

**ECOLOGICAL IMPACTS OF TIMBER HARVEST ON COASTAL BRITISH
COLUMBIA'S RIPARIAN PLANT COMMUNITIES THROUGH FUNCTIONAL
TRAIT ANALYSIS**

by

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Abstract

Riparian areas are fundamental for the function of headwater streams, as they provide nutritional and physical inputs and processes essential for ecosystem function. I examined how timber harvest affects the riparian shrub and herb communities of headwater streams to better understand the associated impacts on ecological processes in British Columbia's coastal small-stream ecosystems. By analyzing effects of environmental gradients at three sites each of three intensities of riparian harvest which were complete tree removal (non-buffered), partial tree retention (buffered) and reference sites, shifts in riparian ecological processes were indicated through plant functional trait responses to conditions such as light and temperature; significant differences were found among species and communities trait values. Buffered sites had intermediate trait values between those of the reference and non-buffered sites. Specific leaf area and leaf nitrogen content values were highest at reference sites, intermediate at buffered sites, and lowest at non-buffered sites; stem specific density and leaf carbon content were highest at non-buffered sites and lowest at reference sites. Directional relations of the six focal traits with the three treatments were consistent for the community-weighted values, and most of the eight focal species' values. These treatment effects were more evident in the physiological plant traits than chemical traits. Buffers of riparian tree retention showed moderating effects to the environmental changes associated with timber harvest that most strongly influence the plant functional traits studied.

Lay Summary

Small streams account for a large area of watersheds but are poorly protected by British Columbia's forest policies. Through assessing riparian plant communities across a gradient of logging intensities, changes to forest understory were observed. Plants adjacent to small streams in unharvested reference forests, harvested forests with tree retention buffers around streams, and harvested forests with no retention buffers were compared, and showed changes both at the individual, and community levels. Changes to these riparian plant communities have impacts on both the small streams adjacent to them, and larger streams into which they flow. The implications of these changes in riparian plants are detrimental to the proper functioning of forest stream ecosystems. The data in this study show that timber harvest changes environmental conditions on which riparian plant communities are dependent, and that cut blocks with trees retained beside these streams have some mitigation capacity to those environmental changes.

Preface

This is an original, independent and unpublished thesis by the author, A. Bryn-Thorn.

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Glossary

7-day-max: the seven-day frame of the study period, during which the moving average temperature was highest for both air and soil, averaged across all nine sites.

B: Buffered (sites); contiguous area of retained trees surrounding both sides of a stream within a timber harvest block.

BC: British Columbia

DEM: Digital elevation model

GW: Groundwater

LME: Linear mixed effects

NA: Not applicable

NB: Non-buffered (sites); no contiguous tree retention on either side of a stream within a timber harvest block

Q-Q: Quantile-quantile

R: Reference (sites); no timber harvest for at least 30 m of either side of the stream

SD: Standard deviation

Tukey's HSD: Tukey's honest significant difference

USA: United States of America

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Dedication

I am honoured to have had the opportunity to work with the lands and water bodies that have been stewarded by the Katzie First Nations peoples since time immemorial. I acknowledge that my access to this research forest is in part due to my privilege as a male descendent of colonial European settlers, whose rights and access to resources supersedes those of First Nations peoples through systemic racism and oppression, and historical genocide.

To my family and friends with such unwavering support during this chapter in my life, this period was an unpredictable roller coaster and I am more resilient from it through my connections with you. My deepest gratitude to Gail, Martin, Tara, Helena, Sabine, and Georgia; thank you for the epic nurturance and encouragement. Lastly, I recognize myself for the perseverance and determination it took to navigate this journey with ambition and passion.

1. INTRODUCTION

As the frequency and magnitude of natural and human-sourced disturbances increase, environmental variability and extreme weather events are also increasing; anthropogenic actions and decisions have altered global ecosystems and their disturbance regimes (Chapin, Matson, & Vitousek, 2011). Historically, ecosystem function could recover from the magnitude of disturbances that occurred; ecosystem resilience is the ability to recover structure and function, re-establishing the capacity of the system to reorganize from subsequent shifts in environmental conditions (Holling, 1973; Walker, Holling, Carpenter, & Kinzig, 2004). Today, ecosystems are shifting towards, and then beyond critical tipping points (those limits of resilience) that lead to alternative ecosystem states, which resist recovery to previous rates of ecological functions (Truitt et al., 2015). Mass extinction, polar ice-cap and glacial melt, and large-scale deforestation are some of the most extreme challenges the Earth has experienced over the last few decades (Capon & Pettit, 2018; Miyamoto, 2020; Scheffer, Carpenter, Foley, Folke, & Walker, 2001; Truitt et al., 2015). Both cumulative and individual effects of urbanization, agricultural land conversion, lack of environmental legislation, and shifts in climate have been documented across the globe (Filbee-Dexter & Scheibling, 2014; Naeem, Thompson, Lawler, Lawton, & Woodfin, 1995).

Deforestation and industrial forestry pressures are evident worldwide, as forest harvesting supports the livelihood of millions of people, the majority of which is done for subsistence fuel wood in many countries (Agrawal et al., 1999; Larson, 2011). Societies that have the economic and political capacity for stewardship must uphold the highest environmental standards, thus developing best-practices and technologies that can address the challenges being faced across the globe (Lambin & Meyfroidt, 2011). In developed countries with rich resource pools, such as

Canada, environmental and natural resource policy needs to be progressive and sustainable. Forest and land managers today face unpredictable and highly dynamic environments; their task is to estimate and assess what historical forms of management have been disruptive to natural systems, and develop management practices that address current and future climatic uncertainty and variability.

1.1 Terrestrial Impacts from Forest Management

Old forestry paradigms from practices before and during the 1900s, such as high-grade timber selection, clear-cut harvest systems, and the absence of riparian protection have left a legacy of mismanaged forest ecosystems, giving rise to more socially and ecologically sustainable forest practices towards the end of the 20th century (Innes, 2003; Niquidet, 2008). Profitability of timber harvest often directly conflicts with the maintenance of ecological and structural diversity; since they cannot be prioritized together, the trade-off often favours industrial forest exploitation (Holland, Lilieholm, & Roberts, 1993). The result is that forest ecosystems across the globe are often managed for maintaining timber production while insufficiently protecting forest function and structure (Krumm, Schuck, & Rigling, 2020; Larson & Lohrengel, 2011). Anthropogenic modifications to forests show significant impacts on their physical, chemical, and biological conditions, impairing the function of forest ecosystems (Clogg, Gage, & Haddock, 2002; Erdozain, Kidd, Kreutzweiser, & Sibley, 2018; Likens, Bormann, Johnson, Fisher, & Pierce, 1970; Warren, Keeton, et al., 2016). Natural systems such as forests are inherently dynamic; however, with such impactful human activities, ecosystem function can shift, and is often not recoverable (Filbee-Dexter & Scheibling, 2014).

There are disproportionate impacts of harvesting trees from riparian zones relative to other forest areas due to their linkages to both in-situ, and related terrestrial and aquatic ecosystem functions

and processes. These include moist microclimate corridor stability (Oldén, Selonén, Lehtonen, & Kotiaho, 2019), riparian obligate species habitat (often prioritized for conservation; Aguiar et al., 2018; Tyler & Peterson, 2004)), and stream morphological, hydrological and ecological maintenance (e.g. Moore, Spittlehouse, & Story, 2005; Richardson, Naiman, Swanson, & Hibbs, 2005; Wipfli, Richardson, & Naiman, 2007). These ecological conditions in riparian areas are mediated by light attenuation and soil temperature fluctuation more strongly by management decisions and climate change than in other forested areas (Capon et al., 2013). Significant shifts in plant and animal community composition that impact many trophic levels and communities – both terrestrial and aquatic – have been linked to anthropogenic stressors in riparian forests, including forest management and timber harvest in riparian areas without sufficient retention buffers (e.g. Johnson, Strengbom, & Kouki, 2014; Kominoski et al., 2013; Oldén, Peura, Saine, Kotiaho, & Halme, 2019; Peter & Harrington, 2018). Terrestrial plants, invertebrates and the soil microbiome facilitate nutrient cycling in the areas adjacent to streams, which converts detritus into labile nutrients, thus supporting microbial, fungal and plant establishment and growth (Chapin et al., 2011). The structural integrity of the riparian zone is dependent on the presence of terrestrial habitat for the biota it supports; vascular plant roots in the riparian zone ensure the maintenance of these terrestrial habitats through their contribution to bank-stability (Pollen, Simon, & Collison, 2004).

1.2 Aquatic Impacts from Timber Harvest

One of the many complex ecosystems susceptible to ecological shifts in forests are the coupled stream-riparian ecosystems. These are the zones of direct interaction between terrestrial communities of plants, animals and micro-biota that influence the taxa and processes of the neighbouring aquatic habitat (Sweeney & Newbold, 2014). The result is an inter-dependent,

coupled ecotone that relies on the function of both its terrestrial and aquatic components (Biswas, Mallik, Braithwaite, & Biswas, 2018; Naiman, Bechtold, Beechie, Latterell, & van Pelt, 2010). These linkages are especially integral to ecosystem function for small, allochthonous source streams (often referred to as headwaters) that are much more closely coupled with their terrestrial riparian area than larger streams (Wipfli et al., 2007; Wohl, 2017).

Stream-riparian ecosystems are very important to protect, as they support organisms through the exchange of subsidies between forest terrestrial and aquatic zones (Hjältén, Nilsson, Jørgensen, & Bell, 2016; Richardson & Sato, 2015; Richardson, Zhang, & Marczak, 2010). Essential services from these systems such as aesthetics, carbon sequestration and storage, production of habitat and food for higher trophic levels, filtration and protection of water quality, in addition to the regulation of climatic conditions (Grizzetti et al., 2016); these are especially integral to the survival of humans and other organisms alike (Richardson & Hanna, in press). Coupled stream-riparian systems provide inputs, and ecological processes - such as aquatic metabolism mediation - that are important to the functioning of streams, and therefore contribute to the function of the forest ecosystems in which they reside (Moore & Richardson, 2003; Warren et al., 2016).

In a coupled stream-riparian system, resistance and resilience to disturbance is supported by many different ecological processes and services; the success of which are largely mediated by functional, structural, and taxonomic diversity (Kominoski et al., 2013; Scheffer et al., 2001; Sweeney & Newbold, 2014b). Implications of timber harvest in the Pacific Northwest on these stream-riparian processes include lowered diversity of aquatic and terrestrial habitats, decreased food web productivity, lowered quality and quantity of terrestrial stream inputs, and loss of stream and riparian temperature regulation (Kiffney, Richardson, & Bull, 2003; Richardson & Béraud, 2014; Kaylor & Warren, 2018). Forestry best-management practices (BMPs) for aquatic

and riparian protection have shown varying capacity to mitigate shifts in ecological function following timber harvest due to inadequate evaluation of these BMPs, and insufficient documentation and legislation for adaptively improving practices (Kuglerová, Hasselquist, et al., 2017; Richardson, Naiman, & Bisson, 2012; Warrington et al., 2017).

Healthy streams - especially headwaters, and streams with high structural heterogeneity - host a gradient of microclimates which provide refugia for taxa with specific habitat requirements, and therefore contribute to the resilience of these systems (Hildrew & Townsend, 1994; Wipfli et al., 2007). Rates of heating and cooling of the riparian soil matrix and the adjacent stream channel are moderated through the interception of solar insolation by riparian plants, in addition to the temperature buffering capacity of the soil matrix itself (Kreutzweiser, Hazlett, & Gunn, 2008). Post-harvest streamflow and temperatures are altered, and can take many years to recover to pre-harvest conditions (Coble et al., 2020; Hicks, Beschta, & Harr, 1991; Kaylor & Warren, 2018; Moore & Wondzell, 2005). In an Oregon, USA study, streams in regenerating Douglas-fir stands aged between 40 to 53 years showed flow rates up to 50% higher than 110 year old reference stands (Coble et al., 2020). Detrital and terrestrial invertebrate inputs into streams, especially into smaller streams, from the riparian zone are essential food resources for the aquatic invertebrate communities; riparian forest harvest can change these inputs, affecting stream productivity and causing trophic responses in downstream reaches (Richardson & Sato, 2015; Studinski & Hartman, 2015; Wallace, Eggert, Meyer, & Webster, 2008; Wipfli et al., 2007). Riparian plants contributing stream shading and detrital inputs are some other important roles these plant communities have in the success of streams and their riparian areas (Warren, Keeton, et al., 2016). These riparian processes and contributions are essential for proper functioning of forest

ecosystems; reciprocally, unimpaired function and structure of forests are essential for supporting healthy riparian processes and contributions (Wipfli et al., 2007; Wohl, 2017).

Riparian and aquatic ecosystem structure and function are altered from industrial development and anthropogenic climatic shifts (Capon & Pettit, 2018). Both direct and indirect effects of human-driven disturbance on terrestrial riparian areas and their associated streams have been monitored, measured and analyzed for decades (e.g. Burt, Howden, McDonnell, Jones, & Hancock, 2015; Likens, Bormann, Johnson, Fisher, & Pierce, 1970; Moore, Spittlehouse, & Story, 2005; Richardson & Béraud, 2014). Demonstrating those shifts in riparian ecosystems is important for assessing impacts on the broad biodiversity that riparian ecosystems support within forests and at the landscape-level (Capon et al., 2013).

1.3 Forest and Riparian Management in British Columbia

Because of their economic and social importance, forested aquatic and terrestrial systems have been studied for their resilience to, and impacts from timber harvest; however, there is insufficient protection for these integrated, inter-dependent forest systems (Erdozain et al., 2018; Likens et al., 1970; Richardson & Béraud, 2014; Sweeney & Newbold, 2014b; Tschaplinski & Pike, 2009). While timber production in British Columbia (BC), Canada has the potential for sustainable long-term use, forest policy has fallen short on both managing for sustainable wood supply and mitigating long-term, deleterious and detrimental impacts of resource management and extraction practices (Beckley, 1998). Environmental legislation in BC demonstrates how short-term use values often dominate forest lands and resources management.

The functional importance of streams and riparian zones in forests is well understood; however, relevant scientific evidence indicating that these systems are inter-dependent is not incorporated

into policy or regulation of BC's forested areas around small streams. This policy-driven deficiency of riparian and stream ecological protection results in forest resource use associated with large impacts on riparian function (Richardson, 2019). Riparian vegetation is linked to forest ecosystem function through contributions of shade, nutrients, sediment storage, food, and habitat (Capon & Pettit, 2018). Variation of traits within these plant communities can have a significant impact on the ecosystem functions to which they contribute (Abakumova, Zobel, Lepik, & Semchenko, 2016). Stream function is influenced by timber harvest; the elimination of riparian vegetation along headwater streams impacts community-level stream processes, thus affecting functioning of the coupled ecosystem as a whole. For example, hydrological and geological modifications of a stream network have been linked to morphological and functional changes in riverine systems (Naiman et al., 2010). These forest management implications are enabled through the discretionary, results-based policy of the Forest and Range Practices Act that until recently was almost exclusively dependent on the professional reliance of a Forester, and their interpretation of the Forest Stewardship Plan specific to the forest license they manage (British Columbia Ministry of Forests and Range, 2002; Innes, 2003; Tschaplinski & Pike, 2009).

Current regulation partially protects riparian zones of large fish-bearing streams and community watersheds from impacts of forestry; however, it does not define legally-binding riparian retention zones for small headwater streams (Tschaplinski & Pike, 2009). Riparian areas adjacent to BC's small streams receive either minimal partial-retention buffers (S4 and S5 streams; fish-bearing streams <1.5 m wide and non-fish bearing streams <3 m wide, respectively), wherein harvesting up to ninety percent of basal area is permitted, or non-buffered streams of any kind (S6; non-fish bearing streams <1.5 m wide). These standards are interpretable to be averaged

over large timber supply areas and over multiple blocks, which allows for small-scale exceptions to ecological protection (British Columbia Ministry of Forests and Range, 2002). These headwaters are the upper reaches of important streams that *do* require strict management practices, and are thus tributaries that provide important subsidies to these protected streams (Gomi et al., 2006). The management of these sensitive ecosystems in BC contrasts with the more scientifically-informed riparian forest policy of Oregon and Washington States, USA, which better protect small streams and associated riparian zones from harvest-related disturbances (Spies et al., 2007; Tyler & Peterson, 2004).

1.4 Plant functional traits

Over the last century, conservation research, and ecological protection in forest management has focused on taxonomic or structural maintenance, rather than sustaining ecosystem function; this has been insufficient for addressing the increasing rates and types of stressors introduced to forests by anthropogenic activities (Long, 2009). Measuring plant functional traits has emerged as a tool for studying community assembly and ecosystem function, which addresses functional composition, instead (Garnier & Navas, 2012). A functional trait approach allows comparisons of communities beyond taxonomic composition through physiological and chemical plant responses to their environment; this enables comparisons of communities with different species assemblages due to the similarity of their habitat filters (Díaz, Kattge, Cornelissen, et al., 2016). This approach allows for better management and conservation decisions based on inference of ecosystem function, rather than species richness (Cadotte, Carscadden, & Mirotchnick, 2011).

Where a plant species lies within the plant economic spectrum can be assessed through its functional trait measurements, providing insights on its strategies on balancing carbon investment with retention of other nutrients, its efficiency of water transport, and overall

regeneration capacity, growth rate, and limits to survival (Cornwell & Ackerly, 2009; Westoby et al., 2004). These physiological adaptations to different growing conditions provide different process rates and relative contributions to ecosystems. Studies using functional traits have also identified challenges associated with the plasticity of traits to abiotic and biotic factors, and as such must be considered when assessing plant functional traits (Abakumova et al., 2016).

Phenotypic plasticity represents variability in physiological trait expression within one genotype and/or morphological acclimation responses which enable individuals to respond to their environment more successfully, based on the filters most strongly influencing them within a generation (Abakumova et al., 2016). This plastic acclimation to the environment allows shifts that account for changes in edaphic conditions at the micro-site scale, rather than genetic selection between generations for adaptations to growth conditions (Callaway, Pennings, & Richards, 2003; Strand & Weisner, 2004). While plasticity can increase the within-species trait variation, the values themselves when weighted by their abundance demonstrate community-level values that are indicative of growing conditions, regardless of species composition (Mouillot, Graham, Bastien Villé Ger, Mason, & Bellwood, 2013).

Functional traits of plant communities along environmental gradients, such as for temperature and light, can help identify influential components on structure and assembly (Petter et al., 2016). Recognizing patterns in plant community trait distributions can help with inference about growth, survival and reproduction strategies within these communities (S. Díaz, Kattge, Cornelissen, et al., 2016). Kominoski et al. (2013) state that shifts in functional traits of riparian plant communities can have impacts on multiple trophic levels, affecting function at the ecosystem level. Using community-level plant functional trait data can enable researchers to identify plant community responses from shifts in environment, and assess the ecological

significance of those changes (e.g. light gradient effects on potential photosynthetic capacity; Wyka et al., 2012, and flood disturbance on competitiveness; Fu et al., 2014).

Nine sites representing a gradient of riparian forest harvest were established in coastal BC for assessing riparian plant community ecology following timber harvest. Six plant functional traits (Table 1) were examined for the eight most abundant understory species found at the study sites. Those traits were specific leaf area (SLA; $\text{mm}^2 \text{mg}^{-1}$), leaf dry-matter content (LDMC; mg/g), leaf nitrogen (Leaf N; % dry mass), and leaf carbon content (Leaf C, % dry mass) by mass, leaf carbon to nitrogen mass ratio (C:N; mass ratio), and stem-specific density (SSD; mg mm^{-3}). This suite of six traits was selected for its capacity to predict plant population responses based on changing environmental conditions. These predictions by extension allow comparisons of plant community-level dynamics following disturbances such as timber harvest (Garnier & Navas, 2012). Analyzing this suite of traits across treatments demonstrates the functional shifts of a plant community in life-history traits along the leaf economics spectrum, prioritizing resource acquisition, resource conservation, or both (Zukswert & Prescott, 2017).

Functional Trait (units)	Ecological significance	Predicted Treatment Response*	Predicted Mechanism	Reference
		R B NB		
Specific leaf area (mm ² mg ⁻¹)	Photosynthetic efficiency	←	Increased growth relative to structural investment from decreased canopy openness	(Wilson, Thompson, & Hodgson, 1999)
Leaf dry-matter content (mg g ⁻¹)	Structural tissue trade-off with liquid phase processes	→	Investment in structural longevity from increased air temperatures	(I. J. Wright et al., 2004)
Specific stem density (mg mm ⁻³)	Growth potential trade-off with stress/mortality risk	→		(Diaz et al. 2016)
Leaf Nitrogen (% dry mass)	Photosynthetic potential trade-off with herbivory risk	←	Increase in photosynthetic prioritization from increased riparian forest density	(Diaz et al. 2016)
Leaf Carbon (% dry mass)	Leaf toughness	→		(I. J. Wright et al., 2004)
Carbon:Nitrogen (mass ratio)	Resource conservation, litter breakdown potential	→	Increased investment in drought resistance from increased solar radiation	(Zukswert & Prescott, 2017)

Table 1. Plant functional traits and associated community ecology relevance with predicted community-level directional response in traits to study treatment. * R = Reference sites, B = Buffered sites, and NB = Non-buffered sites.

SLA was used to represent photosynthetic capacity, gas exchange rates, and associated growth rate; see Table 1 for more trait selection information (Lozanovska, Ferreira, & Aguiar, 2019; Wilson et al., 1999). LDMC indicates structural investment in leaves, and the resultant herbivory potential and drought stress resistance (Wilson et al., 1999). SSD was selected to indicate the trade-off between growth, and hydraulic stress resistance of a plant (Díaz, Kattge, Cerabolini, et al., 2016); SSD was predicted to positively co-vary with LDMC (values increasing with light intensity). Leaf nitrogen content (Leaf N) was chosen for its ability to indicate a plant's trade-off between herbivory risk and photosynthetic potential (Díaz, Kattge, Cerabolini, et al., 2016). Leaf C demonstrates a plant's leaf toughness and longevity (carbon-rich structural tissues greatly influence LDMC and SSD, hence the positive relationship) (Wright et al., 2004). Leaf C:N is an indicator of a plant's resource conservation, as it demonstrates the ratio of toughness (structural investment) and photosynthetic capacity (growth investment) (Zukswert & Prescott, 2017). By studying the effect of timber harvest on this specific suite of traits, the most influential traits on community dynamics that were accessible for measurement were examined.

Studies on plant function and structure have demonstrated that the linkages between a stream and its riparian area are extremely important (e.g. Holmes, Goebel, & Morris, 2010; Kaylor & Warren, 2018; Luke, Luckai, Burke, & Prepas, 2007; M. Wipfli, Richardson, & Naiman, 2007), especially for the more detrital-based, small stream systems (Karlsson, Richardson, & Kiffney, 2005). Unlike studies that focus on species diversity, a functional-trait approach allows comparisons of communities' required growth conditions, and use of resources (Janssen, Piégay, Pont, & Evette, 2018). While Kominoski et al. (2013) explored global patterns of shifting riparian function through plant trait analysis, no research has focused on the altered distribution

of riparian plant traits to represent the community-level shifts that may impact ecosystem function in BC's coastal small-stream riparian areas.

1.5 Objectives and Hypotheses

This thesis aims to contribute to a growing area of scientific literature outlining the historical, and current failures in British Columbia's environmental legislation to protect the forested land that is managed for its citizens. These deficiencies in forest policy lead to environmental changes that have lasting impacts on the ecological function of forested areas, most notably riparian areas of small streams and the downstream systems that are vulnerable to shifts in conditions and subsidies from small, up-stream tributaries. Through the analysis of plant functional traits, this study sought to demonstrate shifts in riparian plant community structure and by inference, address the ecological processes that are impaired by these community shifts following BC's timber harvest practices, which do not require riparian tree retention buffers on small headwater streams.

Given the importance of the riparian area for ecological inputs and processes of small streams, especially relative to larger streams (Richardson, 2019), I focussed on the terrestrial riparian communities directly adjacent to small streams. I tested whether buffers effectively maintain the functional trait distribution of BC's coastal riparian plant communities of small streams compared to reference condition than non-buffered riparian zones. Moreover, I tested a suite of hypotheses based on site-level differences in plant functional trait values.

H₁: the increase in available light will contribute to structural changes in leaves over a growing season, leading to altered water balance strategies in the plants; this will be demonstrated by a lower specific leaf area (SLA);

H₂: the increased growing space will increase the availability of solar radiation, which will decrease soil moisture levels, increasing stem-specific density (SSD) and leaf dry-matter content (LDMC) values;

H₃: at least two years after the initial flush and loss of nutrients following timber harvest, decreases in soil N and growing space will increase competition for nutrients among riparian plants, resulting in a lower leaf nitrogen concentration (Leaf N) and higher leaf carbon concentration (Leaf C);

H₄: The distribution of community-weighted functional trait values at buffered riparian sites will be intermediate to non-buffered and reference sites, indicating microclimate effects of buffers.

Determining the impact of forest management strategies lacking tree retention buffers on riparian vegetation communities may enable policy makers in BC to reconsider the importance of protecting small streams, better protecting the function of both the aquatic and terrestrial communities supported by riparian vegetation (Desroches, 2007). Protecting ecological functions and services in a time of global climate uncertainty should focus on a functional approach, rather than morphological or taxonomic, thus facilitating more adaptable and flexible practices (Capon & Pettit, 2018). This research will contribute to a scientific basis for better protection of BC's small, coastal streams and the downstream networks that they support. This study aims to inform better maintenance of the combined function of forest and stream ecosystems, which provide goods, services, and enjoyment to the inhabitants of BC for whom these forests are managed.

2. METHODS

2.1 Field Description

Prior to the colonization of what is now called British Columbia, Canada, Indigenous Peoples occupied and lived interconnected with the lands and bodies of water in this coastal region. The Katzie First Nation People are the original forest stewards of the focal ecosystems of this research project. Through an agreement with UBC's Faculty of Forestry, they continue to be recognized as the owners and caretakers of these lands. Shared objectives for cultural, spiritual, environmental, economic and social benefits ensure that healthy forest ecosystems are maintained in perpetuity through responsible forest management, shared decision-making, and educational programs (MKRF Staff, 2015).

Study sites were established at the Malcolm Knapp Research Forest (MKRF) in Maple Ridge, British Columbia (BC), located approximately 40 km east of Vancouver, BC (Figure 1). The 5,157-hectare research forest is situated on the windward side of the Coastal Mountain range in the Pacific Northwest (Yeung, Lecerf & Richardson, 2017). The forest is dominated by a temperate maritime climate (Leach & Moore, 2017), and is classified as a Marine West Coast (Cfb) climate under a modified Köppen Geiger Climate Classification System (Larson & Lohrengel, 2011). The oceanic, mesothermal coast experiences cool, wet winters and warm, dry summers (Kiffney, Richardson, & Bull, 2003), though no distinct dry season occurs (Larson & Lohrengel, 2011).

The climate patterns in the region are dominated by Pacific frontal systems that produce orographic precipitation from warm, moist air masses rising up the windward side of the Coast Mountain range (Demarchi, 2011). Annual precipitation over the two years of this study

averaged 1996 mm, which is lower than the historical annual precipitation range (2200-2700 mm (Feller, 1977)), and lower than MKRF Climate Normals (average 2128 mm, period 1981-2010). Seventy percent of annual precipitation falls between October and April (Leach & Moore, 2017). Only five percent of precipitation falls as snow (Feller, 1977); however, both precipitation and the proportion of which falls as snow, vary annually (Kiffney & Richardson, 2010). Average temperature over the two years of this study was 10.6 °C, which is higher than MKRF Climate Normals average of 9.9 °C (period 1981-2010). These values were calculated using meteorological data from the MKRF weather station (ECCC station 1103332).

The temperate forest of MKRF is predominantly occupied by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western red cedar (*Thuja plicata* Donn), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), which is representative of the Coastal Western Hemlock biogeoclimatic zone (Kiffney et al., 2003). The homogeneity of the forest is due to the recent disturbance history in which the forest was harvested early in the 20th century, then burned in 1931; the result is a fire-initiated, densely spaced, second-growth stand (Kiffney & Richardson, 2010). The small deciduous component of the forest is comprised of black cottonwood (*Populus trichocarpa* Torr. & Gray), red alder (*Alnus rubra* Bong.), and vine maple (*Acer circinatum* Pursh) (Kiffney et al., 2003). The understories of forested riparian areas in MKRF are typically dominated by salmonberry (*Rubus spectabilis* Pursh), salal (*Gaultheria shallon* Pursh), western skunk cabbage (*Lysichiton americanus* Hultén & H. St. John), western swordfern (*Polystichum munitum* (Kaulf.) C. Presl), and huckleberry and blueberry species (*Vaccinium* spp.) (Kuglerová, García, Pardo, Mottiar, & Richardson, 2017).

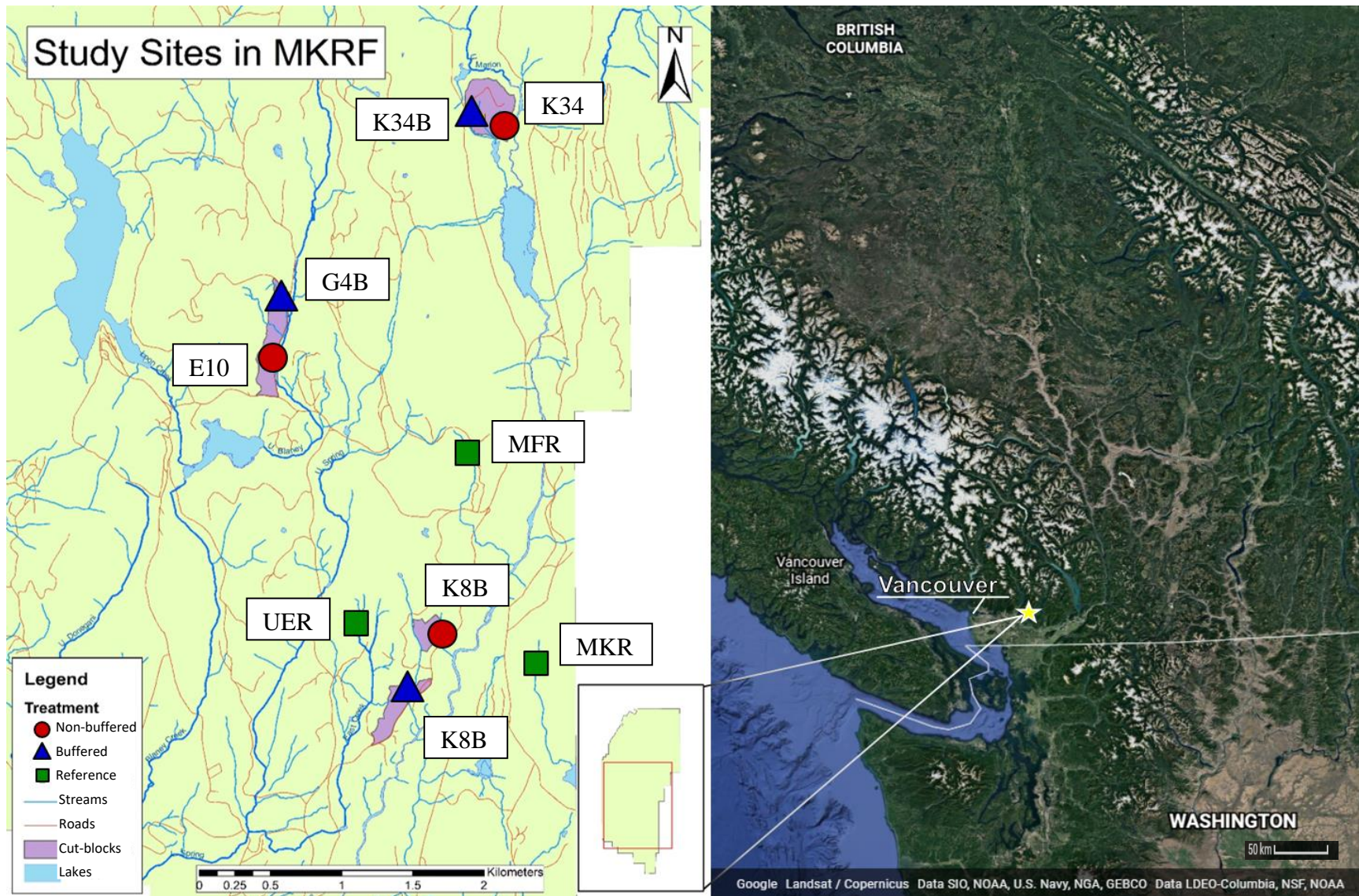


Figure 1. Left: study site locations in Malcolm Knapp Research Forest; non-buffered sites indicated by red circles, buffered sites shown as blue triangles, reference sites as green squares, and relevant cut-blocks indicated by purple shading. Right: study location within British Columbia, Canada indicated by yellow star symbol.

Selection of riparian sites was based predominantly on riparian management practices established within timber harvest blocks at MRKF harvested within the previous five years. Previous experimental and multi-objective harvests were located, and allowed for different riparian harvest intensities on small streams to be the main treatment criterion for this research project. These riparian management practices that formed the different treatments in the observational study were buffered, non-buffered (with machine-free zones), and reference streams. Suitable reaches for buffered sites had a continuous buffer of retained trees with no harvest for at least 5 m from either side of the stream, perpendicular to streamflow direction, for the entire 50 m study reach (buffers at least 10 m total width). All sites had visually similar characteristics for at least 10 m continuously in either stream direction, outside of the established 50 m study reaches; the reach extents for each site were established to maximize treatment-effect conditions, and did not use natural edges for upper or lower extents. Suitable reaches for non-buffered sites were free of continuous forest on either side of the stream for at least 30 m perpendicular to streamflow direction; trees present had to be < 30 cm DBH, and fewer than five stems over the study reach, which was 50 m (slope distance) along the stream. Suitable reference reaches had no harvest or fire disturbance within 30 m on either side of the stream since the 1931 forest fire in MKRF. Reference sites could have harvest outside the 30 m width from the stream, as sampling site options were limited, and effects on functional trait values were assumed to be negligible outside of that threshold.

Site criteria also included absence of disturbance directly upstream, which included no road crossings or recent anthropogenic disturbance. The GIS layer for MKRF indicating the presence of streams was used to identify first- or second-order streams. Once the stream layer was identified, satellite (base) imagery was used in ArcMAP (Environmental Systems Research

Institute, 2019) in order to compare suitable streams present in timber-management blocks. Riparian management practices were then predicted using the site plans (provided by MKRF management and operational staff), and satellite imagery of each possible study site. Each buffered and non-buffered stream reach was walked in early spring, 2019 to determine suitability as a study site. Nine sites were selected in total, three for each of the buffered, non-buffered, and reference treatments.

2.2 Field Measurements

Field data were collected between April and December, 2019. Nine sites (three of each treatment: non-buffered, buffered, references) were established where a small stream was selected for riparian plant community research. Each study site was based on a 50 m stream reach, where the research areas were established on both sides of the stream. At each site, an environmental analysis, including a soil pit, was conducted. Understory plots and tree plots were established on either side of focal stream reaches to assess the taxa and abundance of riparian vascular plants present at each site (Figure 2). In addition to direct measurements, weather data were logged for the duration of field sampling at each study area. Once the relative abundance of shrub and herb taxa present at each site was determined (through understory plot assessment), leaf and stem tissues from the dominant understory vascular plants were collected. All sampling except functional trait measurements were completed in the field; functional trait measurements were conducted in the laboratory (see Section 2.3).

Eight 4 m² understory quadrat plots were established at each site (Figure 2). The plots were evenly spaced along the 50 m reach (starting at 5 m upstream from study reach extent), and alternated sides of the stream every 5 m. The first quadrat was established on the left side of the bank looking upstream, at 5 m of the reach (slope distance, upstream of the lowest elevation section of the reach).

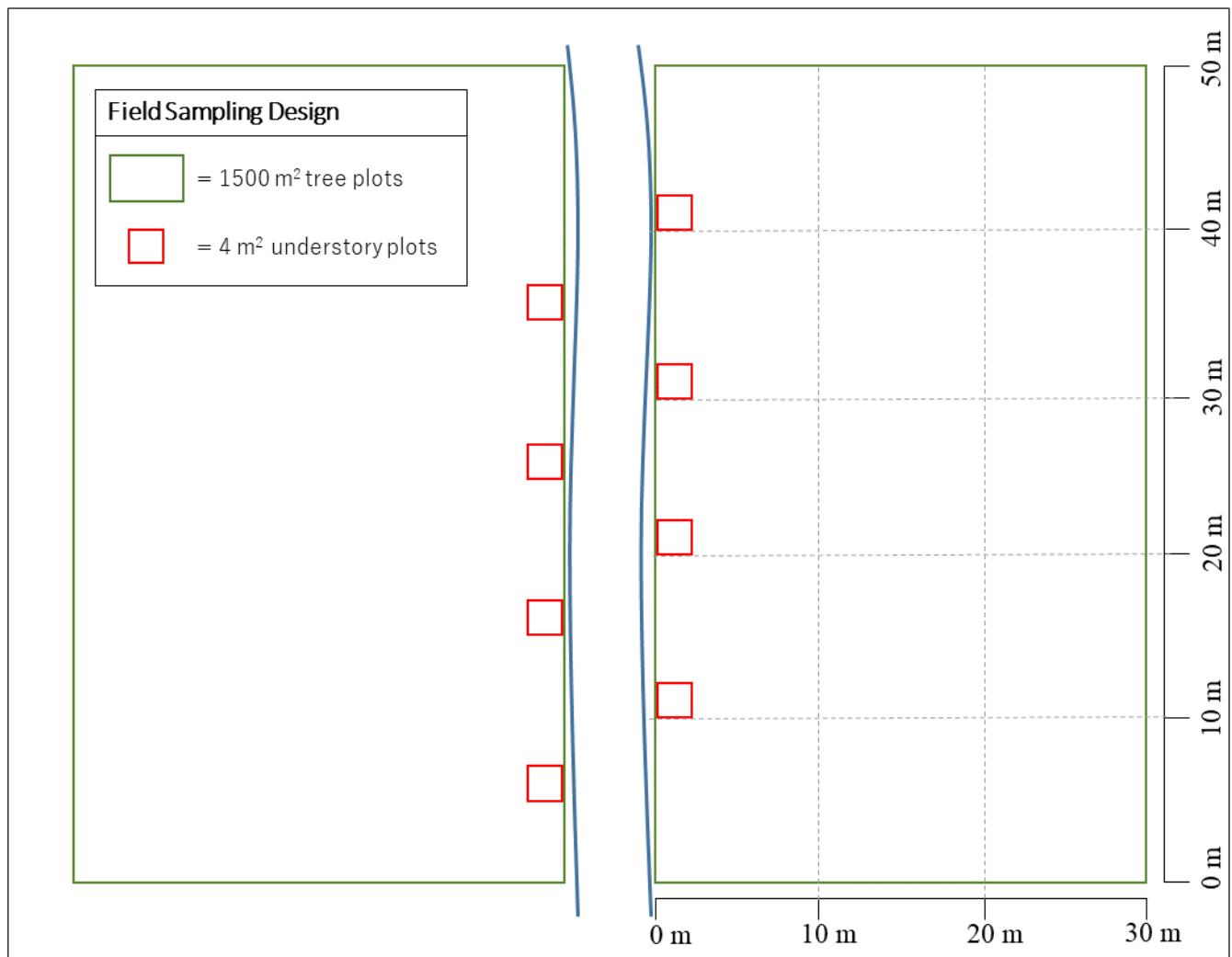


Figure 2. Field design for vegetation sampling protocols established at each of the nine study sites; green rectangle representing tree-level plots, red squares representing understory plant plots. Even sampling occurred across both sides of the stream present at each site.

Relative abundance (RA) was estimated as percent cover for species within the shrub and herb layers present in each quadrat. A field card of 0.2 m x 0.2 m was used to represent 1% cover (of each quadrat), and was the basis for RA estimates for all shrub and herb species. Each vascular plant was identified to species using MacKinnon, Pojar, & Alaback (2004), and was confirmed using Douglas, Meidinger, & Pojar (2000), and Douglas, Straley, Meidinger, & Pojar (1998). Relative abundance of bryophyte and liverwort taxa were together estimated as a percentage within each quadrat using the same procedure as for the herb and shrub layers, but not further identified to lower taxonomic classification. The area within each quadrat unoccupied by vascular plants or bryophytes was classified as “bare” and also given a RA percentage value. Once the RA of each species was determined at the quadrat level, all data were entered into a spreadsheet so that relative abundance for each species at the community (site) level could be calculated. The following equation (1) was used for relative abundance calculations for each species at each site:

$$species\ RA = \frac{sum(\% cover\ spp.)}{sum(\% cover\ total)} \quad (1)$$

The species-specific values at each site were used to select focal species for tissue collection for functional trait analysis. The most abundant species that together comprised at least 80% RA at each site were selected as the focal plant community for functional trait analysis at each site. Tissues for functional trait measurement were collected following this relative abundance analysis at each site. Due to the heterogeneous edaphic conditions at each site and between sites, the assemblage of plant species that determined the focal species at each site was different.

Tree plots were established on either side of the stream at each study site. These plots extended 5 m in both directions of the length of the study reach (40 m + 5 m x 2 = 50 m), and measured 30

m from bankfull margin of each side of the study reach perpendicular to the direction of flow (Figure 2). These 1500 m² plots were designed to account for canopy effects on understory plant communities. Plot area was determined to satisfy error criteria of an alpha of 0.05 (or 5% error), establishing a stem density lower limit of 400 stems / ha; at that density, an average of 60 stems would have been measured per plot, resulting in a sampling error of less than 2% per plot if an individual tree was missed, or misidentified, or incorrectly measured. Higher density forests resulted in lower sampling error values (which was the case for all sites used in this study). The distance of 30 m used for the plot edge perpendicular to the stream was selected to capture all trees that may have a direct effect on the riparian understory plant communities (Elliott & Vose, 2016). A 30 m buffer has also been shown to reduce the effects of timber harvest on small streams, and therefore 30 m was an appropriate distance for tree measurements, thus capturing the canopy effects on riparian plant communities immediately adjacent to these small streams (Sweeney and Newbold 2014). Within each of these 1500 m² plots, all individual stems were identified, and for each tree I collected DBH, species, and x and y-positions relative to study reach (at a coarse scale of 10 m x 10 m = 15 subplots within each plot). Calculations for determining basal area per hectare from the data collected are described in section 2.31.

Microclimate conditions at each site were determined using data collected from iButton dataloggers (DS1923 Hygrochron Loggers and DS1992L ThermoChron Loggers, Maxim Integrated, San Jose, CA, USA), and Onset dataloggers (HOBO U23 Pro v2 Temperature/Relative Humidity Data Loggers, Onset Computer Corporation, Bourne, MA, USA). Hourly air and soil temperature, and humidity measurements at each study site were logged over the period of June to October, 2019. Air temperature and relative humidity data were collected by the HOBO loggers at 0.5 m and 1.5 m from bankfull margin at average slope

locations of each site. The Hygrochrons were buried under 10 cm of mineral soil at the most downstream point (0 m) of each study reach, located 0.5 m from bankfull margin, and were used to measure soil temperature and relative humidity of the soil as a proxy for soil pore conditions. Additional Thermochron Loggers were treated using a Plasti-dip waterproofing protocol developed by Brian Kielstra in the Stream and Riparian Research Lab at the University of British Columbia (Kielstra, 2020). Once sealed, the loggers were buried under 10 cm of mineral soil at the most downstream point (0 m) of each study reach, where they were fastened to stainless steel flags by flexible steel wire. Loggers were installed at 0.5 m and 1.5 m from bankfull margin (adjacent to the Onset weather stations) at each site. These soil and air temperature data were averaged and summarized in Rstudio after being cleaned and interpreted with the procedures described in section 2.32.

For assessing environmental conditions, at each site I collected data for reach slope and aspect; soil group, colour, and texture; humus form; topographical continuity and shape, meso-slope position, average bank side-slope; and soil nutrient and soil moisture regimes (Table 2). These data were collected to characterize sites and to be used as potential environmental covariates for analysis of functional trait responses. Average reach slope at each study site was estimated using a SUUNTO PM-5/360 PC Clinometer, measured in percent gradient along the 50 m study reach. The point of commencement and point of termination used for the slope measurement were used as the reference points for determining reach aspect, which was measured using a SUUNTO MC-2 G Mirror Compass, measured in azimuths (with a magnetic declination set to 16° East).

Table 2. Summary of direct-measured site conditions by treatment; measurement and data collection protocols for all site conditions are found in section 2.21. *Stream classes based on BC's system for stream feature classification.

Treatment		Reference		No Buffer			Buffer		
Site	MFR	MKR	UER	E10	E20	K34	G4B	K8B	K34B
Latest disturbance	1931	1931	1931	2015	2016	2016	2014	2014	2016
Buffer width (m)	-	-	-	-	-	-	18.4	16.2	11.8
Stream bankfull width (m)	0.88	1.97	4.14	0.72	2.15	1.17	2.15	1.38	1.32
Catchment area (ha)	5.4	39.4	37.0	3.4	13.9	2.6	25.3	23.4	3.3
Stream class*	S3	S4	S2	S6	S6	S6	S5	S6	S4
Elevation (m)	339	267	311	318	295	347	259	257	344
Bank slope (%)	24	7	29	12	13	6	17	10	13
Reach slope (%)	26	8	12	19	8	13	34	14	16
Reach aspect (Az°)	194	161	184	136	178	170	221	172	127
Humus form	Leptomoder	Rhizomull	Vermimull	Vermimull	Rhizomull	Rhizomull	Rhizomull	Rhizomull	Vermimull
Soil texture (A horizon)	Sandy loam	Silt	Silty loam	Sandy loam	Silty clay loam	Sandy loam	Sandy loam	Sandy loam	Silty clay loam

A soil pit was dug at each study site, ensuring average site conditions were sampled; slope, slope position, and shape were all factors when choosing pit location. Each pit was dug within 2 m of bankfull stream margin, and was dug to 1 m deep, or deep enough to classify distinctive layers (often Bf or Bfh in this region) in B horizons. Field protocols for soil measurements were based on Watson's (2009) field protocols. Soil group was determined using protocol in Soil Classification Working Group (1998). Soil colour was determined using Munsell Color Firm (2010). Humus form at each site was determined using protocols outlined in Green, Trowbridge, & Klinka (1993).

2.3 Laboratory Procedures and Calculations

2.3.1 Light

In order to estimate light at each study site, two methods were used: forest stem density and hemispherical photo interpretation. Forest stem density was used to capture the effect of the canopy on the understory plant communities (Elliott & Vose, 2016), and was calculated using equations (2), and (3).

The equations used for tree basal area (BA_t), and basal area per hectare (BA_s) were:

$$BA_t = \pi \left(\frac{DBH}{2} \cdot \frac{1 \text{ m}}{100 \text{ cm}} \right)^2 \quad (2)$$

Where DBH is the measured diameter at breast height of an individual tree in cm.

$$BA_s = \frac{BA_t}{a} \cdot \frac{10000 \text{ m}^2}{1 \text{ ha}} \quad (3)$$

Where a is the area of the plot in m^2 .

Eleven hemispherical photos were taken at each site, at 5 m intervals along the study reach from 0 m to 50 m of the reach, inclusive. A Nikon 4500 digital camera, with a Nikon Fisheye Converter FC-E8 lens was used to produce hemispherical photos with a 182.8° field of view. Photos were taken at the camera's highest quality setting, on a tripod, with the sensor located 1.7 m above the channel bed, at stream centre for consistency with published protocols. Photo interpretation for approximation of canopy openness as a proxy for light availability within a 0-30° zenith range was completed using GLA V2.0. Protocols for photo acquisition and interpretation for percent canopy cover at each site was based on published field and lab protocols (e.g., Frazer et al., 1999; Leach & Moore, 2017)

The hemispherical photos from each site were then used as a modelled measure of radiation that reaches the understory plant communities (Yeung et al., 2017), which was calculated in Gap Light Analyzer (GLA) V2.0 software (Simon Fraser University, Burnaby, BC, Canada) (Frazer et al., 1999) with region-specific parameters using equations (4), (5), and (6).

The following region-specific parameters were calculated for photo interpretation in the GLA program: cloudiness coefficient (K_t), spectral fraction (R_p/R_s), and beam fraction (H_b/H). The equation (4) for daily total transmissivity (below: from Leach and Moore (2017)), denoted as τ_t , was used in lieu of the cloudiness coefficient (K_t) equation given in Frazer et al. (1999), but represents the same units and resultant values.

$$\tau_t = A(1 - e^{(-B \cdot \Delta T^C)}) \quad (4)$$

Where A (0.72568), B (0.01735), and C (1.62386) are empirical coefficients specific to MKRF coordinates, based on Leach and Moore's (2017) calculations. The ΔT term represents the diurnal range in temperature for the study period, using weather data from the MKRF weather

station (ECCC station 1103332). The spectral fraction (R_p/R_s), or total daily global Photosynthetically Active Radiation (PAR) relative to total daily global shortwave radiation, was calculated using the following equation from the GLA manual:

$$\frac{R_p}{R_s} = 1 - e^{(-4.99 \cdot K_t^{-0.219})} \quad (5)$$

Where R_p is total daily global PAR, R_s is total daily global shortwave radiation, and $K_t (= \tau_t)$ is the calculated cloudiness index (or daily total transmissivity, which was used instead) (Frazer et al., 1999). The beam fraction (H_b/H), or direct radiation relative to global radiation incident on the Earth's surface, was calculated using the following equation from the GLA manual:

$$\frac{H_b}{H} = 1 - e^{(-3.044 \cdot K_t^{2.436})} \quad (6)$$

Where H_b is direct solar radiation (which is neither scattered nor absorbed by the atmosphere), H is global radiation incident on a horizontal surface, and $K_t (= \tau_t)$ is the calculated cloudiness index (or daily total transmissivity, which was used instead) (Frazer et al., 1999).

An interactive thresholding (IT) approach was used to create a binary image within the GLA. This process was completed manually by selecting a threshold for each image that represented the most accurate canopy gaps, unique to that image. The challenge of IT is in selecting a threshold that avoids overexposure of plant tissue (thus overestimating gap fractions), and simultaneously avoids underexposure of light gaps (thus underestimating gap fractions). Despite the user bias introduced by this method, many studies have completed canopy photo interpretation with user-defined thresholding (See Hale, Edwards, Mason, Price, & Peace, 2009; Yeung et al., 2017). While the accuracy of IT can be increased through iterative thresholding, Inoue, Yamamoto, & Mizoue (2011) found that the discrepancies between repetitive

thresholding on an individual image results in an average of only 0.2% difference in gap fraction estimates. Additionally, Inoue et al (2011) found that gap fraction estimates from IT, and AT algorithms, result in an average of 4.3% difference in gap fraction estimates (Inoue et al., 2011); however, there were no significant differences in gap fraction between the two thresholding methods. Based on the success of IT in other studies assessing canopy gap fractions, and the lack of significant differences between IT and AT, interactive thresholding was used for the hemispherical photo interpretation of this study.

2.3.2 Temperature

Temperature data were summarized by assessing daily values of the minimum, maximum, mean and range in temperatures. These data were also transformed into the maximum 7-day moving average of the daily means, and the maximum 7-day moving average of the daily maximums (Groom, Johnson, Seeds, & Ice, 2017). These values are temperature measures of a single 7-day period based on the averages across all sites – calculated by equations (7) and (8) – that indicate seasonal peak warming while not overly-depending on values from a single day (Swartz, Roon, Reiter, & Warren, 2020).

Daily maximum temperature:

$$T_{7DayMax} = \frac{T_{DailyMax1} + T_{DailyMax2} + T_{DailyMax3} + \dots + T_{DailyMax7}}{7} \quad (7)$$

Where $T_{DailyMaxn}$ is the maximum temperature recorded during the day n .

Daily mean temperature:

$$T_{7DayMean} = \frac{T_{DailyMean1} + T_{DailyMean2} + T_{DailyMean3} + \dots + T_{DailyMean7}}{7} \quad (8)$$

Where $T_{\text{DailyMean}}$ is the arithmetic mean temperature, calculated for the day n . The day n is based on the day in the week during which the highest mean temperatures averaged across all nine sites occurred. This average value was then summed for seven consecutive days, which was compared throughout the summer to assess which seven-day period would be selected as the 7-day-max, representing the time period during which the highest mean temperatures were recorded across all nine sites.

2.3.3 Functional Traits

Plant functional traits were analyzed for each of the species that together comprised at least 80% of the relative abundance at each site, averaged over total understory plot area per site (Figure 3). Individuals of each species were selected based on their proximity to the study reach, and to conspecifics, capturing within-site variation as much as possible across the study reach. Capturing this variation was important to achieve the most representative site-level, species mean values for each trait measured. Due to the heterogeneous distribution of species at each site, tissues were collected as evenly across each study site, and on each side of the stream at each site, as possible given the natural limitations of plant distribution.

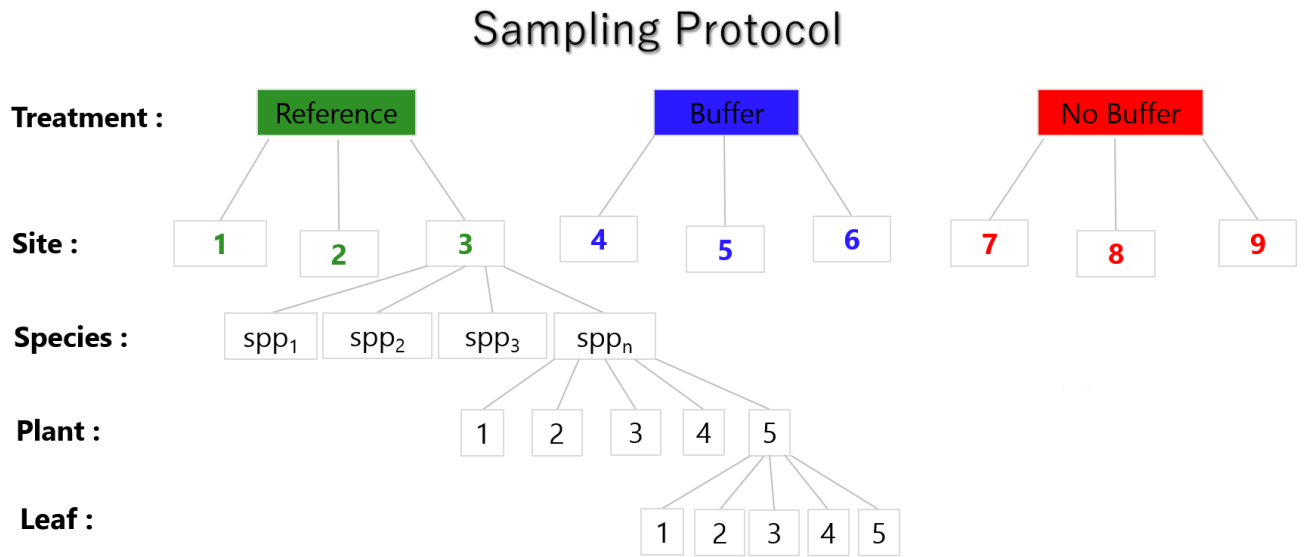


Figure 3. Field sampling protocol for leaf tissue collection for functional trait measurement; n is the number of species selected to comprise 80% understory ground cover. Stem collection was completed as described in section 2.3.3.

Leaves and stems of each focal species were collected from each of the nine sites, based on the protocol for selecting site-specific focal species (section 2.2). Leaves were cut from the twig, as close to the base of the petiole as possible. As with many herbaceous and woody plants, the morphological differences between sun leaves and shade leaves is significant, and distinguishing them should be accounted for prior to tissue collection (Vitousek & Farrington, 1997). The main differences in sun and shade leaves are in response to the differences in light attenuation below the canopy (Fraser, Turkington, & Chanway, 1993). When available, I collected the youngest, fully-formed sun leaves from each plant of each focal species in order to account for these differences, as in Vitousek and Farrington's study (1997). When no sun-leaves were present, the youngest fully-formed leaves at the upper-most portion of the plants were selected.

Stems were cut as close to the ground as possible, capturing the oldest, most site-adapted stem length of each plant; two stems per 5 m segment along the stream were selected and sampled,

when possible. This step was repeated five times per species at each site, capturing within-site heterogeneity, while maintaining close proximity (within 5 m) to the stream bank.

In total, there were 25 leaves and ten stems per focal species collected at each site. Petiole measurements were taken for fern species and reported as stem measurements. Leaf and stem samples from each plant were wrapped together gently in wet paper towel to enable tissues to stay hydrated, minimizing losses through transpiration. The paper towel also served to standardize the hydration of plant tissues at each site. Carbon dioxide was added to the plastic bag through exhalation prior to sealing the bag and placing it into a sealed cooler (maintained below 10 °C with ice packs) in order to maintain stomatal gas exchange function. Samples were transferred to a refrigerator for storing at consistent temperature until tissue measurement, which occurred within 24 hours of collection.

Following tissue collection, leaf and stem fresh measurements were completed within 24 hours of collection to minimize losses from respiration, fungi and bacteria, and herbivory from invertebrates that may have accompanied the plant tissues during collection. Mass measurements (fresh and oven-dried) were completed using an analytical scale (Sartorius BP110S; Sartorius Lab Instruments GmbH & Co. KG, Goettingen, Germany). Leaf and stem tissues were oven-dried at 70 °C for 48 h using a Fisher Scientific 6905 Isotemp Oven (Thermo Fisher Scientific, Marietta, OH, USA).

All field and lab protocols for traits were based on a plant functional trait handbook (Pérez-Harguindeguy et al. 2013). SLA ($\text{mm}^2 \text{mg}^{-1}$) was calculated by dividing the fresh leaf area by the oven-dried mass of the leaf. The leaf area (of the upper surface, including petiole or rachis) was measured using a Li-Cor Model 3100 Area Meter (LI-COR Biosciences UK Ltd., Cambridge,

UK). Fresh, and oven-dried mass of tissues for this study were measured to 0.01 mg, using the Sartorius BP110S scale. Leaf Dry Matter Content (LDMC, mg g^{-1}) was measured by dividing the oven-dry mass in milligrams by the fresh mass of that leaf in grams. Stem-specific density (SSD, mg mm^{-3}) was calculated by dividing the oven-dry mass of a stem section by its previously measured fresh volume. Fresh stem volume was determined using the water-displacement method, whereby the mass of water displaced by each stem length on a balance is equal to the volume of water being displaced by that stem ($1 \text{ mg} = 1 \mu\text{L} = 1 \text{ mm}^3$ of water). Stem samples were held just below the surface of the water by pressing down on the top of them with fine-pointed forceps, assessed to have negligible volume. The epidermis of the stem is included in this metric to capture the inclusive function of the whole stem in hydraulic stress resistance and hydraulic capacity.

Elemental Analysis (EA) of leaf chemistry (carbon and nitrogen concentrations) was determined for each focal species of each site using composite samples. All five oven-dried leaves from each individual plant were ground together using mortar and pestle, or mechanical grinder (depending on the persistence of the petiole or rachis). Each composite sample was then encapsulated to produce five samples per focal species per site. Encapsulation was completed through transferring 3.5 mg of ground leaf tissues into 8 mm diameter tin-antimony alloy capsules (Elemental Microanalysis, Devon, UK) on a Sartorius M2P microbalance (Sartorius Lab Instruments GmbH & Co. KG, Goettingen, Germany), and very carefully compressing encapsulated tissues into a small cylindrical capsule. The samples were then processed using the Elementar Vario EL Cube Elemental Analyzer (Elementar Analysensysteme GmbH, Langenselbold, Germany) at the Stable Isotope Lab of the University of British Columbia. The concentration values are given as a percentage of original sample mass, and have 3.0% precision

for nitrogen, and 1.5% for carbon (percentage relative standard deviation) (Elementar, n.d.). Leaf Nitrogen concentration (Leaf N, % dry mass), and Leaf Carbon concentration (Leaf C, % dry mass) are a percentage of oven-dried mass (Pérez-Harguindeguy et al., 2013). Leaf carbon to nitrogen ratio (Leaf C:N) is the mass ratio.

2.4 Statistical Analysis

Data analyses were conducted in R versions 3.6.3, 4.0.0 – 4.0.5. A correlation matrix was used for selecting explanatory variables by reducing the number of environmental covariates to be considered for analysis. Functional trait data were first organized by species, then treatment and site. This filtering allowed visualization of the raw data in terms of broad relationships between the plant functional traits of interest and how the values differed between species, and across sites and treatments. Community-level functional trait relations with the three treatments were assessed with global models with all species data through Linear Mixed-effects Models (LMMs; section 2.4.1). Species-level functional trait relationships were then assessed through Analyses of Variance (ANOVAs) for the treatment effects (section 2.4.2.1). Analyses of Covariance (ANCOVAs) were used for the combined effects of treatment and selected environmental covariates to assess the species-level effects contributing to the community results of the LMMs. Finally, Non-metric Multidimensional Scaling (NMDS) ordinations were used to visualize results of the plant communities, looking at both species and trait distributions among treatments and sites.

A correlation matrix was created using the “corrplot” package in R in order to select the most influential of the environmental conditions measured (Taiyun & Simko, 2017). These explanatory variables that were considered collinear (with a correlation coefficient value approaching |1|) were assessed, and each variable with the most relations amongst the group of

variables deemed collinear was selected as a focal environmental covariate to be used for the ANOVA, ANCOVA and LMM analyses in addition to the NMDS ordinations.

Outliers in the raw trait data that were related to manual data entry error (obvious when looking at the data) were fixed through visual inspection to correct for apparent outliers. This iterative data cleaning protocol was based on the other measurements specific to that plant, the relationship between the two measurements that accounted for the parameter values being corrected, and finally the closest number keys based on the relative location on the number pad. Outliers that were outside the range of \pm three times the interquartile range ($3 \times (75 \text{ percentile} - 25 \text{ percentile})$) were not eligible for this data cleaning protocol; they were left as outliers and not used for analysis.

2.4.1 Community-level Responses

Plant species distribution and community-level trait value dynamics were assessed through Non-metric Multidimensional Scaling ordinations (NMDS) from the “vegan” package (Oksanen et al., 2020) and Linear Mixed-effects Models (LMMs). The LMMs were used to fit global models for each trait to account for some of the variation in the treatment effect with the explanatory variables of interest modelled independently. The ordination data visualizations were used to augment patterns in the data, and showed trends in the distribution of both species, and functional traits representing both site and treatment relations to multiple environmental covariates together.

For the mixed models, functional trait measurement data were contrasted by site, treatment, and species; this enabled community-level (site-level) averages to be compared between the three treatments for all focal species. While community-level dynamics are inherently dependent on

lower-level measurements, by including the most abundant 80% of species in tissue collection, only the dominant taxa at each site contributed to the community-level values. This enabled examination of the most abundant plant species' responses to environmental conditions through their physiological response to the microclimate observed throughout the plant community at each study site. Only species that represented at least 10% total abundance by spatial cover at three or more sites were selected for tissue collection (Lamb & Mallik, 2003); this selection process ensured uncommon species' data do not influence the community-level trait values (Clarke & Gorley, 2006). All species' relative abundance were \log_{10} -transformed to avoid over-representation of the high abundance species in the ordination (Mallik, Kreutzweiser, Spalvieri, & Mackereth, 2013). This also allowed the species with lower abundance, but significantly present (as per Lamb and Mallik's species selection protocol) to still have an influence on the community patterns analyzed in the ordination (Clarke & Warwick, 2001).

Global mixed models were used for determining community-level responses to the treatment and included influential environmental covariates using the "lme4" package (Bates, Mächler, Bolker, & Walker, 2015). Univariate analysis of mechanisms explaining variation beyond the treatment effect on focal plant functional traits was completed for each trait using Linear Mixed-effects Models (LMMs). These LMMs provided an assessment of what explanatory environmental variables contribute to the variation of the study's focal plant functional traits related to the treatment effect. While these covariates were often collinear with treatment, they explore more detailed mechanistic explanations of the treatment effect than modelling with the treatment alone. Environment explanatory variables such as air and soil temperature metrics and a modelled radiation metric were used individually, in addition to a treatment term for the fixed effects in these models. Species was accounted for by establishing it as a random factor with

random slope and random intercept (Galecki & Burzykowski, 2013). The models were fit by restricted maximum likelihood due to small sample sizes (Bates et al., 2015). The t-tests and F-tests used the Satterthwaite's degrees of freedom method to account for the differences of variance within each site (Kuznetsova, Brockhoff, & Christensen, 2017), which produces an acceptable rate of Type 1 errors for small sample sizes (Luke, 2017). An Akaike's Information Criteria (AIC) comparison was used for LMM selection. AICc for data with small sample sizes was used for the analysis of the data for this study (Harrison et al., 2018). Using the package "AICcmodavg", an AICc comparison table was created using the AICtab function (Mazerolle, 2017). Once the most parsimonious model was selected based on the lowest AICc value, the R-squared and P-values were calculated to identify the proportion of variance explained by the treatment and by the environmental explanatory variable of interest.

2.4.2 Species-level Responses

2.4.2.1 *Treatment Effects*

Species distribution of sites and treatments was visualized using a non-metric dimensional scaling ordination, which helped identify community-level dynamics that were especially influenced by a single species (ordination methods in section 2.4.3). Species relative abundances were used for developing community-weighted mean trait values that were then used for the second part of the trait analysis.

I used linear models to assess the relationship between treatment and focal functional trait values, identifying these differences with a one-way analysis of variance (ANOVA) for each individual focal species. To address the pairwise differences between the three treatment effects on the trait values, I used post-hoc Least-Squares Means tests, with an adjusted p-value using Tukey's Honestly Significant Difference (HSD) test for comparing a family of three estimates

(Underwood, 1997). This test allowed for the comparison between non-buffered, buffered, and reference treatment mean values of functional traits. When sample size was insufficient for a three-way comparison using the Tukey's HSD test, the ANOVA p-values were used to identify significant differences in species-specific trait values between the treatments; these p-values are accompanied by an asterisk throughout this section so as to differentiate the two p-values. Even though the three treatments were not compared directly with the ANOVA, the p-values from that analysis provided a measure for whether the treatment means were significantly different from each other. Unless specified otherwise, the p-values reported in the results section of this paper are the p-values associated with the HSD test. Summary data were used for each species so that site averages were compared to treatment for the linear models.

Once the linear models were created, residuals were plotted for each relationship, so that the distribution could be assessed. Normal distribution of the residuals was important to confirm prior to continuing analyses. The "skewness" function from the "e1071" package was used for quantifying the skewness of the residuals observed in the residual plots (Meyer, Dimitriadou, Hornik, Weingessel, & Leisch, 2020). All data were left untransformed, as the skewness values satisfied the following statement: $-0.5 < x < 0.5$.

After checking that transformations were not necessary for normally distributed residuals, the data were ready for further analysis. Models were used for fitting the data to plot and analyze. Significance was accepted when a comparison yielded a p-value of at most 0.05 (if not further specified in results). Only seven of the eight focal species could be statistically tested with the univariate species-level linear model analyses (ANOVAs), due to an insufficient sample size of two sites for *Blechnum spicant*.

2.4.2.2 Environmental Effects

Analyses of variance were conducted with each environmental variable influential on functional traits as the response, and treatment as the predictor; this allowed environmental conditions to be compared between sites and between treatments, determining significant differences among them. An analysis of covariance was conducted to analyze the effect of environmental covariates on the functional traits of the focal species of this study. Within each species' data, the functional traits were modelled as a linear relation that included treatment and an environmental covariate as the independent factors. There were insufficient degrees of freedom to allow for multiple covariates, so each environmental covariate was modelled separately. Only the variables selected through the correlation matrix were used as covariates in these analyses. P-values less than 0.05 were considered significant. Only six of the focal species could be statistically tested with the ANCOVA analysis, also due to restricted sample size.

There were many individual analyses, given multiple focal species, and multiple environmental covariates to be tested. A high number of such tests can lead to an increased probability for falsely finding significance in the data (an inflated Type 1 error rate); however, no correction was applied to these analyses. The limited sample size of the data did not support the conservative approach of minimizing Type I errors (e.g. Bonferroni correction), which consequently can increase the chance for a Type II error. I did not apply a correction because an increased chance for falsely failing to observe significant relations was not sufficiently justified given my replicate-limited data.

A Shapiro-Wilks test was used to assess the normality of residuals for each relationship from the ANCOVAs. Those with skewed residuals were log₁₀-transformed and re-assessed. While normally-distributed residuals are an assumption for the least-squares approximation of the

regression to which the data were fit, these analyses were limited by a small replicate number for each treatment. As such, the conservative approach of ensuring normality of residuals was not adhered to strictly, for this study.

2.4.3 Community-level Response Visualizations

For the community-weighted mean (CWM) trait value visualizations, transformations were completed in order to select the data that provided the most parsimonious NMDS ordination model for site differences in the community-level trait values. This was assessed through a small stress value, and large non-metric R^2 and linear R^2 values. A square-root transformation on the community-weighted relative abundance values was selected and multiplied by the calculated trait z-score values per species for each site, then summed across all species to get a single standardized trait value with a mean of 0 and a standard deviation of 1 for each site (Garnier et al., 2004). Each site average was representative of the traits present, and the abundance of the plant displaying those trait values at the site. Those CWM trait values were then used for the NMDS ordination to identify the environmental covariates driving the trait-treatment relationships observed at the community level of the nine study sites.

These ordinations were used to determine point-cloud areas that occupy the same space of trait expression, and species distribution between the nine study sites. The axes on which these visualizations exist are unitless, and thus cannot directly show the numerical data of this study; however, they do show the relative influence of environmental factors on the distribution of species and trait values at the community level. Bray-Curtis distances with two dimensions were used for the species ordination. Euclidean distances with three dimensions were used for the traits ordination. Both ordinations used 1000 starting points for the rank-ordering of scaled

species and trait values, which allowed enough iterations to find a converging solution for each of the two ordinations with a low stress value (stress < 0.05).

3. RESULTS

3.1 Site Characteristics

The study sites for this project (Table 2) were distributed across the southern portion of MKRF (Figure 2). Elevations ranged from 259-347 m. The aspect of the sites varied across the azimuth scale, but trended towards the south-west. Average reach slope varied between 8% and 34% across sites. Meso-slope position and site shape were qualitatively identified at each site, but were not influential on any of the results.

Buffered site elevation averaged the lowest among treatments at 287 m, while non-buffered sites averaged 314 m, and the reference treatment had a mean of 306 m. Buffered sites had the steepest study reach gradient at 21% (averaged over 50 m study reach). Slope averages for stream reaches across non-buffered sites and reference sites were similar; i.e. 13% and 15%, respectively. Average aspect was similar across all three treatments, displayed in percent of Southern aspect (% of 180 degrees). Buffered sites averaged 81 % S ($\pm 7.7\%$), non-buffered sites averaged 90 % S ($\pm 7.1\%$), and reference sites averaged 93% S ($\pm 2.4\%$). The most northerly average aspect of study sites was at E10, with an aspect of 75.6°; the most southerly average aspect of study sites was at E20, with an aspect of 98.9° (both non-buffered sites). Catchment area averages for the buffer and reference sites were much larger than that of non-buffered sites. Catchment area of sites with no buffer were on average 6.6 ± 3.6 ha, buffered site catchment area averaged 17.3 ± 7.0 ha, and reference site catchment area averaged 27.3 ± 10.9 ha. Although there was high within-treatment variation, catchment area was not considered one of the focal explanatory variables (supported by AICc value comparison). None of these pre-harvest site-specific environmental conditions were significantly related to plant functional trait values across treatments.

The environmental variables on which this study focused were range and maximum air temperatures, range and maximum soil temperatures, basal area within the riparian area, and modelled potential solar radiation. These environmental variables were used as explanatory variables for the treatment effect on the functional traits, as they were determined to be the most influential variables on the distribution of the plant functional traits (see section 2.41 for details). Additionally, they were chosen based on a collinearity matrix analysis, which aided in the selection of variables that best captured site variation. For example, potential solar radiation and site openness were determined to be collinear with a correlation coefficient close to 1.0; this indicated that all of the variation within a site's trait values explained by site openness is also explained by potential solar radiation. The openness index is therefore captured by the analysis of the potential solar radiation metric.

Mean daily soil temperatures measured between June and September of 2019 averaged lowest at reference sites (10.3 ± 0.7 °C), 28% lower than the buffered treatment and 133% lower than the non-buffered treatment mean ($p = 0.029$; Figure 4). The daily minimum soil temperature averaged across the study period at the three reference sites was 10.0 ± 0.7 °C, which was 24% lower than the buffered treatment mean ($p = 0.045$), and 27% lower than the non-buffered treatment mean (Figure 4; $p = 0.014$). The buffered site treatment's daily maximum temperatures averaged across the study period was 13.2 ± 1.1 °C, 25 % higher than the reference ($p = 0.045$), and 6% lower than the non-buffered treatment mean ($p = 0.599$; Figure 4). The reference treatment mean in daily maximum soil temperature was 31% lower than the non-buffered treatment ($p = 0.014$). Range in daily soil temperatures at reference sites was 0.8 ± 0.1 °C, 10% lower than the buffered treatment mean range ($p = 0.796$), and 85% lower than non-buffered

treatment mean (Figure 4; $p = 0.017$). The mean of the buffered treatment daily range in soil temperature was 67% lower than that of the non-buffered treatment mean ($p = 0.037$).

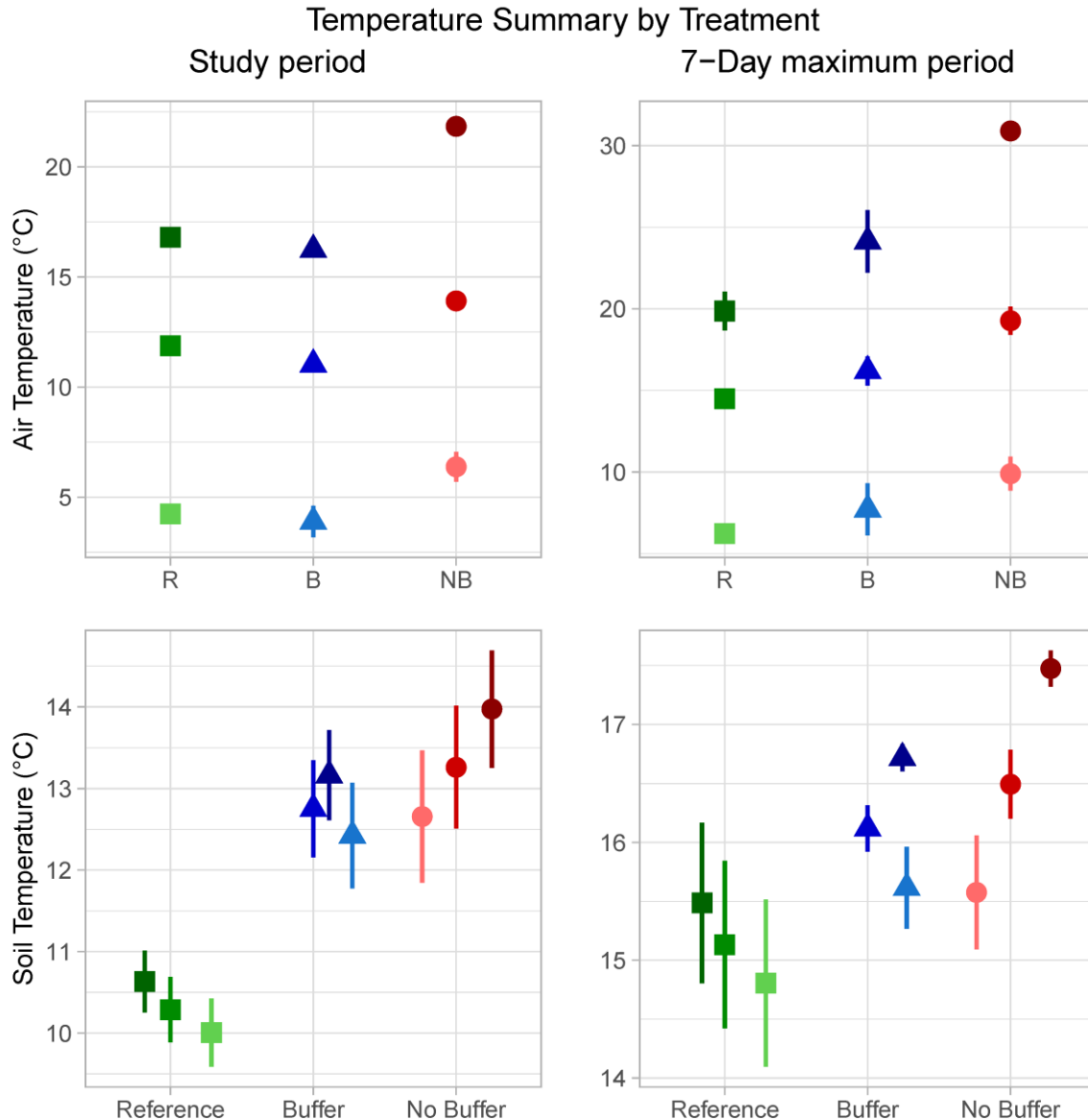


Figure 4. Summary of soil (top) and air (bottom) temperatures during the whole study period (left), and the 7-day-max period (right); average daily minimums in light colour shades, average daily means in medium shades, and average daily maximums in dark shades. Standard deviation shown as lines around the means.

The highest seven-day maximum soil temperature period was during the first week of August (3rd to 9th, 2019). The trends observed during this week (the “7-day-max period”) showed the same trends observed throughout the dry season, but the magnitudes of the differences between

treatments were more pronounced. The reference treatment mean of minimum, maximum, mean and range of soil temperature was the lowest, when compared to both buffer and non-buffered treatment mean values for those metrics (Figure 4).

The mean soil temperature of the 7-day-max period for the buffered treatment was 16.1 ± 0.3 °C, lower than the non-buffered mean of 16.5 ± 0.5 °C ($p = 0.346$), and higher than the reference mean of 15.1 ± 1.2 °C ($p = 0.169$; Figure 4). Minimum daily temperatures averaged the same for the buffered and non-buffered treatments at 15.6 °C (± 0.8 for NB, ± 0.6 for B), which was 5% higher than the reference minimum ($p = 0.594$). Daily maximum soil temperatures during the 7-day-max period averaged highest at non-buffered sites, where the average maximum temperature over that week was 14.0 ± 1.2 °C, which was higher than the buffered maximum of 13.2 ± 1.0 °C ($p = 0.443$), and higher than the reference maximum of 10.6 ± 0.7 °C ($p = 0.032$; Figure 4). Range in soil temperature during this period for the non-buffered treatment was 1.4 ± 0.2 °C, higher than the buffered range of 0.9 ± 0.2 °C ($p = 0.164$), and higher than the reference range of 0.8 ± 0.1 °C ($p = 0.040$; Figure 4).

Air temperatures - measured multiple times daily, between June and September of 2019 - reflected the same directional trend among treatments as the soil temperature metrics: the lowest values were observed at reference sites, intermediate values were observed at buffered sites, and the highest values were observed at the non-buffered sites (Figure 4). The reference treatment mean temperature of 11.9 ± 0.1 °C was higher than the buffered mean of 11.0 ± 0.3 °C ($p = 0.162$) and lower than the non-buffered mean of 13.9 ± 0.8 °C ($p = 0.006$). The treatment average of daily minimum air temperatures displayed the same directional trend (Figure 4). The reference treatment mean for daily minimum air temperature was 4.3 ± 0.2 °C, slightly higher than the buffered minimum of 3.9 ± 1.2 °C ($p = 0.903$), and lower than the non-buffered treatment

minimum of 6.4 ± 1.2 °C ($p = 0.086$). The buffered treatment minimum air temperature average was lower than that of the non-buffered sites ($p = 0.050$). Maximum daily air temperatures were lowest at reference sites, averaging 16.1 ± 1.4 °C, lower than buffered maximum of 16.3 ± 0.5 °C ($p = 0.987$), and lower than non-buffered sites at 21.8 ± 0.4 °C ($p = 0.004$; Figure 4). Buffered treatment daily maximum air temperatures averaged lower than the non-buffered treatment mean ($p = 0.001$). The range in daily air temperatures was highest throughout the sampling period for the non-buffered sites (average range: 15.4 ± 0.8 °C). The range of the buffered treatment's air temperature was 3.7 °C lower than the non-buffered range ($p = 0.002$), while the reference treatment range was 3.4 °C lower ($p = 0.004$; Figure 4).

The seven-day period during which the highest mean air temperatures were observed was August 3rd to 9th; this period is referred to hereafter as the 7-day-max. The 7-day-max showed similar results to the seasonal temperature trends, but as with the soil temperatures, the magnitude in the differences between the treatments was greater during this extreme temperature period. The 7-day-max mean daily air temperature for the 7-day-max at the non-buffered sites was the highest, at 19.3 ± 1.5 °C, three degrees higher than the buffered treatment mean of 16.2 ± 1.5 °C ($p = 0.056$), and almost five degrees higher than the reference mean of 14.5 ± 0.4 °C ($p = 0.009$; Figure 4). The buffered treatment mean of the mean daily air temperature was 1.7 higher than the reference treatment mean ($p = 0.302$). The maximum daily air temperatures during the 7-day-max for the reference treatment averaged 19.9 ± 2.1 °C, 5.6 °C lower than the buffered treatment average of ($p = 0.141$), and 10.9 °C lower than the non-buffered treatment mean of ($p = 0.003$); the buffered maximum was 5.4 °C lower than the non-buffered treatment mean ($p = 0.028$; Figure 4). The minimum daily air temperatures for 7-day-max period averaged 6.2 ± 0.4 °C for the reference treatment, lower than the buffered minimum of 7.7 ± 2.8 °C ($p = 0.634$), and the

non-buffered minimum of 9.90 ± 1.8 °C ($p = 0.125$); minimums were 2.9 °C lower at buffered sites than at non-buffered sites ($p = 0.401$). The range of air temperatures averaged 14.6 ± 0.5 °C for reference sites, lower than the buffered range of 16.4 ± 0.7 °C ($p = 0.126$), and the non-buffered treatment range of 21.0 ± 1.4 °C ($p < 0.001$); the range for buffered sites averaged 4.6 °C lower than the non-buffered sites ($p = 0.003$; figure 4).

Potential solar radiation co-varies with site openness (measure of canopy light from hemispherical photo interpretation), but it is a more robust measure that explains more variation of the treatment effect than site openness. This modelled radiation value represents the light available at the ground that gets through the canopy and accounts for local atmospheric parameters, seasonal sun-paths, and aspect measurements at each site. Potential solar radiation averages in the reference sites were lowest, across all nine sites, when compared to the buffered and non-buffered treatments, while buffered site means were consistently higher than the non-buffered site means (Figure 5). The mean potential solar radiation mean for the reference treatment was 20.5 ± 2.0 %, which was lower than the buffered treatment mean of 38.6 ± 12.9 % ($p = 0.120$), and the on-buffered treatment mean 83.9 ± 9.5 % ($p < 0.001$). The buffered treatment mean potential radiation was 2.2x lower than that of the non-buffered treatment ($p = 0.003$).

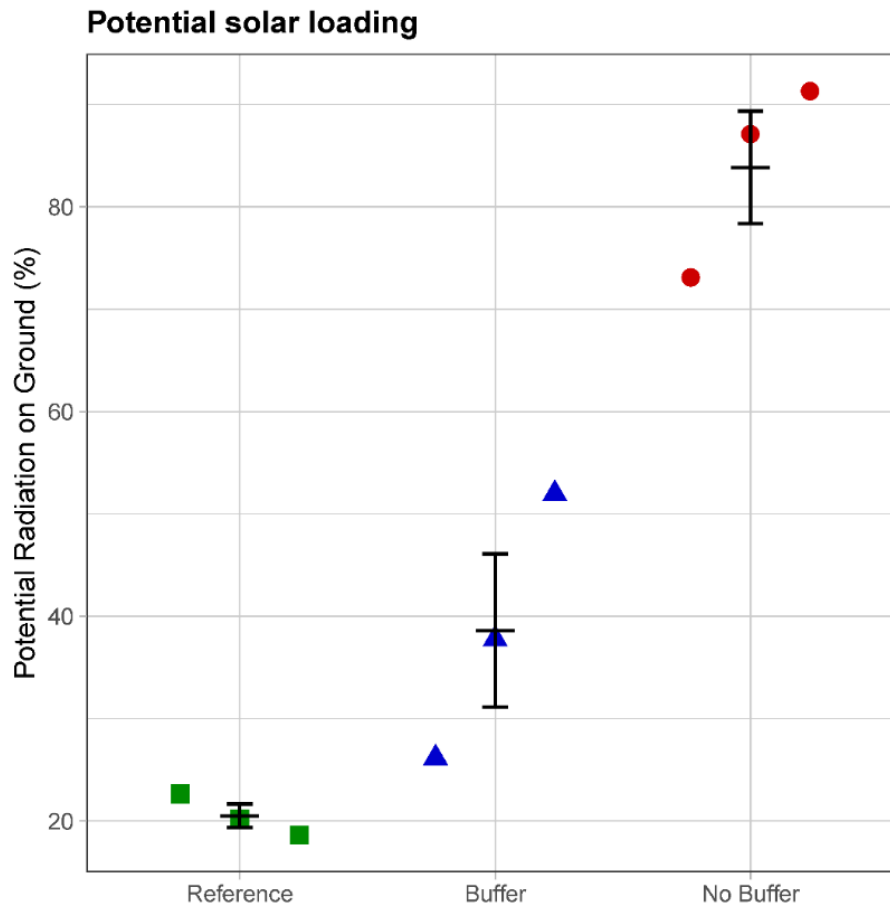


Figure 5. Modelled potential solar radiation reaching the ground surface as a percentage of direct shortwave solar radiation at each of the nine sites; this metric captures aspect of each study site, and region-specific parameters accounting for sun path and seasonality. Black lines indicate treatment mean and standard deviations.

Tree basal area in the riparian area (m^2/ha) was negatively correlated to potential solar radiation. Basal area was lowest at non-buffered sites, intermediate at buffered sites, and highest at reference sites (Figure 6). Basal area quantifies how much of the riparian area is covered by tree stems. The mean basal area for the reference treatment of 67 stems/ha was higher than the buffered treatment density of 34 stems/ha ($p = 0.011$), and the non-buffered treatment mean of 0 stems/ha ($p < 0.001$; Figure 6). The buffered treatment mean was significantly different from the non-buffered treatment mean ($p = 0.011$)

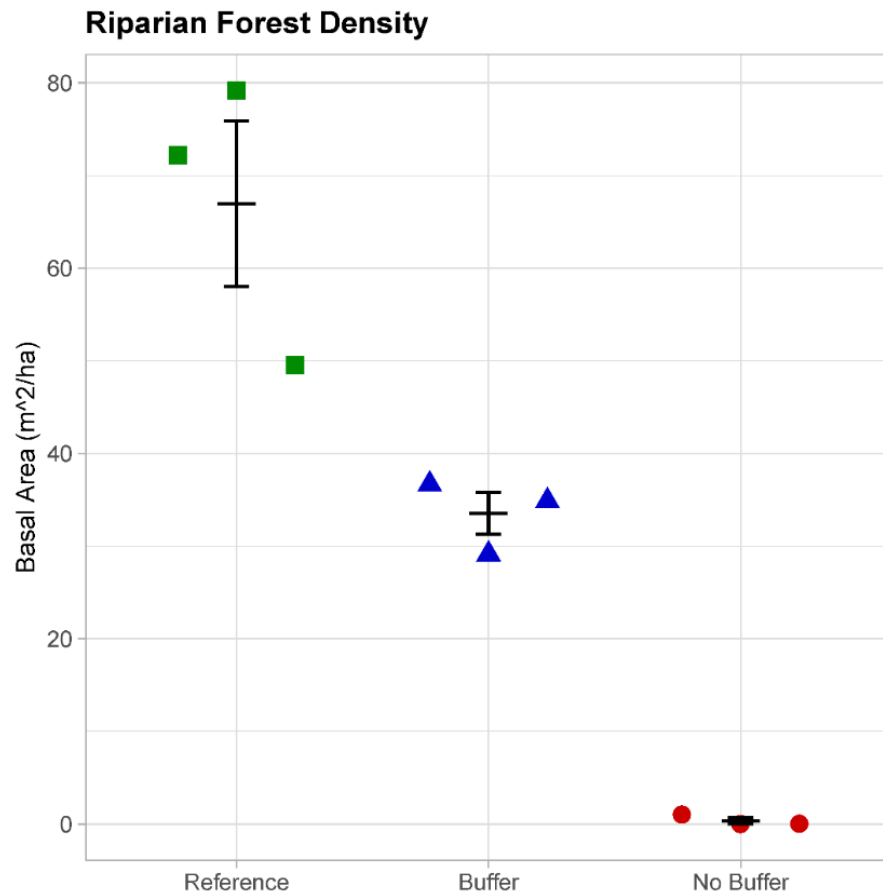


Figure 6. Forest density based on basal area measurements of the adjacent 30 m x 50 m quadrats on either side of study reach at each site; each point represents a site mean value of BA.

3.1.3 Species Composition

The NMDS ordination of species composition among sites and treatments showed that there was more variation in composition between the non-buffered sites than the buffer, and reference sites on the primary axis of variation (Figure 7). The buffered and reference sites have a similar magnitude of variation on that axis; however, the direction of their relations to the ordination axis is inverse. The highest variation in the ordination's primary axis (NMDS1) is among the non-buffered sites, whereas the reference treatment had the most variation in the secondary ordination axis. The species distribution of these plant communities are not well differentiated between the three treatments in this study.

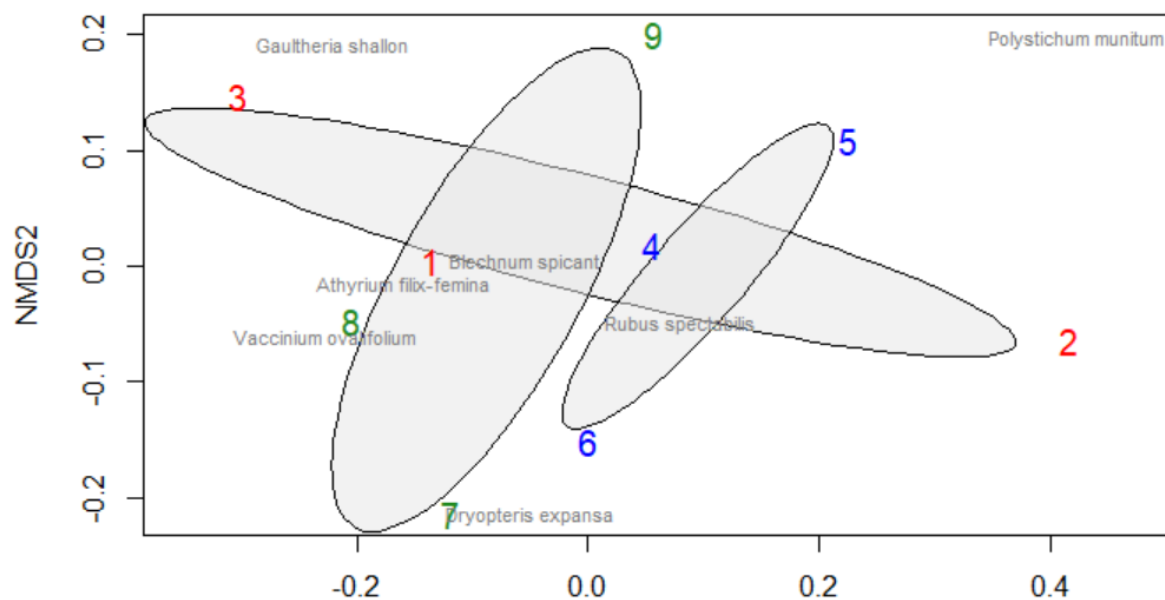


Figure 7. Non-metric dimensional scaling ordination of plant community distribution among study's three treatments; red numbers indicate the three non-buffered sites, blue are buffered sites, and green are reference sites. Relative abundance of the target species; high contribution to site and treatment differences indicated by large distance of species name to centre of plot. Ellipses were drawn to outline relations between and within treatments, and do not represent any statistically significant groupings.

Of the species included in this ordination, *G. shallon* and *P. munitum* had relative abundance that was most different from each other; the higher the percentage of *P. munitum*, the lower the

percent cover of *G. shallon*. Buffered sites differed most in their species composition compared to the other two treatments.

3.2 Community Trait Responses to Treatment and Environment

Linear mixed models demonstrated several explanatory relationships between environmental conditions and functional trait responses. Modelled potential radiation was the most influential environmental factor that contributed to plant functional trait values at the community level.

Other environmental covariates that had significant impact on the variation of those traits were maximum air temperature, maximum soil temperatures, riparian forest stem-density, and the mean daily temperature during the 7-day-max period. A single environmental covariate was selected for all functional trait LMMs except for LDMC, as the other AICc model weights were at least 93% (Table 3). All relationships in this section of results had a p-value of less than 0.001, except where otherwise indicated.

Variation in SLA was most influenced by potential radiation (AICc weight of 1.0) among the community-level (weighted) traits, accounting for 13% beyond the 76% explained by treatment effects. Community LDMC variation was explained by three different environmental parameters, together comprising 84% cumulative AICc weight: potential radiation, accounting for 6% variation ($p = 0.003$; 34% AICc weight), maximum soil temperature, which explained 8% variation in LDMC (34% AICc weight; $p = 0.003$), and riparian forest stem density represented 6% of the variation (16% AICc weight, $p = 0.006$). The environmental covariates influencing LDMC were assessed modelling one variable at a time, meaning that those effects are treated as independent of one another, and were not modelled with any crossed or nested relations.

Treatment effects for LDMC were significant for each of those modelled relationships ($p < 0.001$), and accounted for 55-64% of the remaining variation in those single-factor models. Mean

soil temperature of the 7-day-max period was modelled to be the most influential environmental condition on leaf nitrogen content (AICc weight of 0.97), accounting for 11% of variation along with the 82% accounted for by the treatment. Leaf Carbon content was most significantly impacted by potential radiation (AICc weight of 0.93); 20% of leaf C variation was explained by the radiation parameter in addition to another 24% explained by treatment. The ratio between carbon and nitrogen content in leaves (Leaf C:N) was influenced most significantly by potential radiation (AICc weight of 1.0), which accounted for 21% variation beyond the 65% accounted for by the treatment effects. Specific stem density was modelled as most significantly impacted by maximum air temperature (AICc weight of 0.95), accounting for 21% of variation beyond that of the treatment effect (31%).

Table 3. AICc table for community-weighted functional trait models. The AICc and Cum. Wt. (cumulative weight) were used to assess influential environmental covariates contributing to treatment effects on functional trait values weighted across each site. Lowest AICc value indicates best model fit.

	Modnames	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt		Modnames	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
5	Community_Carb_radiation_model	6	4675.555	0.000000	1.0000000000	0.9326308156	-2331.744	0.9326308	5	Community_CN_ratio_radiation_model	6	7009.171	0.00000	1.000000e+00	1.000000e+00	-3498.552	1
7	Community_Carb_DENSITY_model	6	4682.709	7.153711	0.0279634973	0.0260796193	-2335.321	0.9587104	7	Community_CN_ratio_DENSITY_model	6	7044.359	35.18833	2.285347e-08	2.285347e-08	-3516.146	1
1	Community_Carb_MeanSoilTemp_model	6	4683.662	8.107381	0.0173581987	0.0161887910	-2335.797	0.9748992	1	Community_CN_ratio_MeanSoilTemp_model	6	7060.786	51.61521	6.192992e-12	6.192991e-12	-3524.359	1
2	Community_Carb_MaxSoilTemp_model	6	4684.127	8.571844	0.0137609306	0.0128338680	-2336.030	0.9937731	11	Community_CN_ratio_AirMean7_model	6	7060.931	51.75938	5.762278e-12	5.762278e-12	-3524.431	1
6	Community_Carb_BA_model	6	4684.920	9.364832	0.0092566237	0.0086330125	-2336.426	0.9963661	9	Community_CN_ratio_SoilMean7_model	6	7061.240	52.06878	4.936365e-12	4.936365e-12	-3524.586	1
12	Community_Carb_TROnly	5	4689.451	13.896152	0.0009604813	0.0008957744	-2339.701	0.9972619	10	Community_CN_ratio_AirMax7_model	6	7061.347	52.17565	4.679534e-12	4.679533e-12	-3524.640	1
8	Community_Carb_SoilMax7_model	6	4690.219	14.664084	0.0006542362	0.0006101608	-2339.076	0.9978720	2	Community_CN_ratio_MaxSoilTemp_model	6	7061.361	52.18964	4.646899e-12	4.646899e-12	-3524.647	1
13	Community_Carb_RADOnly	4	4691.075	15.520329	0.0004263863	0.0003976610	-2341.522	0.9982697	8	Community_CN_ratio_SoilMax7_model	6	7065.215	56.04382	6.764540e-13	6.764539e-13	-3526.574	1
9	Community_Carb_SoilMean7_model	6	4691.192	15.636801	0.0004022645	0.0003751643	-2339.562	0.9986449	12	Community_CN_ratio_TROnly	5	7067.984	58.81285	1.694154e-13	1.694154e-13	-3528.968	1
10	Community_Carb_AirMax7_model	6	4691.315	15.759977	0.0003782374	0.0003527559	-2339.624	0.9989976	4	Community_CN_ratio_MaxAirTemp_model	6	7068.451	59.27993	1.341302e-13	1.341302e-13	-3528.192	1
4	Community_Carb_MaxAirTemp_model	6	4691.372	15.817137	0.0003675804	0.0003428168	-2339.652	0.9993404	6	Community_CN_ratio_BA_model	6	7069.887	60.71594	6.541853e-14	6.541853e-14	-3528.910	1
11	Community_Carb_AirMean7_model	6	4691.435	15.879780	0.0003562457	0.0003322457	-2339.684	0.9996727	3	Community_CN_ratio_MeanAirTemp_model	6	7069.996	60.82496	6.194821e-14	6.194821e-14	-3528.964	1
3	Community_Carb_MeanAirTemp_model	6	4691.465	15.909685	0.0003509585	0.0003273147	-2339.699	1.0000000	13	Community_CN_ratio_RADOnly	4	7186.724	177.55299	2.785211e-39	2.785211e-39	-3589.346	1
	Modnames	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt		Modnames	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
5	Community_LDMC_radiation_model	6	12726.63	0.00000000	1.000000e+00	3.448758e-01	-6357.281	0.344875	9	Community_Nitro_SoilMean7_model	6	1087.780	0.000000	1.000000e+00	9.710618e-01	-537.8564	0.9710618
2	Community_LDMC_MaxSoilTemp_model	6	12726.67	0.04397874	9.782506e-01	3.373750e-01	-6357.303	0.682250	8	Community_Nitro_SoilMax7_model	6	1094.830	7.049212	2.946342e-02	2.861080e-02	-541.3810	0.9996726
7	Community_LDMC_DENSITY_model	6	12728.15	1.51914685	4.678660e-01	1.613557e-01	-6358.041	0.843606	6	Community_Nitro_BA_model	6	1103.771	15.990219	3.371072e-04	3.273520e-04	-545.8515	1.0000000
1	Community_LDMC_MeanSoilTemp_model	6	12729.07	2.43799722	2.955260e-01	1.019198e-01	-6358.500	0.945526	5	Community_Nitro_radiation_model	6	1134.882	47.101118	5.917281e-11	5.746046e-11	-561.4070	1.0000000
12	Community_LDMC_TROnly	5	12733.52	6.89080408	3.189194e-02	1.099876e-02	-6361.737	0.956525	3	Community_Nitro_MeanAirTemp_model	6	1141.403	53.622491	2.269990e-12	2.204301e-12	-564.6677	1.0000000
9	Community_LDMC_SoilMean7_model	6	12733.91	7.27796814	2.627903e-02	9.063002e-03	-6360.920	0.965588	10	Community_Nitro_AirMax7_model	6	1143.814	56.033345	6.800077e-13	6.603295e-13	-565.8731	1.0000000
11	Community_LDMC_AirMean7_model	6	12734.24	7.60955738	2.226412e-02	7.678358e-03	-6361.086	0.973266	7	Community_Nitro_DENSITY_model	6	1144.466	56.685612	4.907673e-13	4.765654e-13	-566.1992	1.0000000
6	Community_LDMC_BA_model	6	12734.38	7.74993216	2.075504e-02	7.157912e-03	-6361.156	0.980424	12	Community_Nitro_TROnly	5	1145.807	58.026864	2.509727e-13	2.437100e-13	-567.8795	1.0000000
4	Community_LDMC_MaxAirTemp_model	6	12734.81	8.18084098	1.673220e-02	5.770530e-03	-6361.372	0.986194	4	Community_Nitro_MaxAirTemp_model	6	1146.776	58.995750	1.546093e-13	1.501352e-13	-567.3543	1.0000000
8	Community_LDMC_SoilMax7_model	6	12735.12	8.48756584	1.435319e-02	4.950069e-03	-6361.525	0.991144	11	Community_Nitro_AirMean7_model	6	1147.421	59.640305	1.120140e-13	1.087725e-13	-567.6766	1.0000000
3	Community_LDMC_MeanAirTemp_model	6	12735.29	8.65456048	1.320341e-02	4.553537e-03	-6361.609	0.995698	2	Community_Nitro_MaxSoilTemp_model	6	1147.703	59.922597	9.726877e-14	9.445400e-14	-567.8177	1.0000000
10	Community_LDMC_AirMax7_model	6	12735.40	8.76840006	1.247286e-02	4.301589e-03	-6361.666	1.000000	1	Community_Nitro_MeanSoilTemp_model	6	1147.767	59.986322	9.421840e-14	9.149190e-14	-567.8496	1.0000000
13	Community_LDMC_RADOnly	4	12816.68	90.05406347	2.786176e-20	9.608848e-21	-6404.326	1.000000	13	Community_Nitro_RADOnly	4	1327.581	239.800809	8.470635e-53	8.225510e-53	-659.7746	1.0000000
	Modnames	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt		Modnames	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
5	Community_SLA_radiation_model	6	14702.98	0.00000	1.000000e+00	9.999639e-01	-7345.458	0.9999639	4	Community_SSD_MaxAirTemp_model	6	-1422.629	0.000000	1.000000e+00	9.518563e-01	717.4001	0.9518563
7	Community_SLA_DENSITY_model	6	14723.49	20.50740	3.522686e-05	3.522558e-05	-7355.711	0.9999991	10	Community_SSD_AirMax7_model	6	-1415.843	6.786484	3.359956e-02	3.198196e-02	714.0068	0.9838383
11	Community_SLA_AirMean7_model	6	14730.81	27.82475	9.076781e-07	9.076453e-07	-7359.370	1.0000000	9	Community_SSD_SoilMean7_model	6	-1412.357	10.272179	5.880642e-03	5.597526e-03	712.2640	0.9894358
10	Community_SLA_AirMax7_model	6	14748.72	45.73219	1.173227e-10	1.173185e-10	-7368.324	1.0000000	8	Community_SSD_SoilMax7_model	6	-1411.762	10.866953	4.367885e-03	4.157599e-03	711.9666	0.9935934
9	Community_SLA_SoilMean7_model	6	14753.05	50.07020	1.340891e-11	1.340843e-11	-7370.493	1.0000000	7	Community_SSD_DENSITY_model	6	-1411.451	11.178654	3.737542e-03	3.557603e-03	711.8107	0.9971510
12	Community_SLA_TROnly	5	14754.15	51.16805	7.744613e-12	7.744333e-12	-7372.051	1.0000000	6	Community_SSD_BA_model	6	-1409.472	13.157759	1.389405e-03	1.322514e-03	710.8212	0.9984735
8	Community_SLA_SoilMax7_model	6	14755.72	52.74018	3.528704e-12	3.528577e-12	-7371.828	1.0000000	2	Community_SSD_MaxSoilTemp_model	6	-1407.597	15.031940	5.443218e-04	5.181161e-04	709.8841	0.9989917
3	Community_SLA_MeanAirTemp_model	6	14755.76	52.77623	3.465668e-12	3.465542e-12	-7371.846	1.0000000	1	Community_SSD_MeanSoilTemp_model	6	-1406.770	15.859251	3.599212e-04	3.425932e-04	709.4704	0.9993343
4	Community_SLA_MaxAirTemp_model	6	14755.99	53.00675	3.088373e-12	3.088261e-12	-7371.961	1.0000000	11	Community_SSD_AirMean7_model	6	-1406.188	16.441464	2.690181e-04	2.560666e-04	709.1793	0.9995903
6	Community_SLA_BA_model	6	14756.08	53.09672	2.952527e-12	2.952420e-12	-7372.006	1.0000000	12	Community_SSD_TROnly	5	-1405.497	17.132794	1.903974e-04	1.812310e-04	707.8092	0.9997715
1	Community_SLA_MeanSoilTemp_model	6	14756.11	53.12953	2.904479e-12	2.904374e-12	-7372.022	1.0000000	5	Community_SSD_radiation_model	6	-1405.037	17.592348	1.513108e-04	1.440262e-04	708.6039	0.9999156
2	Community_SLA_MaxSoilTemp_model	6	14756.12	53.13345	2.898798e-12	2.898693e-12	-7372.024	1.0000000	3	Community_SSD_MeanAirTemp_model	6	-1403.858	18.771636	8.390562e-05	7.986610e-05	708.0143	0.9999954
13	Community_SLA_RADOnly	4	14976.19	273.20544	4.722718e-60	4.722547e-60	-7484.078	1.0000000	13	Community_SSD_RADOnly	4	-1398.131	24.498361	4.789039e-06	4.558477e-06	703.1060	1.0000000

3.3 Species Trait Responses to Treatment

The treatment effects on functional traits were observed across all species present at all nine sites. The buffered sites showed intermediate site averages for functional traits between the reference and no buffer values. Statistical power was highest for *R. spectabilis* as it was the only plant species sampled from all nine sites. Not all focal species were collected at each site; in the figures below, absence of a symbol from a treatment indicates that a species was not present at all sites in that treatment.

3.3.1 Specific Leaf Area

Specific Leaf Area had a consistent directional trend across all eight species sampled (Figure 8), where the reference sites had the highest values of SLA for treatment-level means, the non-buffered treatment showed the lowest values, and the buffered sites were intermediate as predicted; however, when sufficient sample size was present, statistical significance varied among the eight focal species studied. The reference treatment mean of $561 \pm 40.0 \text{ mm}^2 \text{ mg}^{-1}$ was 2.42 ($p < 0.001$) and 2.86 ($p < 0.001$) times higher for *R. spectabilis* than the means of the buffered and non-buffered sites, respectively (Figure 8). The buffer mean was higher than the non-buffered mean by 24% ($p = 0.649$). The reference treatment mean of $441 \pm 4.7 \text{ mm}^2 \text{ mg}^{-1}$ for *D. expansa* was higher than buffer and non-buffered treatment means of 279 ($p = 0.146$) and 238 ($p = 0.060$), respectively (Figure 8). The buffered treatment mean was higher than the non-buffered, but not significantly different for *D. expansa* ($p = 0.777$). *Gaultheria shallon* had a reference treatment mean of $210 \pm 13.1 \text{ mm}^2 \text{ mg}^{-1}$, 13% higher than the buffered treatment mean ($p = 0.358$), and 53% higher than the non-buffered treatment mean ($p = 0.040$, Figure 8). The buffered treatment of SLA averaged 36% higher than the non-buffered treatment ($p = 0.122$). The reference treatment mean of *A. filix-femina*'s SLA was $728 \pm 108.8 \text{ mm}^2 \text{ mg}^{-1}$, which was

19% higher than the buffered treatment ($p = 0.549^*$), and 143% higher than the non-buffered treatment means ($p = 0.192^*$); the buffered treatment SLA averaged higher than the non-buffered treatment, but was not statistically testable (Figure 8). *Vaccinium ovalifolium* reference treatment mean was $521 \pm 70.0 \text{ mm}^2 \text{ mg}^{-1}$, higher than the buffered mean of 324 ($p = 0.079$) (Figure 11). The reference treatment mean of *P. munitum* of 210 was 141% higher than the buffered treatment mean ($p = 0.343^*$), and 172% higher than the non-buffered treatment mean ($p = 0.284^*$; Figure 8). For *B. spicant*, the reference treatment mean of $283 \pm 11.8 \text{ mm}^2 \text{ mg}^{-1}$ was significantly higher than the buffer ($p = 0.058$); that mean was also higher than the non-buffered treatment means ($p = 0.171$), but they were not significantly different (Figure 8). This fern species demonstrated an anomalous buffered treatment mean higher than that of the non-buffered treatment mean, but by only 1% ($p = 0.601$). *Rubus ursinus* had a mean at the buffered site that was double (95% higher) than the non-buffered site.

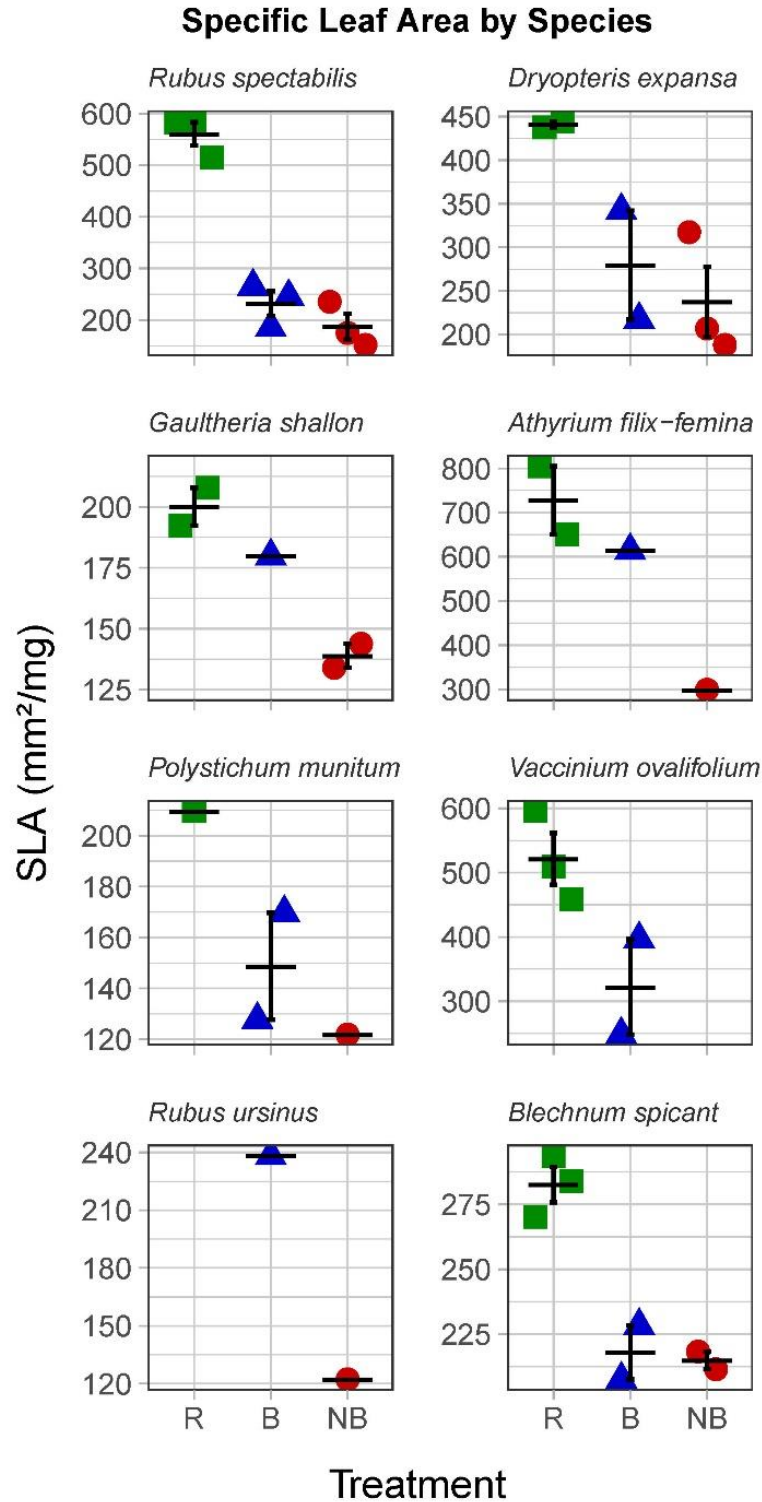


Figure 8. Summary of specific leaf area by species; black bars indicate treatment means with standard error and coloured points indicate site means for which the species were sufficiently abundant for sampling: reference (R) = green squares, buffered (B) = blue triangles, non-buffered (NB) = red circles.

3.3.2 Leaf Dry Matter Content

Leaf Dry Matter Content can often be approximated as the multiplicative inverse of the Specific Leaf Area (Pérez-Harguindeguy et al., 2013). As such, trends for LDMC in this data are approximately inverse of those in Section 3.2.1; LDMC values were highest on average in reference sites and lowest in the non-buffered sites (Figure 9). The buffered treatment mean was intermediate to the other two treatments for all but one species sampled. *Rubus spectabilis* had a reference treatment mean LDMC value of $211 \pm 9.1 \text{ mg g}^{-1}$, which was significantly lower than the buffered ($p = 0.001$) and non-buffered treatments ($p < 0.001$; Figure 9). The mean for the buffered treatment was lower but not significantly different from the non-buffered treatment mean ($p = 0.874$). *Dryopteris expansa* had a non-buffered mean of $295 \pm 20.1 \text{ mg g}^{-1}$, which was 141% higher than the reference mean ($p = 0.067$), and was 110% higher than the buffer mean ($p = 0.014$; Figure 9). The mean LDMC value of *D. expansa* for the buffered treatment was higher than the reference treatment by 28% ($p = 0.325$; Figure 9). The *G. shallon* non-buffered treatment mean was $270 \pm 0.9 \text{ mg g}^{-1}$, higher than the buffered treatment mean of 252 mg g^{-1} (insufficient data for SD, $p = 0.335$), and the reference treatment mean of $248 \pm 10.6 \text{ mg g}^{-1}$ ($p = 0.177$; Figure 9); these differences were insignificant. The reference treatment mean for *G. shallon* was only 2% lower than the buffered treatment mean ($p = 0.889$). *Athyrium filix-femina* reference treatment mean was $166 \pm 14.9 \text{ mg g}^{-1}$, 40% lower than the buffer mean ($p = 0.778^*$), and 46% lower than the non-buffered treatment mean ($p = 0.152^*$; Figure 9). *Vaccinium ovalifolium* had a non-buffered treatment mean higher than the buffered and reference treatment means, neither of which was statistically testable. The buffered treatment mean of $296 \pm 33.1 \text{ mg g}^{-1}$ was 23% higher than the reference treatment mean, for *V. ovalifolium* ($p = 0.140$). *Polystichum munitum* had a reference treatment mean of 319 mg g^{-1} (but had insufficient data for

SD), which was 9% lower than the buffered treatment mean ($p = 0.343^*$), and 15% lower than the non-buffered treatment mean ($p = 0.497^*$). The buffered treatment mean was 6% lower than the non-buffered treatment mean, but that comparison did not have sufficient data for statistical tests. There were no significant differences in LDMC for *B. spicant*; the reference treatment mean was $199 \pm 9.8 \text{ mg g}^{-1}$, and the buffer treatment was 5% lower and non-buffered 4% lower, respectively. *Rubus ursinus* had a non-buffered treatment mean for LDMC at 337 mg g^{-1} , which was 15% higher than the buffered-treatment mean (Figure 9), but not significantly different ($p = 0.627$).

Leaf Dry Matter Content by Species

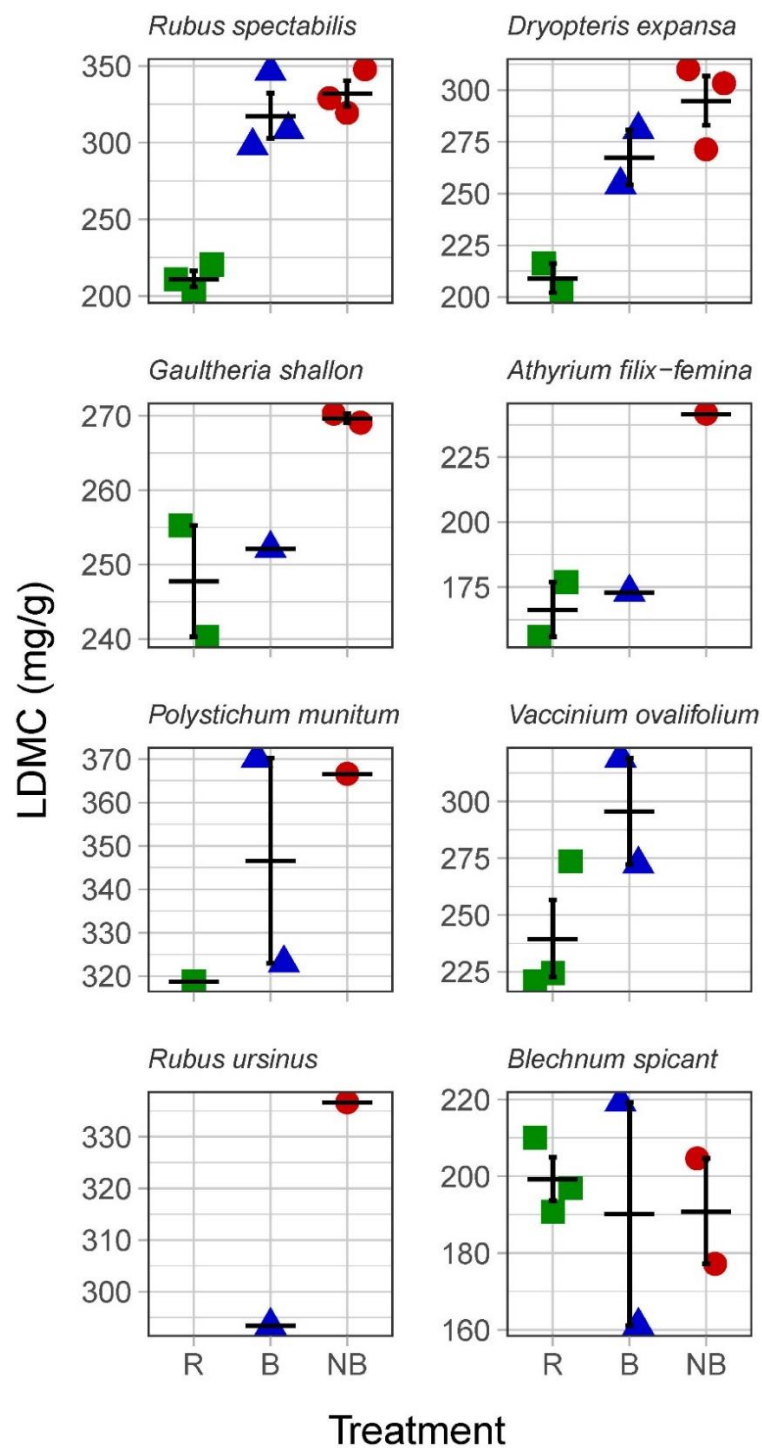


Figure 9. Summary of leaf dry matter content by species; treatment means with standard error in black bars, coloured points indicate site means for which the species were sufficiently abundant for sampling: reference (R) = green squares, buffered (B) = blue triangles, non-buffered (NB) = red circles.

3.3.3 Leaf Nitrogen Content

Leaf nitrogen values had a similar, yet less consistent response as SLA to the treatment; reference means were typically the highest, followed by buffered and non-buffered means. *Rubus spectabilis* had a reference mean of $3.16 \pm 0.2\%$, which was significantly higher than the harvested site means (buffer: $p < 0.001$, no buffer: $p < 0.001$; Figure 10). The buffered treatment mean for *R. spectabilis* was marginally higher than the no buffer mean at $2.20 \pm 0.1\%$ ($p = 0.880$), but not significantly different. For *D. expansa*, the reference treatment mean of $3.04 \pm 0.3\%$ was 1.37 times higher than the buffered treatment mean ($p = 0.069$), and 1.45 times higher than the non-buffered treatment mean ($p = 0.032$); the non-buffered treatment mean was lower than that of the buffered treatment by a factor of 1.06 ($p = 0.833$; Figure 10). *Gaultheria shallon* had a different directional response in Leaf N from the other focal species to treatment effects; the lowest value was the reference at $1.26 \pm 0.1\%$, the buffered treatment mean was the same ($p = 0.994$), and the non-buffered treatment mean was highest at $1.47 \pm 0.1\%$ (relative to reference: $p = 0.268$; relative to buffer: $p = 0.381$). *Athyrium filix-femina* had a reference treatment mean of $3.42 \pm 0.1\%$, which was 1.16 times higher than the buffered treatment mean ($p = 0.090^*$) and 1.43 times higher than the non-buffered treatment mean ($p = 0.042^*$; Figure 10). For *A. filix-femina*, the buffered treatment mean (2.95%; SD N/A) was slightly higher than that of the non-buffered treatment (2.39%; SD N/A). *Vaccinium ovalifolium* had a buffered treatment mean of $2.11 \pm 0.1\%$, which was lower than the reference treatment mean of $2.57 \pm 0.3\%$ ($p = 0.106$). Leaf N content was highest for *P. munitum* in the reference treatment at 1.71% (SD N/A); it was 1.04 times higher than the buffered treatment mean ($p = 0.856^*$) and 1.12 times higher than the non-buffered treatment mean ($p = 0.725^*$). *Blechnum spicant* was the one focal species that had no single directional trend across the treatments (Figure 10); the non-buffered treatment mean

was $1.90 \pm 0.2\%$, not significantly different from the reference, but was 1.24 times higher than the buffered treatment mean ($p = 0.199$). The buffered treatment mean was lower than the reference treatment mean for *B. spicant* by a factor of 1.22 ($p = 0.198$). The non-buffered site had a very close mean value for Leaf N to that of the buffered site for *R. ursinus* (1% relative difference; Figure 10).

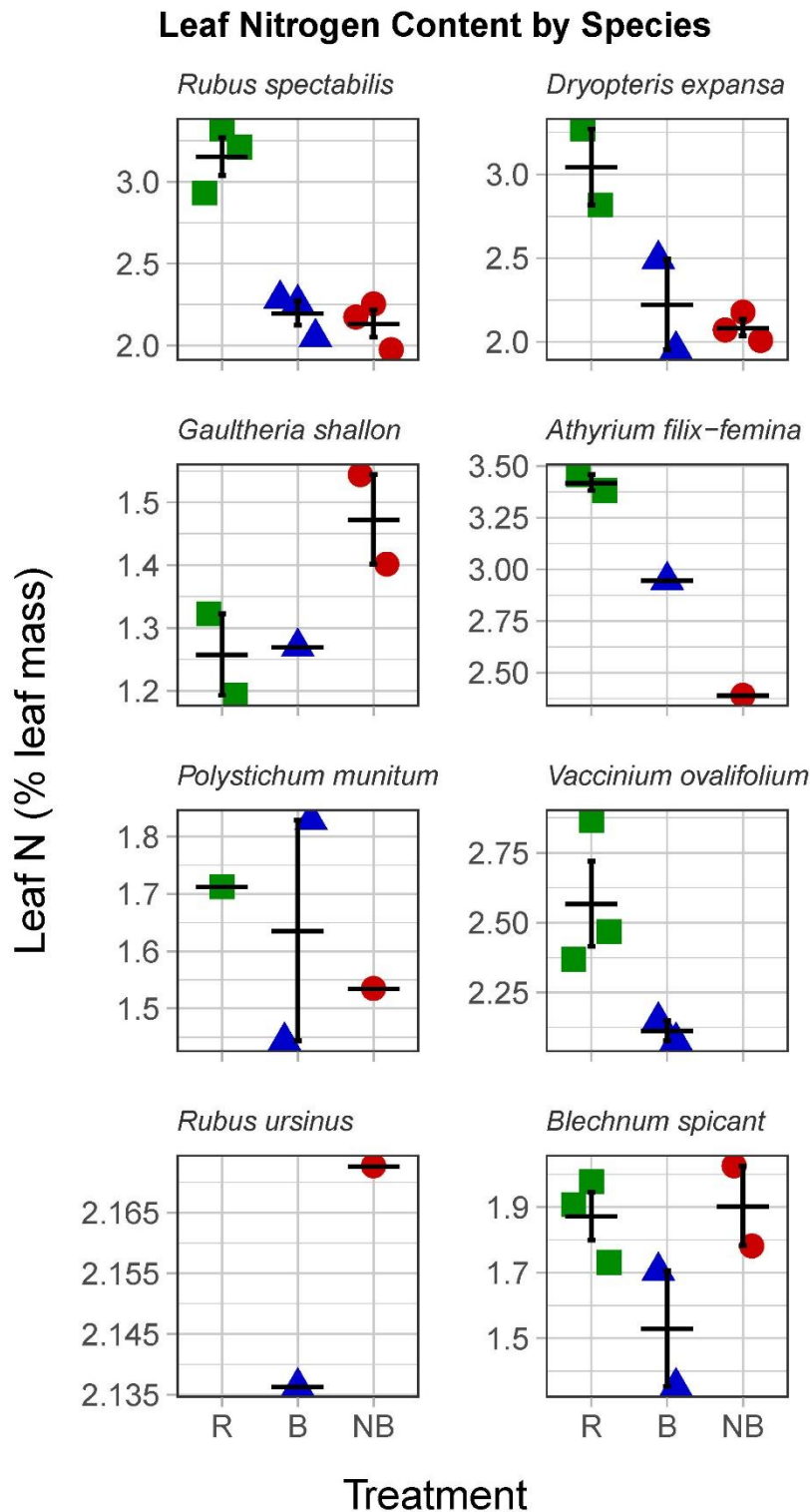


Figure 10. Summary of leaf nitrogen dry mass content by species; treatment means with standard error in black bars, coloured points indicate site means for which the species were sufficiently abundant for sampling: reference (R) = green squares, buffered (B) = blue triangles, non-buffered (NB) = red circles.

3.3.4 Leaf Carbon Content

The effect of treatment on Leaf C was inverse to that on Leaf N, where the majority of species had the highest Leaf C values in the non-buffered sites, intermediate values in the buffered sites, and lowest values at the reference sites (Figure 11). That directional trend was observed in Leaf C treatment means for six of the eight focal species measured. *Rubus spectabilis* had a reference treatment mean of 45.5%, less than 1% leaf C lower than the buffered treatment mean (of 46.1% leaf C; $p = 0.556$), and less than 2% leaf C lower than the non-buffered treatment mean ($p = 0.066$). The non-buffered mean of leaf C was higher at the non-buffered sites than the buffered ones ($p = 0.259$; Figure 11). There were no significant differences among means for leaf C for *D. expansa*: the reference mean was 46.3%, buffered treatment was 47.4%, and the non-buffered treatment was 47.3% (Figure 11). *Gaultheria shallon* had a non-buffered treatment mean of 50.2%, which was not significantly higher than the buffered treatment mean of 49.9%. The reference treatment mean of 49.0 % was not significantly lower than either other treatment (Figure 11). *Athyrium filix-femina* had a non-linear response to treatments, where the non-buffered treatment mean of 46.3% leaf C was higher than both the buffered treatment mean of 43.0 (not statistically testable), and the reference treatment mean of 43.6% leaf C ($p = 0.246^*$); the buffered treatment mean was not significantly lower than that of the reference treatment ($p = 0.680^*$; Figure 11). The buffered treatment mean for *V. ovalifolium* was 48.1%, which is higher than the reference treatment mean of 46.6% ($p = 0.088$, Figure 11). *Polystichum munitum* showed an anomalous response to the treatments, where the reference treatment mean of 45.0% leaf C was the intermediate value between the buffer and non-buffered treatment means (46.7% and 44.7% respectively); the buffered treatment mean was not significantly higher than the reference mean ($p = 0.392^*$), or the non-buffered treatment mean ($p = 0.849^*$; Figure 11).

Blechnum spicant demonstrated the hypothesized directional response (Figure 11), where the reference treatment mean of 44.1% was lower than both buffer (44.3% C) and non-buffered (46.1% C) treatment means ($p = 0.973$, $p = 0.086$, respectively); the non-buffered treatment mean was slightly higher than the buffered treatment mean, but not significantly ($p = 0.136$).

Rubus ursinus had a buffered treatment mean lower only by 0.6% leaf C than the non-buffered treatment mean (not significant; Figure 11).

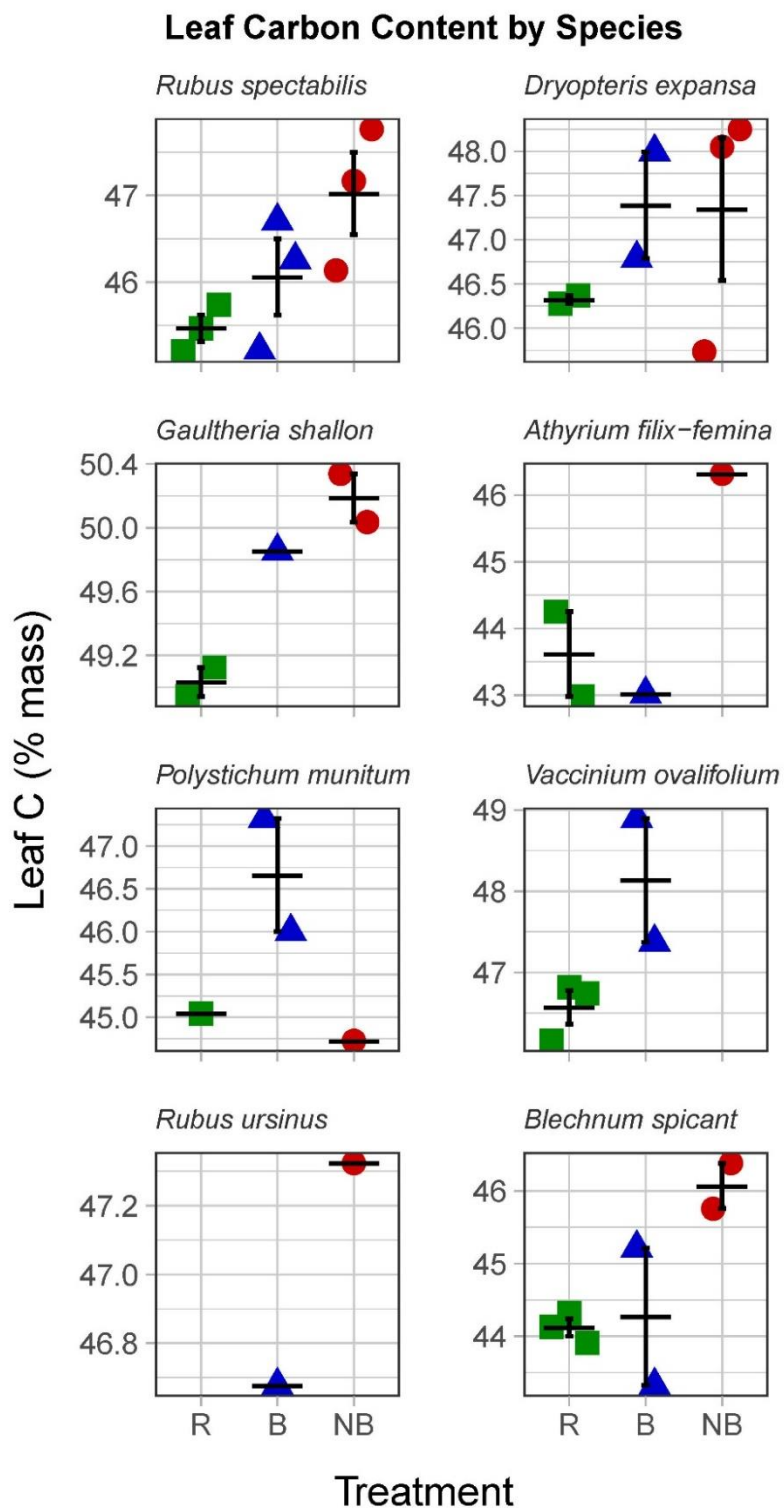


Figure 11. Summary of leaf carbon content by species; treatment means with standard error in black bars, coloured points indicate site means for which the species were sufficiently abundant for sampling: reference (R) = green squares, buffered (B) = blue triangles, non-buffered (NB) = red circles.

3.3.5 Leaf Carbon to Nitrogen ratio

The ratio of percent mass of carbon to percent mass of nitrogen in the leaf is derived directly from the Leaf C and Leaf N measures. Leaf C is generally higher than Leaf N by about an order of magnitude, so C:N is always considerably greater than one. The values in this section therefore show similar trends to those seen in Section 3.2.4. Four of the eight focal species responded in a directional trend where the reference treatment mean was lowest, followed by the buffer mean, followed by the no buffer mean (Figure 12). *R. spectabilis* data demonstrated that trend, where the reference treatment mean of 14.6 was lower than the buffered treatment mean of 21.8 ($p = 0.001$), and the non-buffered treatment mean of 22.0 ($p < 0.001$; Figure 12). The buffered treatment mean was only 3% lower than the non-buffered treatment mean in Leaf C:N for *R. spectabilis* ($p = 0.794$). With *D. expansa*, the non-buffered treatment mean of 23.5 was higher than the buffer mean for Leaf C:N by 5% ($p = 0.890$); the reference treatment mean was 44% lower than the buffered treatment mean ($p = 0.115$), and 51% lower than non-buffered treatment mean ($p = 0.059$; Figure 12). The reference treatment mean of *G. shallon* (39.4) was higher than the buffered treatment, but not significantly, and was 11% higher than the non-buffered treatment mean ($p = 0.615$; Figure 12). The buffered treatment mean was higher than the non-buffered treatment mean ($p = 0.740$), which was inverse to the hypothesized trend observed in the other species. *Athyrium filix-femina* had a non-buffered treatment mean of 19.5, 31% higher than that of the buffered treatment (insufficient data for a statistical test), and 51% higher than that of the reference treatment ($p = 0.005^*$); the buffered treatment mean was 16% higher than the reference treatment mean ($p = 0.0167^*$; Figure 12). *Vaccinium ovalifolium* had a reference treatment mean 26% lower than the buffered treatment mean of 23.1 ($p = 0.031$; Figure 15). The reference treatment mean of Leaf C:N for *P. munitum* was 26.5, 11% lower than that of

the buffered treatment mean ($p = 0.750^*$), and 13% lower than the non-buffered treatment mean ($p = 0.735^*$). There were no significant differences for *B. spicant*, with Leaf C:N values of 24 for the reference, 24.4 for the non-buffered, and 29.5 for the buffered treatment (Figure 12). The buffered treatment mean was essentially the same as the non-buffered treatment mean for *R. ursinus*.

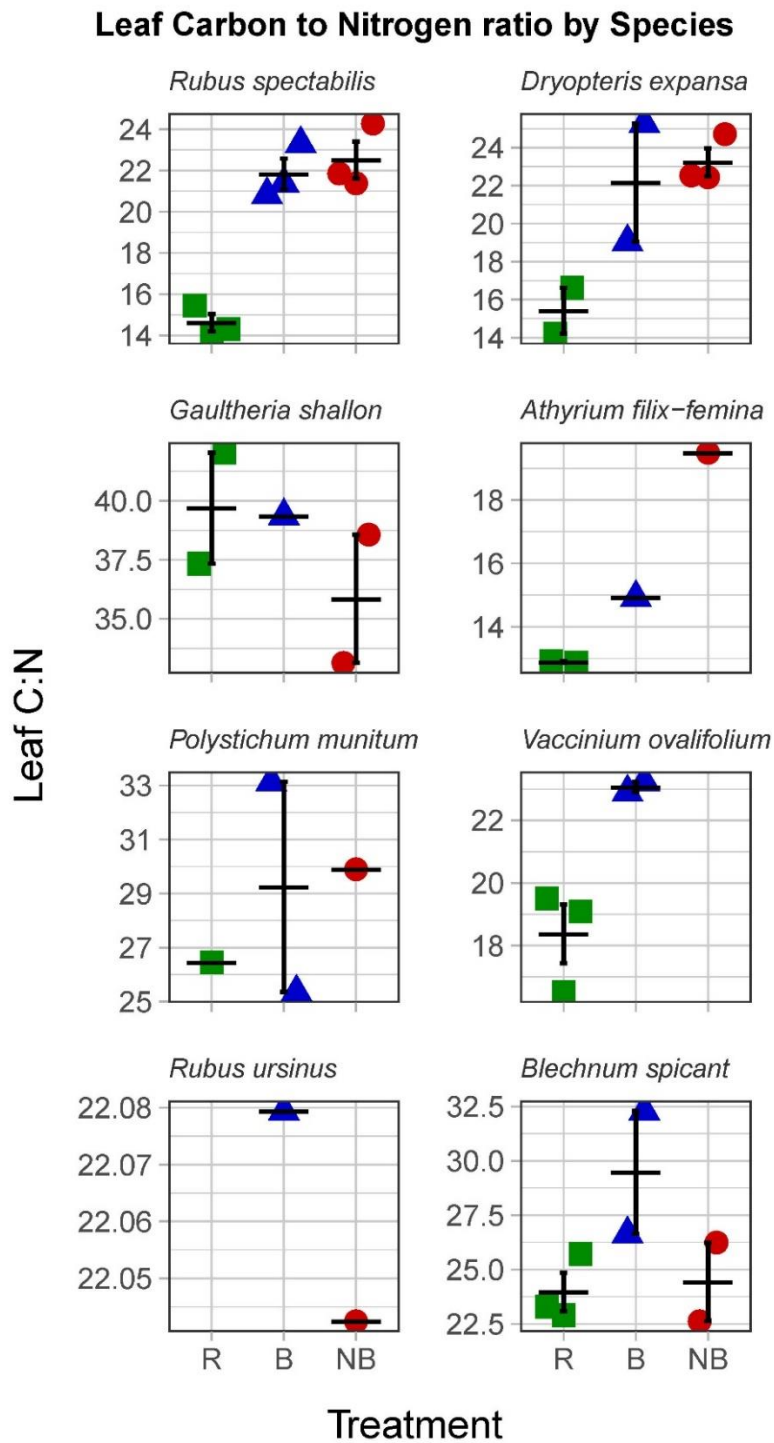


Figure 12. Summary of leaf carbon to nitrogen ratio by species; treatment means with standard error in black bars, coloured points indicate site means for which the species were sufficiently abundant for sampling: reference (R) = green squares, buffered (B) = blue triangles, non-buffered (NB) = red circles.

3.3.6 Stem specific density

Stem specific density (including epidermis) was quite variable in response to the treatment effect. The hypothesized response was represented in only three of the focal species, two of which were the most robustly represented species in the study. There were no significant differences in stem-specific density for *Rubus spectabilis*, with the reference mean of 0.388, a buffered mean of 0.470, and non-buffer mean of 0.481 (Figure 13). *Dryopteris expansa* had a similar directional trend, where the reference treatment mean of 0.135 was 13% lower than the buffered ($p = 0.830$), and 47% lower than non-buffered ($p = 0.142$) treatment means, and the non-buffered treatment mean was much higher than the buffered treatment mean ($p = 0.278$; Figure 13). *Gaultheria shallon*'s trend was different from the other focal species across treatments: the non-buffered treatment mean of 0.339 was lowest, the buffered treatment mean of 0.455 was intermediate ($p = 0.316$), and the reference treatment mean was the higher, at 0.467 ($p = 0.980$) and 38% higher than the non-buffered treatment mean ($p = 0.203$) (Figure 13). *Athyrium filix-femina* had a higher mean value for the non-buffered treatment (0.114) than both the buffered treatment (0.091; $p = 0.030^*$), and the reference treatment (0.082; $p = 0.008^*$) (Figure 13). *Vaccinium ovalifolium*, *P. munitum*, and *R. ursinus* showed a directional trend opposite to the hypothesized response (Figure 13). The reference treatment mean for SSD of *V. ovalifolium* of 0.517 was higher than the buffered treatment mean by 3% ($p = 0.053$). The reference treatment mean of *P. munitum* SSD of 0.240 was 5% higher than the buffered treatment mean ($p = 0.623^*$) and 14% higher than the non-buffered treatment mean ($p = 0.385^*$), while the buffered treatment mean was 8% higher than that of the non-buffered treatment, but the data did not support a comparative statistical test (Figure 13). *Blechnum spicant* had non-linear effects from the treatment on SSD, as it did with the Leaf C:N and Leaf N metrics (Figure 13).

The reference treatment mean for *B. spicant* was intermediate (0.269) between the buffered treatment mean (which was 16% higher; $p = 0.349$), and the non-buffered treatment mean (which was 19% lower; $p = 0.369$). The buffered treatment mean was 38% higher than the non-buffered treatment mean for *B. spicant* ($p = 0.096$). *Rubus ursinus* had a higher mean value of SSD in the buffered treatment (0.261) than the non-buffered treatment (0.241; Figure 13).

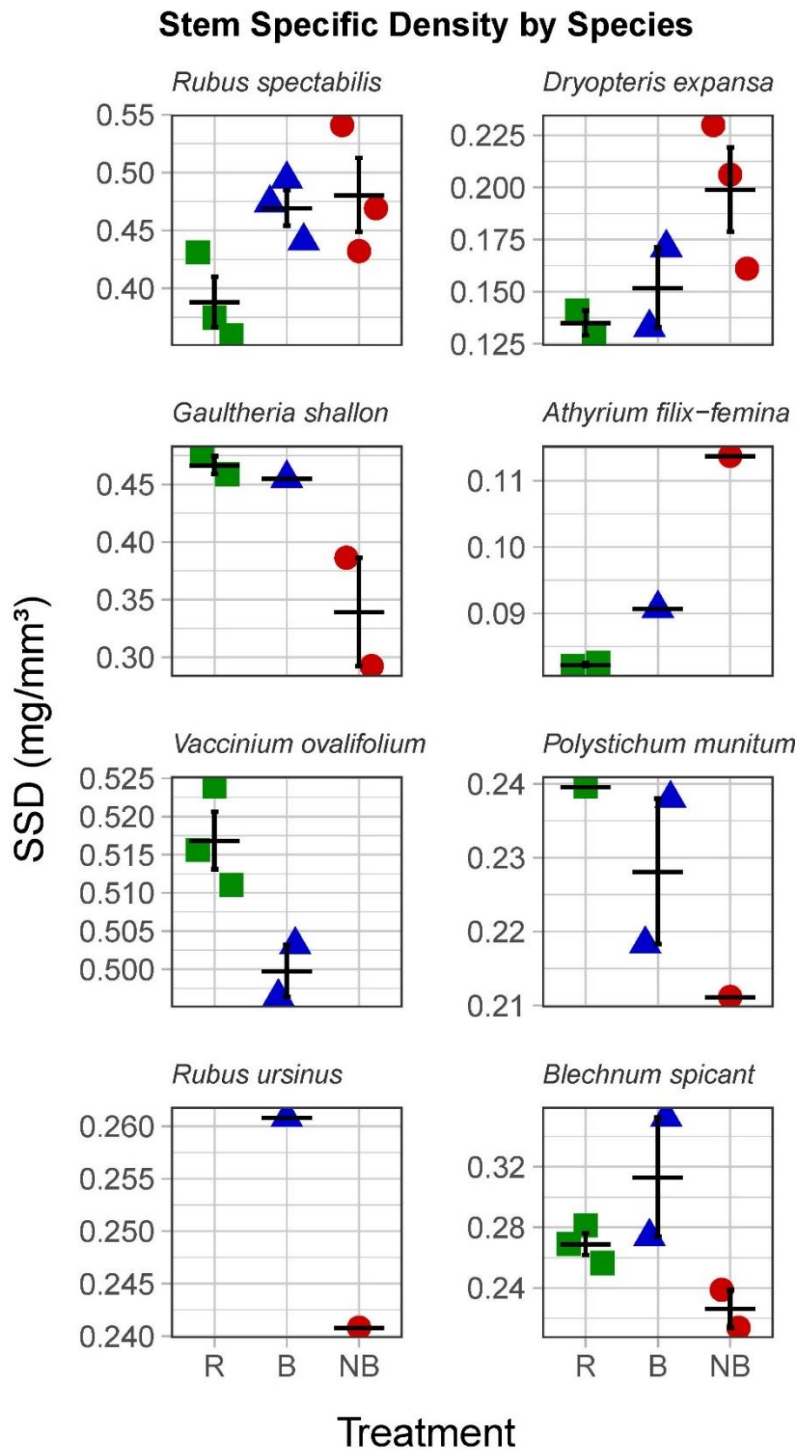


Figure 13. Summary of stem specific density by species; treatment means with standard error in black bars, coloured points indicate site means for which the species were sufficiently abundant for sampling: reference (R) = green squares, buffered (B) = blue triangles, non-buffered (NB) = red circles.

3.4 Species Trait Responses to Environment

3.4.1 Specific Leaf Area

The results of the ANCOVAs showed a significant impact of both radiation and daily maximum air temperature during the 7-day-max period on the focal plants' expression of traits. *Rubus spectabilis*, *V. ovalifolium*, *G. shallon*, *D. expansa* and *B. spicant* were the species that had sufficient data for these two-factor analyses. Of all environmental covariates of interest, potential radiation accounted for the most variation in SLA for *R. spectabilis* ($p = 0.026$), and *D. expansa*. Radiation accounted for 44% of variation for *D. expansa* ($p = 0.002$), in addition to the 40% explained by the treatment effect ($p = 0.006$). Only 4% variation in SLA for *R. spectabilis* was explained by radiation ($p = 0.026$), beyond that explained by the treatment effect ($R^2 = 0.62$; $p = 0.001$). For *G. shallon*, the daily maximum air temperature of the 7-day-max period accounted for 39% of variation in SLA beyond the 60% explained by the treatment ($p = 0.019$ and $p = 0.024$, respectively).

Although *R. spectabilis*, *D. expansa* and *G. shallon* were the three focal species for which statistically significant relationships were identified in this analysis, directional trends of the linear relationships identified were consistent for both environmental variates across all of the other four focal species analyzed. Specific Leaf Area was inversely related to both potential radiation and daily maximum air temperature for the 7-day-max period. The buffered treatment mean values were intermediate for both the radiation, and maximum air temperature effect on SLA, and resulted in the intermediate treatment values of SLA for all analyzed species but *B. spicant* (see figure 8 for species-level treatment responses of SLA to treatment).

3.4.2 Leaf Dry Matter Content

The ANCOVA analyses resulted in significant relationships for both mean daily air temperature, and basal area with leaf dry matter content. Mean daily air temperature of the 7-day-max period accounted for 35% variation of LDMC for *G. shallon* ($p = 0.025$), and 24% variation for *B. spicant* ($p = 0.035$), beyond the treatment effects of an additional 63% for *G. shallon*, and 15% for *B. spicant* in those linear relations ($p = 0.029$ and $p = 0.130$, respectively). Variation in LDMC for *B. spicant* was significantly influenced by mean soil temperature ($R^2 = 0.29$; $p = 0.018$), and maximum soil temperature over the study period ($R^2 = 0.24$; $p = 0.029$), while treatment accounted for a remaining 27% ($p = 0.042$) and 24% ($p = 0.064$) in each of those relations, respectively. Basal area also had a significant impact on LDMC, accounting for an additional 37% of the variation for *G. shallon* ($p = 0.037$), with the treatment effect accounting for 60% of variation in that two-factor linear relation ($p = 0.046$).

The statistically significant linear relations for *G. shallon* demonstrated a direct relation of LDMC with basal area, but an inverse relation with mean daily air temperature for the 7-day-max period for all focal species except *B. spicant*, which had opposite directional relations of both environmental factors with leaf dry matter content.

3.4.3 Leaf Nitrogen Content

Mean, and maximum daily soil temperatures, mean daily air temperatures as well as mean and maximum daily air temperatures over the 7-day-max period were found to have a significant influence on the variation of leaf N. *Vaccinium ovalifolium*'s Leaf N values were accounted for most by maximum daily soil temperatures (78% variation of Leaf N; $p = 0.005$); treatment effect accounted for an additional 11% variation in that linear relation ($p = 0.036$). Mean daily soil

temperature was significant for both *V. ovalifolium* ($p = 0.036$), and *G. shallon* ($p = 0.046$), accounting for 50%, and 41% of variation in Leaf N, respectively; treatment accounted for an additional 4% for *V. ovalifolium* ($p = 0.302$), and 54% for *G. shallon* ($p = 0.063$) in those linear relations. Daily mean soil temperatures during the 7-day-max period were significantly influential on Leaf N for *R. spectabilis*, accounting for 5% ($p = 0.024$), while the majority of variation was explained through the treatment effect ($R^2 = 0.74$; $p < 0.001$). Daily maximum soil temperature over the 7-day-max period explained 6% variation in Leaf N for *R. spectabilis* ($p = 0.018$), with treatment effect accounting for most of the variation in that relation ($R^2 = 0.71$, $p < 0.001$).

Although *V. ovalifolium*, *G. shallon*, and *R. spectabilis* data all demonstrated significant influence from environmental variates on their leaf N values, directional relations were not consistent for all focal species analyzed. Leaf nitrogen content had inverse relations with mean and maximum daily soil temperatures during both the whole study period, and for the 7-day-max period, which were consistent for four of the five species analyzed. The exception was for *G. shallon*, which had direct relations between Leaf N and mean and maximum daily soil temperatures over both the whole study period, and the 7-day-max period. Mean air temperature showed a significant relation to Leaf N; however, the directional relations were inconsistent between focal species analyzed; it was a direct relation for *V. ovalifolium*, *G. shallon*, and *D. expansa*, and an inverse relation for *R. spectabilis*, and *B. spicant*.

3.4.4 Leaf Carbon Content

Leaf carbon content was significantly influenced by radiation, and mean air temperatures during both the whole study period, and the 7-day-max period. Radiation accounted for 31% variation of Leaf C for *D. expansa* ($p = 0.015$); in this linear relation, treatment accounted for an additional

27% variation ($p = 0.040$). Leaf C was significantly influenced by daily mean air temperatures; study period values accounted for 23% variation with *B. spicant* ($p = 0.032$), while 7-day-max period values accounted for 42% variation with *V. ovalifolium* ($p = 0.047$). In these relations with mean air temperatures, the treatment effect accounted for an additional 23% for *B. spicant* ($p = 0.069$), and only 4% for *V. ovalifolium* ($p = 0.319$).

The direct relation between Leaf Carbon Content and radiation was consistent across all five species analyzed. Mean air temperature averaged for the 7-day-max period and leaf C also had a direct relation across all species; mean air temperature over the whole study period, however, had a direct relation with Leaf C for all species analyzed except *V. ovalifolium*, for which the data had inverse relations.

3.4.5 Leaf Carbon to Nitrogen Ratio

The results of the ANCOVA analyses showed that leaf carbon to nitrogen ratio was influenced by a combination of factors that were significant to leaf C and leaf N concentrations. The most influential of the environmental covariates on the leaf C:N were mean and maximum soil temperatures, and mean air temperature. Maximum soil temperature accounted for 75% variation for *V. ovalifolium* ($p = 0.013$) in the linear relation for which treatment accounted for no additional variation in Leaf C:N. Mean air temperature also significantly influenced the leaf C:N site means for *V. ovalifolium*, accounting for 55% of the variation ($p = 0.020$), in addition to another 17% explained by the treatment effect ($p = 0.062$). Mean soil temperature explained 61% of variation in leaf C:N for *G. shallon* ($p = 0.029$). The treatment effect for that linear relation with *G. shallon* accounted for an additional 36% variation ($p = 0.061$).

The directional relations of mean and maximum soil temperatures with Leaf C:N were direct for all species except *G. shallon*, which had inverse relations for both temperature metrics. Mean air temperature had mixed directional relations for the five focal species analyzed; both *G. shallon* and *B. spicant* had the same inverse relation demonstrated by *V. ovalifolium*, whereas *R. spectabilis* and *D. expansa* had direct relations for mean air temperature and Leaf C:N.

3.4.6 Stem-specific Density

ANCOVA analyses showed significant influence on stem specific density from solar radiation, and mean and maximum air temperatures of the 7-day-max period. Radiation was statistically influential on SSD for *G. shallon*, accounting for 73% variation ($p = 0.021$), with an additional 25% explained by the treatment effect ($p = 0.057$). Mean air temperature over the 7-day-max period explained 17% variation in SSD values *B. spicant* ($p = 0.021$), while maximum air temperatures over that same 7-day-max period accounted for 16% variation in SSD ($p = 0.036$); treatment effects accounted for an additional 55%, and 54% for those air temperature relations, respectively ($p = 0.009$; $p = 0.016$).

Directional relations were not as consistent across species as with other traits in this portion of analysis. The direct relation of radiation with SSD shown by *G. shallon* data was also demonstrated with *V. ovalifolium* and *B. spicant* data, whereas *R. spectabilis* and *D. expansa* had inverse relations for radiation and SSD. Mean and maximum air temperatures over the 7-day-max period were both inversely related to SSD for *V. ovalifolium*, *G. shallon* and *B. spicant*, but directly related for *R. spectabilis* and *D. expansa*.

3.5 Ordination: Community Weighted Mean Trait Values

This NMDS ordination demonstrated the relative patterns of plant functional traits within and among the three treatments. The relative position of trait values and environmental covariates among ordination space of the nine study sites is shown in Figure 14.

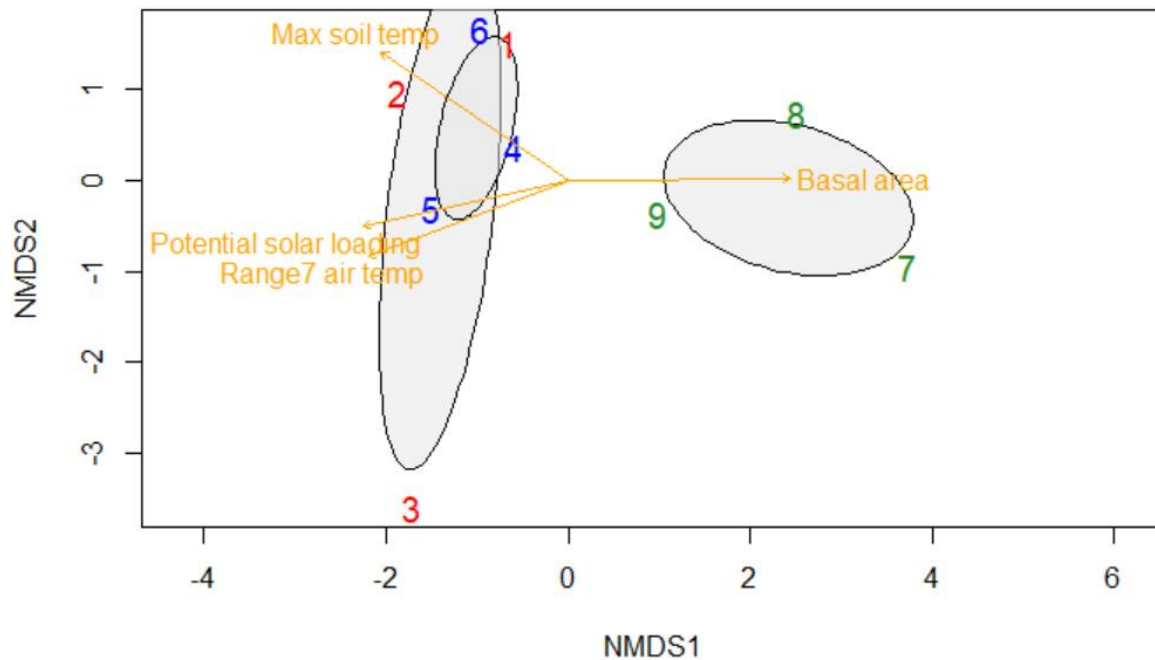


Figure 14. Non-metric dimensional scaling ordination showing the relative distribution of functional trait values in ordination space across sites and treatments; explanatory environmental covariation with relative magnitude of effect represented by yellow arrows, red numbers = non-buffered sites, blue = buffered, green = reference. Sites that are close together have the most similar variation in community-level trait values weighted across all six focal plant functional traits. Ellipses were drawn to outline relations between and within treatments, and do not represent any statistically significant groupings.

Despite not finding clear differentiation of species distribution among treatments, the treatments show a difference on the primary axis of variation between the harvested sites and the reference sites. From the ordination of plant functional trait values weighted for the community, the buffered and non-buffered sites had a very similar distribution of functional traits, which was different from the distribution of the reference sites. The non-buffered sites had slightly more

variation in the primary axis of variance (NMDS1) than the non-buffered sites, but were not considered different. The secondary axis showed that the buffered and reference sites had similar variation in that dimension, which was less variable on that axis than the non-buffered sites. Study site K34 (indicated by a red “3” in Figure 14), with no buffer, was the most different from the other two non-buffered sites, and accounted for most of the variation in the y-axis (NMDS2) on the ordination plot.

Minimum soil temperatures, solar radiation, and the range of air temperatures over the 7-day-max period were the three most influential environmental covariates that contributed to the distribution of functional trait values at the site-level. These factors all had a similar magnitude of effect on the variation of those traits.

4. DISCUSSION

My results demonstrate how timber harvest in coastal BC affects the distribution of plant functional traits in riparian areas of small streams due to altered environmental conditions from the industrial removal of the tree canopy. All six of the functional traits studied showed trends consistent with the hypotheses that sites with riparian buffers, even narrow buffers (5.9 – 9.2 m on both sides of stream), would have trait values intermediate between the non-buffered and reference site values. These trends were evident both at the species level, and through the community weighted, site-level trait means. Differences between the trait values of the three treatments represent the altered plant physiology and community structure when growing conditions are changed through timber harvest. These impacts on the physiology and the resulting ecology of the riparian plant communities can be mitigated through establishing tree retention buffers in riparian areas adjacent to small streams.

4.1 Physical Environmental Variability

There is inherent variation of site conditions in treatments that are not manipulated explicitly for a particular study; the heterogeneity of riparian forest structure can also contribute to high environmental variation (Warren, Collins, Purvis, Kaylor, & Bechtold, 2016). Potential radiation, soil and air temperatures, tree density, stream width, bank slope, aspect, and reach slope had high variation between sites in this study. Some of these components of each study reach impacted the responses, while others had minimal impact on the response variables. Many field measurements addressing the environmental conditions were measured multiple times, in a stratified way at each site, which produced site-level means that were representative of the average conditions at each study site. These within-site measurements and site means captured the extent of site-level

environmental variation for which I was able to account. I completed other measurements in only one location at each site, when replicated measures were not feasible, and/or when single point measurements were considered sufficient for capturing the average site conditions.

Understory light levels were estimated by a modelled potential radiation parameter based on hemispherical photography (Leach and Moore 2010, Yeung et al. 2017), and replicated 10 times per site, to represent average light intensity at the site level. Studies looking at within-site variation of riparian light conditions such as Swartz, Roon, Reiter, and Warren (2020) have used a similar method, but with less replication per site. Consistent camera sensor height relative to the streambed enabled a consistent standard for light availability along the study reach, like Yeung et al. (2017) and Swartz et al. (2020). Since the sensor was placed at 1.3 m above the streambed, as in Lilles et al. (2018), all modelled potential radiation values were likely overestimates for the stream bottom, but an appropriate approximation of light conditions in the shrub stratum. Interactive thresholding was an introduced bias, and was justified by accounting for the over-estimation associated with the binary classification of foliage that is not optically black (Díaz & Lencinas, 2018; Inoue et al., 2011).

I did not account for within-site variation in air and soil temperatures given only one temperature logger for each per site; this was similar to other studies with single-point temperature measurements at each of their study sites (e.g. Edmonds & Tuttle, 2010; Mallik, Kreutzweiser, Spalvieri, & Mackereth, 2013). By selecting areas at each site that looked typical of average site conditions, each site had temperature values that were considered representative of the whole reach (Silverthorn & Richardson, 2021). Air temperatures measured at a single location at each site were determined to be sufficient for suite averages, like Gray, Spies, and Easter's (2002) measurements in their study of BC's coastal Douglas-fir forest microclimates. In that same study,

they found low variation in soil temperatures among relative cardinal directions within small forest gaps (Gray et al., 2002), confirming that the relative position of the temperature logger in my study reaches was unlikely to influence the data in a major way. Soil temperatures were taken at 10 cm below the surface of the mineral horizons, like Edmonds and Tuttle (2010) in their western Washington riparian forest study. The general trend of low soil temperatures in reference sites relative to harvested sites was consistent with Kreutzweiser, Hazlett, and Gunn (2008), who suggested that soil temperatures are more variable with lower amounts of organic matter accumulated at harvested sites than in in-tact forests. Moore et al. (2005) in their review on riparian microclimate determined that on average, surface soil temperatures in the Pacific Northwest can be between 10-15 °C cooler in reference sites than harvested sites during the day; my research did not have such contrasting values, but still showed significant differences consistent in direction between harvest and unharvested sites. The smaller differences in temperatures between sites may have been due to the limited temporal and spatial scales of my measurements, in addition to being a temperate climate which has far less daily and seasonal variability in temperatures than continental ones, which dominate the majority of the Pacific Northwest (Larson & Lohrengel, 2011).

Based on treatment averages, both the soil and air temperatures were lowest and least variable at reference sites, highest and most variable at non-buffered sites, and intermediate at the buffered sites. Sweeney and Newbold's (2014) findings were that small streams are more vulnerable to thermal extremes than larger ones, and that the extent of riparian buffer present determines the temperature control in riparian areas. While I did not measure stream temperatures, our riparian temperature measurements suggest that this temperature variability may also be present in the streams at my study sites.

Study reaches were selected with reach and bank slopes within an acceptable range between and among treatments; they were considered suitable for study sites, since reach slopes were low and uniform, relative to studies involving similar study systems. In their Oregon coast study on riparian detrital subsidies, Hart, Hibbs, and Perakis (2013) also considered that bank steep slopes should be avoided when selecting study sites for comparing riparian plant communities; as such, the variation of slopes within and between each treatment of this study were considered low and appropriate.

4.2 Functional Traits

Understory plant species vary in their physiological responses to microclimate changes (Abella & Springer, 2015). The functional trait data from this study show that many of the focal plant species responded with similar directional trends relative to the treatments applied, but varied significantly in the magnitude to which each species at each site responded to the treatment. To account for such varied measures of functional traits within a plant community, Perez-Hardingway et al. (2017) suggest collecting tissues from the local species that together comprise the most abundant 80% of ground cover at each site. While each species responded to the changes in growing conditions from the buffer and no buffer treatments in this study individually, the directional trend of the response of community weighted site-level means allows for inference about the community-level ecological processes and growing conditions (Bjorkman et al., 2018; Garnier et al., 2004).

4.2.1 Trait responses to environment

The purpose of assessing the focal traits of this study at the species level was to represent the range of variation in the trait values between species within each site, and how the species-level

responses contribute to the overall community-level values. By analyzing the response of each focal species at each site, I determined directional relationships for the focal species between the treatment effects and the focal trait values. I was able to account for between-species variation in trait differences due to treatment, when making inferences from the values at the community-level.

Habitat filters have a strong influence on SLA values (Cornwell & Ackerly, 2009) and Petter et al. (2016) concluded that environmental conditions significantly influence SLA. Low SLA is correlated with leaf longevity in response to warm, dry conditions in which plants must invest more in conservative growth strategies like low specific leaf areas in order to regulate gas exchange rates relative to photosynthate production (Bjorkman et al., 2018; Carbone & Aguilar, 2016; S. Díaz, Kattge, Cerabolini, et al., 2016; McCoy-Sulentic et al., 2017; Meng et al., 2015). While some of these studies were comparing environmental responses in communities with different species composition, these shifts are consistent, and still represent community-level responses, regardless of species composition. With higher water availability through precipitation and streamflow in riparian areas, SLA values shift upwards (Westoby, 1998; Wright et al., 2017). My study demonstrated that the seasonally drier, non-buffered sites had the lowest SLA values compared to the other two treatments. Mallik et al. (2013) found that SLA was negatively correlated to canopy openness, which was something that my results also supported. Caplan and Yeakley (2013) found that experimentally augmenting water supply yields high SLA values for *R. spectabilis*, which was consistent with the results of this study. Based on my results, decreases in community level SLA values will occur in non-buffered riparian areas of small streams in BC's timber harvest blocks.

While I did not directly measure soil moisture, soil temperatures are often used as a reliable proxy for that measure due to their positive correlation, and are therefore justified in their use as covariates (Verhoef, Fernández-Gálvez, Diaz-Espejo, Main, & El-Bishti, 2006). This directional trend of high SLA at low temperature sites and low SLA at high temperature sites was consistent for all focal plant species; however, mean SLA values for *Blechnum spicant* at the two harvested sites were not significantly different from each other. Menéndez, Revilla, and Fernández (2006) found that sexual development and growth in *B. spicant* are strongly associated with the growing medium, which could indicate that the treatment responses for this species in my study was more heavily dependent on microsite conditions than the other focal species. Because I measured average site conditions for this study, I may have not captured the conditions that most influenced SLA in *B. spicant*.

Leaf dry matter content can vary independently of leaf thickness and is typically less variable within sites than SLA (Roche, Díaz-Burlinson, & Gachet, 2004), as it is less plastic than SLA in response to light availability, which can make it a very effective proxy for productivity (Smart et al., 2017). Both measurements indicate leaf investment priorities and overall plant growth strategies, so Wilson et al. (1999) suggest using a combination of the two traits for most accurately predicting strategies. Leaf dry matter content (LDMC) was found to be higher in logged riparian areas than in buffered or reference riparian areas in the study by Mallik et al. (2013), consistent with my results. Warm temperatures yield high LDMC (Meng et al., 2015), which I also found. Plants adapted to dry conditions have high LDMC for maintaining hydration of leaves even in drought conditions, through investment in protection such as leaf cuticle and epidermal thickness (Zukswert & Prescott, 2017) when water potentials are low (Bartlett, Scoffoni & Sack, 2012). LDMC was also positively related with soil temperature, which is

consistent with the positive relations between soil temperature and soil moisture (Bjorkman et al., 2018). Variation in this study for LDMC was highest in *P. munitum* and *B. spicant* which may relate to LDMC values being higher in ferns, as Petter et al. (2016) found. The tissues collected for those two species in this study had a large amount of reproductive propagules relative to the other two focal fern species, which may account for high variation in fresh and dry mass measurements that were used to calculate the LDMC values. Only fertile fronds from *B. spicant* were collected. The within-treatment variation of buffered sites was high for the LDMC values for those two species, which may relate to strong relations to microsite conditions (Kennedy & Quinn, 2001; Menéndez et al., 2006). Brodersen, Rico, Guenni, and Pittermann (2016), found that *P. munitum*'s drought stress tolerance is adapted to withstand a loss of up to 50% hydraulic conductivity before any loss of stomatal conductance occurs. This could suggest that without extreme changes to microclimate, *P. munitum* may not demonstrate shifts in physiological trait values as expected.

The C:N ratio is often referred to in stream and riparian forest metabolism studies, as it is a valuable indicator of leaf breakdown rates, both chemically and physically, and used as a measure of detritivore nutrition (e.g. Edmonds & Tuttle, 2010; Follstad Shah et al., 2017; Kominoski, Marczak, & Richardson, 2011). The ratio of carbon to nitrogen generally decreases after timber harvest, according to Warren et al. (2016) in their theoretical paper on riparian ecosystem function. Given its inverse relationship with leaf carbon content in the form of lignin, a high N content, relative to C (low C:N) can indicate a leaf's high initial decomposition rate (Berg & McClaugherty, 2020).

Results for leaf chemistry in this study were generally consistent with the hypotheses; however, there were some inconsistencies – notably with *B. spicant* and *G. shallon*. *Blechnum spicant* can

have trait responses representative of its microsite, and not as influenced by average edaphic conditions in its community as the other focal plant species of this study, which may explain the non-linear relationship between treatment and leaf chemistry values (Menéndez et al., 2006). The inverse to the hypothesized relationship between treatment and Leaf N, Leaf C and Leaf C:N was observed for *G. shallon*. This species forms dense, complex root association systems with mycorrhizae and bacteria in the rhizosphere that assist in its acquisition of nutrients such as nitrogen (Fraser, Turkington, & Chanway, 1993). There are also significant contributions of *G. shallon* to the humus content present in its habitat following disturbance, through the retention of soil moisture by accumulated leaf litter, and through reduction of soil erosion from its dense root systems (Sabhasri, 1961 cited in Fraser et al., 1993). This species is considered a good competitor; Fraser, Turkington, and Chanway (1993) refer to *G. shallon* as a “persistent and pervasive plant [and a] serious competitor” (p. 1235), especially in open habitats near the coastal Pacific Northwest. These features may explain this species’ ability to maintain chemical exchange rates in the dry, exposed (non-buffered) sites of this study. According to Minami, Oba, Kojima, & Richardson (2015), *G. shallon* does especially well on exposed mineral soil, which may be why leaf nitrogen content was highest at non-buffered sites and lowest at reference sites. In those exposed dry areas, *G. shallon* has the ability to maintain high photosynthetic capacity due to its investment in a very waxy cuticle, protecting the leaves from water loss, and enabling the maintenance of high photosynthetic rate even in drought stress conditions.

Among variation in trait responses to our treatment, specific stem density was also consistent with my hypotheses and the literature. Kennedy and Quinn (2001) found that when comparing *P. munitum* growing on stumps versus on the ground, stem specific density was much higher on the ground; they attributed this to higher moisture content maintained in coarse wood. While my

study did not assess the impact of soil moisture on stem density, I measured soil temperature which is directly linked to moisture availability (Bjorkman et al., 2018); I also found that the drier and warmer non-buffered sites yielded a higher stem density for *P. munitum*.

Because of the relatively long life span of the focal perennial plant species analyzed in this study, trait responses observed are likely shifts in trait values due to plasticity, as these individuals probably established on these study sites prior to the application of timber harvest treatments. Plant phenotypic plasticity can be mediated by local abiotic conditions, species and location of neighbouring plant taxa, and by herbivory patterns; in turn, those factors can be very influential on the variation in trait distribution in these plant communities (Callaway et al., 2003). Interactions within these communities are somewhere between competitive and facilitative, and where individuals fall within this spectrum is dependent largely on environmental conditions (Callaway et al., 2003).

Although leaf hydration is a large determinant of leaf mass, and therefore influential on SLA (albeit minimally, due to fresh area calculation) and LDMC values, Wilson, Thompson, and Hodgson (1999) indicated that the challenge of ensuring full hydration of leaf tissues is heightened in arid plants such as succulents. This was not outlined as an important consideration for plants in temperate climates, where published field protocols sufficiently account for that source of variation in leaf hydration (S. Díaz, Kattge, Cerabolini, et al., 2016; Pérez-Harguindeguy et al., 2013). The hydration conditions of riparian plant communities reflect the physical conditions of the riparian area (Politti, Bertoldi, Gurnell, & Henshaw, 2018). The trait measurements when based on proper collection protocols are therefore accepted to reflect the community growing conditions from which they come.

4.2.2 Community responses

The site-level community averages of each trait were weighted so that the most abundant species have the highest influence on the community averages, while the species with lower abundance have a more limited effect on the community-level values. While this is appropriate based on the published protocols for the assessment of plant communities through functional trait measurements (Pérez-Harguindeguy et al., 2013), Newaz, Mallik, and Mackereth (2019) found that generalist plant species will remain abundant post-harvest, but the disturbance-sensitive species will disappear. This can result in no net loss of species richness due to the establishment of generalist and often invasive species (e.g. *Rubus laciniatus*, *Rubus discolor*, *Cytisus scoparius*; personal observation), but a shift in community composition nonetheless. The most dominant species are perhaps not as indicative of ecosystem-function due to their generalist edaphic amplitudes and high plasticity compared to less abundant, more specialized species with narrower niches of growing conditions that may or may not have existed prior to timber harvest; lower abundance indicator species can be the most predictive of local edaphic conditions (Pojar, Klinka, & Meidinger, 1987). In this study, it is assumed that the abundance of each species represents the proportion to which they represent the function of the ecosystem in which their community exists, as supported by Pérez-Harguindeguy et al. (2013). Whether it be regional effects, environmental effects, or effects from biotic interactions, the representation of plant functional traits present at the community-level *does* represent the community dynamics responding to their habitat, regardless of which filter is most influential to each species response (Cornwell & Ackerly, 2009).

The community responses seen in my study are supported by the literature on the assessment of functional traits as an inferential tool for determining changes in ecosystem processes and overall

function following changes in environment (e.g., Fajardo & Siefert, 2019; Fukami, Bezemer, Mortimer, & Van Der Putten, 2005; Garnier et al., 2004; McCoy-Sulentic et al., 2017; Wilson et al., 1999). Mouillot, Graham, Bastien Villé Ger, Mason, and Bellwood (2013) in their review determined that a functional trait approach is an effective tool for predicting ecosystem processes and function through community-level responses to disturbance. However, directional shifts in the plant traits assessed in this study show the plants' phenotypic plasticity, as local growing conditions change and interactions with neighbours shift (Abakumova et al., 2016). While each of the plastic responses to altered growing conditions is different between species, the trends I observed at the community level still show that the ecosystem as a whole was impacted. The directional relations of trait results consistent with all four hypotheses - H₁: SLA will decrease with more light; H₂: SSD and LDMC will increase with higher temperatures; H₃: decreased soil N availability will drive leaf N down, and more growing space will drive leaf C up; and (generally) H₄: buffered sites will have intermediate trait values - demonstrate that the community shifts were in response to the treatment. Many of the shrubs and herbs demonstrated the capacity to thrive as ruderal species, demonstrating competitiveness in disturbed areas with new growing space, while other species show that their success depends on the growing conditions in pre-harvest ecosystem conditions.

Riparian plant communities with lower SLA values can contribute less shading from their leaf area to the soils and adjacent streams, provide less habitat availability for terrestrial invertebrates and amphibians, and moderate temperatures and moisture content less effectively. Combined with high LDMC, low SLA values result in smaller, more recalcitrant detrital inputs from riparian areas into the adjacent small streams. Studies have shown that the breakdown of these

dense litter inputs with lower labile nutrients are more strongly mediated by temperature than more easily decomposed detritus (Martínez, Larrañaga, Pérez, Basaguren, & Pozo, 2013).

Increased C:N ratio is another response to timber harvest shown in my data; this is the chemical component to the leaf responses, showing prioritization of high structural content in relation to photosynthetic tissues. A high C:N ratio leads to slower breakdown rates and lower nutritional value for aquatic detritivorous invertebrates (Follstad Shah et al., 2017; Warren, Keeton, et al., 2016). The deposition of organic N back into the soil matrix is largely determined by the litter that falls to the forest floor, which is variable with timber harvest (Fraser et al., 1993; Kaylor & Warren, 2018). With lower N concentrations, less nitrogen is involved in the nutrient cycles and the plant communities can be less productive as a result (Amatangelo et al., 2017).

The chemical and physical functional trait responses in the understory plant communities to the treatments applied in this study can lead to changes in both terrestrial and aquatic riparian ecological processes, impacting ecosystem function at, and downstream of, the focal small stream systems. In their meta-analysis Duguid and Ashton (2013) find that plant community recovery may take up to 150 years following disturbance, indicating that these shifts in ecosystem function may be a more long-lasting legacy than the rotation cycle of a coastal forest. Canopy closure in riparian areas of the Pacific Northwest can take up to thirty years following timber harvest, and can have long-lasting bottom-up impacts on multiple trophic levels of stream organisms even after this recovery period (Kaylor & Warren, 2018).

During the period in which my study sites recover from their treatments, I predict that the magnitude of structural and chemical variation in traits will continue to be highest at non-buffered sites, lowest at reference sites, and an intermediate magnitude of traits will occur at the

buffered sites. At the non-buffered sites, fast-growing generalist, and shade-intolerant species adapted to wide edaphic conditions will continue to dominate for the first seral stage of development (stand initiation 0-15 years; Duguid & Ashton, 2013). During stem exclusion, understory community cover decreases significantly due to canopy closure and the resulting loss of growing space (~ 40 years; Lilles, Dhar, Coates, & Haeussler, 2018). In their study, Lilles et al. (2018) found that recovery time for vascular plant cover to return to pre-harvest levels was less than eight years for both 40% and 70% BA retention, but was more than 24 years for the treatment with no retention. I anticipate the trajectories at my study sites to be similar to Lilles et al. (2018), where full understory recovery to pre-treatment conditions occurs within the first decade at the buffered sites, but occurs much later for the non-buffered sites.

4.3 Limitations and Next Steps

Sites within each treatment were selected to meet the requirements of conditions described in section 2. This site selection process aimed to best represent the buffered, non-buffered, and reference treatments while ensuring viable study sites, given both logistical and practical considerations. There was limited availability of buffered streams in MKRF's cut blocks that were harvested within 5 years prior to this study's data collection period, which meant variation both within, and among treatment environmental characteristics was noticeable. Limited resources available for temperature sampling replication at each site contributed to the single-point measurement method as the selected protocol, which was the part of this study that least accounted for within-site environmental variability.

The high variation in buffered-site conditions is due to the combined effect of management strategies at the research forest and BC's forest policy that informs operational practices. The

research forest is a fully functioning lumber producer with an on-site mill that deals mainly with custom wood products. Many of the funds that continue to make the forest available for research purposes come from the value of timber harvested and sold from the property. Many of the timber harvest blocks in MKRF were not designed with research in mind, but rather a balance of environmental and economic objectives. While the forest upholds a very high level of integrity in the sustainable management of forest resources, it continues to depend on logging for sustained use. The other major operational constraint that limited the availability of buffered sites at MKRF is that of BC's forest policy. As discussed in the introduction, small streams in BC have minimal operational protection in timber harvest blocks of BC. The result is that very few low-order streams with buffered riparian areas contained within a harvest block exist at MKRF.

While the physical features of the reference sites differed greatly from the buffer and no buffer sites, a large assumption made in the site selection process was that the study reaches used as reference sites were truly representative of reference forest conditions. Due to the disturbance history of MKRF, it was difficult to locate reference conditions where small streams existed in pristine maturing seral (or later succession) stands. As land-use and forest management continue in BC, the extent of old growth forests is being depleted; thus, the question arises, to what natural forest conditions should an experimentally or industrially manipulated forest area be compared? The comparison of study forests to forests harvested or burned early in the 20th century may well be emerging as the most realistic and important comparison to "baseline" conditions in a quickly changing landscape (Richardson, Kuglerová, Muotka, Chellaiah, & Jyväsjärvi, in preparation). Are we looking at a shifted baseline in which conditions, structure and function of an old growth stand are no longer the appropriate reference? I speculate that due to current forest policy, and as the salience of protecting old growth forests continues to grow for citizens, BC's forestry

industry will be forced to consider second growth plantations as target timber-producing ecosystems that represent ecological conditions reflecting current forest management and changing environment.

Due to the strong influence of soil and air temperatures and radiation on both species-level and community-level functional traits, future research could focus more specifically on the impact of seasonal variation of temperatures on riparian plant structure and function. Since my study only used individual values for daily temperatures, more focus on replicated temperature measurement that accounts for within-site variation may contribute to a more robust analysis of trait changes resulting from environmental shifts in riparian plant communities following timber harvest. Finer-scale temperature data collection would likely only provide limited improvements in management applications to this study. Additionally, a field sampling protocol for plant tissue collection designed around community-weighted mean trait values rather than species-level ones would provide the replication necessary to run mixed models at the species-level in addition to the community-level. Not only would this provide a more thorough analysis of the species-level trait values, but would also account for within-site variation, which the two-factor analyses for the focal species did not.

4.4 Management Implications

Due to the inference capacity of functional trait studies (Lozanovska et al., 2019; Westoby & Wright, 2006), this study was designed to measure the most impacted components of microclimate from the existence or absence of riparian buffers in timber harvest block in coastal BC. The data show clear trends in increased potential radiation, contributing to both air and soil temperatures with higher peak values throughout the growing season at riparian features with no

retained tree buffer. With regards to the observed trends, assembly processes and mechanisms - such as intraspecific competition, mycorrhizal symbioses, and niche partitioning - occur in addition to the edaphically-adapted plastic leaf and stem responses observed in my focal species data (Mccoy-Sulentic et al., 2017).

The importance of small stream-riparian systems is beyond the *in-situ* function and health of these headwaters, and their associated terrestrial riparian areas of forests. Failing to protect the riparian areas of small streams in BC may lead to losses of the physical and chemical composition of the riparian plant communities, and consequently, decreases in the quality of the remaining inputs that are essential for the function of downstream ecosystems (Kuglerová, Hasselquist, et al., 2017; Wipfli et al., 2007; Wohl, 2017; Yeung et al., 2017). Small streams account for up to 80% of stream length in watersheds and are integral to the function of larger streams due to the linkages between upper and lower reaches in a catchment (Leopold, Wolman, & Miller, 1964; Moore & Richardson, 2003; Wipfli & Gregovich, 2002). Headwaters are important for thermal, detrital and faunal inputs to large, fish-bearing streams and community watersheds that BC's environmental legislation is designed to protect (Moore et al., 2005; Richardson, 2019; Tschaplinski & Pike, 2009).

Deficiencies in these natural resource protection policies exhibit limited preservation of these headwater areas; the integrated relationship between large stream systems and these source streams that provide subsidies and services that are essential for ecosystem function are not addressed through BC's current forest policy. This study has demonstrated riparian plant community-level shifts as a result of changes to riparian environments following timber harvest, and the data show that buffered riparian areas maintain physiological structure and chemical composition of understory plant communities better than those without buffers.

References

- Abakumova, M., Zobel, K., Lepik, A., & Semchenko, M. (2016). Plasticity in plant functional traits is shaped by variability in neighbourhood species composition. *New Phytologist*, 211, 455–463. <https://doi.org/10.1111/nph.13935>
- Abella, S. R., & Springer, J. D. (2015). Effects of tree cutting and fire on understory vegetation in mixed conifer forests. *Forest Ecology and Management*, 335, 281–299. <https://doi.org/10.1016/j.foreco.2014.09.009>
- Agrawal, A., Gibson, C. C., Britt, C., Coward, W., Engel, S., Greenberg, J., ... Walker, J. (1999). Enchantment and Disenchantment: The Role of Community in Natural Resource Conservation. *World Development*, 27(4), 629–649. Retrieved from https://ac.els-cdn.com/S0305750X98001612/1-s2.0-S0305750X98001612-main.pdf?_tid=3669cd66-121b-4899-a0be-715556ae9427&acdnt=1537816335_1b3519e7788d6f81c57568d9fddee73e
- Aguiar, F. C., Segurado, P., Martins, M. J., Bejarano, M. D., Nilsson, C., Portela, M. M., & Merritt, D. M. (2018). The abundance and distribution of guilds of riparian woody plants change in response to land use and flow regulation. *Journal of Applied Ecology*, 55(5). <https://doi.org/10.1111/1365-2664.13110>
- Amatangelo, K. L., Johnson, S. E., Rogers, D. A., Donald, M., Amatangelo, K. L., Johnson, S. E., ... Waller, D. M. (2017). Trait — environment relationships remain strong despite 50 years of trait compositional change in temperate forests Published by : Wiley on behalf of the Ecological Society of America Stable URL : <http://www.jstor.org/stable/43494860> Trait- environment re. *Ecology*, 95(7), 1780–1791.

- Bartlett, M. K. Scoffoni, C., & Sack, L. . (2012). The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: a global meta-analysis, 15, 393–405, 2012. *Ecol. Lett.*, 15, 393–405.
- Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Staistical Software*, 67(1), 1–51.
- Beckley, T. M. (1998). Moving toward consensus-based forest management: A comparison of industrial, co-managed, community and small private forests in Canada. *The Forestry Chronicle*, 74(5), 736–744. Retrieved from <http://pubs.cif-ifc.org/doi/pdf/10.5558/tfc74736-5>
- Berg, B., & McClaugherty, C. (2020). Role of Chemical Constituents in Regulating Decay Rates and Stable Fractions: Effects of Initial and Changing Chemical Composition on Decomposition and Organic Matter Accumulation. In *Plant Litter: Decomposition, Humus Formation, Carbon Sequestration* (4th ed., pp. 129–163). <https://doi.org/10.1007/978-3-030-59631-6>
- Biswas, S. R., Mallik, A. U., Braithwaite, N. T., & Biswas, P. L. (2018). Effects of disturbance type and microhabitat on species and functional diversity relationship in stream-bank plant communities. *Forest Ecology and Management*, 432, 812–822. <https://doi.org/10.1016/j.foreco.2018.10.021>
- Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Rüger, N., A Beck, P. S., ... Weiher, E. (2018). Plant functional trait change across a warming tundra biome. *Nature*, 562, 57–62. <https://doi.org/10.1038/s41586-018-0563-7>
- British Columbia Ministry of Forests and Range. (2002). *Forest and Range Practices Act*.

Victoria.

- Brodersen, C. R., Rico, C., Guenni, O., & Pittermann, J. (2016). Embolism spread in the primary xylem of *Polystichum munitum*: Implications for water transport during seasonal drought. *Plant Cell and Environment*, 39(2), 338–346. <https://doi.org/10.1111/pce.12618>
- Burt, T. P., Howden, N. J. K., McDonnell, J. J., Jones, J. A., & Hancock, G. R. (2015). Seeing the climate through the trees : observing climate and forestry impacts on stream flow using a 60-year record. *Hydrological Processes*, 480, 473–480. <https://doi.org/10.1002/hyp.10406>
- Cadotte, M. W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, 48(5), 1079–1087. <https://doi.org/10.1111/j.1365-2664.2011.02048.x>
- Callaway, R. M., Pennings, S. C., & Richards, C. L. (2003). Phenotypic plasticity and interactions among plants. *Ecology*, 84(5), 1115–1128. [https://doi.org/10.1890/0012-9658\(2003\)084\[1115:PPAIAP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[1115:PPAIAP]2.0.CO;2)
- Caplan, J. S., & Yeakley, J. A. (2013). Functional morphology underlies performance differences among invasive and non-invasive ruderal *Rubus* species. *Oecologia*, 173(2), 363–374. <https://doi.org/10.1007/s00442-013-2639-2>
- Capon, S. J., Chambers, L. E., Mac Nally, R., Naiman, R. J., Davies, P., Marshall, N., ... Williams, S. E. (2013). Riparian Ecosystems in the 21st Century: Hotspots for Climate Change Adaptation? *Ecosystems*, 16(3), 359–381. <https://doi.org/10.1007/s10021-013-9656-1>
- Capon, S. J., & Pettit, N. E. (2018). Turquoise is the new green: Restoring and enhancing

- riparian function in the Anthropocene. *Ecological Management and Restoration*, 19, 44–53.
<https://doi.org/10.1111/emr.12326>
- Carbone, L. M., & Aguilar, R. (2016). Contrasting effects of fire frequency on plant traits of three dominant perennial herbs from Chaco Serrano. *Austral Ecology*, 41(7), 778–790.
<https://doi.org/10.1111/aec.12364>
- Chapin, F. S., Matson, P. A., & Vitousek, P. M. (2011). *Principles of Terrestrial Ecosystem Ecology* (Second). <https://doi.org/10.1007/978-1-4419-9504-9>
- Clarke, K. R., & Gorley, R. N. (2006). *Primer v6: User Manual/Tutorial* (Primer-E, Ed.). Plymouth.
- Clarke, K. R., & Warwick, R. M. (2001). *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation* (2nd ed.). Plymouth: Primer-E.
- Clogg, J., Gage, A., & Haddock, M. (2002). *A Results-Based Forest and Range Practices Regime for British Columbia*. Retrieved from
[https://www.wcel.org/sites/default/files/publications/A Results-Based Forest and Range Practices Regime for British Columbia.pdf](https://www.wcel.org/sites/default/files/publications/A%20Results-Based%20Forest%20and%20Range%20Practices%20Regime%20for%20British%20Columbia.pdf)
- Coble, A. A., Barnard, H., Du, E., Johnson, S., Jones, J., Keppeler, E., ... Wagenbrenner, J. (2020). Long-term hydrological response to forest harvest during seasonal low flow: Potential implications for current forest practices. *Science of the Total Environment*, 730, 138926. <https://doi.org/10.1016/j.scitotenv.2020.138926>
- Cornwell, W. K., & Ackerly, D. D. (2009). Community Assembly and Shifts in Plant Trait Distributions across an Environmental Gradient in Coastal California. *Source: Ecological*

- Monographs*, 79(1), 109–126. Retrieved from
<https://www.jstor.org/stable/pdf/27646168.pdf?refreqid=excelsior%3A6260e1d3bc049231ff3e8e56f2142a4>
- Demarchi, D. A. (2011). *An Introduction to the Ecoregions of British Columbia*. Retrieved from
https://www2.gov.bc.ca/assets/gov/environment/plants-animals-and-ecosystems/ecosystems/broad-ecosystem/an_introduction_to_the_ecoregions_of_british_columbia.pdf
- Desroches, C. T. (2007). Policy advice for public participation in British Columbia forest management. *The Forestry Chronicle*, 83(5), 672–681. Retrieved from <http://pubs.cif-ifc.org/doi/pdf/10.5558/tfc83672-5>
- Díaz, G. M., & Lencinas, J. D. (2018). Model-based local thresholding for canopy hemispherical photography. *Canadian Journal of Forest Research*, 48(10), 1204–1216.
<https://doi.org/10.1139/cjfr-2018-0006>
- Díaz, S., Kattge, J., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., ... Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, 529, 167–171.
<https://doi.org/10.1038/nature16489>
- Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., ... Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, 529(7585), 167–171.
<https://doi.org/10.1038/nature16489>
- Douglas, G. W., Meidinger, D., & Pojar, J. (2000). *Illustrated flora of British Columbia* (3,4,5). Victoria, BC: B. C. Ministry of Environment, Lands and Parks, B.C. Ministry of Forests.

- Douglas, G. W., Straley, G. B., Meidinger, D., & Pojar, J. (1998). *Illustrated Flora of British Columbia* (1,2). Victoria, BC: B.C. Ministry of Environment, Lands and Parks, Ministry of Forests.
- Duguid, M. C., & Ashton, M. S. (2013). A meta-analysis of the effect of forest management for timber on understory plant species diversity in temperate forests. *Forest Ecology and Management*, 303, 81–90. <https://doi.org/10.1016/j.foreco.2013.04.009>
- Edmonds, R. L., & Tuttle, K. M. (2010). Red alder leaf decomposition and nutrient release in alder and conifer riparian patches in western Washington, USA. *Forest Ecology and Management*, 259, 2375–2381. <https://doi.org/10.1016/j.foreco.2010.03.011>
- Elementar. (n.d.). *Vario EL CUBE User Manual*. Retrieved from http://www.spektronika.ru/sites/default/files/vario_el_cube.pdf
- Elliott, K. J., & Vose, J. M. (2016). Effects of riparian zone buffer widths on vegetation diversity in southern Appalachian headwater catchments. *Forest Ecology and Management*, 376, 9–23. <https://doi.org/10.1016/j.foreco.2016.05.046>
- Environmental Systems Research Institute. (2019). *ArcGis*. Retrieved from <https://desktop.arcgis.com/en/arcmap/>
- Erdozain, M., Kidd, K., Kreutzweiser, D., & Sibley, P. (2018). Linking stream ecosystem integrity to catchment and reach conditions in an intensively managed forest landscape. *Ecosphere*, 9(5), 1–29. <https://doi.org/10.1002/ecs2.2278>
- Fajardo, A., & Siefert, A. (2019). The interplay among intraspecific leaf trait variation, niche breadth and species abundance along light and soil nutrient gradients. *Oikos*, 128, 881–891.

<https://doi.org/10.1111/oik.05849>

- Feller, M. C. (1977). Nutrient Movement Through Western Hemlock-Western Redcedar Ecosystems in. *Ecology*, 58(6), 1269–1283. Retrieved from <https://www-jstor-org.ezproxy.library.ubc.ca/stable/pdf/1935080.pdf?refreqid=excelsior%3Af1bc7a4a917b184a99cce066876c4228>
- Filbee-Dexter, K., & Scheibling, R. E. (2014). Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. *Marine Ecology Progress Series*.
<https://doi.org/10.3354/meps10573>
- Follstad Shah, J. J., Kominoski, J. S., Ardón, M., Dodds, W. K., Gessner, M. O., Griffiths, N. A., ... Zeglin, L. H. (2017). Global synthesis of the temperature sensitivity of leaf litter breakdown in streams and rivers. *Global Change Biology*, 23(8), 3064–3075.
<https://doi.org/10.1111/gcb.13609>
- Fraser, L., Turkington, R., & Chanwayz, C. P. (1993). Biology of Canadian Weeds: Gaultheria shallon Pursh. *Canadian Journal of Plant Sciences*, 1247, 1233–1247.
- Frazer, S., Canham, C. D., & Lertzman, K. P. (1999). *Gap light analyzer (GLA): Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation*. Retrieved from [http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Gap+Light+Analyzer+\(+GLA+\):+Users+manual+and+program+documentation,+version+2.0#5%5Cnhttp://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Gap+light+analyzer+\(GLA\).+Users+m anual+and+pro](http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Gap+Light+Analyzer+(+GLA+):+Users+manual+and+program+documentation,+version+2.0#5%5Cnhttp://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Gap+light+analyzer+(GLA).+Users+m anual+and+pro)
- Fukami, T., Bezemer, T. M., Mortimer, S. R., & Van Der Putten, W. H. (2005). Species

- divergence and trait convergence in experimental plant community assembly. *Ecology Letters*, 8, 1283–1290. <https://doi.org/10.1111/j.1461-0248.2005.00829.x>
- Galecki, A., & Burzykowski, T. (2013). Linear Mixed-Effects Models Using R. In G. Casella, S. E. Fienberg, & I. Olkin (Eds.), *Springer Texts in Statistics*. <https://doi.org/10.4127/ch.2012.0065>
- Garnier, E., Cortez, J., Billès, G., Navas, M. L., Roumet, C., Debussche, M., ... Toussaint, J. P. (2004). Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, 85(9), 2630–2637. <https://doi.org/10.1890/03-0799>
- Garnier, E., & Navas, M.-L. (2012). A trait-based approach to comparative functional plant ecology: concepts, methods and applications for agroecology. A review. *Agronomy for Sustainable Development*, 32(2), 365–399. <https://doi.org/10.1007/s13593-011-0036-y>
- Gomi, T., Johnson, A. C., Deal, R. L., & Hennon, P. E. (2006). Factors affecting distribution of wood, detritus, and sediment in headwater stream draining managed young-growth red alder - conifer forests in southeast Alaska. *Canadian Journal of Forest Research*, 36(3), 725–737. Retrieved from <https://search-proquest-com.ezproxy.library.ubc.ca/docview/230526229/fulltextPDF/8BB8DF8939504A0EPQ/1?accountid=14656>
- Gray, A. N., Spies, T. A., & Easter, M. J. (2002). Microclimatic and soil moisture responses to gap formation in coastal Douglas-fir forests. *Canadian Journal of Forest Research*, 32, 332–343. <https://doi.org/10.1139/X01-200>
- Grizzetti, B., Lanzasova, D., Liqueste, C., Reynaud, A., & Cardoso, A. C. (2016). Assessing water ecosystem services for water resource management. *Environmental Science and*

Policy, 61, 194–203. <https://doi.org/10.1016/j.envsci.2016.04.008>

Groom, J. D., Johnson, S. L., Seeds, J. D., & Ice, G. G. (2017). Evaluating Links Between Forest Harvest and Stream Temperature Threshold Exceedances: The Value of Spatial and Temporal Data. *Journal of the American Water Resources Association*, 53(4), 761–773. <https://doi.org/10.1111/1752-1688.12529>

Hale, S. E., Edwards, C., Mason, W. L., Price, M., & Peace, A. (2009). Relationships between canopy transmittance and stand parameters in Sitka spruce and Scots pine stands in Britain. *Forestry*, 82(5), 503–513. <https://doi.org/10.1093/forestry/cpp020>

Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher, D. N., Goodwin, C. E. D., ... Inger, R. (2018). A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ*, 2018(5), 1–32. <https://doi.org/10.7717/peerj.4794>

Hart, S. K., Hibbs, D. E., & Perakis, S. S. (2013). Riparian litter inputs to streams in the central Oregon Coast Range. *Source: Freshwater Science*, 32(1), 343–358. <https://doi.org/10.1899/12-074.1>

Hicks, B. J., Beschta, R. L., & Harr, R. D. (1991). Long-term Changes in Streamflow Following Logging in Western Oregon and Associated Fisheries Implications. *Water Resources Bulletin*, 27(2), 217–226.

Hildrew, A. G., & Townsend, C. R. (1994). Species traits in relation to a habitat templet for river systems. *Freshwater Biology*, 31, 265–275.

Hjältén, J., Nilsson, C., Jørgensen, D., & Bell, D. (2016). Forest–Stream Links, Anthropogenic Stressors, and Climate Change: Implications for Restoration Planning. *BioScience*, 66(8),

646–654. <https://doi.org/10.1093/biosci/biw072>

Holland, D. N., Lilieholm, R. J., & Roberts, D. W. (1993). Economic trade-offs of managing forests for timber production and vegetative diversity. *Canadian Journal of Forest Resources*, 24, 1260–1265. Retrieved from www.nrcresearchpress.com

Holling, C. S. (1973). Resilience and Stability of Ecological Systems. *Annual Review of Ecology and Systematics*, 4, 1–23.

Holmes, K. L., Goebel, P. C., & Morris, A. E. L. (2010). Characteristics of downed wood across headwater riparian ecotones: integrating the stream with the riparian area. *Canadian Journal of Forest Research*, 40, 1604–1614. <https://doi.org/10.1139/X10-106>

Innes, J. L. (2003). The incorporation of research into attempts to improve forest policy in British Columbia. *Forest Policy and Economics*, 5(4), 349–359.
[https://doi.org/10.1016/S1389-9341\(03\)00034-0](https://doi.org/10.1016/S1389-9341(03)00034-0)

Inoue, A., Yamamoto, K., & Mizoue, N. (2011). Comparison of automatic and interactive thresholding of hemispherical photography. *Journal of Forest Science*, 57(2), 78–87.
<https://doi.org/10.17221/68/2010-jfs>

Janssen, P., Piégay, H., Pont, B., & Evette, A. (2018). How maintenance and restoration measures mediate the response of riparian plant functional composition to environmental gradients on channel margins: Insights from a highly degraded large river. *Science of the Total Environment*, 656, 1312–1325. <https://doi.org/10.1016/j.scitotenv.2018.11.434>

Johnson, S., Strengbom, J., & Kouki, J. (2014). Low levels of tree retention do not mitigate the effects of clearcutting on ground vegetation dynamics. *Forest Ecology and Management*,

330, 67–74. <https://doi.org/10.1016/j.foreco.2014.06.031>

Karlsson, O. M., Richardson, J. S., & Kiffney, P. M. (2005). Modelling organic matter dynamics in headwater streams of south-western British Columbia, Canada. *Ecological Modelling*, 183, 463–476. <https://doi.org/10.1016/j.ecolmodel.2004.08.022>

Kaylor, M. J., & Warren, D. R. (2018). Canopy closure after four decades of postlogging riparian forest regeneration reduces cutthroat trout biomass in headwater streams through bottom-up pathways. *Canadian Journal of Fisheries and Aquatic Sciences*, 75, 513–524. <https://doi.org/10.1139/cjfas-2016-0519>

Kennedy, P. G., & Quinn, T. (2001). Understory plant establishment on old-growth stumps and the forest floor in western Washington. *Forest Ecology and Management*, 154(1–2), 193–200. [https://doi.org/10.1016/S0378-1127\(00\)00622-8](https://doi.org/10.1016/S0378-1127(00)00622-8)

Kielstra, B. W. (2020). *Using multiple scales for enhancing predictive capacity in modelling responses to the cumulative effects of disturbance in streams (Doctoral dissertation)*. University of British Columbia.

Kiffney, P. M., & Richardson, J. S. (2010). Organic matter inputs into headwater streams of southwestern British Columbia as a function of riparian reserves and time since harvesting. *Forest Ecology and Management*, 260, 1931–1942. <https://doi.org/10.1016/j.foreco.2010.08.016>

Kiffney, P. M., Richardson, J. S., & Bull, J. P. (2003). Responses of periphyton and insects to experimental manipulation of riparian buffer width along forest streams. *Journal of Applied Ecology*, 40(6), 1060–1076. <https://doi.org/10.1111/j.1365-2664.2003.00855.x>

- Klinka, K., Krestov, P., & Fons, J. (1997). Towards a taxonomic classification of humus forms; third approximation. *Scientia Silvica, Extension*(9), 1–4.
- Kominoski, J. S., Follstad, J. J., Canhoto, C., Fischer, D. G., Giling, D. P., González, E., ... Tiegs, S. D. (2013). Forecasting functional implications of global changes in riparian plant communities. *Ecology and the Environment*, 11(8), 423–432. Retrieved from <https://www-jstor-org.ezproxy.library.ubc.ca/stable/pdf/43187655.pdf?refreqid=excelsior%3A577c5825fc8db c83ad84d22f86731aad>
- Kominoski, J. S., Marczak, L. B., & Richardson, J. S. (2011). Riparian forest composition affects stream litter decomposition despite similar microbial and invertebrate communities. *Ecology*, 92(1), 151–159. <https://doi.org/10.1890/10-0028.1>
- Kreutzweiser, D. P., Hazlett, P. W., & Gunn, J. M. (2008). Logging impacts on the biogeochemistry of boreal forest soils and nutrient export to aquatic systems: A review. *Environmental Reviews*, 16, 157–179. <https://doi.org/10.1139/A08-006>
- Krumm, F., Schuck, A., & Rigling, A. (Eds.). (2020). *How to balance forestry and biodiversity conservation – A view across Europe*. Birmensdorf: European Forest Institute; Swiss Federal Institute for Forest, Snow and Landscape Research.
- Kuglerová, L., García, L., Pardo, I., Mottiar, Y., & Richardson, J. S. (2017). Does leaf litter from invasive plants contribute the same support of a stream ecosystem function as native vegetation? *Ecosphere*, 8(4), 1–18. <https://doi.org/10.1002/ecs2.1779>
- Kuglerová, L., Hasselquist, E. M., Richardson, J. S., Sponseller, R. A., Kreutzweiser, D. P., & Laudon, H. (2017). Management perspectives on *Aqua incognita*: Connectivity and

- cumulative effects of small natural and artificial streams in boreal forests. *Hydrological Processes*, 31, 4238–4244. <https://doi.org/10.1002/hyp.11281>
- Kuznetsova, A., Brockhoff, P., & Christensen, R. (2017). lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software*, 82(13), 1–26.
- Lamb, E. G., & Mallik, A. U. (2003). Plant species traits across a riparian-zone/forest ecotone. *Journal of Vegetation Science*, 14(6), 853–858. <https://doi.org/10.1111/j.1654-1103.2003.tb02218.x>
- Lambin, E. F., & Meyfroidt, P. (2011). Global land use change, economic globalization, and the looming land scarcity. *Proceedings of the National Academy of Sciences of the United States of America*, 108(9), 3465–3472. <https://doi.org/10.1073/pnas.1100480108>
- Larson, A. M. (2011). Forest tenure reform in the age of climate change: Lessons for REDD+. *Global Environmental Change*, 21(2), 540–549. <https://doi.org/10.1016/j.gloenvcha.2010.11.008>
- Larson, P. R., & Lohrengel, C. F. (2011). A new tool for climatic analysis using the Köppen climate classification. *Journal of Geography*, 110(3), 120–130. <https://doi.org/10.1080/00221341.2011.537672>
- Leach, J. A., & Moore, D. (2017). Insights on stream temperature processes through development of a coupled hydrologic and stream temperature model for forested coastal headwater catchments. *Hydrological Processes*, 31(18), 3160–3177. <https://doi.org/10.1002/hyp.11190>
- Leopold, B., Wolman, M., & Miller, J. (1964). *Fluvial Processes in Geomorphology*. New York:

Dover Publication.

- Likens, G. E., Bormann, F. H., Johnson, N. M., Fisher, D. W., & Pierce, R. S. (1970). Effects of Forest Cutting and Herbicide Treatment on Nutrient Budgets in the Hubbard Brook Watershed-Ecosystem. *Source: Ecological Monographs*, 40(1), 23–47. Retrieved from <https://www.jstor.org/stable/pdf/1942440.pdf?refreqid=excelsior%3A962aa42f9034eba77b99439dacdeeff2>
- Lilles, E., Dhar, A., Coates, K. D., & Haeussler, S. (2018). Retention level affects dynamics of understory plant community recovery in northern temperate hemlock-cedar forests. *Forest Ecology and Management*, 421, 3–15. <https://doi.org/10.1016/j.foreco.2017.12.033>
- Long, J. N. (2009). Emulating natural disturbance regimes as a basis for forest management: A North American view. *Forest Ecology and Management*, 257, 1868–1873. <https://doi.org/10.1016/j.foreco.2008.12.019>
- Lozanovska, I., Ferreira, M. T., & Aguiar, F. C. (2019). Functional diversity assessment in riparian forests – Multiple approaches and trends: A review. *Ecological Indicators*, 95, 781–793. <https://doi.org/10.1016/j.ecolind.2018.08.039>
- Luke, S. G. (2017). Evaluating significance in linear mixed-effects models in R. *Behaviour Research and Therapy*, 49, 1494–1502. <https://doi.org/10.3758/s13428-016-0809-y>
- Luke, S. H., Luckai, N. J., Burke, J. M., & Prepas, E. E. (2007). Riparian areas in the Canadian boreal forest and linkages with water quality in streams. *Environ. Rev.*, 15, 79–97. <https://doi.org/10.1139/A07-001>
- MacKinnon, A., Pojar, J., & Alaback, P. B. (2004). *Plants of coastal British Columbia including*

- Washington, Oregon & Alaska. Retrieved from
<http://webcat1.library.ubc.ca/vwebv/holdingsInfo?bibId=5881393>
- Mallik, A. U., Kreutzweiser, D. P., Spalvieri, C. M., & Mackereth, R. W. (2013). Understory plant community resilience to partial harvesting in riparian buffers of central Canadian boreal forests. *Forest Ecology and Management*, 289, 209–218.
<https://doi.org/10.1016/j.foreco.2012.09.039>
- Martínez, A., Larrañaga, A., Pérez, J., Basaguren, A., & Pozo, J. (2013). Leaf-litter quality effects on stream ecosystem functioning: a comparison among five species. *Fundamental and Applied Limnology*, 183(3), 239–248.
- Mazerolle, M. J. (2017). AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). *R Package Version 2.1-1*, p. R Packag. version 2.1-1. Retrieved from
<https://cran.r-project.org/package=AICcmodavg>.
- Mccoysulentic, M. E., Kolb, T. E., Merritt, D. M., Palmquist, E., Ralston, B. E., Sarr, D. A., & Shafroth, P. B. (2017). Changes in Community-Level Riparian Plant Traits over Inundation Gradients, Colorado River, Grand Canyon. *Wetlands*, 37, 635–646.
<https://doi.org/10.1007/s13157-017-0895-3>
- Menéndez, V., Revilla, M. A., & Fernández, H. (2006). Growth and gender in the gametophyte of *Blechnum spicant* L. *Plant Cell, Tissue and Organ Culture*, 86(1), 47–53.
<https://doi.org/10.1007/s11240-006-9095-1>
- Meng, T. T., Wang, H., Harrison, S. P., Prentice, I. C., Ni, J., & Wang, G. (2015). Responses of leaf traits to climatic gradients: Adaptive variation versus compositional shifts. *Biogeosciences*, 12(18), 5339–5352. <https://doi.org/10.5194/bg-12-5339-2015>

- Meyer, D., Dimitriadou, E., Hornik, K., Weingessel, A., & Leisch, F. (2020). *e1071: Misc Functions of the Department of Statistics, Probability Theory Group*. Vienna, Austria.
- Minami, Y., Oba, M., Kojima, S., & Richardson, J. S. (2015). Distribution pattern of coniferous seedlings after a partial harvest along a creek in a Canadian Pacific northwest forest. *Journal of Forest Research*, 20(3), 328–336. <https://doi.org/10.1007/s10310-015-0479-0>
- Miyamoto, M. (2020). Poverty reduction saves forests sustainably: Lessons for deforestation policies. *World Development*, 127, 104746. <https://doi.org/10.1016/j.worlddev.2019.104746>
- MKRF Staff. (2015). Malcolm Knapp Research Forest: History. Retrieved from MKRF Webpage website: <https://www.mkrf.forestry.ubc.ca/about/history/>
- Moore, R. D., & Richardson, J. S. (2003). Progress towards understanding the structure, function, and ecological significance of small stream channels and their riparian zones. *Canadian Journal of Forest Research*, 33, 1349–1351.
- Moore, R. D., Spittlehouse, D. L., & Story, A. (2005). Riparian microclimate and stream temperature response to forest harvesting: A review. *Journal Of The American Water Resources Association*, 7(4), 813–834. <https://doi.org/10.1111/j.1752-1688.2005.tb04465.x>
- Moore, R. D., & Wondzell, S. M. (2005). Physical hydrology and the effects of forest harvesting in the Pacific Northwest: A review. *Journal of the American Water Resources Association*, 41(4), 763–784. <https://doi.org/10.1111/j.1752-1688.2005.tb04463.x>
- Mouillot, D., Graham, N. A. J., Bastien Villé Ger, S., Mason, N. W. H., & Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, 28(3), 167–177. <https://doi.org/10.1016/j.tree.2012.10.004>

Munsell Color (Firm). (2010). *Munsell soil-colour charts : with genuine Munsell color chips*. Grand Rapids, MI: Munsell Colour.

Naeem, S., Thompson, L., Lawler, S. P., Lawton, J. H., & Woodfin, R. M. (1995). Empirical evidence that declining species diversity may alter the performance of terrestrial ecosystems. *Philosophical Transactions: Biological Sciences*, 347(1321), 249–262.
Retrieved from <http://www.jstor.org/stable/55946>

Naiman, R. J., Bechtold, J. S., Beechie, T. J., Latterell, J. J., & van Pelt, R. (2010). A Process-based view of floodplain forest patterns in coastal river valleys of the Pacific Northwest. *Ecosystems*, 13(1), 1–31. <https://doi.org/10.1007/s10021-009-9298-5>

Newaz, M. S., Mallik, A. U., & Mackereth, R. W. (2019). Riparian vegetation recovery in a 23 year chronosequence of clear-cuts along boreal headwater streams. *Forest Ecology and Management*, 443, 69–83. <https://doi.org/10.1016/j.foreco.2019.04.010>

Niquidet, K. (2008). Revitalized? An event study of forest policy reform in British Columbia. *Journal of Forest Economics*, 14(4), 227–241. <https://doi.org/10.1016/j.jfe.2007.10.001>

Oksanen, J., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., ... Wagner, H. (2020). *vegan: Community Ecology Package*.

Oldén, A., Selonen, V. A. O., Lehtonen, E., & Kotiaho, J. S. (2019). The effect of buffer strip width and selective logging on streamside plant communities. *BMC Ecology*, 19(1), 1–9. <https://doi.org/10.1186/s12898-019-0225-0>

Oldén, Anna, Peura, M., Saine, S., Kotiaho, J. S., & Halme, P. (2019). The effect of buffer strip width and selective logging on riparian forest microclimate. *Forest Ecology and*

Management, 453. <https://doi.org/10.1016/j.foreco.2019.117623>

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., ... C Cornelissen, J. H. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, 61, 167–234.
https://doi.org/10.1071/BT12225_CO

Peter, D. H., & Harrington, T. B. (2018). Effects of forest harvesting, logging debris, and herbicides on the composition, diversity and assembly of a western Washington, USA plant community. *Forest Ecology and Management*, 417, 18–30.
<https://doi.org/10.1016/j.foreco.2018.01.045>

Petter, G., Wagner, K., Wanek, W., Sánchez Delgado, E. J., Zotz, G., Cabral, J. S., & Kreft, H. (2016). Functional leaf traits of vascular epiphytes: Vertical trends within the forest, intra- and interspecific trait variability, and taxonomic signals. *Functional Ecology*, 30(2), 188–198. <https://doi.org/10.1111/1365-2435.12490>

Pojar, J., Klinka, K., & Meidinger, D. V. (1987). Biogeoclimatic ecosystem classification in British Columbia. *Forest Ecology and Management*, 22(1–2), 119–154.
[https://doi.org/10.1016/0378-1127\(87\)90100-9](https://doi.org/10.1016/0378-1127(87)90100-9)

Politti, E., Bertoldi, W., Gurnell, A., & Henshaw, A. (2018). Feedbacks between the riparian Salicaceae and hydrogeomorphic processes: A quantitative review. *Earth-Science Reviews*, 176, 147–165. <https://doi.org/10.1016/j.earscirev.2017.07.018>

Pollen, N., Simon, A., & Collison, A. (2004). Advances in Assessing the Mechanical and Hydrologic Effects of Riparian Vegetation on Streambank Stability. In S. J. Bennett & A. Simon (Eds.), *Riparian Vegetation and Fluvial Geomorphology* (Volume 8, pp. 125–139).

<https://doi.org/10.1029/008WSA10>

Richardson, J. (2019). Biological Diversity in Headwater Streams. *Water*, 11(366), 1–19.

<https://doi.org/10.3390/w11020366>

Richardson, J., & Béraud, S. (2014). Effects of riparian forest harvest on streams: a meta-analysis. *Journal of Applied Ecology*, 51(6), 1712–1721. <https://doi.org/10.1111/1365-2664.12332>

Richardson, J.S., & Hanna, D. E. L. (n.d.). Leaf Litter Decomposition as a Contributor to Ecosystem Service Provision. In C. M. Swan, L. Boyero, & C. Canhoto (Eds.), *The Ecology of Plant Litter Decomposition in Stream Ecosystems*. Springer-Nature.

Richardson, J.S., & Sato, T. (2015). Resource subsidy flows across freshwater-terrestrial boundaries and influence on processes linking adjacent ecosystems. *Ecohydrology*, 8(3), 406–415. <https://doi.org/10.1002/eco.1488>

Richardson, J.S., Zhang, Y., & Marczak, L. B. (2010). Resource subsidies across the land-freshwater interface and responses in recipient communities. *River Research and Applications*, 26, 55–66. <https://doi.org/10.1002/rra>

Richardson, John S., Kuglerová, L., Muotka, T., Chellaiah, D., & Jyväsjärvi, J. (n.d.). *Protecting our streams by defining clear targets for riparian management*.

Richardson, John S., Naiman, R. J., & Bisson, P. A. (2012). How did fixed-width buffers become standard practice for protecting freshwaters and their riparian areas from forest harvest practices? *Freshwater Science*, 31(1), 232–238. <https://doi.org/10.1899/11-031.1>

Richardson, John S., Naiman, R. J., Swanson, F. J., & Hibbs, D. E. (2005). Riparian

- communities associated with pacific northwest headwater streams: Assemblages, processes, and uniqueness. *Journal of the American Water Resources Association*, 41(4), 935–947.
<https://doi.org/10.1111/j.1752-1688.2005.tb04471.x>
- Roche, P., Díaz-Burlinson, N., & Gachet, S. (2004). Congruency analysis of species ranking based on leaf traits: Which traits are the more reliable? *Plant Ecology*, 174(1), 37–48.
<https://doi.org/10.1023/B:VEGE.0000046056.94523.57>
- Scheffer, M., Carpenter, S., Foley, J., Folke, C., & Walker, B. (2001). Catastrophic Shifts in Ecosystems. *Nature*, 413(6856), 591–596. <https://doi.org/10.1038/35098000>
- Silverthorn, T. K., & Richardson, J. S. (2021). Forest Management Impacts on Greenhouse Gas Fluxes from Riparian Soils Along Headwater Streams. *Ecosystems*.
<https://doi.org/10.1007/s10021-021-00621-z>
- Smart, S. M., Glanville, H. C., Blanes, M. del C., Mercado, L. M., Emmett, B. A., Jones, D. L., ... Hodgson, J. G. (2017). Leaf dry matter content is better at predicting above-ground net primary production than specific leaf area. *Functional Ecology*, 31(6), 1336–1344.
<https://doi.org/10.1111/1365-2435.12832>
- Soil Classification Working Group. (1998). *The Canadian system of soil classification* (3rd ed.; R. H. Haynes, Ed.). Ottawa: National Research Council of Canada Research Press.
- Spies, T. A., Johnson, K. N., Burnett, K. M., Ohmann, J. L., McComb, B. C., Reeves, G. H., ... Garber-yonts, B. (2007). *Cumulative Ecological and Socioeconomic Effects of Forest Policies in Coastal Oregon*. 17(1), 5–17.
- Strand, J. A., & Weisner, S. E. B. (2004). Phenotypic plasticity - Contrasting species-specific

- traits induced by identical environmental constraints. *New Phytologist*, 163(3), 449–451.
<https://doi.org/10.1111/j.1469-8137.2004.01144.x>
- Studinski, J. M., & Hartman, K. J. (2015). The effects of riparian logging on terrestrial invertebrate inputs into forested headwater streams. *Hydrobiologia*, 743(1), 189–198.
<https://doi.org/10.1007/s10750-014-2036-9>
- Swartz, A., Roon, D., Reiter, M., & Warren, D. (2020). Stream temperature responses to experimental riparian canopy gaps along forested headwaters in western Oregon. *Forest Ecology and Management*, 474(118354). <https://doi.org/10.1016/j.foreco.2020.118354>
- Sweeney, B. W., & Newbold, J. D. (2014a). Streamside forest buffer width needed to protect stream water quality, habitat, and organisms: A literature review. *Journal of the American Water Resources Association*, 50(3), 560–584. <https://doi.org/10.1111/jawr.12203>
- Sweeney, B. W., & Newbold, J. D. (2014b). Streamside forest buffer width needed to protect stream water quality, habitat, and organisms: A literature review. *Journal of the American Water Resources Association*, 50(3), 560–584. <https://doi.org/10.1111/jawr.12203>
- Taiyun, W., & Simko, V. (2017). *R package “corrplot”: Visualization of a Correlation Matrix*.
- Truitt, A. M., Granek, E. F., Duveneck, M. J., Goldsmith, K. A., Jordan, M. P., & Yazzie, K. C. (2015). What is Novel About Novel Ecosystems: Managing Change in an Ever-Changing World. *Environmental Management*, 55, 1217–1226. <https://doi.org/10.1007/s00267-015-0465-5>
- Tschaplinski, P. J., & Pike, R. G. (2009). Riparian management and Effects on Function. In *Compendium of Forest Hydrology and Geomorphology in British Columbia*. (pp. 479–525).

- Tyler, M. W., & Peterson, D. L. (2004). Effects of forest policy on landscape pattern of late-seral forest of the Western Olympic Peninsula, Washington. *Agriculture, Ecosystems and Environment*, 101(2–3), 289–306. <https://doi.org/10.1016/j.agee.2003.09.020>
- Underwood, A. J. (1997). *Experiments in Ecology: their Logical Design and Interpretation Using Analysis of Variance*. Cambridge, UK: Cambridge University Press.
- Verhoef, A., Fernández-Gálvez, J., Diaz-Espejo, A., Main, B. E., & El-Bishti, M. (2006). The diurnal course of soil moisture as measured by various dielectric sensors: Effects of soil temperature and the implications for evaporation estimates. *Journal of Hydrology*, 321(1–4), 147–162. <https://doi.org/10.1016/j.jhydrol.2005.07.039>
- Vitousek, P. M., & Farrington, H. (1997). Nutrient limitation and soil development: Experimental test of a biogeochemical theory. *Biogeochemistry*, 37(1), 63–75. Retrieved from <https://about.jstor.org/terms>
- Walker, B., Holling, C. S., Carpenter, S. R., & Kinzig, A. (2004). Resilience, adaptability and transformability in social-ecological systems. *Ecology and Society*, 9(2). <https://doi.org/10.5751/ES-00650-090205>
- Wallace, A. J. B., Eggert, S. L., Meyer, J. L., & Webster, J. R. (2008). Multiple Trophic Levels of a Forest Stream Linked to Terrestrial Litter Inputs Published by : American Association for the Advancement of Science Stable URL : <http://www.jstor.org/stable/2893227>. *Science*, 277(5322), 102–104.
- Warren, D. R., Collins, S. M., Purvis, E. M., Kaylor, M. J., & Bechtold, H. A. (2016). Spatial Variability in Light Yields Colimitation of Primary Production by Both Light and Nutrients in a Forested Stream Ecosystem. *Ecosystems*, 20, 198–210. <https://doi.org/10.1007/s10021->

- Warren, D. R., Keeton, W. S., Kiffney, P. M., Kaylor, M. J., Bechtold, H. A., & Magee, J. (2016). Changing Forests – Changing Streams: Riparian forest stand development and ecosystem function in temperate headwaters. *Ecosphere*, 7(8), 1–19.
<https://doi.org/10.1002/ecs2.1435>
- Warrington, B., Aust, W., Barrett, S., Ford, W., Dolloff, C., Schilling, E., ... Bolding, M. C. (2017). Forestry Best Management Practices Relationships with Aquatic and Riparian Fauna: A Review. *Forests*, 8(9), 331. <https://doi.org/10.3390/f8090331>
- Watson, K. (2009). *Soils Illustrated - Field Descriptions* (2nd ed.). Kamloops: International Remote Sensing Surveys Ltd.
- Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, 199(2), 213–227. <https://doi.org/10.1023/A:1004327224729>
- Westoby, M., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Diemer, M., ... Cornelissen, J. H. . (2004). The worldwide leaf economics spectrum. *Nature*, 428, 821–827.
- Westoby, M., & Wright, I. J. (2006). Land-plant ecology on the basis of functional traits. *TRENDS in Ecology and Evolution*, 21(5). <https://doi.org/10.1016/j.tree.2006.02.004>
- Wilson, P. J., Thompson, K., & Hodgson, J. G. (1999). Specific Leaf Area and Leaf Dry Matter Content as Alternative Predictors of Plant. *Source: The New Phytologist*, 143(1), 155–162.
Retrieved from <https://www-jstor-org.ezproxy.library.ubc.ca/stable/pdf/2588523.pdf?refreqid=excelsior%3Abbf22997c177a8df71e34798c82e2c25>

- Wipfli, M., Richardson, J., & Naiman, V. (2007). Ecological linkages between headwaters and downstream ecosystems. *Jawra*, 43(1), 72–85.
- Wipfli, M. S., & Gregovich, D. P. (2002). Export of invertebrates and detritus from fishless headwater streams in southeastern Alaska: Implications for downstream salmonid production. *Freshwater Biology*, 47(5), 957–969. <https://doi.org/10.1046/j.1365-2427.2002.00826.x>
- Wipfli, M. S., & Musslewhite, J. (2004). Density of red alder (*Alnus rubra*) in headwaters influences invertebrate and detritus subsidies to downstream fish habitats in Alaska. *Hydrobiologia*, 520, 153–163. Retrieved from <https://search-proquest-com.ezproxy.library.ubc.ca/docview/821543976?pq-origsite=summon&accountid=14656>
- Wohl, E. (2017). The significance of small streams. *Frontiers in Earth Science*, 11(3), 447–456. <https://doi.org/10.1007/s11707-017-0647-y>
- Wright, A. J., de Kroon, H., Visser, E. J. W., Buchmann, T., Ebeling, A., Eisenhauer, N., Fischer, C., ... Mommer, L. (2017). Plants are less negatively affected by flooding when growing in species-rich plant communities. *New Phytologist*, 213(2), 645–656.
- Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., ... Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, 428, 821–827.
- Wyka, T. P., Oleksyn, J., Żytkowiak, R., Karolewski, P., Jagodziński, A. M., & Reich, P. B. (2012). Responses of leaf structure and photosynthetic properties to intra-canopy light gradients: a common garden test with four broadleaf deciduous angiosperm and seven evergreen conifer tree species. *Oecologia*, 170(1), 11–24. <https://doi.org/10.1007/s00442-012-2279-y>

Yeung, A. C. Y., Lecerf, A., & Richardson, J. S. (2017). Assessing the long-term ecological effects of riparian management practices on headwater streams in a coastal temperate rainforest. *Forest Ecology and Management*, 384, 100–109.
<https://doi.org/10.1016/j.foreco.2016.10.044>

Zukswert, J. M., & Prescott, C. E. (2017). Relationships among leaf functional traits, litter traits, and mass loss during early phases of leaf litter decomposition in 12 woody plant species. *Oecologia*, 185, 305–316. <https://doi.org/10.1007/s00442-017-3951-z>