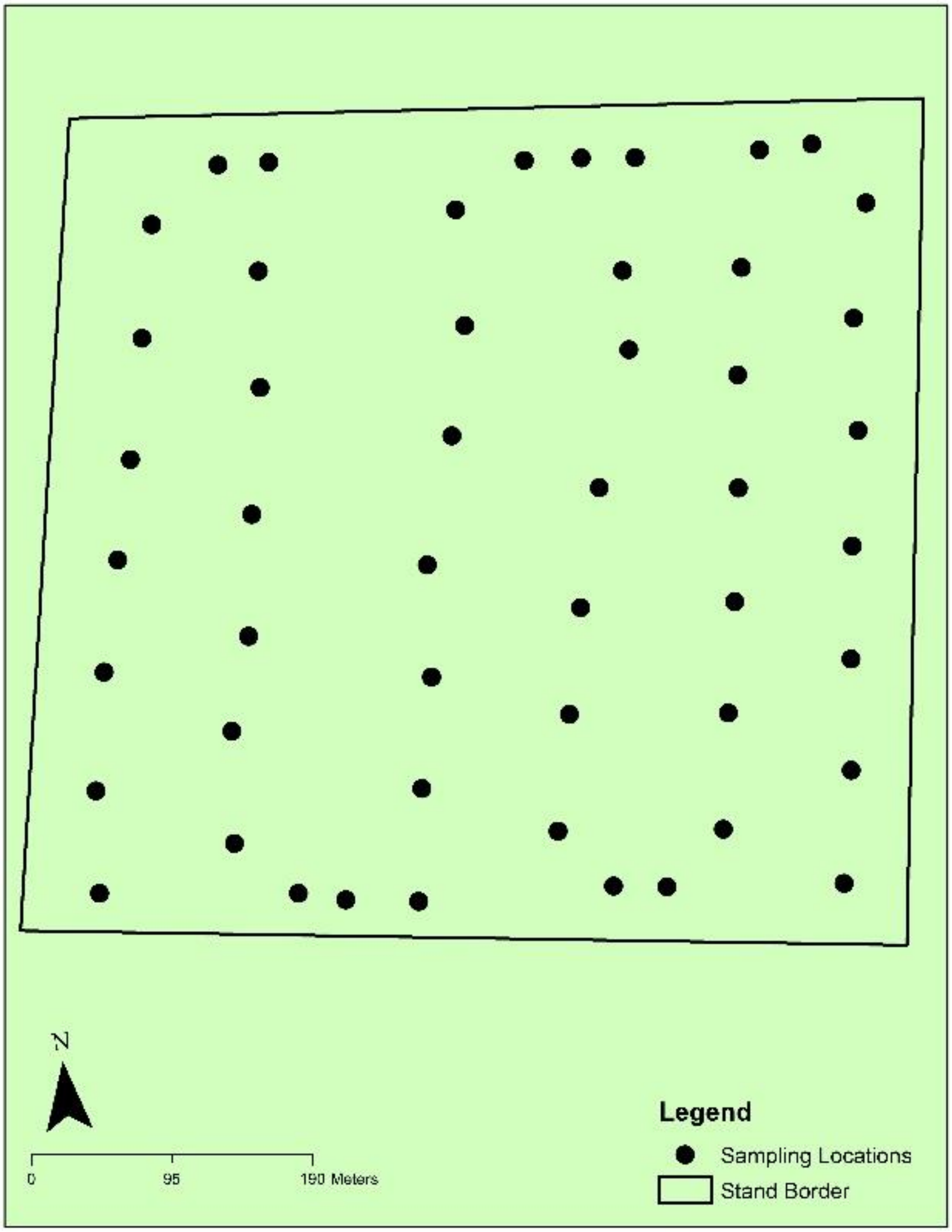

Figure A-1. Approximation of meandering transect lines and location of 50 sample plots for each 500 m x 500 m study site (4 in total).

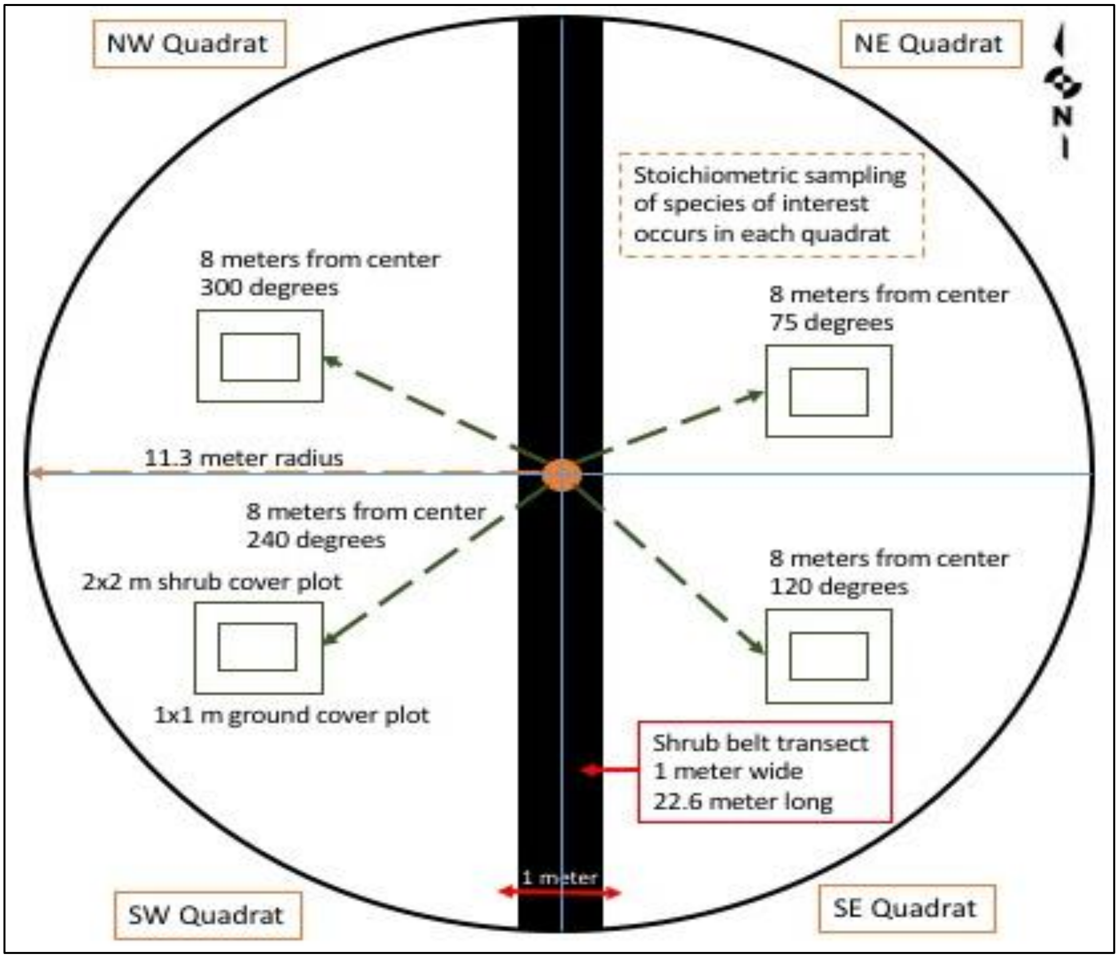

Figure A- 2. Sampling plot layout for species density and vegetative sampling, that was carried out at each of the 50 sampling points shown in Figure S1.

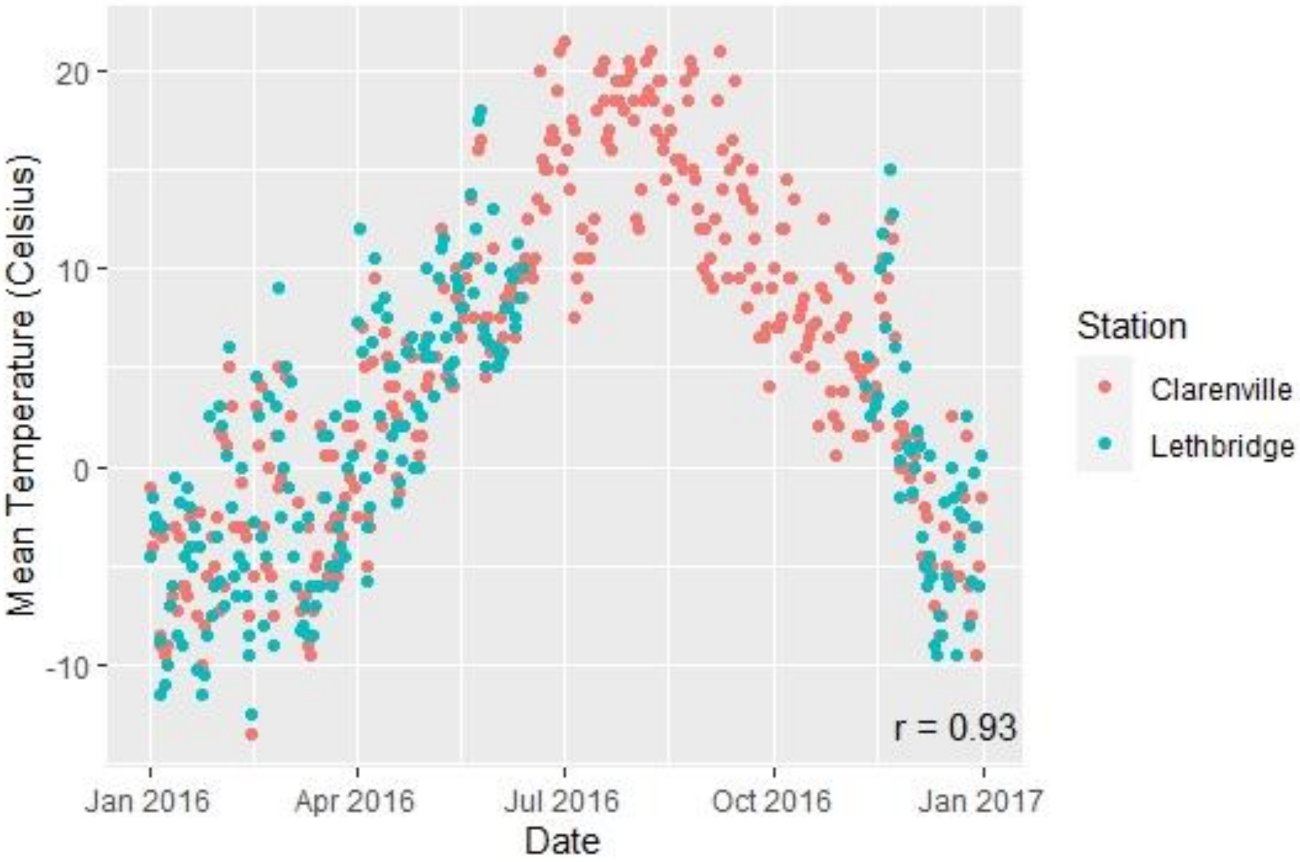

Figure A-3. Mean temperatures collected at the Clarenville and Lethbridge weather stations from January 2016 - January 2017. Data are highly correlated (Pearson correlation coefficient is 0.93), missing data from Lethbridge weather station during the study period was replaced with Clarenville weather station data. Data were obtained from the historical weather dataset at Environment and Climate Change Canada (https://climate.weather.gc.ca/historical_data).

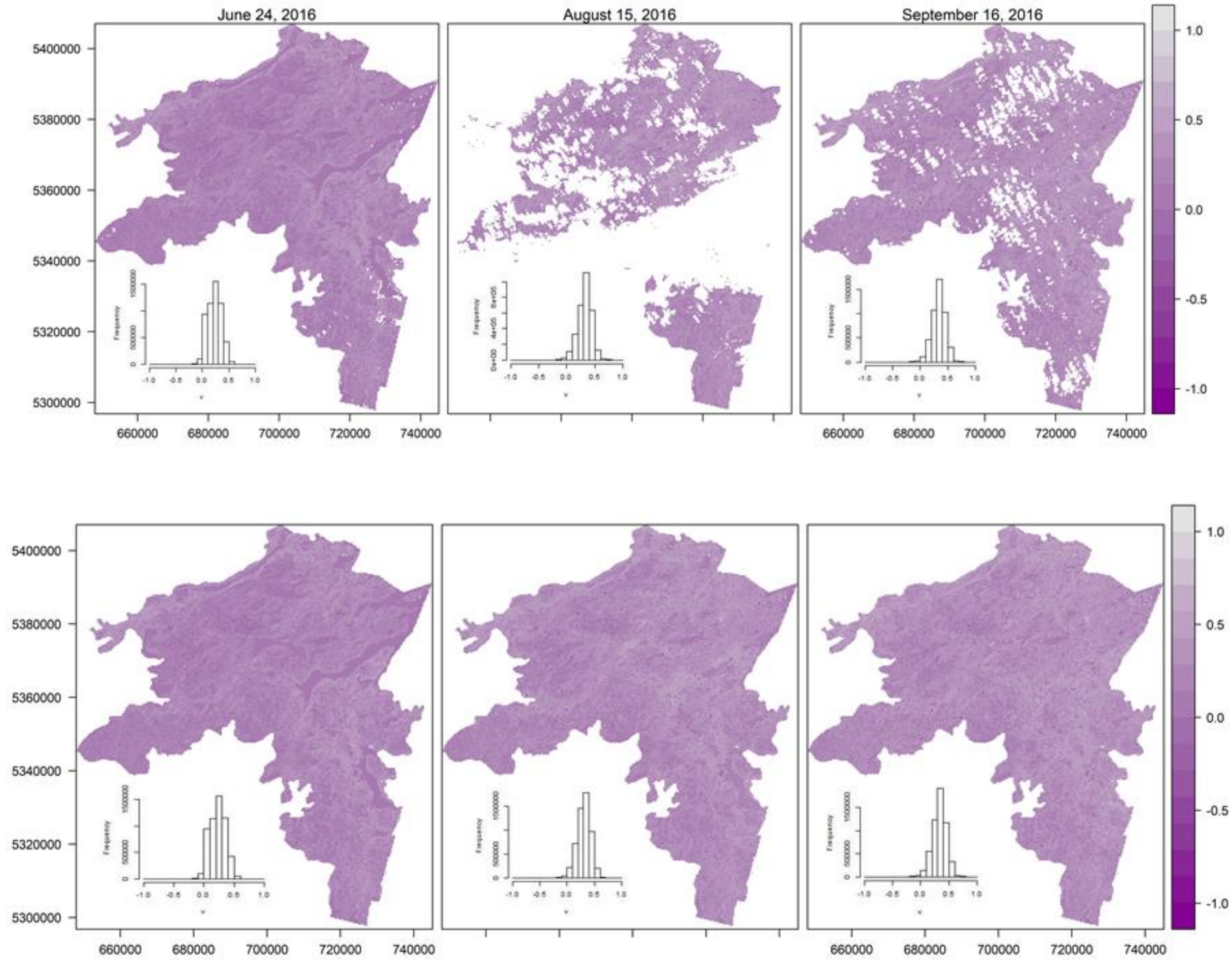

Figure A-4a. Using the ‘approxNA’ function from the ‘raster’ package in R, we performed a linear temporal interpolation to determine Normalized Difference Moisture Index (NDMI) pixel values for areas obscured by cloud. Dates analyzed were chosen within the growing season; for 2016 they included June 28, August 15, and September 16. The top panel shows each scene before interpolation, and the bottom panel shows each scene after interpolation. Accompanying histograms are provided for each EVI scene, demonstrating the change in pixel value distribution after interpolation. Values were averaged across all dates and extracted for sampling locations at each grid.

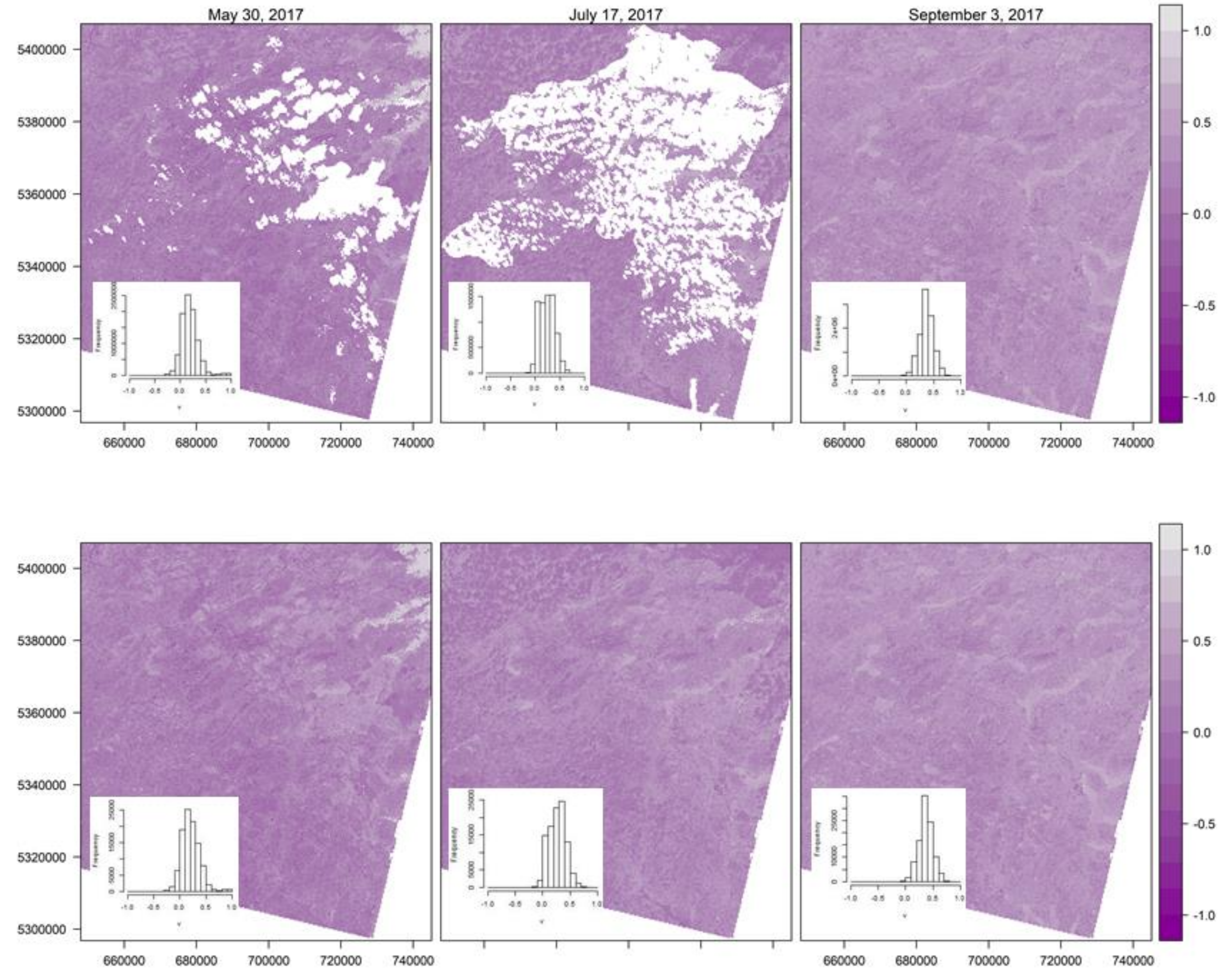

Figure A-4b. Using the ‘approxNA’ function from the ‘raster’ package in R, we performed a linear temporal interpolation to determine Normalized Difference Moisture Index (NDMI) pixel values for areas obscured by cloud. Dates analyzed were chosen within the growing season, for 2017 they included May 30, July 17, and September 3. The top panel shows each scene before interpolation, and the bottom panel shows each scene after interpolation. Accompanying histograms are provided for each EVI scene, demonstrating the change in pixel value distribution after interpolation. Values were averaged across all dates and extracted for sampling locations at each grid.

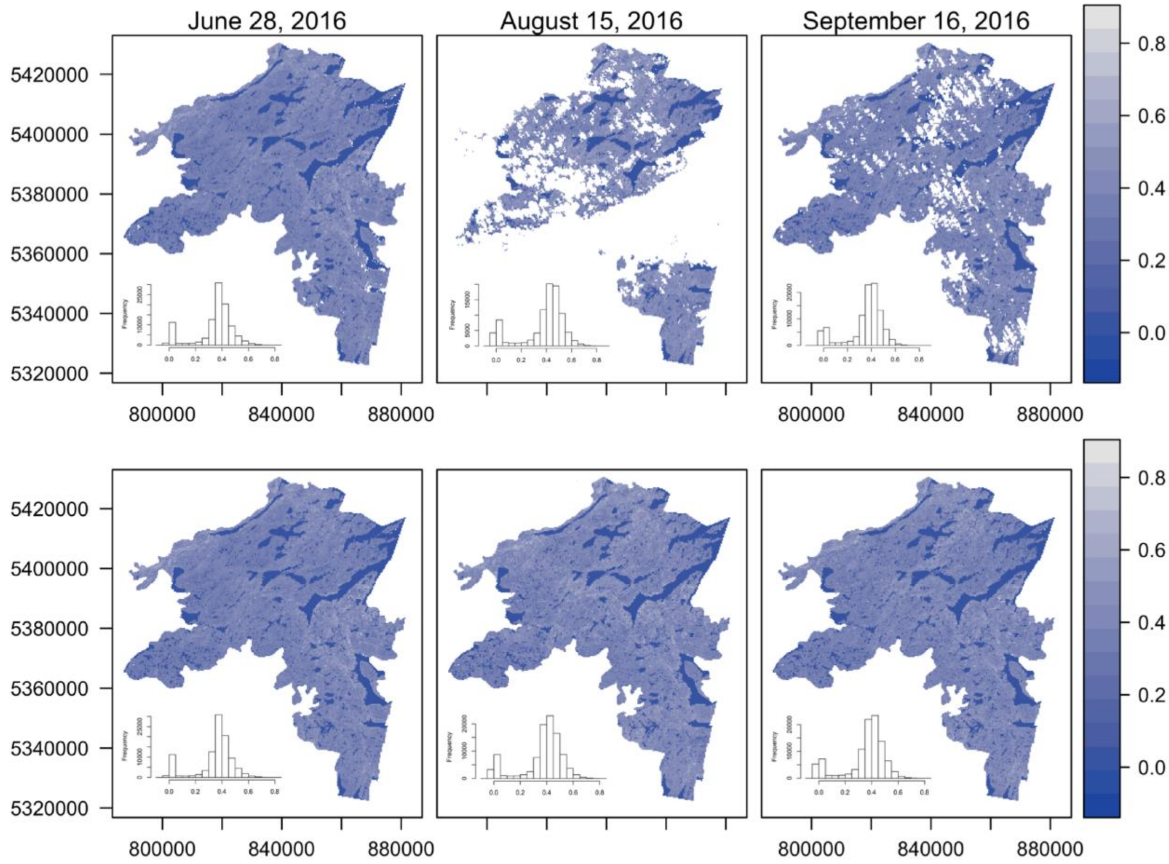

Figure A-5a. Using the ‘approxNA’ function from the ‘raster’ package in R, we performed a linear temporal interpolation to determine Enhanced Vegetation Index (EVI) pixel values for areas obscured by cloud. Dates analyzed were chosen within the growing season, for 2016 they included June 28, August 15, and September 16. The top panel shows each scene before interpolation, and the bottom panel shows each scene after interpolation. Accompanying histograms are provided for each EVI scene, demonstrating the change in pixel value distribution after interpolation. Values were averaged across all dates and extracted for sampling locations at each grid. Reproduced with permission from Heckford et al. (in review).

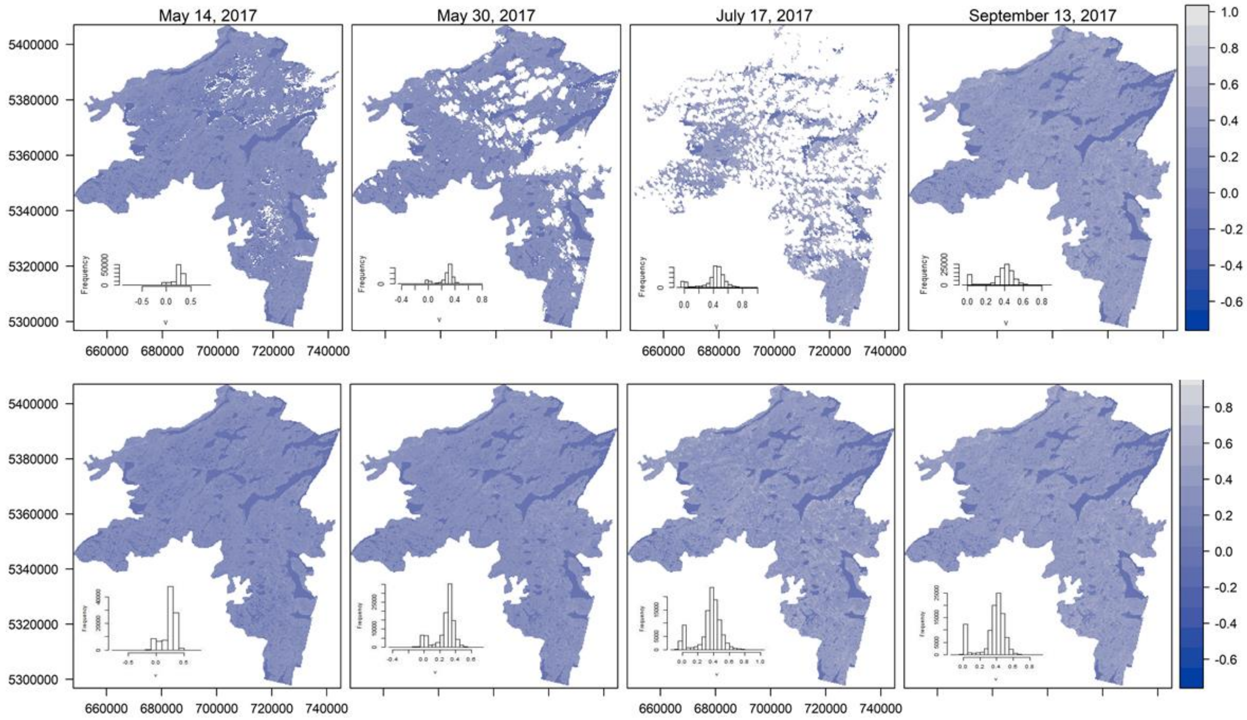

Figure A-5b. Using the ‘approxNA’ function from the ‘raster’ package in R, we performed a linear temporal interpolation to determine Enhanced Vegetation Index (EVI) pixel values for areas obscured by cloud. Dates analyzed were chosen within the growing season, for 2017 they included May 14, May 30, July 17, and September 13. The top panel shows each scene before interpolation, and the bottom panel shows each scene after interpolation. Accompanying histograms are provided for each EVI scene, demonstrating the change in pixel value distribution after interpolation. Values were averaged across all dates and extracted for sampling locations at each grid

Additional Results

Below, I provide additional details on the thesis results. Figure A-6 shows the results of variance partitioning for each of the response variables, based on year, site, and species.

Tables A-1 to A-8 are AIC tables for the first round modelling, Model = model variables; K = number of estimated parameters; AICc = estimate of the expected relative distance between model and true mechanism, corrected for small sample size; ΔAICc = difference in AICc value from next highest model; AICc Weight = normalized relative likelihood of a model; Log Likelihood = relative likelihood of the model or relative strength of evidence. Models are general linear models with a Gaussian error distribution.

Tables A-9 to A-12 are AIC tables for the second round of models. Models were only run for the response variables that had year in the top-ranked model in the first round. Growing Degree Days = GDD, Normalized Difference Moisture Index = NDMI, Enhanced Vegetation Index = EVI. Models were ranked using AICc. Model = model variables; K = number of estimated parameters; AICc = estimate of the expected relative distance between model and true mechanism, corrected for small sample size; ΔAICc = difference in AICc value from next highest model; AICc Weight = normalized relative likelihood of a model; Log Likelihood = relative likelihood of the model or relative strength of evidence. Models are general linear models with a Gaussian error distribution.

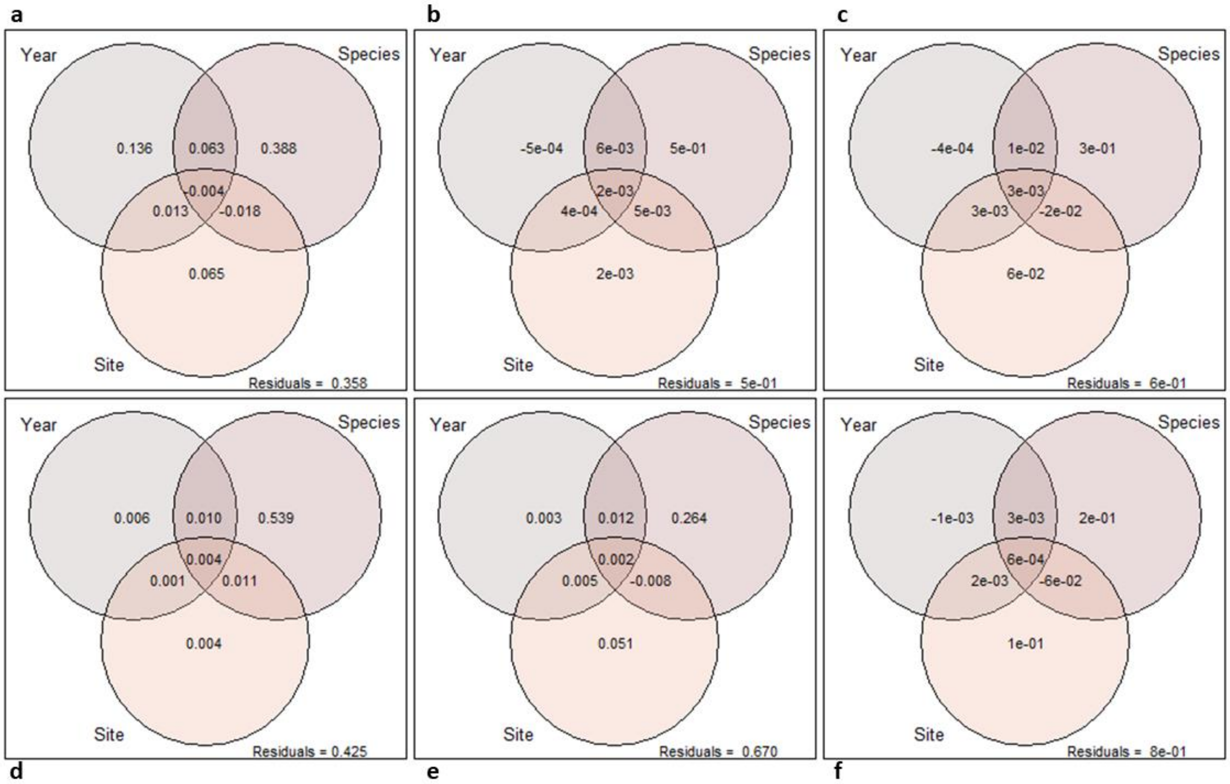

Figure A-6. Variance partitioning (by year, species, and site) for each response variable tested in our study a) % Carbon, b) % Nitrogen, c) % Phosphorus, d) Carbon:Nitrogen, e) Carbon:Phosphorus, f) Nitrogen:Phosphorus. Variation partitioning was done using linear regression in the package "vegan" (Oksanen et al. 2019).

Table A-1a-c. AIC tables for the first round of balsam fir percent composition models.

Table A-1a. AIC table for the first round of balsam fir percent carbon models.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
Year*Site	8	227.26	0	1	-104.94
Year	3	303.07	75.81	3.46E-17	-148.42
Site	5	313.72	86.46	1.68E-19	-151.58
Null	2	326.62	99.36	2.65E-22	-161.26

Table A-1b. AIC table for the first round of balsam fir percent nitrogen models.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
Year*Site	8	299.31	0	0.97	-140.97
Year	3	306.88	7.57	0.02	-150.33
Site	5	308.60	9.29	0.019	-149.02
Null	2	326.62	27.31	1.14E-06	-161.26

Table A-1c. AIC table for the first round of balsam fir percent phosphorus models.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
Year*Site	8	301.73	0	0.93	-142.18
Site	5	307.05	5.33	0.06	-148.25
Year	3	314.49	12.76	1.58E-03	-154.13
Null	2	326.62	24.90	3.67E-06	-161.26

Table A-2a-c. AIC tables for the first round of balsam fir stoichiometric ratio models.

Table A-2a. AIC table for the first round of balsam fir carbon:nitrogen models.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
Year*Site	8	901.41	0	0.98	-442.02
Year	3	909.55	8.15	0.07	-451.67
Site	5	912.26	10.85	4.31E-03	-450.85
Null	2	930.97	29.56	3.73E-07	-463.43

Table A-2b. AIC table for the first round of balsam fir carbon:phosphorus models.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
Year*Site	8	1811.09	0	0.86	-896.86
Site	5	1814.74	3.65	0.14	-902.09
Year	3	1825.73	14.64	5.69E-04	-909.76
Null	2	1836.91	25.82	2.13E-06	-916.40

Table A-2c. AIC table for the first round of balsam fir nitrogen:phosphorus models.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
Site	5	796.11	0	0.87	-392.78
Year*Site	8	800.24	4.13	0.11	-391.44
Year	3	805.00	8.89	0.01	-399.39
Null	2	806.39	10.28	5.11E-03	-401.14

Table A-3a-c. AIC tables for the first round of red maple percent composition models.

Table A-3a. AIC table for the first round of red maple percent carbon models.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
Year*Site	9	237.49	0	1	-108.92
Year	3	304.20	66.71	3.27E-15	-149.00
Site	5	342.70	105.22	1.42E-23	-166.09
Null	2	343.64	106.16	8.88E-24	-169.77

Table A-3b. AIC table for the first round of red maple percent nitrogen models.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
Year	3	342.71	0	0.48	-168.25
Null	2	343.64	0.93	0.30	-169.77
Year*Site	9	345.70	2.98	0.11	-163.03
Site	5	345.73	3.02	0.11	-167.60

Table A-3c. AIC table for the first round of red maple percent phosphorus models.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
Null	2	343.64	0	0.66	-169.77
Year	3	345.45	1.80	0.27	-169.62
Site	5	348.28	4.64	0.06	-168.88
Year*Site	9	355.56	11.91	1.71E-03	-167.96

Table A-4a-c. AIC tables for the first round of red maple stoichiometric ratio models.

Table A-4a. AIC table for the first round of red maple carbon:nitrogen models.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
Null	2	766.43	0	0.48	-381.16
Year	3	767.73	1.30	0.25	-380.76
Site	5	768.16	1.73	0.20	-378.81
Year*Site	9	770.75	4.32	0.06	-375.56

Table A-4b. AIC table for the first round of red maple carbon:phosphorus models.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
Null	2	1769.16	0	0.65	-882.53
Year	3	1771.09	1.92	0.25	-882.44
Site	5	1773.00	3.84	0.10	-881.24
Year*Site	9	1779.37	10.20	3.96E-03	-879.87

Table A-4c. AIC table for the first round of red maple nitrogen:phosphorus models.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
Null	2	885.73	0	0.71	-440.82
Year	3	887.82	2.09	0.25	-440.81
Site	5	891.46	5.73	0.04	-440.47
Year*Site	9	895.13	9.39	6.43E-03	-437.74

Table A-5a-c. AIC tables for the first round of white birch percent composition models.

Table A-5a. AIC table for the first round of white birch percent carbon models.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
Year*Site	9	241.92	0	1.00	-110.95
Year	3	266.95	25.02	3.68E-06	-130.35
Site	5	274.31	32.39	9.25E-08	-131.83
Null	2	284.07	42.15	7.04E-10	-139.97

Table A-5b. AIC table for the first round of white birch percent nitrogen models.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
Site	5	283.37	0	0.49	-136.36
Null	2	284.07	0.70	0.34	-139.97
Year	3	285.90	2.53	0.14	-139.82
Year*Site	9	288.97	5.60	0.03	-134.47

Table A-5c. AIC table for the first round of white birch percent phosphorus models.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
Site	5	278.90	0	0.88	-134.12
Null	2	284.07	5.17	0.07	-139.97
Year	3	285.54	6.65	0.03	-139.65
Year*Site	9	286.70	7.81	0.02	-133.34

Table A-6a-c. AIC tables for the first round of white birch stoichiometric ratio models.

Table A-6a. AIC table for the first round of white birch carbon:nitrogen models.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
Null	2	817.52	0	0.44	-406.70
Site	5	817.97	0.45	0.35	-403.66
Year	3	819.04	1.52	0.20	-406.39
Year*Site	9	824.71	7.20	0.01	-402.35

Table A-6b. AIC table for the first round of white birch carbon:phosphorus models.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
Null	2	1596.58	0	0.57	-796.23
Site	5	1598.52	1.94	0.22	-793.94
Year	3	1598.59	2.01	0.21	-796.17
Year*Site	9	1606.52	9.94	3.96E-03	-793.25

Table A-6c. AIC table for the first round of white birch nitrogen:phosphorus models.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
Null	2	698.88	0	0.58	-347.38
Year	3	700.99	2.11	0.20	-347.37
Site	5	701.22	2.34	0.18	-345.29
Year*Site	9	704.74	5.86	0.03	-342.36

Table A-7a-c. AIC tables for the first round of lowbush blueberry percent composition models.

Table A-7a. AIC table for the first round of lowbush blueberry percent carbon models.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
Year*Site	9	352.01	0	1	-166.51
Year	3	458.72	106.71	6.72E-24	-226.30
Site	5	510.62	158.61	3.61E-35	-250.15
Null	2	545.10	193.09	1.18E-42	-270.52

Table A-7b. AIC table for the first round of lowbush blueberry percent nitrogen models.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
Null	2	545.10	0	0.52	-270.52
Site	5	546.65	1.56	0.24	-268.16
Year	3	547.16	2.06	0.18	-270.52
Year*Site	9	549.29	4.20	0.06	-265.15

Table A-7c. AIC table for the first round of lowbush blueberry percent phosphorus models.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
Site	5	434.75	0	0.98	-212.21
Year*Site	9	442.84	8.08	0.02	-211.92
Null	2	545.10	110.34	1.08E-24	-270.52
Year	3	546.15	111.40	6.34E-25	-270.01

Table A-8a-c. AIC tables for the first round of lowbush blueberry stoichiometric ratio models.

Table A-8a. AIC table for the first round of lowbush blueberry carbon:nitrogen models.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
Site	5	1340.40	0	0.54	-665.04
Null	2	1341.61	1.21	0.30	-668.77
Year	3	1343.26	2.86	0.13	-668.57
Year*Site	9	1346.10	5.70	0.03	-663.55

Table A-8b. AIC table for the first round of lowbush blueberry carbon:phosphorus models.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
Site	5	2849.71	0	0.98	-1419.69
Year*Site	9	2857.76	8.05	0.02	-1419.38
Null	2	2920.54	70.84	4.08E-16	-1458.24
Year	3	2920.94	71.23	3.34E-16	-1457.41

Table A-8c. AIC table for the first round of lowbush blueberry nitrogen:phosphorus models.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
Site	5	1339.87	0	0.98	-664.77
Year*Site	9	1347.26	7.39	0.02	-664.13
Null	2	1406.36	66.49	3.56E-15	-701.15
Year	3	1407.78	67.91	1.75E-15	-700.83

Table A-9a-e. AIC tables for the second round of balsam fir models.

Table A-9a. AIC table for the second round of balsam fir percent carbon models. EVI was removed as a pretending variable.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
GDD+NDMI+GDD*NDMI	5	277.45	0	0.82	-133.45
GDD+NDMI	4	280.48	3.03	0.18	-136.06
GDD	3	289.54	12.09	1.94E-03	-141.66
NDMI	3	314.95	37.50	5.89E-09	-154.37
Null	2	326.62	49.17	1.72E-11	-161.26

Table A-9b. AIC table for the second round of balsam fir percent nitrogen models. The EVI-GDD interaction term was removed as a pretending variable.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
EVI+GDD+NDMI+EVI*NDMI	6	292.22	0	0.71	-139.72
EVI+GDD+NDMI	5	295.00	2.77	0.18	-142.22
GDD+NDMI	4	296.16	3.94	0.10	-143.90
GDD	3	300.62	8.40	0.01	-147.20
EVI+GDD	4	302.07	9.84	5.16E-03	-146.85
EVI+NDMI+EVI*NDMI	5	318.04	25.81	1.76E-06	-153.74
NDMI	3	319.49	27.26	8.51E-07	-156.64
EVI+NDMI	4	321.55	29.32	3.04E-07	-156.59
Null	2	326.62	34.40	2.40E-08	-161.26
EVI	3	328.10	35.88	1.15E-08	-160.94

Table A-9c. AIC table for the second round of balsam fir percent phosphorus models.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
EVI+GDD+NDMI+EVI*NDMI +GDD*NDMI	7	296.09	0	0.64	-140.52
EVI+GDD+NDMI+EVI*GDD+ EVI*NDMI+GDD*NDMI	8	298.25	2.15	0.22	-140.44
EVI+GDD+NDMI+EVI*NDMI	6	300.46	4.37	0.07	-143.84
EVI+GDD+NDMI+EVI*GDD+ EVI*NDMI	7	301.55	5.46	0.04	-143.25
GDD+NDMI+GDD*NDMI	5	304.35	8.26	0.01	-146.90
GDD+NDMI	4	304.53	8.43	9.41E-03	-148.08
EVI+GDD+NDMI+GDD*NDMI	6	306.58	10.48	3.38E-03	-146.90
EVI+GDD+NDMI	5	306.71	10.62	3.16E-03	-148.08
EVI+NDMI+EVI*NDMI	5	308.30	12.20	1.43E-03	-148.87
EVI+GDD+NDMI+EVI*GDD+ GDD*NDMI	7	308.62	12.53	1.22E-03	-146.78
EVI+GDD+NDMI+EVI*GDD	6	308.94	12.84	1.04E-03	-148.08
NDMI	3	313.90	17.81	8.67E-05	-153.84
GDD	3	314.67	18.57	5.92E-05	-154.22
EVI+NDMI	4	315.36	19.27	4.18E-05	-153.50
EVI+GDD	4	315.70	19.58	3.59E-05	-153.65
EVI+GDD+EVI*GDD	5	317.86	21.76	1.20E-05	-153.65
EVI	3	324.45	28.36	4.45E-07	-159.12
Null	2	326.62	30.53	1.50E-07	-161.26

Table A-9d. AIC table for the second round of balsam fir carbon:nitrogen models. The EVI-GDD and NDMI-GDD interaction terms were removed as pretending variables.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
EVI+GDD+NDMI+EVI*NDMI	6	894.24	0	0.91	-440.73
EVI+GDD+NDMI	5	899.22	4.98	0.08	-444.33
GDD+NDMI	4	902.54	8.30	0.01	-447.09
GDD	3	908.02	13.77	9.28E-04	-450.90
EVI+GDD	4	908.64	14.40	6.79E-04	-450.14
EVI+NDMI+EVI*NDMI	5	918.70	24.46	4.44E-06	-454.07
NDMI	3	922.82	28.58	5.66E-07	-458.30
EVI+NDMI	4	924.28	30.04	2.72E-07	-457.96
Null	2	930.97	36.72	9.64E-09	-463.43
EVI	3	932.94	38.69	3.60E-09	-463.36

Table A-9e. AIC table for the second round of balsam fir carbon:phosphorus models. The EVI-GDD interaction term was removed as a pretending variable.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
EVI+GDD+NDMI+EVI*NDMI +GDD*NDMI	7	1808.30	0	0.79	-896.62
EVI+GDD+NDMI+EVI*NDMI	6	1811.08	2.78	0.20	-899.14
EVI+NDMI+EVI*NDMI	5	1819.23	10.93	3.35E-03	-904.34
GDD+NDMI	4	1819.27	10.97	3.28E-03	-905.45
GDD+NDMI+GDD*NDMI	5	1820.32	12.02	1.94E-03	-904.88
EVI+GDD+NDMI	5	1821.19	12.89	1.26E-03	-905.32
EVI+GDD+NDMI+GDD*NDMI	6	1822.33	14.03	7.10E-04	-904.77
GDD	3	1825.71	17.42	1.31E-04	-909.75
EVI+GDD	4	1827.64	19.34	4.99E-05	-909.64
NDMI	3	1828.11	19.89	3.94E-05	-910.95
EVI+NDMI	4	1830.11	21.81	1.45E-05	-910.87
EVI	3	1836.78	28.48	5.17E-07	-915.28
Null	2	1836.91	28.61	4.85E-07	-916.40

Table A-10. AIC table for the second round of red maple models. NDMI was removed as a pretending variable.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
EVI+GDD+EVI*GDD	5	319.36	0	0.78	-154.42
EVI+GDD	4	322.58	3.22	0.16	-157.12
GDD	3	324.33	4.70	0.06	-159.06
EVI	3	335.49	16.13	2.45E-04	-164.64
Null	2	343.64	24.28	4.16E-06	-169.77

Table A-11. AIC table for the second round of white birch modelsEVI was removed as a pretending variable.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
GDD	3	264.44	0	0.66	-129.09
GDD+NDMI	4	266.61	2.17	0.22	-129.09
GDD+NDMI+GDD*NDMI	5	267.80	3.36	0.12	-128.58
Null	2	284.07	19.63	3.58E-05	-139.97
NDMI	3	286.20	21.76	1.24E-05	-139.97

Table A-12. AIC table for the second round of lowbush blueberry models.

Model	K	AICc	Δ AICc	AICc Weight	Log Likelihood
EVI+GDD+NDMI+EVI*GDD+ EVI*NDMI+GDD*NDMI	8	488.33	0	0.33	-235.77
EVI+GDD+NDMI+EVI*GDD+ GDD*NDMI	7	489.13	0.79	0.22	-237.26
EVI+GDD+NDMI+EVI*GDD+ EVI*NDMI	7	489.76	1.43	0.16	-237.57
EVI+GDD+NDMI+EVI*GDD	6	489.90	1.56	0.15	-238.72
EVI+GDD+NDMI+EVI*NDMI	6	492.07	3.74	0.05	-239.81
EVI+GDD+NDMI	5	492.35	4.01	0.04	-241.01
EVI+GDD+NDMI+EVI*NDMI+ GDD*NDMI	7	493.63	5.30	0.02	-239.51
EVI+GDD+NDMI+GDD*NDMI	6	494.12	5.79	0.02	-240.83
GDD+NDMI	4	499.65	11.32	1.15E-03	-245.72
GDD+NDMI+GDD*NDMI	5	501.42	13.09	4.73E-04	-245.55
GDD	3	509.64	21.29	7.83E-06	-251.75
EVI+GDD	4	509.84	21.51	7.03E-06	-250.81
EVI+GDD+EVI*GDD	5	510.37	22.04	5.38E-06	-250.02
EVI+NDMI	4	516.38	28.05	2.67E-07	-254.08
EVI+NDMI+EVI*NDMI	5	518.10	29.77	1.13E-07	-253.89
NDMI	3	525.86	37.53	2.33E-09	-259.87
Null	2	545.10	56.76	1.55E-13	-270.52
EVI	3	545.63	57.30	1.19E-13	-269.75

Appendix B. Chapter 3 Supplementary Figures and Tables

Additional Methods

In this appendix, I provide additional details on my chapter 3 methods. Figures B-1 and B-2 show the principal component analyses (PCAs) used to analyze the group of habitat complexity variables that we measured. The first axis (PC1) was extracted from each at every sampling point and used as explanatory variables for perceived predation risk in subsequent models. Figure B-1 represents understory habitat complexity and Figure B-2 represents overstory habitat complexity.

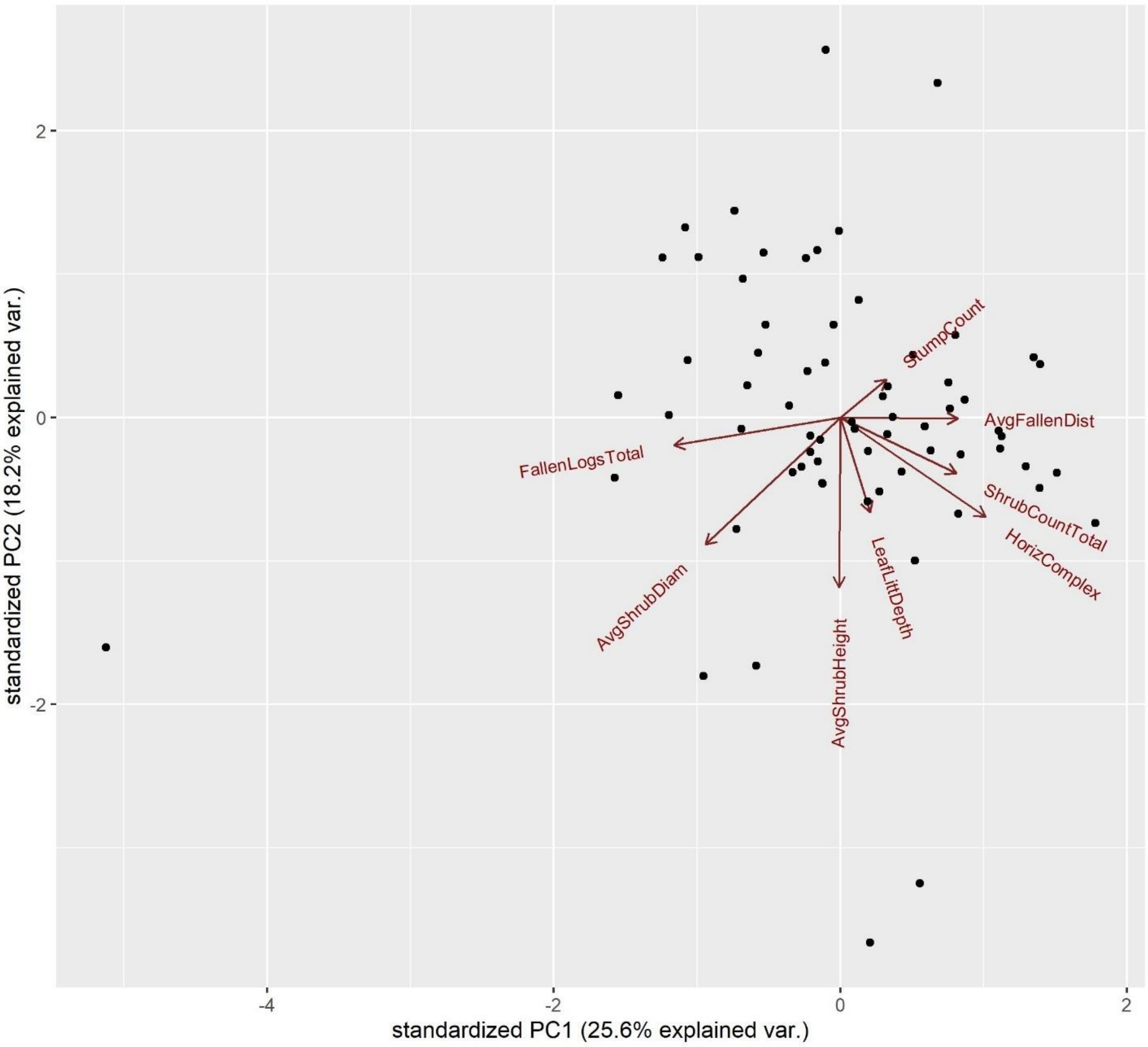

Figure B-1. Principal components analysis (PCA) for all understory habitat complexity variables. Vectors represent magnitude and direction of effect of each understory habitat complexity variable measured. Points represent the sampling points where habitat complexity data was measured (n = 72 originally, after removing for any NA values n = 67). Values of PC1 for each sampling point were extracted and used in further analysis.

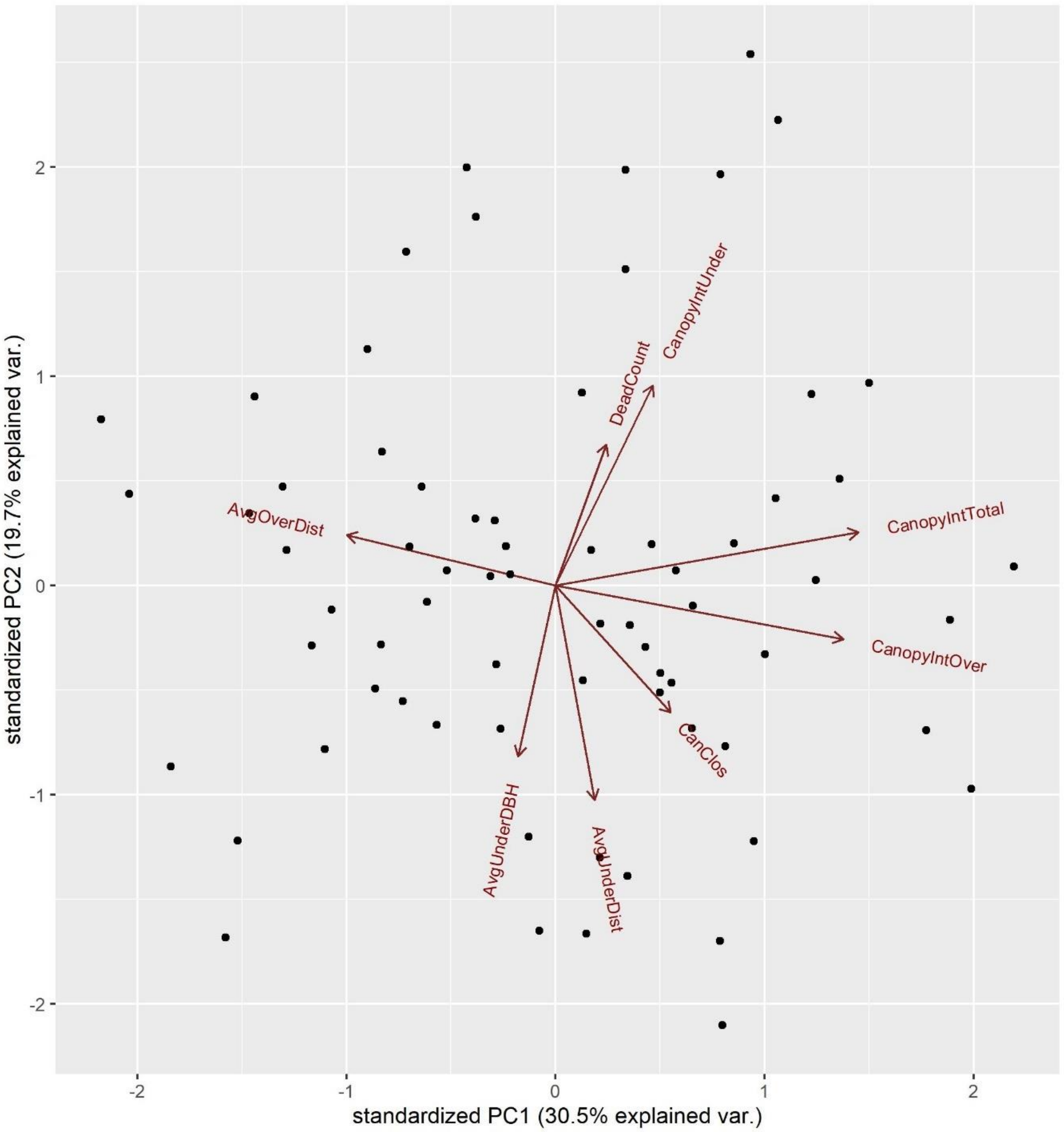

Figure B-2. Principal components analysis (PCA) for all overstory habitat complexity variables. Vectors represent magnitude and direction of effect of each overstory habitat complexity variable measured. Any highly correlated vectors were removed prior to PCA. Points represent the sampling points where habitat complexity data was measured (n = 72 originally, after removing for any NA values n = 67). Values of PC1 for each sampling point were extracted and used in further analysis.

Additional Results

In this appendix, I provide additional details on chapter 3 results. Tables B-1 and B-2 are the full summary tables for the top-ranking model in both groups of models. For both groups, population and individual effects, food quality was the top-ranking models. All models were general linear models with Gaussian error distribution. The response variable, kernel utilization distribution (KUD), was log-transformed prior to analysis. Table B-1 shows the summary table for the population effect and Table B-2 shows the summary table for the individual effect. Figure B-3 shows the variation in lowbush blueberry C:N and C:P, as well as the variation in understory and overstory habitat complexity across the study site.

Table B-1. Summary table of our top-ranking model in our model comparison. Fixed effects indicate population level effects and random effects indicate individual level effects. The top ranked model was Food Quality. The Food Quality model included kernel utilization distribution as the response variable. Fixed explanatory variables included lowbush blueberry C:N, lowbush blueberry C:P, and their interaction. C:N had variable slopes across individuals. The model was a linear mixed effects model with a Gaussian error distribution. The response variable, kUD (kernel utilization distribution) was log-transformed to meet assumptions of normality. Explanatory variables were scaled prior to analysis. C:N = Lowbush blueberry carbon:nitrogen, C:P = Lowbush blueberry carbon:phosphorus, understory = understory habitat complexity, overstory = overstory habitat complexity.

Fixed Effects	**Estimates**	**CI**
Intercept	-2.31	-2.38 – (2.24)
C:N	0.19	0.07 – 0.30
C:P	-0.044	-0.111 – 0.022
C:N*C:P	-0.046	-0.114 – 0.022
Random Effects	**Variance**	**Standard Deviation**
Individual (Intercept)	0.05	0.22
C:N	0.19	0.44
Residual	3.55	1.88

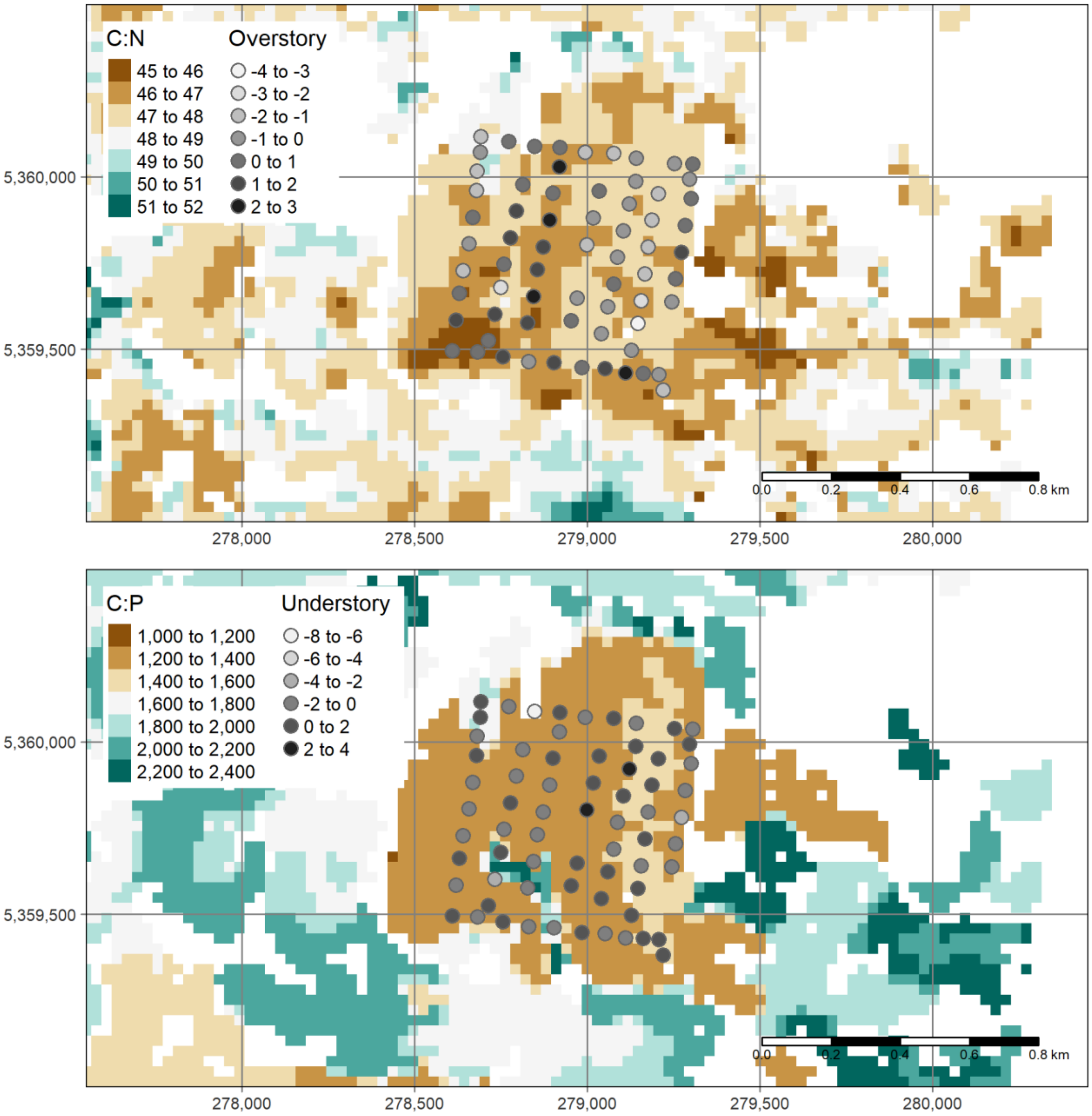

Figure B-3a. Top panel showing the lowbush blueberry C:N surrounding the study site, with lower values of C:N indicating a higher quality forage. Overlaid on the food quality raster are the overstory habitat complexity sampling points, colour represents the value from the extracted overstory complexity PCA axis. **3b.** Bottom panel showing the lowbush blueberry C:N surrounding the study site, with lower values of C:P indicating a higher quality of forage. Overlaid on the food quality raster are the understory habitat complexity sampling points, colour represents the value from the extracted understory complexity PCA axis. A darker colour of bubble indicates a more complex habitat and therefore more shelter from predators. Map projection is in WGS 86 UTM 22N (epsg: 32622).

Appendix C. Bayesian Analysis for Chapter 3

In this appendix, I provide the methods and results for an additional Bayesian analysis done post-examination. This analysis was done due to the non-Gaussian nature of the data in Chapter 3. The methods other than the statistical analysis remain the same. Table C-1 shows the model construction of the four competing models. Table C-2 shows the results of the model comparison using the Deviance Information Criterion. Figure C-1 shows the varying slopes of random effects in food quality and perceived predation risk models across all individual hares. Figure C-2 shows the relationship between the slopes of each individual hare for each random effect in the food quality and perceived predation risk models. Figure C-3 shows the relationships between intensity of space use (measured using kernel utilization distribution of snowshoe hare, n = 30) and each of the explanatory variables at the population level.

Methods

We extracted the normalized probability density function of the 95% KUD, a measure of the intensity of space use, at each habitat complexity sampling point for every individual hare. No hare home ranges overlapped all habitat complexity sampling points. Therefore, when a snowshoe hare home range did not overlap with one of the 72 habitat complexity sampling points and the extracted value was therefore zero, we changed the value to NA. In addition, we extracted predicted lowbush blueberry C:N, C:P, understory complexity, and overstory complexity at each of the habitat complexity sampling points. Before analysis, we centered and scaled all explanatory variables by subtracting the variable mean from each value and then dividing the subtracted value by the variable's standard deviation. After extracting and scaling the data, we ran four generalised mixed effects models with the KUD values as our response variable. The models were run using a Markov chain Monte Carlo (MCMC) sampler from the *MCMCglmm* package with 420,000 iterations each, a burn-in period of 20,000, and a thinning internal of 100 (Hadfield 2010). We used a Bayesian approach for our generalised models due to the non-Gaussian structure of the data. We designed the models to test the effect of the predation risk/food quality trade-off at the population level using the fixed effects, and at the individual level using the random effects. Our fixed effect explanatory variables were lowbush blueberry C:N and C:P, and the overstory and understory complexity. Our random effect explanatory variables were lowbush blueberry C:N, lowbush blueberry C:P, understory complexity, and overstory complexity with varying slopes and intercepts across individuals. We evaluated the four competing models using Deviance Information Criterion (Table C-1, DIC, Spiegelhalter et al. 2002).

We compared three models plus a null (intercept-only) model with DIC. Our first model was the global model which included lowbush blueberry C:N and C:P, overstory and understory complexity, all two-way interaction terms of fixed effects, and all four variables varying across individuals as random effects. Our second model was a food quality model, with lowbush blueberry C:N and C:P, their interaction term, and C:N and C:P varying across individuals as random effects. Our third model was a perceived predation risk model, with overstory complexity, understory complexity, their interaction term, and understory complexity and overstory complexity varying across individuals as random effects. Finally, our last model was a null model, which included the intercept and individuals as a random effect. Lastly, we regressed the random slopes to test for individual-based trade-offs between all random effects from the food quality and perceived predation risk models (Fig. C-2). We extracted the slope value of each random effect for each individual hare and regressed them against each other to visualize the trade-offs occurring at the individual level. We calculated all generalised linear mixed effects models using the *MCMCglmm* package and completed all DIC using the *MuMIn* package. We performed all statistical analysis in R 4.0.0 (Hadfield 2010; Barton 2020; R Core Team 2020). All code and data used for our analyses are available at https://github.com/icrichmond/HareSpaceUse.

Table C-1. Model construction of our four models. Fixed effects test the predation risk food quality trade-off at the population level and random effects test the trade-off at the individual level. The models were run using a Markov Chain Monte Carlo sampler and had 420,000 iterations each. The explanatory variables were scaled before analysis. kUD = kernel utilization distribution, C:N = lowbush blueberry Carbon:Nitrogen, C:P = lowbush blueberry Carbon:Phosphorus, understory = understory habitat complexity, overstory = overstory habitat complexity.

Model Name	Model Parameters
1 – Global	kUD ~ overstory + understory + C:N + C:P + overstory*understory + C:N*C:P + overstory*C:N + overstory*C:P + understory*C:N + understory*C:P + (1+C:N|Individual) + (1+C:P|Individual) + (1+understory|Individual) + (1+overstory|Individual)
2 – Habitat Complexity	kUD ~ overstory + understory + overstory*understory + (1+understory|Individual) + (1+overstory|Individual)
3 – Food Quality	kUD ~ C:N + C:P + C:N*C:P + (1+C:N|Individual) + (1+C:P|Individual)
4 – Intercept	kUD ~ 1 + (1|Individual)

Results

Overview

Values of lowbush blueberry C:N ranged from 45.41 to 48.64 (mean = 46.96) and variation in C:P ranged from 1205.04 to 1899.04 (mean = 1349.83) at the points sampled for analysis. Understory complexity at each sampling point, as measured using values from the first PCA axis of the understory variable PCA, ranged from -7.34 to 2.55, with a mean very close to zero (1.03×10^{-16}). Overstory complexity at each sampling point, as measured using the values from the first PCA axis of the overstory variable PCA, ranged from -3.37 to 2.61 with a mean very close to zero (-4.52×10^{-16}). KUD values were bound by 0 and 1 so they could be compared across individuals, with a mean of 0.13 at the points sampled for analysis.

Model Comparison

We used DIC to compare four models that explored our predictions for the effect of the perceived predation risk food quality trade-off (Table C-1). The fourth model, our null model, ranked highest in our DIC (Table C-2). All other models had greater than 10 ΔDIC. None of the fixed effects was highly correlated in our models.

Population & Individual Variation

There were no ecologically significant trends at the population level in our models (Fig. C-3). Individual hares exhibited different strategies of space use depending on all observed measures of food quality and perceived predation risk (Fig. C-1). The direction of the effect and the magnitude depended on the individual for lowbush blueberry C:N (-0.15 to 0.71, Fig. C-1A), lowbush blueberry C:P (-0.15 to 0.71, Fig. C-1B), understory habitat complexity (-0.088 to 0.49, Fig. C-1C), and overstory habitat complexity (-0.088 to 0.49, Fig. C-1D).

Food Quality-Predation Risk Interaction

We found no consistent correlation for the food quality-predation risk interaction at the individual level. There were two statistically significant correlations found, the first was a negative correlation between lowbush blueberry C:P and overstory complexity (R = -0.40, p = 0.037, Fig. C-2A) and the second was a positive correlation between lowbush blueberry C:N and understory complexity (R = 0.50, p = 0.0085, Fig. C-2D). The other two correlations were negative but insignificant, between lowbush blueberry C:N and overstory complexity (R = -0.29, p = 0.15, Fig. C-2B) and lowbush blueberry C:P and understory complexity (R = -0.33, p = 0.097, Fig. C-2C).

Table C-2. DIC table showing the model comparison for the four competing models. Habitat complexity was used as a proxy for perceived predation risk and the intercept model refers to our null model. df = degrees of freedom; Δ DIC = difference in DIC value from next highest model; DIC = deviance information criteria value; DIC Weight = normalized relative likelihood of a model; Log Likelihood = relative likelihood of the model or relative strength of evidence. Models are generalised mixed effects models run using a Markov chain Monte Carlo sampler with 420,000 iterations each.

Model name	df	Δ DIC	DIC	DIC Weight	Log Likelihood
4 – Intercept	3	0.00	-89.79	0.999	60.01
2 – Food Quality	9	15.19	-74.60	0.001	81.89
3 – Predation Risk	9	32.96	-56.83	0.000	73.24
1 – Global	18	67.06	-22.73	0.000	86.04

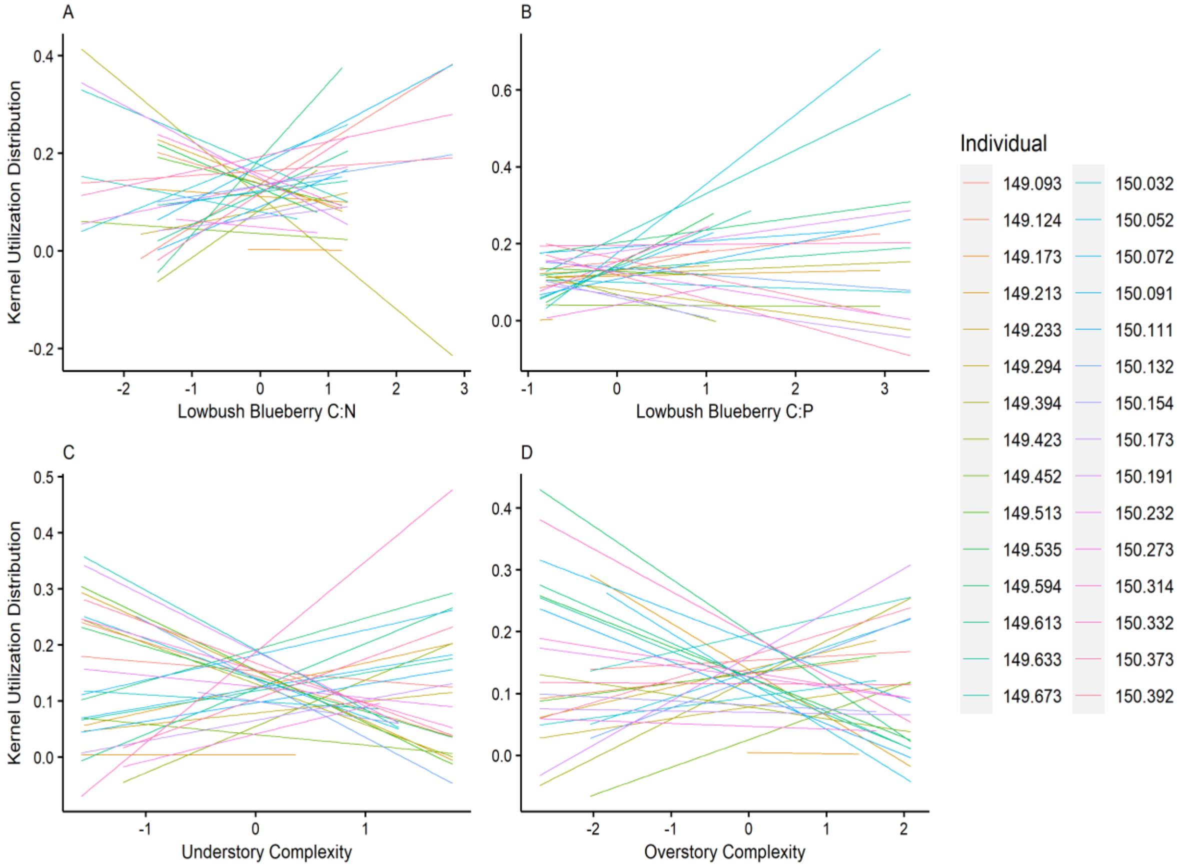

Figure C-1. The varying slopes of random effects in food quality and perceived predation risk models. The random effects vary across each individual snowshoe hare (n = 30). A) predicted lowbush blueberry C:N B) predicted lowbush blueberry C:P C) understory habitat complexity D) overstory habitat complexity.

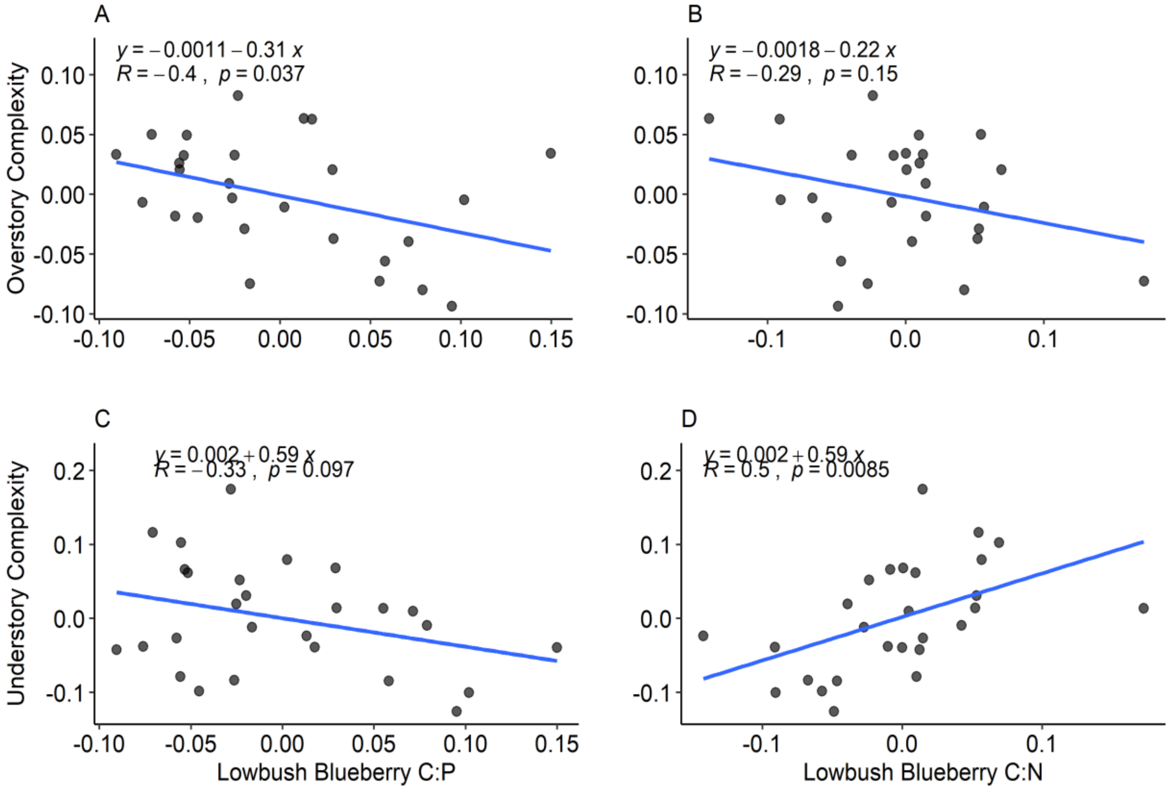

Figure C-2. Relationship between the slopes of each individual hare for each random effect in the food quality and perceived predation risk models. A) lowbush blueberry C:P and overstory habitat complexity, B) lowbush blueberry C:N and overstory habitat complexity, C) lowbush blueberry C:P and understory habitat complexity, D) lowbush blueberry C:N and understory habitat complexity. Slopes were extracted from the food quality and predation risk models from the second group of models. The line represents a linear regression line. Each point represents one individual hare in the study (n = 30). R indicates the Pearson correlation coefficient, p represents the associated p-value with the Pearson correlation, and the equation represents the linear regression.

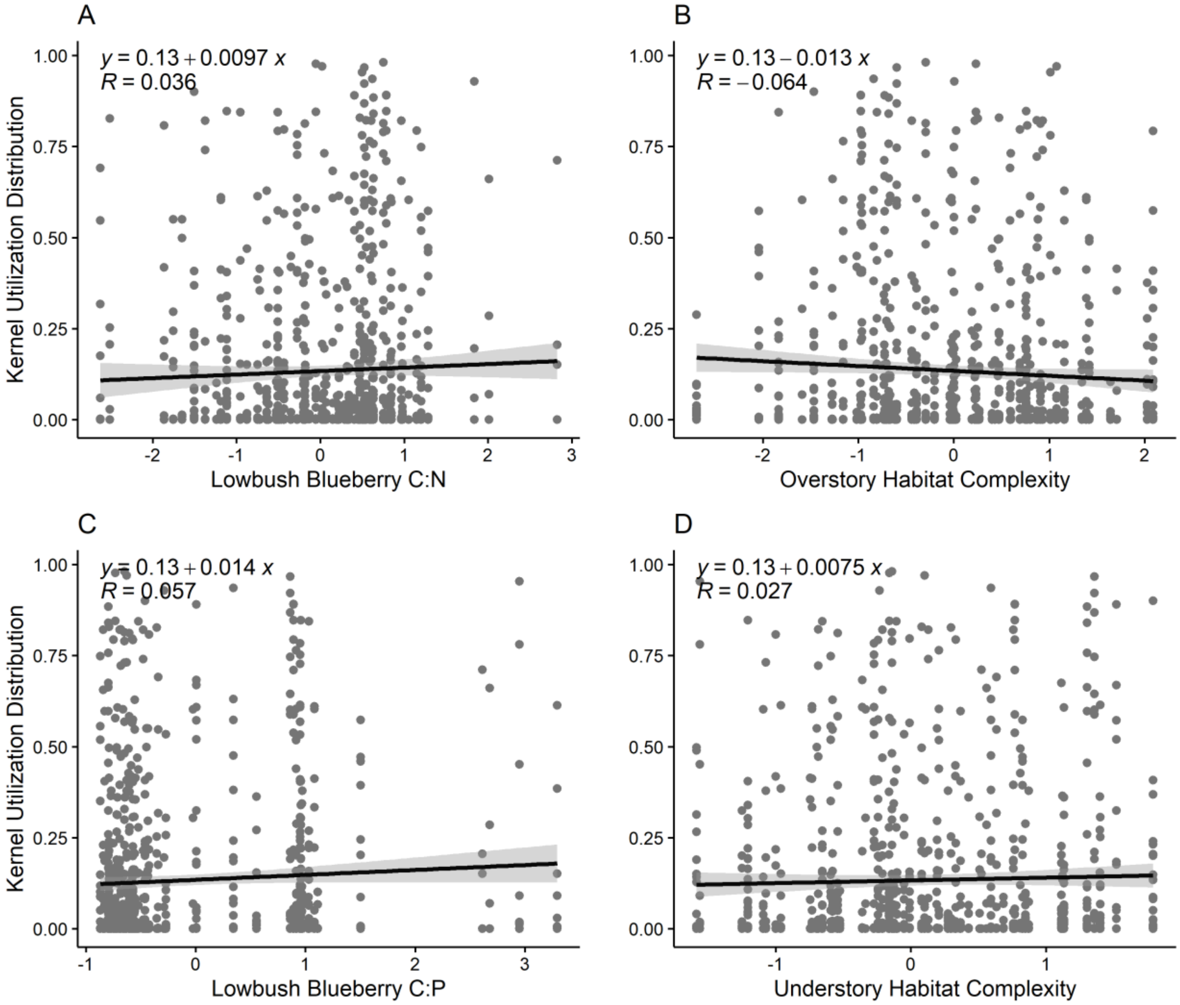

Figure C-3. Relationship between intensity of space use (measured using kernel utilization distribution of snowshoe hare, n = 30) and each of the explanatory variables at the population level. A) lowbush blueberry C:N (carbon:nitrogen), B) overstory habitat complexity, C) lowbush blueberry C:P (carbon:phosphorus), D) understory habitat complexity. The line represents a linear regression line and the ribbon depicts the 95% confidence intervals. Each point represents a sampled value (n = 938).

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