Local topography is more important than climate as a determinant of regional alpine plant diversity in southwestern British Columbia

by

Katharine Baldwin-Corriveau
B.Sc., McGill University, 2009

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of the Requirements for the Degree of

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in the School of Environmental Studies

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Abstract

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Mountain ecosystems are considered highly sensitive to the impacts of climate change, and are experiencing a magnitude of change that far exceeds global averages, particularly with respect to increases in average temperature and precipitation. As such, scientists are predicting a rapid habitat reduction or even the loss of the coolest climatic alpine zones, thus threatening the continued survival of high elevation specialists. However, many of these 'doomsday' predictions are based primarily on models with coarse-resolution changes to atmospheric climate parameters, and do not take into account the potential buffering effects of other environmental gradients known to structure alpine plant communities, related to topography and soils. To assess the accuracy of predictions regarding the state of vulnerability of alpine plant communities to climate change, this thesis examined the relative importance of climate, topography and soils as determinants of regional alpine plant diversity for all species, as well as for forbs, graminoids and woody species separately, in alpine meadows of southwestern British Columbia. Through redundancy analyses and variation partitioning, results show that topography and soils are more important than climate as determinants of regional alpine plant diversity. Within these groups, elevation, slope, soil moisture and mean summer temperature were most

significant. Interestingly, precipitation played only a small role, even though the study area spanned a precipitation gradient of over 1200 mm/year. The stronger influence of temperature, especially for woody species beta diversity, supports findings of shrub expansion in arctic-alpine systems. The lower importance of climate as a determinant of regional alpine plant diversity, especially for forbs, the dominant life form in alpine meadow ecosystems, suggests that these productive environments may be more resilient to on-going changes in atmospheric climate conditions than previously believed.

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Chapter 1

1.0 Introduction

1.1 Mountain Ecosystems and Climate Change

Mountain ecosystems are considered highly sensitive to the impacts of climate change (Diaz *et al*., 2003; Grabherr *et al*., 2010; Klanderud & Totland, 2005; Pauli *et al*., 1996), and are experiencing a magnitude of change that far exceeds global averages, particularly with respect to increases in average temperature and precipitation (Böhm. *et al*., 2001; Demezhko & Golovanova, 2007; Devi *et al.,* 2008; Luckman & Kavanagh, 2000).

High-elevation mountain ecosystems, broadly referred to as "alpine", are defined as sections of mountain summits that are above the low-temperature determined treeline (Grabherr *et al*., 2010). Due primarily to their complex topography, alpine ecosystems host a wide array of microhabitats, are highly biodiverse, and are home to a disproportionate abundance of endemic species that have become isolated at high elevations (Barthlott *et al*., 1996; Beniston, 2003; Diaz *et al*., 2003). In addition to their hosting a rich biota, the vulnerability of alpine environments to climate change is enhanced because they a) are nutrient-limited and predictions show enhanced rates of decomposition and mineralization, thus increasing nutrient availability; b) have high relief and thus heterogeneous local environmental conditions; and c) are home to strong gradients where narrow, elevation-controlled vegetation belts are analogous to latitude-driven climatic zones (Bowman *et al*., 1993; Diaz *et al*., 2003; Krannitz & Kesting, 1997;

Rustad *et al.*, 2001). Moreover, alpine systems are considered high-stress as plant life is limited by low temperature, insufficient water availability, high winds, and strong solar radiation, among others (Körner & Larcher, 1988; Pauli *et al*., 1996). As a consequence, small shifts in any of these parameters due to climate change may have large impacts on species and communities present. Most concerning are alpine species that thrive near mountain summits, as they are unable to climb higher in an attempt to escape encroaching climate conditions and are thus at a higher risk of extinction (Beniston, 2003).

1.2 Overview of Climate Change Impacts in the Alpine

Globally, the last century has seen mean surface temperatures rise by 0.74°C, general increases in precipitation, more frequent extreme climatic events, and changing trends in cloud cover (IPCC, 2007). Like the arctic, however, many mountain ecosystems have experienced a magnitude of climatic change greater than the global average. For example, the average annual temperature in the European Alps increased approximately 1.1°C since 1890 (Böhm *et al*., 2001), the Ural Mountains in western Russia warmed at a rate of 1.6°C/100yrs from 1930 to 2001 and experienced doubling of winter precipitation during the 20th century (Demezhko & Golovanova, 2007; Devi *et al.,* 2008), and the Canadian Rockies warmed 1.5°C during the last century (Luckman & Kavanagh, 2000). Additionally, in most regions increases in temperature and precipitation have been greater in winter months, substantially influencing snow cover and duration, the magnitude and timing of spring freshet, and the length of the growing season (Beniston, 2003; IPCC, 2007).

There is a growing body of evidence to suggest that alpine vegetation is already responding to these shifts in climate conditions (Grabherr *et* al., 2010; McCarthy, 2001;

Pauli *et al.*, 2012). Observations include elevational shifts in species' ranges (Cannone *et al.,* 2007; Crimmins *et* al., 2011; Grabherr *et al.*, 1994; Krannitz & Kesting, 1997; Lenoir *et al.*, 2008; Parmesan, 1996; Pauli *et al.*, 2012), average increases in species richness at higher elevations (Grabherr *et al*., 1994; Grabherr *et al.,* 2001; Holzinge*r et al.,* 2008; Pauli *et al.*, 2012), changes to alpine community composition through increases in the abundance of thermophilic species and decreases in cold-adapted ones (Gottfried *et al.*, 2012), diebacks of alpine trees (Fisher, 1997; Hamburg & Cogbill, 1988; Smith *et al*., 2008), losses of mountain endemics and invasions by lower elevation species (Dirnböck *et al*., 2011; Grabherr *et al.,* 2010; Pounds *et al.,* 1999), and altered plant reproductive phenologies (Dunne *et al*., 2003).

Though the above changes have been noted, they cannot be generalized as changes may vary depending on the region under study (Engler *et al*., 2011). Most notably, Pauli *et al*. (2012) recorded an increase of 3.9 species from 2001 to 2008 on alpine summits on European temperate-boreal mountains, but a loss of 1.4 species on the drier alpine summits of Mediterranean ranges, suggesting that the historical climate type and water availability of a region may dictate how alpine biodiversity responds to climate change. As the impacts of global climate change are expected to be most ecologically relevant at the regional scale (Walther *et al.*, 2002), such results suggest that we must first understand how our present-day alpine plant communities are structured by local and regional environment factors in order to predict how they will change in the years to come.

1.3 Scale and the Environmental Determinants of Diversity

Species richness is a numerical value given to a community based on the number of species present in a sample containing a specified number of individuals or amount of biomass (Hurlbert, 1971). In conjunction with species abundances (or evenness), it is used to measure the total species diversity of a given area (Lloyd & Ghelardi, 1964; Pielou, 1966; Simpson, 1949; Whittaker, 1972). At its most basic, the diversity of plant species in a community depends on both abiotic and biotic factors (Ricklefs, 1987). Given the extreme environmental conditions characteristic of mountain ecosystems, abiotic factors typically prevail over biotic ones as determinants of diversity (Körner, 2003; Pauli et al., 1996; Webster, 1961).

At a global scale, evidence supporting the water-energy hypothesis (O'Brien, 1993, 2006) has established that environmental energy and water availability are primary determinants of species diversity (Evans *et al*., 2005; Hawkins *et al.*, 2003). This theory hypothesizes that species richness is controlled primarily by water at lower latitudes and energy at higher latitudes (Hawkins *et al*., 2003). Typically, estimates of potential evapotranspiration within vegetative communities are used to represent the "energy" portion of the water-energy hypothesis, and annual precipitation as a measure of "water availability" (O'Brien, 1993, 2006; Hawkins *et al.,* 2003). Though this theory has been able to explain almost 80% of the variation in global species richness (O'Brien, 1993), it is likely that other environmental factors begin to override evapotranspiration and water availability as determinants of diversity at regional and local scales.

Indeed, local species diversity is in part linked to local environmental gradients, but is also mediated by regional effects (e.g. Cornell, 1993; Harrison *et al*., 2006;

Ricklefs, 2004; Starzomski *et al.*, 2008). At the local scale, individual plants and communities in the alpine rely heavily on elements of the microenvironment to generate the means for their own survival (Körner, 2003). For instance, the local climate experienced by alpine plants can be drastically disconnected from ambient air temperature, even up to 25°C higher on a clear summer day as a result of micro-topography, slope exposure, solar radiation and plant growth form (Körner & Cochrane, 1983; Moser *et al*., 1977; Scherrer & Körner, 2010). Furthermore, relief can alter the flow of air and protect alpine vegetation from high winds, creating calm oases in an otherwise turbulent environment (Körner, 2003; Nägeli, 1971; Whitehead, 1959). The facilitative effects of neighboring plants sheltering one another in the vegetative matrix can also accentuate this phenomenon (Choler et al., 2001). Thus, at such a small scale the assumption that life at high elevations is limited by severe climate conditions is not entirely justified because these habitats represent "normal" conditions for well-adapted alpine species, rather than extremes or limits (Körner, 1999).

At a larger regional scale where many plant communities are involved over several hundred square kilometers, the importance of the micro-environment is reduced to noise and larger abiotic systems such as climate and geology increase in significance as determinants of diversity and species distribution (Harrison et al., 2006; Huston, 1999; Parmesan & Yohe, 2003; Pearson & Dawson, 2003; Whittaker *et al*., 2001). The determinants of diversity at a regional scale are perhaps the least understood, as they appear to be comprised of both local and large-scale factors such as climate parameters that define biogeographic zones and site-specific soil characteristics (e.g. Harrison *et al.*, 2006; Moser *et al.,* 2005; Vonlanthen *et al.,* 2006).

1.4 Climate Change Modeling and Predictions for the Future

As the alpine is experiencing a higher rate of warming than lower elevations (Beniston *et al*., 1997; Diaz & Bradley, 1997), scientists are predicting a rapid habitat reduction or even the loss of the coolest climatic alpine zones, thus threatening the continued survival of high elevation specialists (e.g. Beniston, 2003; Dirnböck *et al*., 2003; Dirnböck *et al*., 2011; Guisan & Theurillat, 2000; Hamann & Wang, 2006; Keller *et al*., 2005; Theurillat & Guisan, 2001; Thuiller *et al*., 2005). However, many of these 'doomsday' predictions are based primarily on models with coarse-resolution changes to atmospheric climate parameters (e.g. Dirnböck *et al.*, 2011; Engler *et al*., 2011; Trivedi *et al.*, 2008), and do not take into account the potential buffering effects of other environmental gradients known to structure alpine plant communities, based on topography and soils (Randin *et al*., 2009; Scherrer & Körner, 2010 & 2011). Since the impacts of global climate change are expected to be most ecologically relevant at the regional scale (Walther *et al*., 2002), it is critical that we understand the relative importance of climate, topography and soils as determinants of regional alpine plant diversity to increase the accuracy of our predictions and assess the true state of vulnerability of alpine plant communities in the face of climate change.

1.5 Environmental Determinants of Alpine Plant Diversity

Multiple abiotic factors play a role in structuring plant life in alpine ecosystems: climatic factors such as temperature, precipitation, short growing seasons, snow cover, and high winds (Friedel, 1961; Klanderud, 2005; Körner & Larcher, 1988; Pauli et al., 1996; Walker et al., 1994); soil factors relating to nitrogen and/or phosphorus availability, soil moisture, pH and frost disturbance (Billings & Bliss, 1959; Bowman *et al*., 1993;

Bowman, 1994; Fox, 1981; Körner, 2003; Marini *et al*., 2007; Sala *et al*., 2000; Walker *et al*., 1994); and topographic factors like slope, altitude and aspect (Bennie *et al*., 2008; Bhattarai & Vetaas, 2003; Bruun *et al*., 2006; Geiger, 1965; Holland & Steyn, 1975; Kazakis *et al*., 2007; Körner, 2003; Moser *et al*., 1977; Stanisci *et al*., 2005; Wallace, 1878**)**.

Though we understand that these environmental variables significantly impact the plant community composition in alpine ecosystems, the first order effects of each variable remain unclear, and even less is known about their interactions. Without knowing which abiotic factors are most important in explaining alpine plant diversity patterns at the regional scale where global climate change impacts gain ecological relevancy (Walther *et al*., 2002), we cannot make accurate predictions as to how community composition might change over the coming decades. In basing our outlook regarding the future loss of alpine habitat largely on coarse resolution changes to climate parameters (e.g. Hamann & Wang, 2006; Thuiller *et al*., 2005), we are ignoring the potentially stabilizing role of more fine-scale environmental factors, such as those related to topography and soils, in maintaining current patterns of alpine plant diversity, or at least in promoting the resilience of certain species or communities in the face of climate change (Randin *et al*., 2009; Scherrer & Körner, 2010 & 2011).

Several studies, summarized in Table 1, have examined the relative importance of climate, topography and soil variables as determinants of alpine plant diversity at local or regional scales. Using statistical techniques such as variation partitioning (Legendre, 2008; Peres-Neto *et al*., 2006), generalized linear modeling (GLM; McCullagh & Nelder, 1989) and structural equation modeling (SEM; Mitchell, 1992), some researchers have

extracted the amount of variance in diversity patterns that is explained by each explanatory variable (Table 1). In many of these studies, species richness is often regarded as a proxy for species diversity (Magurran, 1988; Whittaker *et al*., 2001). This assumption ignores the importance of species abundance (or evenness), implying equal roles for rare and dominant species with regard to ecosystem function and response to environmental gradients (Walker *et al*., 1999; Wisley & Potvin, 2000).

Overall, results from Table 1 suggest that more than half of the time, topography and soil are of greater importance than climate as determinants of regional alpine plant diversity. Specifically, patterns of diversity and richness appear to be most strongly regulated by soil pH and other factors relating to local bedrock characteristics, soil phosphate and nitrogen dynamics, elevation, slope exposure, habitat heterogeneity including nearby anthropogenic land-use regimes, annual and growing season precipitation, and various measures of atmospheric temperature.

Table 1: Summary of studies examining the amount of variance in alpine plant diversity or richness explained by climate, topography and/or soil variables. A range of variance explained is included if the analysis was performed on many different plant types instead of on overall species diversity or richness. Cells left blank mean that these variables were not tested. Scale is local (L - one mountain or series of connected peaks) or regional (R - many mountains covering a large area). Note that few studies were performed in North America.

Study	**Location**	**Community Sampled & Diversity Measure**	**Scale**	**% Variance Explained**			**Significant variables**
				Climate	**Topography**	**Soil**	
Austrheim *et al*. (1999)	Budalen valleys, Norway	Richness of subalpine semi-natural grasslands	R		18%	34 %	*Topography*: enclosure or pasture, altitude, heat index *Soil:* pH, P, plowing, grazing, mowing, LOI, fertilization, K, NH_4
Choler *et al*. (2001)	French Alps	Alpine tundra richness & diversity	R		~12% (Rich. & Div.)		*Topography:* elevation, slope, aspect, mesotopography
Harrison *et al*. (2006)	California Mountain Ranges	Endemic serpentine plant richness	L & R	17 % (L) 42 % (R)	19 % (L)	34 % (L) 26-34 % (R)	*Climate:* mean annual regional precipitation *Topography*: rock cover *Soil:* Mg/Ca ratio
Kampmann *et al*. (2008)	Swiss Alps	Alpine grassland richness	R		20.9 %		*Topography:* elevation, slope, habitat diversity
Kikvidze *et al.* (2005)	Northern Hemisphere	High mountain subalpine & alpine meadow richness	R	45 %			*Climate*: growing season precipitation
Li *et al.* (2011)	Qinghai-Tibetan plateau, China	Alpine meadow diversity	L		4 – 16 % (Topography + Soil)		*Topography*: aspect *Soil*: pH, organic C, total P, available P, total N, NH_4N, NO_3N, available N, C/N ratio
Lobo *et al*. (2001)	Iberian Peninsula	All species richness	R	Not significant	39 %	7.5 %	*Topography:* Mean & maximum elevation, scrub area, sea area *Soil:* calcareous & acid rock surface
Marini *et al*. (2007)	Southern Alps, Italy	Alpine hay meadow richness & diversity	R	Not significant	32 % (Rich.) 17 % (Div.)	45 % (Rich.)/ 17 % (Div.)	*Topography:* altitude, slope *Soil:* clay fraction < 0.002 mm, amount of N fertilizer, Olsen P_2O_5, pH

Marini *et al*. (2008a)	Southern Alps, Italy	Richness of rare and common alpine species	R	59 – 62 %	7 %	2 - 12 %	*Climate:* mean annual minimum temperature & its standard deviation, mean summer precipitation *Topography:* forest area, urban elements area, grasslands area, land-cover type heterogeneity *Soil:* bedrock heterogeneity, calcareous bedrock area
Marini *et al*. (2008b)	Southern Alps, Italy	Alpine hay meadow richness	R	Not significant	11 %	12 %	*Topography*: slope, % urban elements (500 m radius), length of meadow edges *Soil:* amount of N fertilizer
Marini *et a*l. (2009)	Southern Alps, Italy	Richness of native and alien species	R	~ 43 % (independent contribution)	~ 31 % (independent contribution)	~ 8 % (only a joint contribution)	*Climate*: mean annual temperature *Topography*: slope, human population density *Soil*: area covered by calcareous bedrock
Moser *et al.* (2005)	Austrian Alps	All alpine zones	R	16 %	1 %	6 %	*Climate:* mean maximum of PET for Jun. 21 & its variation for Dec. 21 *Topography:* # of land-cover & landscape types *Soil:* calcareous bedrock area, # of geological units
Rey Benayas & Scheiner (2002)	Iberia, including mountains	Plant richness & diversity of many habitat types	R	24% (Rich.) (Climate + Topography + Soil) 21% (Div.) (Climate + Topography + Soil)			*Climate*: total precipitation, actual evapotranspiration, temperature (SD) *Topography*: altitudinal range *Soil*: # bedrock types & soil water holding capacity
Sebastià (2004)	Southeastern Pyrenees	Subalpine calcareous grassland diversity	R		63 %	73 %	*Topography:* altitude, slope, aspect, micro- & macro-topography. *Soil:* stoniness, loam, pH, assimilable P, Mg, total C, $CaCo_3$, Ca
Sherman *et al*. (2008)	Hengduan Mountains, China	Alpine meadow, shrub and scree community richness	R		9-55 %		*Topography*: elevation, slope, sun index
Vonlanthen *et al.* (2006)	Swiss Alps	Richness above the timberline	L	43–72 %		46-52 %	*Climate*: daily maximum & mean temperature, daily maximum pressure, length of growing season *Soil*: pH, Mg, NH_4
Wohlgemuth (2002)	Swiss Alps	Richness above the timberline	R	42 %		71 %	*Climate*: continentality index *Soil*: ln(area of calcareous bedrock), # bedrock types
Wohlgemuth *et al*. (2008)	Switzerland	All species richness	R	~ 56 %	~ 61 %	> 11 %	*Climate*: average annual temperature & its range of annual variation, average March radiation *Topography*: range & average of elevation, slope, aspect *Soil*: calcareous & siliceous substrate

1.5.1 Determinants of Plant Functional Diversity

As shown in Table 1, the diversity patterns of entire plant communities are correlated with various environmental gradients relating to climate, topography and soils. However, plant functional groups have been shown to respond separately to environmental conditions, and with climate change these disparities may result in altered competitive interactions and dominance hierarchies, with subsequent adjustments to community structure and composition (Klanderud & Totland, 2005). Forbs, graminoids and woody species are three such functional groups, whose relative diversity may be regulated by different abiotic factors. Of greatest interest may be evidence that woody species diversity is more strongly influenced by climate than the diversity patterns of other life forms, at least in habitats where shrub or tree abundance and/or richness is high (Bhattarai & Vetaas, 2003; Ohlemüller & Wilson, 2000; Wilson & Nilsson, 2009). For instance, Bhattarai & Vetaas (2003) found that temperature- and precipitation-related climate variables in a Nepalese mountain range explained 70% of the variance in woody species richness along an elevation gradient, but did not show any correlation with herbaceous species richness. Wilson & Nilsson (2009) also found that herbaceous species richness decreased significantly with increasing woody species cover in an alpine heath community over a period of 20 years. Moreover, though not exclusively in the alpine, Ohlemüller & Wilson (2000) demonstrated through a review of diversity patterns in New Zealand forests that woody species increased significantly in richness with altitude (and thus with decreasing temperature), while herbaceous species exhibited no such trend. What is interesting to consider is whether climate parameters would increase in significance for herbaceous species such as forbs and graminoids in ecosystems like

alpine meadows where woody species are a minority. In sync with this, Klanderud & Totland (2005) detected no significant effect of experimental warming alone on the diversity, richness or abundance of woody species, forbs and graminoids in an alpine heath meadow. Though this site was dominated by a dwarf shrub (gen. *Dryas*) with a percent cover of approximately 35%, overall forb and graminoid richness and abundance was much higher than that for woody species, suggesting that climate is less influential for woody species diversity in habitats rich in herbaceous species. In a herb-dominated alpine meadow system, Yang *et al*. (2011) found that experimentally increased precipitation positively influenced species richness, thereby contradicting Bhattarai & Vetaas (2003) who found precipitation not to be related to herbaceous species richness in subtropical montane forests. Equally intriguing is a study by Rustad *et al.* (2001) that measured changes to soil respiration in response to warming in both woody and non-woody sites in various ecosystems around the world, and found that effect sizes were only significant for woody sites. This slew of evidence begs for discussion of the possibility that herbaceous plant communities may have some sort of innate climate 'buffer' serving to boost their resilience in the face of climate change.

1.6 Thesis Objectives

Given the complicated patterns described above, this study seeks to explore the magnitude of the relationships between environmental variables and regional plant diversity in numerous alpine meadows in southwestern British Columbia, both in terms of turnover in community composition (β-diversity) and species richness. Specifically, I address the following questions:

(1) How much of the variance in alpine plant diversity is explained by climate, soil, and topography, respectively?

    i. How do environmental determinants differ for alpine plant β-diversity and species richness?

(2) Since different plant functional groups can respond uniquely to environmental stress gradients, how do the environmental determinants of diversity differ for forbs, graminoids and woody species in alpine meadow ecosystems?

    i. How much of the variance in woody species diversity is due to climate and how does this compare to the other life forms?

(3) How many distinct plant species assemblages comprise the alpine meadows surveyed, and what are the primary differences in ecological requirements for the species in each group?

(4) Does the level and extent of recreational access to alpine sites constitute an important determinant of alpine plant diversity?

Chapter 2

2.0 Intensive Plot sampling of alpine meadows in British Columbia to establish the environmental determinants of β–diversity and species richness.

2.1 Introduction

Considered highly vulnerable to global climate change (Diaz et al., 2003; Grabherr et al., 2010; Klanderud & Totland, 2005; Pauli et al., 1996), alpine ecosystems and species are already responding to warmer temperatures and altered precipitation patterns (Böhm *et al*., 2001; Demezhko & Golovanova, 2007; Devi *et al.,* 2008; Luckman & Kavanagh, 2000). Located in nutrient-limited and cold temperature environments where growing seasons are short and vegetation distribution is heavily structured by snowpack (Körner, 2003), the long-term persistence of most high-altitude plant communities in a warming world is questionable (Beniston, 2003; Dirnböck *et al*., 2011; Hamann & Wang, 2006).

Over the past century, British Columbia has experienced regional warming between 0.6°C and 1.7°C (Gayton, 2008). Under a moderate climate change scenario, mean annual temperature and precipitation in southwestern British Columbia is predicted to further rise by over 3°C and 130 mm/yr, respectively, by 2080 (ClimateWNA - Mbogga *et al.,* 2009 and Wang *et al.,* 2012). With such significant long-term changes to climate

parameters, it is critical that we uncover the relative importance of climatic, topographic and soil-related determinants of alpine plant diversity in this region to better understand how affected communities will respond to climate change in the years to come.

In this chapter, alpine meadow sites in southwestern British Columbia were surveyed for species richness and β-diversity, and these data were analyzed in relation to site-specific abiotic conditions to distinguish the relative importance of climate, topography, and soil as determinants of alpine plant diversity for all species and functional groups. The difference in environmental determinants for species richness and β-diversity was also contrasted. Finally, findings were compared to results from Table 1, a literature review of similar studies conducted over the past 15 years, to reveal any underlying trends and thoughts are offered regarding the state of resilience of alpine meadow systems in the face of impending climate change.

2.2 Methods

2.2.1 Site Descriptions

Data for this project were collected from seven high-elevation sites distributed over approximately 6,200 km^2 in southwestern British Columbia from late July to mid-September 2011 (Fig. 1; see Plates 1-7 in Appendix 1 for site photographs). Six sites are located within the Coast Mountain range and one straddles the region dividing the southeast Coast Mountains from the Chilcotin plateau, on the border of the South Chilcotin Mountains Provincial Park (Fig.1). The Coast Mountains are a 100-200 km wide belt of high relief extending for 1700 km from southwestern British Columbia to the St. Elias Mountains of southwestern Yukon Territory and Alaska (Monger & Journeay, 1994; Reyes & Clague, 2004). The Chilcotin plateau, lying to the east, spans 50,000 km^2

in south-central British Columbia between the Coast Mountains and the Quesnel Highlands (Bevier, 1983).

The physiography of the southern Coast Mountains is dominantly granitic with volcanic intrusions and areas of folded volcanic and sedimentary rocks, and glaciers and icefields are common (BC Parks Division & TFE Consultants, 1999; Reyes & Clague, 2004). The Chilcotin plateau is composed primarily of marine and non-marine sedimentary (mainly chert) and basaltic volcanic rocks, and granitic intrusions (BC Parks Division, 2005; Bevier, 1983; Monger & Journeay, 1994; see Table 2 for coordinates and ecological description of each site).

Biogeographically, both Marriott Basin and Singing Pass are located within the Coast and Mountains Ecoprovince of British Columbia, whereas the remaining sites (Blowdown Pass, Texas Creek, McGillivray Pass, Downton Creek and Cinnabar Basin) are found in the Southern Interior Ecoprovince (see Demarchi (1993) for an overview of British Columbia's ecoregions). As the names suggest, the climate changes dramatically when transitioning between the two Ecoprovinces, moving from a warm, humid coastal climate to a colder, dry interior one. Though Blowdown Pass and Texas Creek are located within the Southern Interior Ecoprovince, they are near the boundary with the Coast and Mountains Ecoprovince, and thus remain strongly influenced by the coastal climate to the west. Records from the nearest weather stations indicate that annual precipitation ranges from 320 mm/yr in Lillooet to 1255 mm/yr in Whistler, with up to 50% falling as snow (Fig. 1) (Environment Canada, 2012; BC Parks Division & TFE Consultants, 1999).

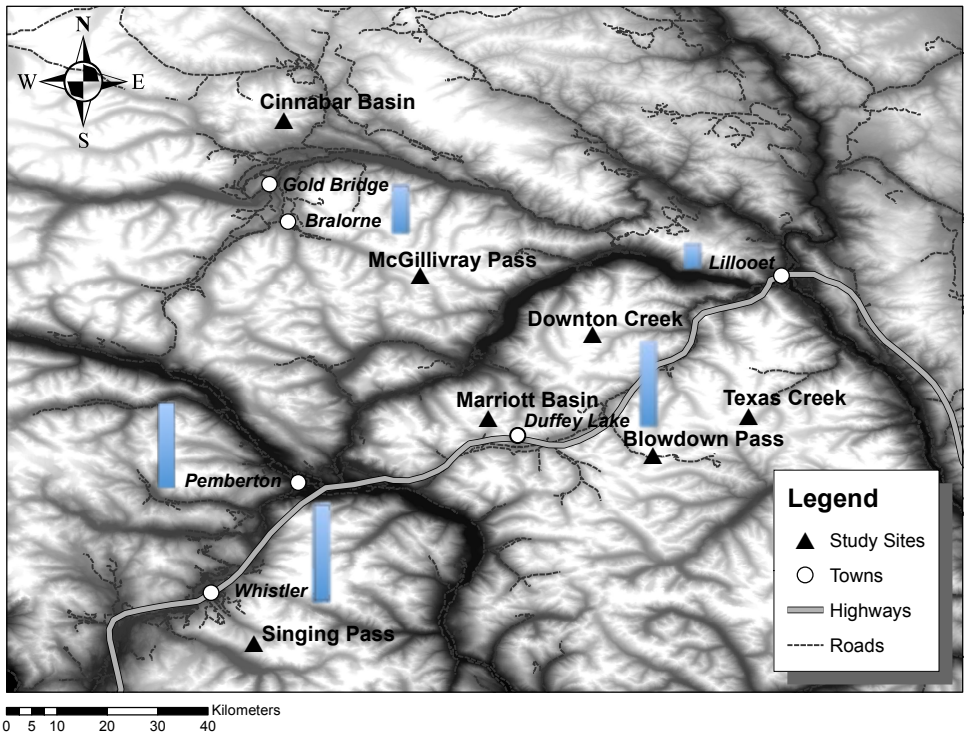


Figure 1: Location of study sites (black triangles) in relation to weather stations (white circles, in italics) in the study region. Average annual precipitation at each weather station is depicted by the relative height of the blue bars. Average annual precipitation and standard deviation for each weather station are as follows: Lillooet: 320 ± 65 mm/yr, N = 24 years; Duffey Lake: 1104 ± 251 mm/yr, N = 15 years; Bralorne: 625 ± 156 mm/yr, N = 28 years; Pemberton: 1089 ± 201 mm/yr, N = 17 years; and Whistler: 1255 ± 200 mm/yr, N = 27 years. Elevations scales from low (black) to high (white).

Along this transition zone, sites were located in south-facing alpine meadows between 1925 m and 2125 m in elevation. The vegetation was dominated by herbaceous forbs such as *Anemone occidentalis*, *Arnica cordifolia*, *Artemisia norvegica*, *Erigeron peregrinus*, *Lupinus arcticus*, *Lupinus nootkatensis*, *Minuartia rubella*, *Potentilla flabellifolia*, *Solidago multiradiata* and *Valeriana sitchensis*; graminoids such as *Bromus sitchensis*, *Carex macrochaeta*, *Carex phaeocephala*, *Carex podocarpa* and *Carex spectabilis*; and/or woody species such as *Phlox diffusa* and *Vaccinium caespitosum*. This habitat type is characteristic of the alpine tundra biogeographic zone, which in this region

occurs at elevations above approximately 1650 m where vegetation is primarily comprised of shrubs, herbs, bryophytes and lichens, with occasional patches of trees in krummolz form (Pojar & Stewart, 1991). At high altitude and on north-facing slopes, the landscape can be largely devoid of vegetation and dominated by rock, ice and snow (Pojar & Stewart, 1991).

Table 2: Physical description and dominant vegetation of study sites. Climate Type refers to the climatic region in which a site is found, 'coastal' being more humid and warm than the dry 'interior' (see Demarchi (1993) for an overview of British Columbia's ecoregions, including the warmer and humid Coast and Mountains Ecoprovince and the colder and drier Southern Interior Ecoprovince). Elevation and slope are averages and species names are described in Table 9, Appendix II. Higher access ratings represent more easily accessed or human disturbed sites, whereas lower ratings indicate more remote or pristine sites (for more details on the development of this rating, see Table 8, Appendix I).

Site	Coordinates	Climate Type	Associated Range	Elevation (m)	Slope (°)	Access Rating	Dominant Species
Texas Creek	50°26'12.067"N 121°59'72.95"W	Coastal - Interior	Coast Mountains	2085	31	13	PHDI, THOC, BRSI
Blowdown Pass	50°21'99.114"N 122°09'95.73"W	Coastal - Interior	Coast Mountains	2132	30	17	PHDI, LUNO, ARNO
Downton Creek	50°35'00.471"N1 22°16'43.64"W	Interior	Coast Mountains	2119	9	15	PHDI, ARNO, VACA
Marriott Basin	50°25'93.186"N 122°27'64.99"W	Coastal	Coast Mountains	2044	39	18	VASI, CAMA, ARCO
McGillivray Pass	50°41'24.214"N 122°34'91.10"W	Coastal - Interior	Coast Mountains	2049	27	15	VASI, CAPO, ARCO
Cinnabar Basin	50°57'81.986"N 122°4949.96"W	Interior	Chilcotin Plateau	2088	26	20	MIRU, SOMU, ARNO
Singing Pass	50°01'84.80"N 122°52'71.54"W	Coastal	Coast Mountains	1950	17	18	CASP, VASI, POFL

2.2.2 Sampling Design

Sites were chosen by examining topographic maps of the region followed up by Google Earth images, and finally through consultation with experts familiar with the area. Sites were further selected based on the accessibility of large (> 500 m wide), relatively uninterrupted stretches of alpine meadow via roads and hiking trails, and were visited

during snow-free conditions. Even with these regulations imposed, the survey was inclusive and covered the majority of accessible and known sizeable south-facing alpine meadows in the region. GPS equipment and detailed topographical maps of the area (Ernst, 2010) were used to locate the sites when in the field.

To sample plant richness and community composition in each alpine meadow, I used Barnett & Stohlgren's (2003) 100 m^2 Intensive Plot (Fig. 2). This plot design is practical and efficient for sampling alpine meadows as its relatively small size limits sampling time per plot and allows for flexible placement in a potentially fragmented landscape, thereby enhancing coverage of broad spatial patterns (Barnett & Stohlgren, 2003). The Intensive Plot contains four 1 m^2 subplots and one 10 m^2 subplot nested within the 100 m^2 plot (Fig. 2). Richness and abundance of vascular species is assessed within the 1 m^2 subplots, whereas only species richness is recorded in the larger 10 m^2 and 100 m^2 plots (Barnett & Stohlgren, 2003). This multi-scale plot design facilitates the recording of rare species that may not be detected in conventional 1 m^2 sampling plots. The 1 m^2 subplot was constructed with 3/4" polyvinyl chloride (PVC) piping and the 10 m^2 and 100 m^2 plots were laid out in the field using fluorescent twine and metal tent pegs (Appendix 1, Plate 8).

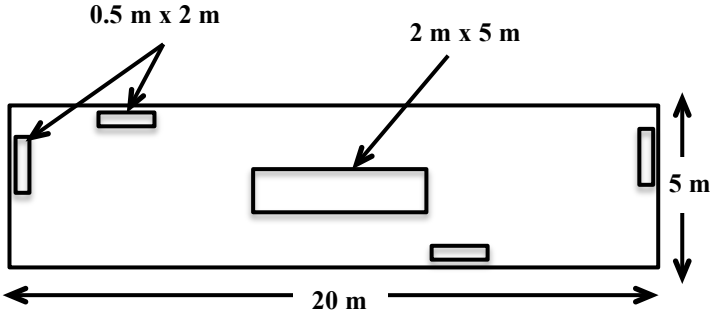


Figure 2: The Intensive Plot designed by Barnett & Stohlgren (2003) uses a nested design that allows diversity to be sampled at multiple scales (1 m^2, 10 m^2 & 100 m^2) within each plot. Species richness is recorded at all scales, while species cover is only assessed in the 1 m^2 subplots.

To estimate the sample sizes required for this study, power analyses were conducted using G*Power© software (Faul *et al.*, 2006, 2009). As a pilot study was not feasible, I used data collected by Adler & Levine (2007) in US grasslands, Theodose & Bowman (unpublished data) at Niwot Ridge, Colorado, and Douglas & Bliss (1977) in the North Cascade Range (see results summary in Table 3). Although the Adler & Levine (2007) study was not conducted in alpine meadows, it was one of only a few studies measuring the relationship between climate and plant diversity on a smaller regional scale. Most studies explicitly studying this association function on large regional or global scales where changes in precipitation or evapotranspiration are represented primarily by large changes in latitude (Francis & Currie, 2003; Hawkins *et al.*, 2003). In this sense, this dataset (Adler & Levine, 2007) can provide a modest estimate for the variation in plant species richness expected over the coastal-interior transition zone of southwestern British Columbia, excluding the effects of topography.

Table 3: Comparison of plot size, average species richness, between-group standard deviation and effect size (f) of studies conducted in alpine meadow and grassland communities. The sample size necessary to maintain a power (1- β) of 0.95 is indicated on the far right.

Study	Ecosystem Type	Location	Plot Size (Samples; Sites)	Richness (StDev)	Effect Size	Sample Size
Douglas & Bliss (1977)	Alpine Meadow	North Cascade Range (OR, WA, BC)	0.1 m^2 (1000; 10)	29.3 (8.2)	0.938	40
Theodose & Bowman (unpublished data)	Alpine Meadow	Niwot Ridge Saddle, CO	4 m^2 (5; 2)	17.9 (5.7)	0.707	20
Adler & Levine (2007)	Grassland	Precipitation gradient from CO to KS	1 m^2 (250; 6)	11.9 (2.2)	0.999	30

Results from these power analyses indicated that a minimum total sample size between 40 0.1 m^2 and 20 4 m^2 plots is necessary to achieve a power (1-probability of Type II error [β]) greater than 0.95 and alpha of 0.05 (probability of Type I error [α]) in this ecosystem type, meaning that these sample sizes would ensure a 95 % likelihood of accurately detecting a difference in diversity between sites. Based on these values, I aimed for a sample size of 49 plots divided equally among 7 sites, totaling 4,900 m^2 of vegetation surveyed using the 100 m^2 Intensive Plots. In the end, I was forced to reduce the sample size to 48 plots, because the meadow at Texas Creek was only large enough to accommodate 6 plots. I chose to sample a greater area than statistically suggested by the power analyses (Table 3) because it was logistically possible and it improved the likelihood of detecting rare species responsible for important differences in diversity between sites. Due to the multi-scale plots design, species abundance data was collected at between 24 and 28 1 m^2 plots per site (for a total of 192 m^2), whereas species richness data was taken from between 6 and 7 100 m^2 plots per site (for a total of 4,900 m^2). Though there was a discrepancy in the total area sampled for species abundances and species richness, very few species were detected in the larger 10 m^2 and 100 m^2 plots that

were not found in the 1 m^2 plots in the same Intensive Plot. Additionally, these species were typically rare and therefore would not have contributed greatly to our abundance datasets.

To maintain consistency between sites, the 6-7 Intensive Plots were arranged along a belt transect at mid-slope (halfway between the observed treeline and top edge of meadow or summit) on a south-facing alpine meadow following the topographic isocline (like in Li *et al*., 2011). Plots were placed approximately 50-100 m apart, depending on the width of the meadow being sampled, and this same distance was maintained between the plots and meadow edges to avoid transition zones between ecosystem types. Sampling south-facing meadows at mid-slope controlled for differences in community composition due solely to aspect and elevation between plots at each site, as both of these parameters are known to have significant effects on plant diversity (Bennie *et al*., 2008; Geiger, 1965; Holland & Steyn, 1975; Kampmann *et al*., 2008; Marini *et al*., 2007; Sebastià, 2004; Sherman *et al*., 2008).

2.2.3 Explanatory Variables

The 15 environmental variables measured at each plot were divided into 3 categories pertaining to climate, topography and soil (Table 4).

Topography variables were measured at each plot, except for Accessibility (Acc), which was the same for all plots at a site as it is measured at too coarse a scale to pick up differences between plots. *Accessibility* is a value created specifically for this study, where each site was ranked using an index reflecting the approximate level of anthropogenic use. There were 7 characteristics that contributed to the final "access" value for each site based on road and trail quality, distance from city hubs and highways,

and the presence of domestic grazing, among others (see Table 8, Appendix I). Lower numbers reflect more remote, pristine or inaccessible meadows, and higher numbers easy to access or more human-disturbed meadows. Finally, though all sites surveyed were on south-facing slopes, aspect was recorded to capture differences in plant community composition that may be caused by small changes in aspect creating unique microhabitats within the larger meadow. Aspect was measured as the 360° compass direction faced by the slope on which the plot was placed, and then combined with slope to generate a "sun index" reflecting the amount of solar radiation received by the plot (Gibson *et al*., 2004; Sherman *et al*., 2008). The sun index is comprised of both an east-west (SI.E) and south-north (SI.S) component ranging from -1.0 to 1.0: a value of 1.0 represents a steep slope facing due east or south and -1.0 a steep slope facing due west or north, respectively.

Table 4: Explanatory variables pertaining to climate, topography and soil measured at each plot. Variables in square brackets were removed prior to analysis due to strong collinearity with other variables (see section 2.2.5).

Category	Variable	Code	Units	Method
Climate	[Mean Annual Temperature]	[MAT]	° C	ClimateWNA*
	Mean Summer Temperature (May-September)	MST	° C	ClimateWNA*
	[Mean Annual Precipitation]	[MAP]	mm	ClimateWNA*
	Mean Summer Precipitation (May-September)	MSP	mm	ClimateWNA*
Topography	Slope	Slo	°	Clinometer
	Elevation	Elev	m	Hand-held GPS
	Sun Index East	SI.E	-	360° compass & clinometer Formula: sin(aspect) x sin(slope)
	Sun Index South	SI.S	-	360° compass & clinometer Formula: cos(aspect) x sin(slope)
	Accessibility	Acc	-	Sum from Table 8, Appendix 1
Soil**	pH	pH	pH	1:1 H_2O (USDA, 2011)
	Moisture Content	SMo	%	Field-moisture weight: oven-dry weight
	[Organic Matter Content]	[LOI]	%	Loss-on-ignition (Cambardella *et al.*, 2001)
	Available Phosphorus	P	mg/Kg	Bray 1 (Bray & Kurtz, 1945)

Total Nitrogen	N	%	SSL combination method (USDA, 2004)
C:N ratio (index of rate of N mineralization)	C.N	-	Total carbon: total nitrogen (USDA, 2004)

* See Wang *et al*., 2012 and Mbogga *et al*., 2009 for more detail on the Climate WNA modeling. Software is available online at: http://www.genetics.forestry.ubc.ca/cfcg/ClimateWNA/ClimateWNA.html#references.
**All soil analyses were conducted by the British Columbia Ministry of Environment Knowledge Management Branch Laboratory (Environmental Sustainability and Strategic Policy Division) in Victoria, BC.

Due to the lack of weather stations at any of the study sites (Fig. 2), precipitation and temperature variables were estimated using ClimateWNA, an online software package that generates scale-free climate data by combining interpolations of weather station data with elevation adjustments derived from a digital elevation model, along with expert meteorological knowledge (for more information, see Mbogga *et al.,* 2009 and Wang *et al.,* 2012). Since small increases in elevation can bring about substantial climatic changes in mountainous terrain (Beniston, 2003; IPCC, 1996; Whiteman, 2000), it was critical that I use the ClimateWNA interpolations as estimates of site climate parameters rather than climatic data retrieved from weather stations nearer to sea level. Here, I assume that the climate variables at a site are the same for all plots since the meadow landscapes surveyed were relatively homogeneous and likely experience very similar atmospheric climate conditions at any one time. To obtain climate parameter estimates for each site, I used the mean of the values obtained for each plot in that site. To avoid significant error in the values derived from the ClimateWNA model, climate estimates in more remote locations have been validated with weather station data (Wang *et al*., 2012). My sites were in comparable topographic locations and similarly distant from the closest weather stations, and therefore any error present should be relatively constant. Somewhat coarse atmospheric climate estimates are sufficient for the purpose of our study since the differences between sites are representative of the true climatic differences spanning the

study region based on comparisons with weather station data (Environment Canada, 2012).

Soil samples were collected with a trowel from the four corners and center of each Intensive Plot and pooled into a composite sample weighing approximately 400 g (method approved by Dr. Wanli Wu, Ecosystem Scientist with the Parks Canada Agency, pers. comm.). They were retrieved from beneath the living biomass at a depth between 5 and 10 cm and weighed in the field using a Pesola scale. Following collection, samples were kept in double Ziploc© freezer bags in a dark cooler and shipped within 2 days to the British Columbia Ministry of Environment Knowledge Management Branch Laboratory in Victoria, BC, to be analyzed for pH, soil moisture (SMO), total nitrogen (N), available phosphorus (P), and organic matter content (LOI) (see Table 4 for methods).

2.2.4 Response Variables

Response variables assessed in each Intensive Plot were overall species richness and abundance, and life form (forbs, graminoids and woody species) richness and abundance. Only vascular plants were identified and estimated for abundance – the presence of lichens, mosses, rocks, litter and bare ground was not recorded. Forb, graminoid and woody species life forms were distinguished using the USDA Plants (USDA, 2012) descriptions, a widely regarded and broadly utilized database for classifying plant species. The life form "woody species" includes both shrubs and subshrubs for the purpose of this study.

Species abundance was measured using percent cover to the nearest 1%, a respected method for estimating species abundance in single-canopy communities

(Bråkenhielm & Qinghong, 1995; Vanha-Majamaa *et al*., 2000). Percent cover is especially useful in providing an index reflecting the abundance of species whose individuals are too densely packed or abundant for stems to be efficiently counted, as is the case in alpine meadow systems. Species that could not be identified in the field were pressed and given a unique identification code until they could be identified in the lab. There was a small number of cases where immature or desiccated specimens could not be keyed to species – since this happened only 9 times out of 1213 observations, they were removed from the dataset before conducting diversity analyses. A rough rule of thumb states that when sampling site-to-site variability in species diversity or composition, capturing approximately 90% of species present is sufficient to maintain maximum statistical power in detecting the true differences in diversity between sites (Vellend *et al*., 2008). Therefore, ignoring a small fraction of the species present may not be detrimental to the accuracy or credibility of diversity analyses conducted on datasets that include the large majority of species that were present in the community (Vellend *et al*., 2008).

2.2.5 Data Analysis

All analyses were performed using the statistical software package R 2.12.1 (R Development Core Team, 2010). To prepare the data for analysis, all soil variables except pH and the C:N ratio were log-transformed to improve linearity and the entire explanatory dataset was standardized (converted to z-scores) to remove dimensional heterogeneity. Unlike the explanatory dataset, the response data were not standardized prior to analysis unless explicitly stated, because this would imply similar roles for abundant and rare species, an incorrect assumption in ecological systems (Borcard *et al*.,

2011). Using the response data, eight response matrices were created: a presence-absence (0=absent, 1=present; reflective of species richness) and abundance (reflective of community similarity/β–diversity) matrix and for all species, forbs, graminoids and woody species (see Tables 11 and 12 in Appendix IV, respectively). The presence-absence matrices were constructed using data obtained from 48 100 m^2 plots and the abundance matrices from 192 1 m^2 plots distributed throughout 7 sites in southwestern British Columbia.

These matrices were transformed using a Hellinger transformation, where abundance and presence/absence values are divided by the plot's total abundance or total number of species, respectively, and then square-root transformed (Borcard *et al*., 2011). This method is an asymmetric measure of association appropriate for species composition data and richness data with many zeros and reduces the importance of very high abundance values (Borcard *et al*., 2011; Legendre, 2005; Legendre & Gallagher, 2001). The presence/absence data tables were transformed to reduce the skewedness of the dataset resulting from there being few common species and many rare species, as is the case in most ecological systems (Borcard *et al*., 2011).

Kendall's W coefficient of concordance was used to detect positive and significant species associations over the 48 plots that could suggest differing community types (Legendre, 2005). This method uses k-means partitioning to detect species associations irrespective of any known environmental differences between sites, and then forms the most encompassing assemblages with the smallest number of groups possible (Borcard *et al*., 2011; Legendre, 2010). K-means partitioning identifies high-density regions in the Hellinger-transformed and standardized abundance data (all species),

thereby detecting the "best" number of groups. Kendall's W test follows up by extracting the significant species assemblages that compose these groups (α=0.05) from the unstandardized Hellinger-transformed response data.

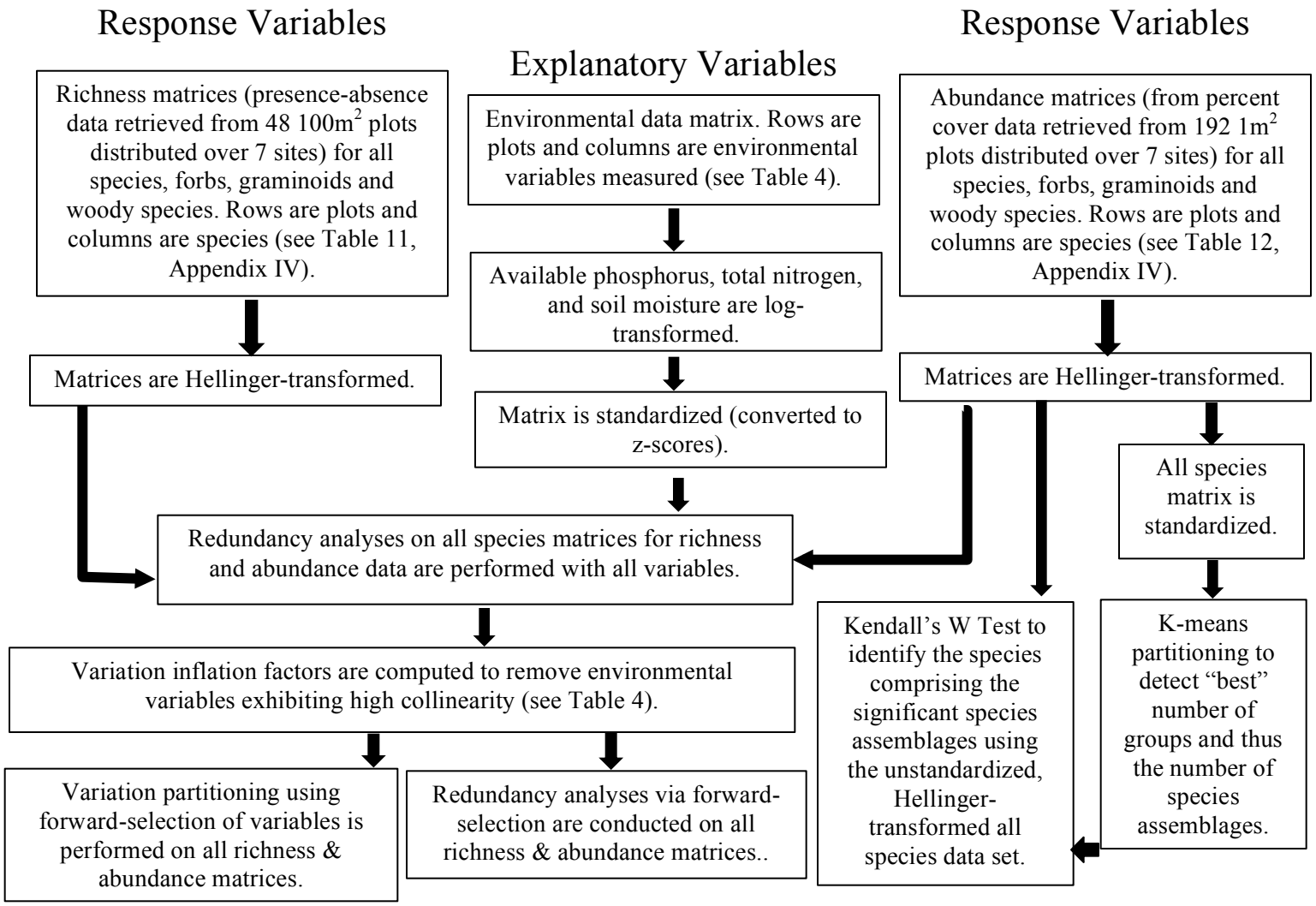
Redundancy analyses (RDAs) were carried out on all response matrices and the explanatory matrix to identify the combination of explanatory variables that play a significant role as determinants of alpine plant diversity and richness in the study region. RDA combines both multiple linear regression and principal component analysis (PCA) and achieves a visualization of both the response and explanatory datasets in a constrained ordination space (Borcard *et al*., 2011). To detect and remove any environmental variables exhibiting strong collinearity, variance inflation factors (VIFs) were computed prior to conducting the RDAs (Borcard *et al*., 2011). The variables excluded from the models are presented in Table 4 in square parentheses. Further, for each model, the number of explanatory variables was reduced by forward selection to include only variables contributing significantly to the amount of variance explained (Borcard *et al*., 2011). The resulting adjusted R^2 value describes the amount of variation explained by the explanatory variables included in the model (Borcard *et al*., 2011; Peres-Neto *et al*., 2006). Finally, the significance (α=0.05) of all RDA results and canonical axes was assessed using an ANOVA permutation test.

Variation partitioning was used to quantify the amount of variance in the abundance dataset explained independently and jointly by soil, topography and climate parameters (Legendre, 2008; Peres-Neto *et al*., 2006). To do so, the standardized explanatory data were divided into three subsets pertaining to soil, topography, and climate variables. Then, for each response matrix, explanatory subsets were subjected to

redundancy analyses and forward-selected to identify the most parsimonious models. Variation partitioning was applied to the parsimonious models to yield adjusted R^2 values for soil, topography and climate subsets, and all fractions were tested for significance using an ANOVA permutation test. A flowchart summarizing the data analysis process can be viewed in Figure 3.

Last, the Principle Coordinates of Neighbour Matrices (PCNM) method (Dray *et al.*, 2006) was applied to test for spatial structure in the response data (i.e., spatial dependence of plots) using a matrix of geographical coordinates and distance matrices generated from the detrended and Hellinger-transformed abundance dataset. This analysis involves an RDA that plots the response data with respect to spatially-derived canonical axes and uses Moran's *I* to identify spatial correlation at a series of distance classes (Borcard *et al.*, 2011). The results were tested for significance (α=0.05) using an ANOVA permutation test.

Figure 3: Flowchart describing the data analysis procedure.



2.3 Results

2.3.1 Species Richness

The 48 alpine meadow plots surveyed were located in the following sites: Blowdown Creek (BD - plots BD1 to BD7), Cinnabar Basin (CB - CB1 to CB7), Downton Creek (DT - DT1 to DT7), Marriott Basin (MB - MB1 to MB7), McGillivray Pass (MC - MC1 to MC7), Singing Pass (SP - SP1 to SP7) and Texas Creek (TC - TC1 to TC6) (Fig. 1). Overall, 101 vascular plant species were recorded in the study region: 65 forbs, 24 graminoids and 12 woody species (for the full list of species, see Appendix II, Table 9). A principal coordinates of neighbour matrices (PCNM) analysis was carried out to detect any positive spatial autocorrelation in the community composition between plots, but results were not significant ($p=0.0783$), implying that plots are stochastically independent from one another (Borcard & Legendre, 2002).

The geographic location, species richness and environmental parameters for each plot are listed in Table 10 (Appendix III). Species richness ranged from a low of 15 species in plots SP4 and SP7 to a high of 37 in plot TC5, for an average richness of 24.8 species per 100 m^2. In decreasing order, total species richness by site was 54 (TC), 53 (CB), 50 (MB), 41 (DT), 37 (SP), 36 (BD) and 29 (MC) (Fig. 4).

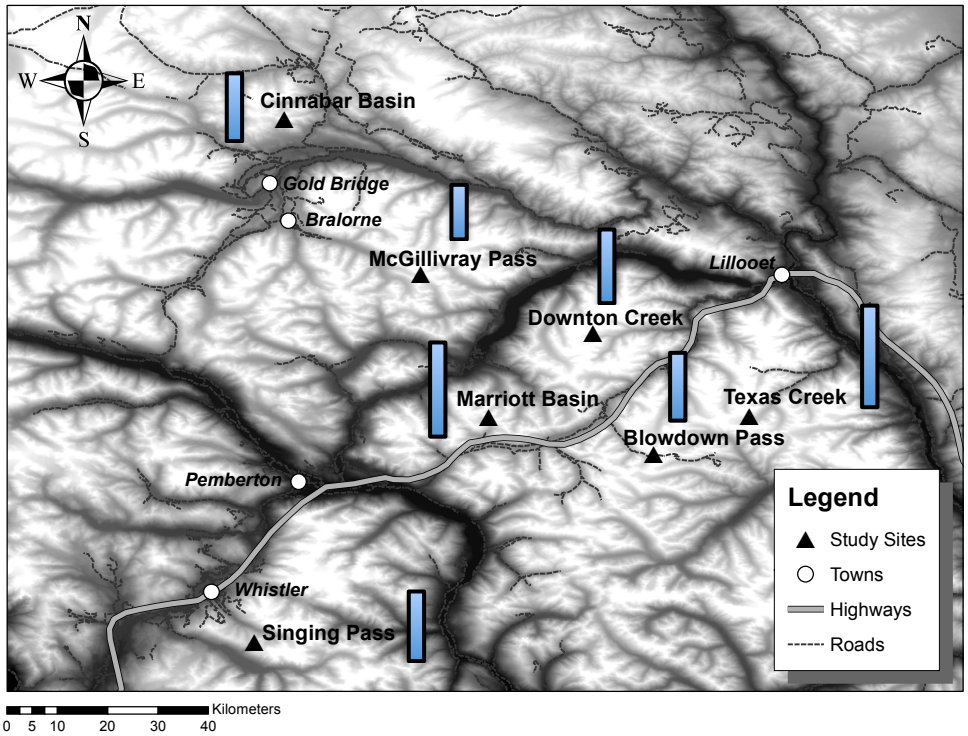


Figure 4: Relative species richness at each site depicted by the relative length of the blue bars (Texas Creek (TC) = 54, Cinnabar Basin (CB) = 53, Marriott Basin (MB) = 50, Downton Creek (DT) = 41, Singing Pass (SP) = 37, Blowdown Pass (BD) = 36 and McGillivray Pass (MC) = 29).

2.3.2 Species Assemblages

K-means partitioning and a Kendall W Test of concordance were used to detect positive and significant species assemblages among the 48 plots. Two groups representing distinct community types were identified. The first group is comprised of *Achillea millefolium*, *Agoseris glauca*, *Arnica diversifolia*, *Bromus sitchensis*, *Carex phaeocephala*, *Eriogonum umbellatum*, *Lupinus arcticus*, *Minuartia rubella*, *Poa abbreviata*, *Potentilla diversifolia*, *Senecio integerrimus*, *Silene douglasii*, *Solidago multiradiata*, *Thalictrum occidentale* and *Trisetum spicatum*; and the second group of *Arnica cordifolia*, *Carex macrochaeta*, *Claytonia lanceolata*, *Erigeron peregrinus*, *Erythronium grandiflorum*, *Potentilla flabellifolia* and *Valeriana sitchensis*. The first

assemblage is strongly associated (>70% of species from the assemblage present in the plot) with plots from Cinnabar Basin (CB2 to CB7) and Texas Creek (TCI & TC3 to TC5); and the second species assemblage with all plots from Marriott Basin and McGillivray Pass, as well as with plots from Blowdown Creek (BD2 to BD5 & BD7), Downton Creek (DT1), Singing Pass (SP5 to SP7) and Texas Creek (TC5) (see Fig. 1 for area map).

2.3.3 Redundancy Analyses (RDA)

2.3.3.1 All Species

Table 5 shows the RDA results for all parsimonious models. For all species, explanatory models predicted 58% and 47% of the variation in β-diversity and species richness among plots, respectively. The identity and strength of determinants found to be significant in both models were similar in terms of climate and topography, but differed in the variables pertaining to soil. Specifically, the β-diversity model incorporated soil moisture (SMo), the C:N ratio (C.N), total nitrogen (N) and available phosphorus (P); whereas the richness model only included soil moisture, available phosphorus and soil pH. Generally, the variables in the β-diversity model each explained slightly more variation in the response data than those in the richness model, with the exception of mean summer temperature (MST), slope (Slo) and available phosphorus. In both models, elevation (Elev), soil moisture, mean summer temperature (MST) and slope were revealed as the most important determinants of diversity among plots, with greater diversity at higher elevations, steeper slopes and drier sites. To ensure that soil moisture was not correlated to the date of collection following snowmelt, a linear regression and t-test were conducted, but results were not significant ($p=0.2163$). This result confirms that

I was able to control for the impact of snowmelt on soil moisture by sampling each site at approximately the same time following snowmelt.

The response of the 20 most abundant (β-diversity) and frequent (richness) species to the significant explanatory variables and their distribution among plots is depicted in a pair of RDA triplots (Figure 5a).

2.3.3.2 Life Forms

Life forms were affected in different ways by the environmental variables measured (Table 5). Most obviously, it is within the life forms that the discrepancy between the β-diversity and richness models becomes most apparent. 8 determining factors dominated by elevation and soil moisture came together to explain 54% and 47% of forb β-diversity and richness, respectively, with mean summer precipitation and pH in the richness model replacing total nitrogen and the C:N ratio in the β-diversity model as significant determinants of diversity. 53% and 50% of graminoid β-diversity and richness are each explained by 7 significant explanatory variables that primarily differ from the models describing the other life forms by the increased importance of mean summer precipitation. The richness model for graminoids can be distinguished from the β-diversity model by a drop in the significance of soil moisture and the replacement of phosphorus by pH as an explanatory variable. Finally, the parsimonious models derived for woody species β-diversity and richness had less explanatory power than for other life forms, explaining only 53% and 34% of the variation with 9 and 6 variables, respectively. The model for woody species richness is strongly influenced by accessibility, elevation and pH, in contrast to the β-diversity model, which is heavily dominated by the mean summer temperature (18 %). The richness model for woody species is the only one to

include the south-north sun index (SI.S) as a significant explanatory factor, as well as the only model to exclude slope. The β-diversity model for woody species is also unique due to the presence of the east-west sun index. Within the climate category, mean summer temperature tended to hold a higher level of importance as a determinant of diversity for all species and life forms, with the exception of the model for woody species richness, where mean summer precipitation dominated and mean summer temperature was not found to be significant at all. The RDA triplots depicting the species in each life form and the plots as they relate to the significant explanatory variables are displayed in Figures 5b-d.

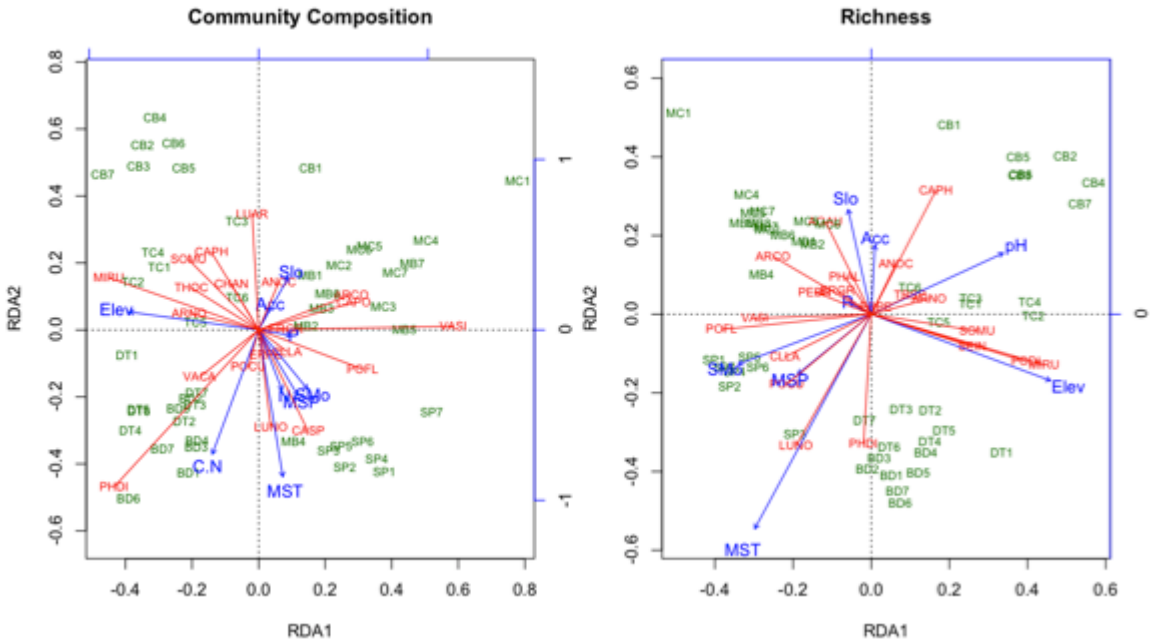
On a side note, to delve deeper into how forbs, the dominant life form in alpine meadows, are influenced by their abiotic environment, I performed an RDA on only the forb species found at six or more of my sites. This way, I could assess more carefully how their abundances were influenced by soil, topography and atmospheric climate (Fig. 6). Results from this analysis show that the importance of elevation and soil moisture remain paramount, explaining 20% and 10% of the variation in species abundance, respectively. Total nitrogen came in third, increasing the amount of variation explained by the model by 6%, followed by access (5%), slope (3%), the C:N ratio (3%), mean summer temperature (3%), and available phosphorus (2%). Mean summer precipitation was not selected by the model as a significant variable in explaining the variance in the abundance of the most common forbs in British Columbia (Fig. 6).

Table 5: Results from the forward selection of environmental variables for the RDA analyses on species composition (β-diversity) and richness of all species, forbs, graminoids and woody species in alpine meadows. The contribution of all significant variables to the total percentage of variance explained by each model is shown (adjusted R^2), along with its significance ($p<0.05$), and the direction of any significant linear trends (+ = positive; - = negative).

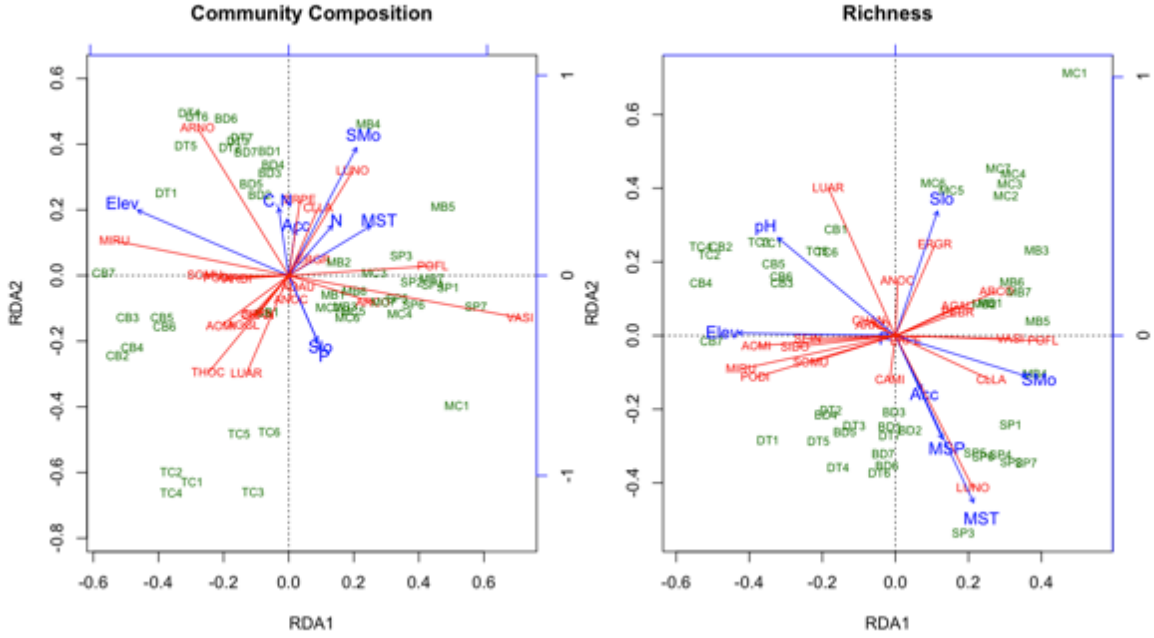
Variables[a]	All Species		Forbs		Graminoids		Woody Species	
	β-diversity	**Richness**	**β-diversity**	**Richness**	**β-diversity**	**Richness**	**β-diversity**	**Richness**
Elev	0.137*** (+)	0.082*** (+)	0.176*** (+)	0.106*** (+)	0.075*** (+)	0.071***	0.094***	0.074***
Acc	0.064***	0.062***	0.050***	0.057***	0.079***	0.061***	0.022*	0.083***
Slo	0.075*** (+)	0.084*** (+)	0.060*** (+)	0.074*** (+)	0.101***	0.122***	0.087***	-
SI.E	-	-	-	-	-	-	0.017*	-
SI.S	-	-	-	-	-	-	-	0.020*
SMo	0.092***	0.089*** (-)	0.105*** (-)	0.099*** (-)	0.085***	0.035*** (-)	0.064***	0.019*
C.N	0.021***	-	0.021**	-	-	-	0.031** (+)	-
N	0.018***	-	0.039*** (-)	-	-	-	0.019* (+)	-
P	0.023**	0.013***	0.014*	0.017***	0.023**	-	0.016*	-
pH	-	0.015*** (+)	-	0.018** (+)	-	0.011*	-	0.074***
MSP	0.046*** (-)	0.048***	-	0.041***	0.088***	0.092***	-	0.071***
MST	0.101*** (-)	0.076*** (-)	0.076*** (-)	0.058*** (-)	0.076*** (-)	0.103***	0.182***	-
Model	0.577***	0.468***	0.541***	0.469***	0.526***	0.495***	0.532***	0.342***

[a] Variable names are according to Table 4.

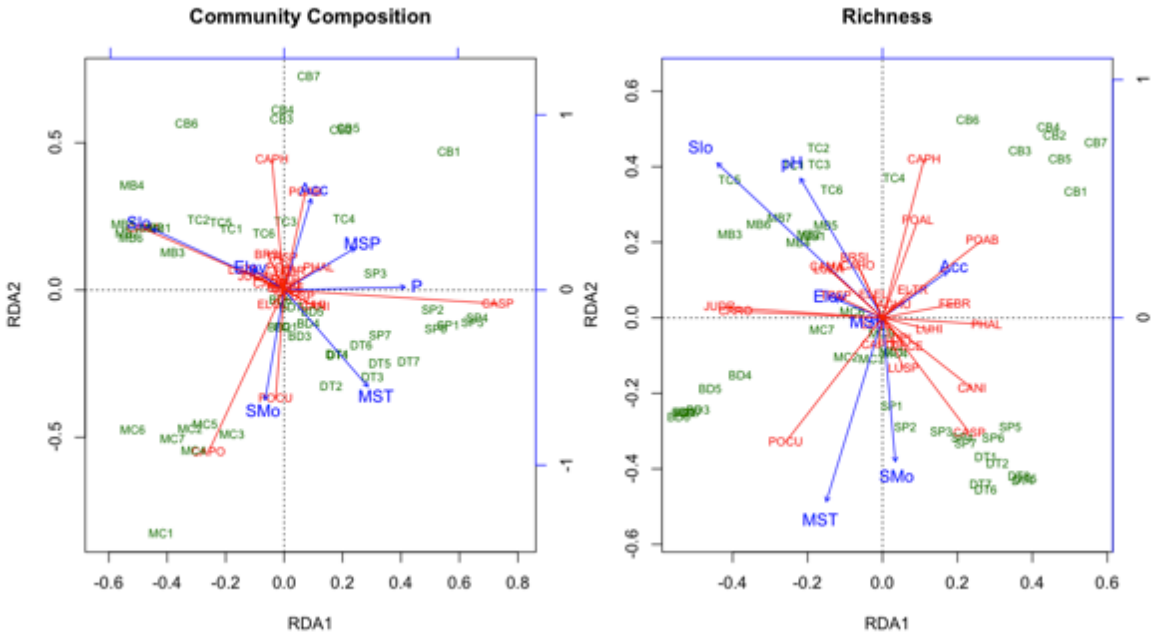
*** $P < 0.001$, ** $P = 0.001$ - 0.01, * $P = 0.01$ - 0.05 and "–" $P > 0.05$.



(a) All Species



(b) Forbs



(c) Graminoids

(d) Woody Species

Figure 5: Ordination plots of community composition and richness of all species (a) and functional groups (b-d), respectively, and environmental variables and plots, along the first 2 RDA axes (scaled in standard deviation units) constrained with significant explanatory variables obtained via forward selection. Arrow length reflects the relative explanatory power of environmental variables (blue) and the relative abundance (composition plots) or frequency (richness plots) of each vascular plant species (red) in

48 plots distributed over 7 alpine meadows in southwestern British Columbia. Only the 20 most common species are shown in plots (a) and (b). The first two axes of the RDA triplots explain 20% and 14%, 22% and 16%, 22% and 16%, and 20% and 14% of the variation in all species, forb, graminoids and woody species β-diversity and richness, respectively. See Table 4 and Table 9 (Appendix II) for a description of the abbreviations of environmental variables and species names, respectively. Abbreviations of site names: Blowdown Creek (BD1-BD7), Cinnabar Basin (CB1-CB7), Downton Creek (DT1-DT7), Marriott Basin (MB1-MB7), McGillivray Pass (MC1-MC7), Singing Pass (SP1-SP7) and Texas Creek (TC1-TC6).

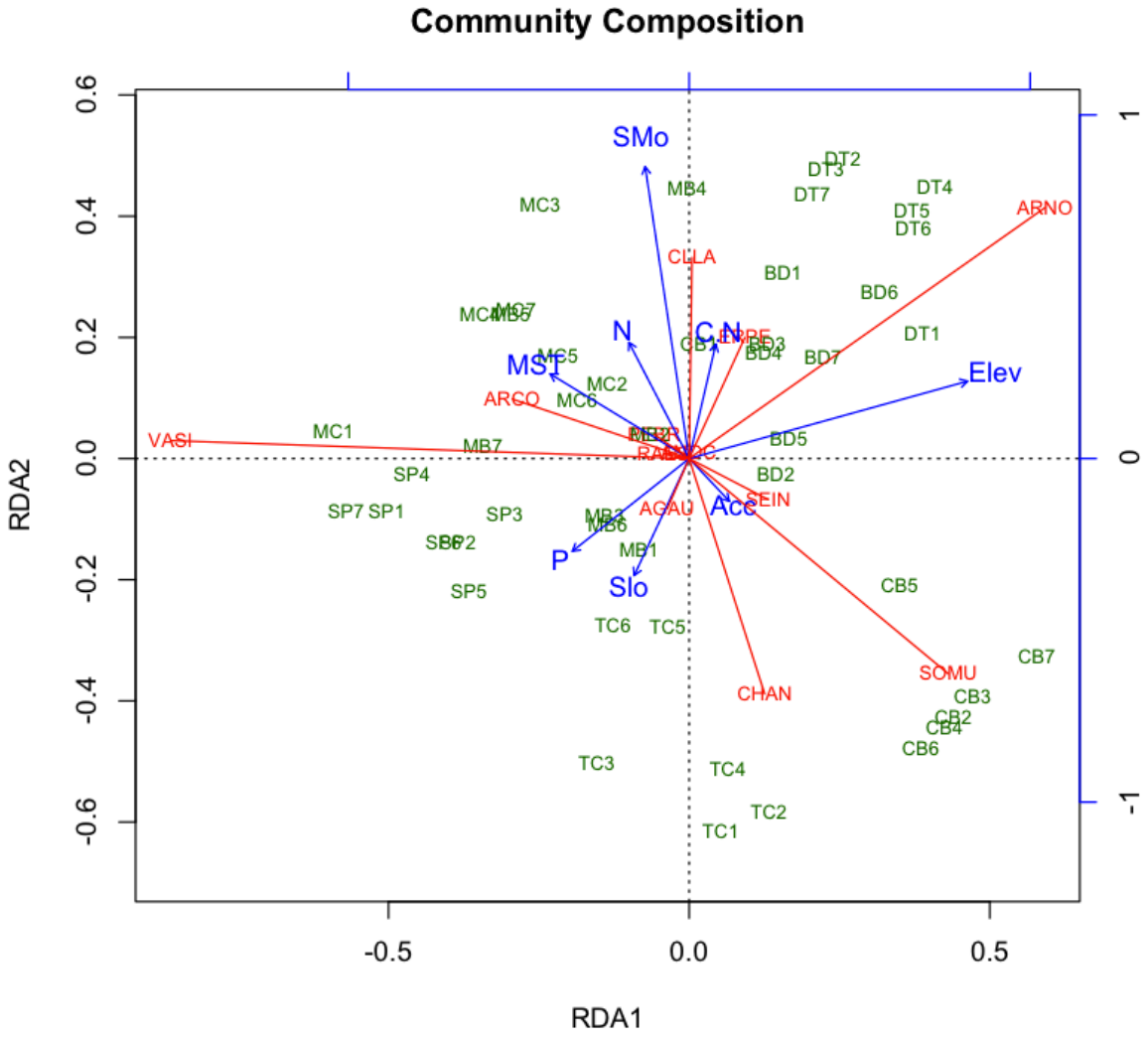


Figure 6: Ordination plot of forb community composition for the 12 species found in the majority of sites (6 or 7) in southwestern British Columbia. The first two axes of the RDA triplot represent 20% of the variation in forb abundance. See Table 4 and Table 9 (Appendix II) for a description of the abbreviations of environmental variables and species names, respectively. Abbreviations of site names: Blowdown Creek (BD1-BD7),

Cinnabar Basin (CB1-CB7), Downton Creek (DT1-DT7), Marriott Basin (MB1-MB7), McGillivray Pass (MC1-MC7), Singing Pass (SP1-SP7) and Texas Creek (TC1-TC6).

2.3.4 Variation Partitioning

Results from the variation partitioning were relatively consistent across all species and life forms (Fig. 7; Table 6). For overall β-diversity and richness, topography and soil were the most significant determinants, explaining almost 18% and 11% of the variation in β-diversity and richness between plots, respectively, whereas climate played a smaller part, with an independent contribution of 8%. The variation explained by the intersection of the amount of variation accounted for by each explanatory subset was highest for both the joint effects of soil and climate, at 13.4% and 10.6%, and the joint effects of soil and topography, at 13.2% and 11%, for the β-diversity and richness models, respectively.

For independent contributions among life forms, results for forbs β-diversity and richness, and for woody species richness and graminoid β-diversity were fairly similar to results for all species. In contrast, the explanatory power of soil increased to 13.3% and that of topography decreased to 8.2% as predictors of woody species β-diversity. Additionally, the importance of soil fell to 4.3% as a predictor of graminoid richness. The independent importance of climate remained steady for all life forms in all models. There were also some differences among life form β-diversity in the amount of variance explained by the intersections of variance between subsets: the most important joint effects were that of topographically structured soil variables for forbs (13.6%), and climatically structured soil for graminoids (12.1%) and woody species (9.5%) (Fig. 7). Apart from a drop in significance in each subset, the same patterns were visible in the richness models for forbs and woody species, but topographically structured soil overtook climatically structured soil as the most important intersection for graminoid species.

By listing each explanatory variable deemed significant within the climate, topography and soil categories, Table 7 further explores the variation partitioning results for all species and life forms. The variables Acc, Slo, SMo, C.N, MSP and MST were retained via forward selection in all models. In contrast, available phosphorus (P) was only selected 3 out of 8 times, exclusively in β-diversity models, and the sun indices did not contribute significantly to any of the models.

Table 6: Variation partitioning results (adjusted R^2 values (R^2_a)) for the β-diversity and richness of all species and three plant functional groups. Fractions are as follows: [C] = variation explained by climate independent of soil and topography; [T] = variation explained by topography independent of climate and soil; [S] = variation explained by soil independent of climate and topography; [CΠT] = variation explained by the topographically structured climate variables; [SΠC] = variation explained by climatically structured soil variables; [TΠS] = variance explained by topographically structured soil variables; [CΠTΠS] = variation explained by the intersection of the amounts of variation explained by the three explanatory models; [M] = total amount of variation explained by the model; and [R] = residual variation. Fractions [CΠT], [SΠC], [TΠS] and [CΠTΠS] represent the intersection, not the interaction, of the amount of variation explained by each explanatory model involved, and cannot be tested for significance (Borcard *et al*., 2011).

All Species	**[C]**	**[T]**	**[S]**	**[CΠT]**	**[SΠC]**	**[TΠS]**	**[CΠTΠS]**	**[M]**	**[R]**
β-diversity	0.083***	0.175***	0.108***	0.051	0.135	0.132	-0.105[a]	0.594***	0.406
Richness	0.082***	0.166***	0.070***	0.025	0.106	0.110	-0.096[a]	0.464***	0.536
Forbs									
β-diversity	0.082***	0.179***	0.089***	0.078	0.115	0.136	-0.135[a]	0.544***	0.456
Richness	0.075***	0.155***	0.078***	0.040	0.107	0.119	-0.113[a]	0.461***	0.539
Graminoids									
β-diversity	0.085***	0.168***	0.097***	0.048	0.121	0.096	-0.074[a]	0.540***	0.460
Richness	0.099***	0.190***	0.043***	0.016	0.108	0.116	-0.080[a]	0.492***	0.508
Woody Species									
β-diversity	0.078***	0.082***	0.133***	0.001	0.095	-0.003[a]	0.054	0.439***	0.561
Richness	0.085***	0.165***	0.049**	-0.038[a]	0.056	0.018	0.019	0.355***	0.645

[a] A negative R^2 can result from suppressor variables or strongly correlated predictors (see Peres-Neto *et a*l., 2006 for more details).

*** $P < 0.001$, ** P =0.001 - 0.01, * P 0.01 - 0.05 and not significant: ns= $P > 0.05$.

Figure 7: Visual representation of Table 6: independent (solid colors) and joint (patterns) contributions of considered explanatory subsets for β-diversity derived via variation partitioning for 48 alpine meadow plots in southwestern British Columbia. The very top bar section represents the joint contribution of soil and climate variables.

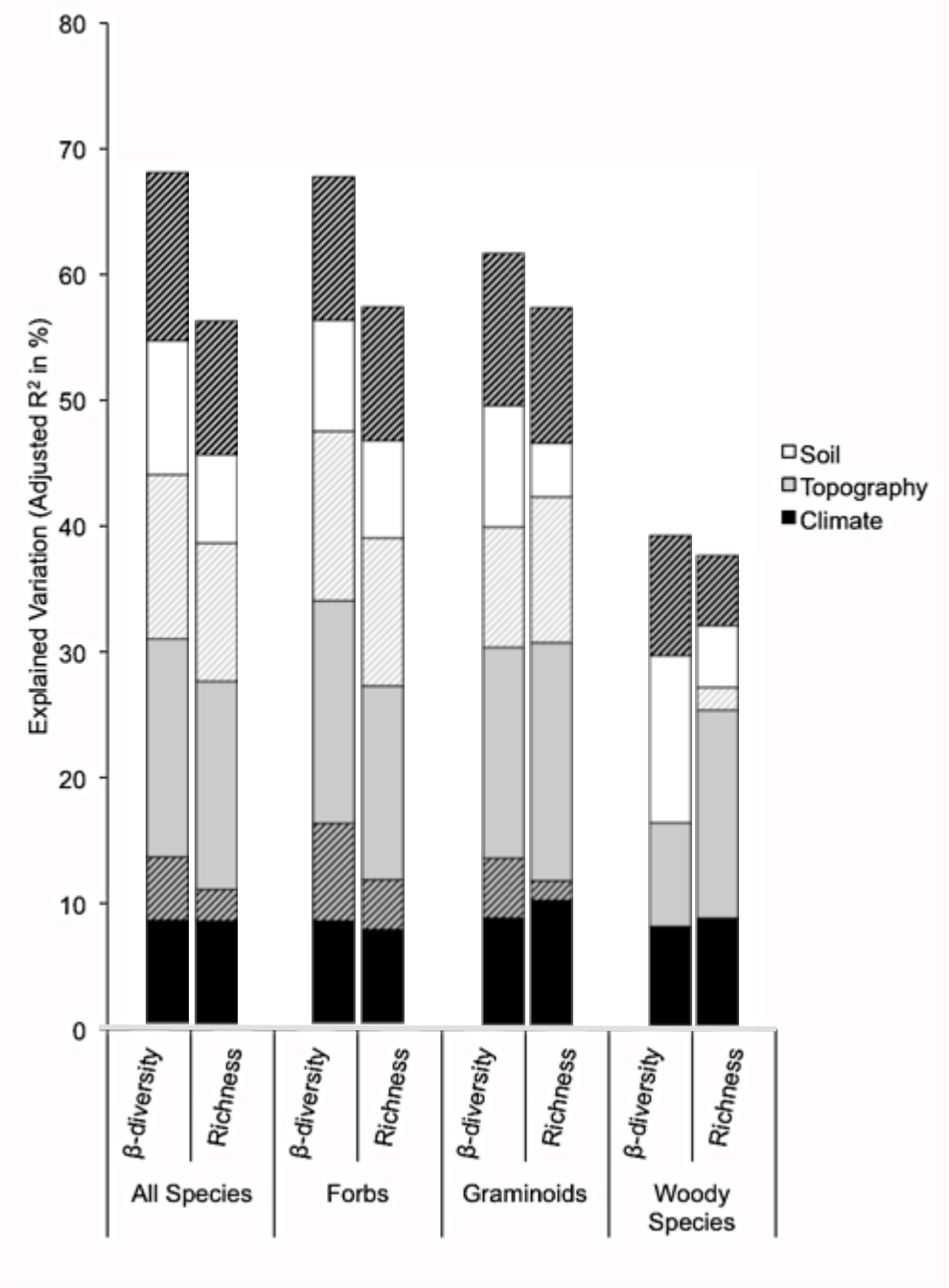


Table 7: Significant variables detected through forward selection for each variation-partitioning model. Explanatory variable names are according to Table 4.

	MST	MSP	SI.E	SI.S	Elev	Acc	Slo	SMo	C.N	N	P	pH
All Species												
β-diversity	■	■			■	■	■	■	■	■	■	■
Richness	■	■			■	■	■	■	■	■		■
Forbs												
β-diversity	■	■			■	■	■	■	■	■		■
Richness	■	■			■	■	■	■	■	■		■
Graminoids												
β-diversity	■	■			■	■	■	■	■	■	■	
Richness	■	■			■	■	■	■	■	■		■
Woody Species												
β-diversity	■	■				■	■	■	■		■	
Richness	■	■			■	■	■	■	■			

2.4 Discussion

2.4.1 Results Summary

Both my redundancy analyses and variation partitioning results suggest that on a regional scale, the high topographic heterogeneity and varied soil types characteristic of mountain environments are more important than climate in structuring alpine plant communities in southwestern British Columbia (Figures 5a & 7, Tables 5 & 6). Also of note, this study shows that on a broad level in this system, species richness is an appropriate proxy for species β-diversity (Table 6; Magurran, 1988; Whittaker et al., 2001). Though the richness models had a lower level of 'fit' than the β-diversity models, the relative importance of each subset from the variation partitioning was generally maintained. Finally, the two species assemblages generated from Kendall's W test of concordance appear to differ primarily on their soil moisture requirements (see sections 2.3.2 and 2.4.4 for further details). Essentially, the first group is

comprised of species that flourish in xeric to mesic soils, whereas the second group is formed by species preferring a much wetter environment.

2.4.2 Topography and soil as primary determinants of regional alpine plant diversity

On a regional scale, the high topographic heterogeneity and varied soil types characteristic of mountain environments explain more of the variance in alpine plant β-diversity and species richness in southwestern British Columbia (Figures 5a & 7, Tables 5 & 6). These findings are consistent with studies conducted in the European Alps, Iberian Peninsula, and California (Harrison *et al.*, 2006; Lobo *et al.*, 2001; Marini *et al*., 2007 & 2008b; Wohlgemuth, 2002; Wohlgemuth *et al.*, 2008), but contradict other results exclusively from the European Alps (Marini *et al*., 2008a & 2009; Moser *et al.*, 2005; Vonlanthen *et al.*, 2006) (Table 1). This contradiction does not seem to be a result of the specific variables chosen to be measured in each study, as often the same parameters have been deemed significant and insignificant, even in the same region (e.g. Marini *et al*., 2007 & 2008b versus 2008a). However, many studies that show climate to be of greatest importance used broad-scale estimates of species richness within cells of a grid spanning the study region, and averaged environmental variables to accommodate the cell size (e.g. the *average* elevation in a 35 km^2 area) (Marini *et al*., 2008a & 2009; Moser *et al*., 2005), with some exceptions (Vonlanthen *et al*., 2006; Wohlgemuth *et al*., 2008). On the other hand, studies finding climate to be of lesser importance often used data from specific sites within the larger study region, with the exception of Lobo *et al*. (2001) (Harrison *et al*., 2006; Marini *et al*., 2007 & 2008b). Using estimates of richness and environmental parameters over large areas ignores the influence of the microenvironment in mountain ecosystems, particularly with regards to soil. As my study and several others show, local soil parameters are responsible for large

changes in alpine plant diversity at the regional scale (Austrheim *et al*., 1999; Harrison *et al*., 2006; Marini *et al*., 2007 & 2008b; Sebastiá, 2004; Vonlanthen *et al*., 2006). By blurring the effects of the micro-environment, extrapolations of diversity and environmental datasets over vast areas may be more accurately reflecting larger, even global scale patterns, where environmental energy and water availability are the most significant determinants of diversity (Evans *et al*., 2005; Hawkins *et al*., 2003).

2.4.2.1 Topography

It is well known that topography affects plant community composition in mountain systems (e.g. Bennie *et al*., 2008; Bhattarai & Vetaas, 2003; Bruun *et al*., 2006; Geiger, 1965; Holland & Steyn, 1975; Kazakis *et al*. 2007; Körner, 2003; Moser *et al*., 1977; Stanisci *et al*., 2005; Wallace, 1878**)**. In concordance with results from Table 1, elevation, slope and accessibility were consistently selected as important topographic variables in my study (Tables 5 & 7). Particularly, there has been a heavy focus on trends of species diversity along elevational gradients and conclusions reflect an overall *decrease* of species diversity with altitude (e.g. Alexander & Hilliard, 1969; Bhattarai & Vetaas, 2003; Bruun *et al*., 2006; Kazakis *et al*., 2007; Stanisci *et al*., 2005; Wallace, 1878). However, my results show that diversity tends to *increase* with elevation (Table 5). Indeed, a unimodal relationship with elevation exists, where plant diversity peaks at some intermediate elevation, before decreasing as it reaches the summit (e.g. Bhattarai & Vetaas, 2003; Brunn *et al.*, 2006; Grytnes & Vetaas, 2002; Wang *et al*., 2003; Wohlgemuth *et al*., 2008). Since the elevational range in my study was not large (1925 to 2141 m) and sampling was exclusively conducted midway up the meadows, it is possible that species diversity was still near its peak and would have shown a downward trend if I had sampled along an altitudinal gradient at each site. This said, it is interesting that given the small range in

elevational differences between plots, elevation was still consistently chosen as one of the most significant determinants of diversity in my models (Fig. 5; Table 5), demonstrating that even slight elevational changes in alpine systems of southwestern British Columbia are important in structuring plant communities. Indeed, Spehn & Körner (2005) noted an average regional decline in richness of 40 species per 100 m of elevation in mountain ecosystems across Europe, Greenland and Asia, though the change in richness in my study was nowhere near as large.

Second, alpine species diversity generally increased with slope steepness (Table 5). Steeper slopes often exhibit higher species richness because they experience more extreme environmental conditions than level ground, and thus prevent competitive species from monopolizing resources and potentially excluding rare species (Geiger, 1965; Kampmann *et al*., 2008; Marini *et al*., 2008b; Pykälä *et al*., 2005). Though known to significantly affect diversity (Badano *et al*., 2005; Bennie *et al*., 2008; Geiger, 1965; Holland & Steyn, 1975; Sherman, 2008), the sun indices (SI.S & SI.E, measures of slope exposure), were not selected as important determinants of diversity (except for a minor effect on woody species diversity – Table 6). This is likely because all of my sites were situated on south-facing slopes, and thus there was not much variation in the amount of sunlight experienced by plots.

A reflection of the relative isolation and human 'use' of each site, *accessibility* (Acc) influenced patterns of regional diversity in southwestern British Columbia, explaining 6% of the variance in overall β-diversity and richness (Fig. 5a; Table 5). For life forms, this number increased to 8% for graminoid β-diversity and woody species richness, and decreased to 2% for woody species β-diversity (Fig. 5c & d; Table 5). Factors relating to human land use and management regimes both within the site and in the surrounding landscape repeatedly are found to be significant determinants of plant diversity in mountainous ecosystems (Table 1). In general,

by increasing exotic invasions, replacing natural disturbance regimes and promoting habitat fragmentation, anthropogenic disturbance has served to alter patterns of regional and local diversity (Higgins *et al*., 2003; Olsson *et al*., 2000; Parmesan & Yohe, 2003; Sax & Gaines, 2003; Spehn & Körner, 2005; Thuiller *et al*., 2005). Therefore, in Europe, where mountainous landscapes have long been transformed by agricultural activity and urban development, it is not surprising that factors relating to anthropogenic land-use can explain between 13% and 77% of the variance in the alpine plant diversity datasets (Table 1 - Austrheim *et al*., 1999; Marini *et al*., 2007, 2008a & b, 2009). However, in more intact (and inevitably under-studied) mountain systems, it can be expected that anthropogenic influences will be much lower (Holzinger *et al*., 2008). Sure enough, my results show that though *accessibility* is a statistically significant determinant of alpine plant diversity in southwestern British Columbia, it is of lower importance than elevation, slope, soil moisture and mean summer temperature (Table 5). Using G*Power© (Faul *et al.*, 2006, 2009), the effect size of the accessibility rating as a determinant of diversity is 0.15, with can be considered 'low' (Cohen, 1988), therefore suggesting that there is some, but not much, biological significance in accessibility. The biological significance that does exist could be primarily related to the varying levels of grazing pressure present at each site: from baseline (wildlife only), to horses, to cattle. Grazing is known to impact species diversity, which is especially obvious in Europe where alpine agriculture is widespread (Austrheim *et al*., 1999; Marini *et al*., 2007 & 2008b). Only one of my sites was occasionally grazed by cattle (Texas Creek), and two by horses (McGillivray Pass & Cinnabar Basin).

2.4.2.2 Soil

Soil moisture was by far the most significant soil-related determinant of diversity for both models (Table 5). Even in the cases where total nitrogen, available phosphorus, the C:N ratio and

soil pH were found to be significant, individually they did not contribute more than 2% of explained variance in species β-diversity or richness (Table 5). This pattern was also evident in all life-form models, except woody species richness, where the contribution of soil pH increased and that of soil moisture decreased to only 2% (Table 5).

Soil moisture is influenced by multiple factors including snowmelt & rain events, elevation, aspect, slope, and soil clay content and porosity (Billings & Bliss, 1959; Famiglietti *et al*., 1998; Isard, 1986). The sites I visited were released from snow cover only a few weeks prior and there was no significant correlation between rainfall in the week leading up to sampling and soil moisture ($p=0.3992$), between mean annual precipitation and soil moisture ($p=0.3499$) or between the date of sampling and soil moisture ($p=0.2163$), meaning that my soil moisture values were likely representative of each plot based on general climate, micro-topography and soil characteristics. Moreover, though many alpine plants have sections of longer roots that extend deep into the soil profile where moisture is more consistent, my study shows that even the moisture content of the top 10-15 cm (Körner, 2003), where my soil samples were taken, is still important in maintaining the observed patterns of community composition.

As shown in Table 1, models with pH as a factor (Austrheim *et al*., 1999; Li *et al*., 2011; Marini *et al*., 2007; Sebastià, 2004; Vonlanthen *et al*., 2006) were generally more successful in explaining the variation in species diversity in the 'soil' category. This trend is not surprising as soil pH can reflect soil nutritional status and has been linked to strong differences in plant community composition in other systems (Gough et al., 2000; Tilman & Olff, 1991). Further, high values of soil pH are associated with calcareous bedrock (Schaetz & Schwenner, 2006), such as limestone, and in turn, alpine plant distribution is strongly influenced by the abundance of calcium (Körner, 2003; Wohlgemuth, 2002). Calcium and magnesium cations can be

weathered from the bedrock (Vonlanthen *et al*., 2006) and are essential for cell structure and functioning (White & Broadley, 2003), and enzyme performance (Shaul, 2002), respectively. In my study, pH was more often a significant determinant of species richness than β-diversity, but did not contribute greatly to the overall strength of the 'soil' category, except for woody species richness (Tables 5 & 7). The relatively low independent contribution of pH could be a result of all sites being underlain by comparable bedrock features that were dominantly granitic and thus generally non-calcareous.

Finally, available phosphorus was consistently a significant determinant of β-diversity and richness for all species and life forms, whereas total nitrogen and the C:N ratio tended to be significant only as determinants of β-diversity (Table 5). However, neither phosphorus, nitrogen nor the C:N ratio contributed a great deal to the explained variance in the models of alpine plant diversity in southwestern British Columbia, and had very low effect sizes of around 0.05 (Cohen, 1988) (generated with G*Power© software (Faul *et al.*, 2006, 2009)) (Table 5). In Europe where many mountain regions are heavily impacted by agricultural activity, Austrheim *et al*. (1999) and Marini *et al*. (2007 & 2008b) found that the use of N-based fertilizers significantly reduced alpine plant richness, and that meadows with high levels of fertilization were dominated by competitive species (as per Grimes *et al*., 1997). Since the majority of alpine meadows in southwestern British Columbia are free from agricultural pressure, and are not subject to pulses of anthropogenic nitrogen inputs, this may explain why the importance of nitrogen in my study was so low. The low importance of phosphorus may be a result of alpine plants having evolved to match their growth and acquisition efficiency to the long-term phosphorus supply (Körner, 2003). Additionally, since carbonate content and pH modulate phosphorus availability in the soil (Gough *et al*., 2000; Passama, 1970), community level effects of phosphorus availability may be

largely regulated through indirect pathways, theoretically reducing its relative importance as a determinant of diversity. Fertilization experiments in alpine ecosystems have provided evidence for this hypothesis by demonstrating an increase in biomass production and/or the abundance of certain species following P addition, but with little to no effect on species richness (Seastedt & Vaccaro, 2001; Theodose & Bowman, 1997). Finally, being negatively correlated with the rate of net nitrogen mineralization, the C:N ratio reflects soil microflora activity and consequently the amount of N available to plants in the soil organic matter (Björk *et al*., 2007; Zeller *et al*., 2000). High C:N ratios and thus low levels of net nitrogen mineralization are often found in dwarf shrub-dominated ecosystems, as this group has a greater abundance of carbon and lignin-rich material and lower leaf nitrogen levels (Zeller *et al*., 2000); this may explain my findings regarding the slightly stronger and positive correlation between the C:N ratio and woody species β-diversity in alpine meadows (Table 5). Moreover, warming experiments conducted in arctic-alpine systems have shown dramatic increases to C:N ratios and the abundance of dwarf shrubs, (Arft *et al*., 1999; Walker *et al.,* 2006), which suggests that the minor relationship between the C:N ratio and plant diversity in my study is likely due to the overall dearth of woody species.

2.4.2.3 Climate

Though topography and soil were generally the most important determinants of alpine plant diversity in my study region, mean summer precipitation and temperature did contribute significantly to the β-diversity and richness models (Fig. 7; Tables 5 & 6). As an individual variable, mean summer temperature was most important for the diversity of all species and life forms, with the exception of graminoid β-diversity and woody species richness, where mean summer precipitation was the dominant climatic factor (Table 5). Additionally, as a determinant of the abundance of the most common forb species, mean summer precipitation was not

significant, whereas mean summer temperature explained a mere 3% of the variation (Fig. 6). These results do not support the recent European and American evidence for the greater importance of precipitation or water availability in dictating climate-related changes to plant richness on mountain summits (Crimmins *et al.*, 2011; Pauli *et al*., 2012). Instead, my results show that temperature tends to be more important than precipitation as a determinant of alpine plant diversity, at least in the coastal-interior transition zone of the Coast Mountains of southwestern British Columbia.

The positive correlation between precipitation and plant species richness is well known (e.g. Adler & Levine, 2007; Pausas & Austin, 2001; Whittaker *et al.*, 2007; Yang *et al.*, 2011), and yet precipitation has been identified as a significant and insignificant (Table 1) determinant of alpine plant richness. Moser *et al*. (2005) brought up the possibility that precipitation is only correlated with regional alpine plant richness in more arid regions where water availability is limiting to plant growth. Yet, recent evidence shows that over the last decade, species richness has increased significantly on European mountain summits in temperate and boreal regions, but decreased at sites with a drier Mediterranean climate where warming temperatures have been accompanied by decreasing or stable precipitation events (Pauli *et al*., 2012). Also, as is the case with my study, Table 1 shows that three out of four studies noting precipitation as a significant determinant of alpine plant diversity were located either in relatively humid climates such as the Alps or the Iberian Peninsula (Marini *et al*., 2008a; Rey Benayas & Scheiner, 2002), or incorporated a mixture of both dry and humid sites to obtain a global perspective (Kikvidze *et al*., 2005). My study detected a negative correlation between overall diversity and precipitation (Table 5), but the trend seems to be due to my wettest site (Singing Pass) being especially species-poor. By removing the Singing Pass plots, the trend becomes positive, indicating that

other environmental factors must be overriding precipitation to keep diversity low; for one, Singing Pass is found at the lowest elevation of all sites. Since I recorded a significant positive relationship between species richness and elevation, this finding further highlights how topography may have the potential to outweigh the effects of climate in structuring diversity patterns in mountain landscapes (Tables 5 & 6).

Mean summer temperature was significantly negatively correlated with the β-diversity of alpine meadow communities in southwestern British Columbia. This is interesting because the average temperature difference between sites was quite low at a maximum difference of 2°C, meaning that even small changes in growing season temperature can be enough to alter patterns of regional alpine plant diversity. Many studies finding temperature-related parameters to be significant determinants of alpine plant diversity usually surveyed a region where temperature ranges were much greater, such as 14°C for Rey Benayas & Scheider (2002) and 23°C for Moser *et al*. (2005). Temperature in mountain ecosystems is negatively linked to altitude (Körner, 2003), but since I noted an increase in diversity with elevation, the negative correlation between temperature and diversity does not reflect an elevational trend. Rather, it may be representative of the location of the meadows along the coast to interior climate transition zone. Meadows furthest inland (e.g. Texas Creek & Cinnabar Basin) tend to be colder and fairly species rich, whereas those nearest the coast (e.g. Singing Pass & Blowdown Pass) are warmer and less diverse. This pattern cannot be explained through glacial history as glacial refuges are noted biodiversity hotspots (Médail & Diadema, 2009) and in British Columbia these are known to be located near the coast and in the Rocky Mountains (Wilson *et al*., 2007). Therefore, if distance from the nearest glacial refugia was playing a role in the diversity patterns measured in this

study, the sites nearest the coast should have been more diverse, rather than the other way around.

Life forms showed similar relationships with climate as overall species β-diversity and richness, with the exception of woody species (Tables 5 & 6). For woody species richness, mean summer temperature did not make any significant contribution to the model; but for woody species β-diversity, the importance of temperature greatly increased to 18.2% (Table 5). In arctic-alpine systems, increases in woody species cover and production have been documented in response to actual and experimental warming over the long term (Chapin *et al*., 1995; Molau & Alatalo, 1998; Wilson & Nilsson, 2009). My study provides support for these observational and experimental results by highlighting how woody species β-diversity is strongly influenced by temperature (Table 5). However, when species abundances are not included, woody species richness alone is not influenced by temperature (Table 5). Similarly, Klanderud & Totland (2005) showed that while the relative cover of a dominant dwarf shrub in an alpine heath community was significantly reduced by experimentally increasing temperature and nutrients, woody species richness remained unaltered.

2.4.3 Species richness as an appropriate proxy for diversity in alpine plant communities (exception: species-poor groups)

In the redundancy analyses and variation partitioning performed, environmental models were able to explain about 10% and 13% more of the variation in overall species community composition than in species richness, respectively, and were comprised of one more variable (Tables 5 & 7). Even with the slight difference in explanatory power between models, my results suggest that both diversity and species richness are satisfactory measures to describe overall regional alpine plant diversity in its relationship to topography and climate (Tables 5 & 7). The

models mainly differed in terms of the soil variables they included, but those factors that were not consistent between models (N, P, C:N, pH) were of low importance compared to soil moisture, which always contributed to the fit of both models (Table 5). Therefore, it is difficult to say whether species richness and community composition are indeed affected by soil parameters in different ways, or if the importance of certain variables was simply too low to be detected by one model or the other. This high degree of compatibility provides some validation for the common use of species richness as a proxy for species diversity (Magurran, 1988; Whittaker *et al*., 2001), but does conflict with the findings of other studies comparing the two measures in mountain systems where the variables composing each model differed (e.g. Marini *et al*., 2007; Rey Benayas & Scheiner, 2002). However, the systems examined by Marini *et al*. (2007) and Rey Benayas & Scheiner (2002) have been long affected by anthropogenic nutrient inputs through agricultural, silvicultural and pastoral practices, and this may have altered the mechanisms controlling species richness and composition in those communities. Additionally, Marini *et al*. (2007) demonstrated the greatest difference between their richness and community composition models, but did not include any climatic parameters in their analysis. With the addition of climate variables such as temperature and precipitation it is very likely that the proportion of variance explained by their community composition model would have increased, as it is well known that climate plays a large role in dictating species abundances in alpine habitats (e.g. Klanderud & Totland, 2005).

On another note, the community composition model for woody species, the minority life form in the alpine meadow communities, included a greater number of factors than those describing species richness in the redundancy analyses, and had much greater explanatory power (Table 5). Similarly, Scrosati *et al*. (2011) showed that in contrast to a very diverse group, two

species-poor life forms in an intertidal community showed inconsistent trends along environmental stress gradients when examined using species richness versus species diversity. In combining the two life forms into a single group and rerunning the analyses, the authors were able to achieve greater compatibility in how species richness and diversity trended along the environmental gradients in question.

In alpine meadows, the dominant functional type (in my study, forbs) may be monopolizing available resources and thus competitively controlling species identity and richness in groups that are relatively species-poor. Consequently, environmental models for *diversity* in species-poor groups may have more explanatory power because though biotic interactions might largely dictate species *identity* (and thus richness), environmental factors may still play a significant role in determining how productive, and thus abundant, each of these species will be. For instance, Klanderud & Totland (2005) showed that the relative cover of *Dryas*, a dwarf woody species dominating an alpine heath community, was significantly reduced by experimentally increasing temperature and nutrients, while graminoid and forb diversity surged. This species was part of the most species-poor "dwarf shrub" functional group, and sure enough, species richness was not significantly altered by changes to the abiotic environment, only *Dryas* cover. In contrast, the more diverse functional groups (forbs & graminoids) showed comparable changes in both richness and diversity measures.

2.4.4 Species identity linked to soil moisture in alpine meadows

Species comprising the assemblages derived from Kendall's W test of concordance differed primarily in their overall moisture requirement. The first assemblage is mainly composed of species that flourish in xeric to mesic soils, such as *Eriogonum umbellatum* *Minuartia rubella*, *Poa abbreviata* and *Solidago multiradiata* (UBC, 2012; USDA, 2012). In

contrast, all seven species making up the second assemblage prefer a wetter environment, such as *Arnica cordifolia*, *Carex macrochaeta*, *Erigeron peregrinus* and *Valeriana sitchensis* (UBC, 2012; USDA, 2012). Concordantly, average soil moisture for the plots in group 1 (9.6%) was significantly different from that of group 2 (28.4%) (Student's t-test, $p<0.001$).

The compartmentalization of alpine plant community types based on soil moisture requirements was also demonstrated by Sebastià (2004). Soil moisture regulates the establishment of plant communities (Legates *et al.*, 2011) and influences the distribution of these communities in alpine habitats through interactions with topography and climate (Billings & Bliss, 1959; Isard, 1986; Körner, 2003). Moreover, a linear increase in species richness has been demonstrated by experimentally elevating soil moisture levels in an alpine system (Yang *et al*., 2011). Soil moisture (SMo) was identified in this study as a significant explanatory variable for all redundancy analysis models, explaining approximately 9% of the variation in the overall β-diversity and species richness of alpine meadows (Table 5). However, contrary to Yang *et al*.'s study (2011), my study found soil moisture to be negatively correlated with species richness, similar to results from Niwot Ridge in Colorado where snowbed and mesic meadows have fewer species than dry meadows (Seastedt & Vaccaro, 2001). Seastedt and Vaccaro (2001) also found that though dry meadows are most species-rich, they have the lowest foliage production, suggesting that high-moisture sites allow for a few dominant species to monopolize resources and exclude rare species, as is likely the case in southwestern British Columbia.

2.4.5 Potential resilience of alpine plant communities to climate change

The relatively low importance of climate as a determinant of regional alpine plant diversity in this study comes as a bit of a surprise, considering the ubiquitous emphasis placed on the heightened vulnerability of mountain ecosystems to climate change (Diaz *et al*., 2003;

Grabherr *et al*., 2010; Hamann & Wang, 2006; Klanderud & Totland, 2005; Körner, 2003; Pauli *et al.*, 1996), and fresh evidence of a continental-scale change in European alpine plant communities over the past decade through an increase in thermophilic species and a decrease in cold-adapted species (Gottfried *et al*., 2012). For all species and life forms, variation partitioning results show that topography and soil are far greater determinants of β-diversity than climate in alpine meadows (Fig. 7; Table 6). The importance of climate did rise above that of soil for models of overall species richness, as well as for graminoid and woody species richness, but topography remained by far the most significant determinant.

Though growing season precipitation and temperature does influence overall alpine species diversity to some extent, my results suggests that alpine meadow ecosystems may be less threatened by climate change than previously suspected. Throughout Canada increases in the range of +20% for mean annual precipitation and between 1°C and 5°C for mean annual temperature are expected with future climate change (IPCC, 2007b). From such climate projections, predictions were that the area occupied by the alpine zone in British Columbia would decrease by a dramatic 97% by 2085 (Hamann & Wang, 2006). However, as shown by my study, and by research conducted by Harrison *et al*. (2006), Lobo *et a*l. (2001), Marini *et al.* (2007 & 2008b) and Wohlgemuth (2002), abiotic factors other than climate strongly influence patterns of plant diversity in highly heterogeneous mountain environments. The persistence of individual species and functional groups may depend on the presence of topographically induced gradients that create the specific soil and micro-climatic characteristics necessary to provide refuge from changing atmospheric climate conditions (Pauli *et al*., 1999).

Indeed, Scherrer and Körner (2010 & 2011) recently argued for the potential of such resilience in a study examining the thermal habitat preferences of alpine plant species across

topographically derived microhabitats. Observing a large range of seasonal soil and surface temperatures, and season lengths over a small area covering 2 km^2, they concluded that the majority of species could find suitable "escape" habitats close to their current distribution should atmospheric temperatures increase by 2°C. These results supported an earlier study by Randin *et al*. (2009) in the Swiss Alps whose fine-scale models predicted the high-elevation persistence of up to 100% of alpine species that had been showed by coarse scale models to lose all suitable habitat over the next few decades. In conjunction with my study demonstrating the lower importance of atmospheric climate as a determinant of alpine plant diversity, these findings suggest that projections of alpine habitat loss due to climate change are likely overestimated. Moreover, Johnson *et al*. (2011) modeled the transition of between various alpine ecosystems over the period from 1971 to 2001 and found that the abundance of "moist", "wet", and "dry" meadows have been relatively stable over time, that snowbed and fell-field habitats were decreasing, and shrub tundra vegetation increasing. In southwestern British Columbia, the alpine meadows I surveyed likely fell into the "wet" and "dry" meadow types, as supported by the fact that my species assemblages were distinguishable based on soil moisture requirements (section 2.4.4), and that my species lists were comparable in terms of species identity to those from wet and dry meadows at Niwot Ridge (Theodose & Bowman,1997). This further suggests the potential for resilience to changes in atmospheric climate conditions in alpine meadow environments.

Chapter 3

3.0 General Discussion

3.1 Overview of Results

With little hope of significantly curbing anthropogenic greenhouse gas emissions over the upcoming decades, there is increasing concern as to how our sensitive alpine ecosystems will respond to global climate change (Grabherr *et al.*, 2010; Parmesan & Yohe, 2003; Walker *et al.*, 2006). Already, region-specific changes to species richness have been noted as species are moving along elevational gradients according to the predictions of climate change models (Crimmins *et al.*, 2011; Lenoir *et al.*, 2008; Pauli *et al.*, 2012; Rubidge *et al*., 2011), and overall shrub density is increasing in alpine tundra habitats (Hallinger *et al.*, 2010; Johnson *et al*., 2011). Models predicting the future distribution of alpine habitat offer conflicting predictions. For instance, Hamann & Wang (2006) and Dirnböck *et al.* (2003 & 2011) predicted a severe contraction of alpine zones in British Columbia and the European Alps, respectively, over the upcoming decades. These models were primarily based on the current and future climate and land-use envelopes available to a species or plant community. In contrast, updated fine-scale modeling work using species distributions and abiotic variables have yielded rather different results, and conclude that the likelihood of persistence for many species and plant communities in the alpine zone in a warming world is actually much higher than previously believed (Johnson *et al.*, 2011; Randin *et al.*, 2009; Scherrer & Körner, 2010 & 2011).

In response to these predictions, Table 1 was developed to summarize the state of knowledge on the importance of the abiotic environment (topography, soil & climate) in

structuring present-day alpine plant communities, and especially alpine meadow systems. Following this, the species composition, topographic, soil, and climatic characteristics of 48 alpine meadow plots at 7 sites in southwestern British Columbia were thoroughly surveyed during the summer of 2011. These data were analyzed with redundancy analyses and variation partitioning to determine (1) the relative importance of topography, soil and climate as overarching determinants of overall regional alpine plant β-diversity and richness, as well as for individual life forms (forbs, graminoids, and woody species), and (2) the identity of the most important individual variables within those categories.

With the support of the literature review in Table 1, my study makes its most significant contribution by revealing that in highly heterogeneous mountain landscapes, topography, and soil to a lesser degree, are the primary determinants of regional alpine plant diversity, whereas climate is the least important of the three (Fig. 7; Table 6). As individual variables, elevation, slope, mean summer temperature and soil moisture play the greatest roles as determinants of overall species β-diversity and richness (Table 5). My rating of the recreational accessibility of each site was significant (6% of variation explained), but is not nearly as important in the relatively pristine Coast Mountain environment as it is in Europe where anthropogenic activity through urbanization and agriculture is far more prominent (Austrheim *et al*., 1999; Marini *et al*., 2007, 2008a & b, 2009). Soil moisture was the most significant soil-related variable by a wide margin, highlighted through Kendall's W test of concordance (sections 2.3.2 and 2.4.4) when two distinct species assemblages distinguishable mainly based on their soil moisture requirements were detected within the alpine meadows sampled. The importance of soil moisture as a determinant of β-diversity in alpine meadows is in line with findings from Niwot Ridge, Colorado (Theodose & Bowman, 1997; Johnson *et al*., 2011).

For life forms, results were generally similar to those for overall species with some interesting exceptions: a) for graminoid β-diversity and richness, the importance of mean summer precipitation roughly doubled; and b) for woody species β-diversity the importance of mean summer temperature rose dramatically to explain 18% of the variation (Table 5). The stronger effect of precipitation on graminoid diversity has been experimentally demonstrated in alpine meadows by Yang *et al.* (2011), and may be the result of graminoids having higher water-use efficiency than forbs (Bowman *et al*., 1995). For woody species, shrub cover in the alpine has been shown to respond significantly to changing temperatures, while richness did not (Klanderud & Totland, 2005). This strong connection also supports the recent evidence for long-term increasing woody cover and production in arctic-alpine systems (Chapin *et al*., 1995; Molau & Alatalo, 1998; Wilson & Nilsson, 2009).

As a side question, I asked whether the determinants of diversity were different for species richness and β-diversity models. For all species, both environmental models describing β-diversity and species richness were quite similar, and could be used interchangeably (Fig. 7; Tables 5 & 6). However, for life forms, the fewer species included within the life form group, the greater was the disparity between the β-diversity and richness models. As such, the most species-poor group, woody species, exhibited the greatest difference between β-diversity and richness models. I concluded that for species-poor groups, the two measures of diversity should not be used as proxies for one another unless species-poor groups are combined with others to create a larger species pool before analysis, as in Scrosati *et al*. (2011).

3.2 Methodological Strengths and Weaknesses

Any observational study in ecology comes with inherent limitations and weaknesses, primarily because without experimentation, one cannot truly get at the mechanisms yielding a

pattern observed in a natural ecosystem. Rather, one can only speculate about the nature of the mechanisms by examining correlations between the chosen response and explanatory variables, as was done in this study. However, with careful planning and an extensive review of pertinent literature, observational studies in ecology can be very valuable indeed as they offer a snapshot of an ecosystem in its present, living state, and create the groundwork for future experimentation to decipher the correlations uncovered and answer hypotheses generated.

Within these constraints, every precaution was taken to ensure a high quality of data collection and analysis. A thorough series of power analyses were conducted to ensure an appropriate sample size for my study system, and to increase the power of detection, I exceeded the suggestions offered (section 2.2.2). To collect the necessary response data on alpine plant community composition, multi-scale 100 m^2 Intensive Plots were selected for their optimum balance of large size and reasonable sampling time (Barnett & Stohlgren, 2003). These plots also allowed for a thorough inventory of species present. Once in the field, this method was further confirmed as suitable for sampling alpine meadows, as on many occasions the 7 plots spread out along a transect following the topographic isocline fit the length of the meadow perfectly, and thus the entire span of the meadow was sampled. Moreover, the meadows sampled included the majority of known and accessible meadows in the 6,200 km^2 study area. By placing plots along a transect running horizontally midway up each meadow, I had hoped to somewhat control for elevation as it is already well-known as a determinant of alpine plant diversity. However, as all meadows sampled were on different mountains and at slightly different elevations, this did not work out as planned and elevation still remained my most significant explanatory variable. In future years, it might be useful to sample plots at the same elevation on each mountain to determine how plant communities are structured by their abiotic environment when elevation is

held constant. Finally, there is a possibility that the discrepancies witnessed among environmental models for β-diversity and richness were due to the difference in sampling area for each measure of diversity. For β-diversity, species cover was measured in approximately 28 1 m^2 plots in each meadow, whereas species richness was assessed in 7 100 m^2 plots, meaning that far more area was sampled to determine species richness than community composition. However, all species located in the larger 100 m^2 plot that were not found in the 1 m^2 plot were very rare in the overall community and rarely consisted of more than 4 or 5 individuals. Therefore, their presence in the analysis for overall species β-diversity likely would not have made much of a difference considering that capturing 90% of species present is sufficient to maintain maximum statistical power in detecting differences in diversity between plots (Vellend *et al.*, 2008).

During data analysis, redundancy analysis (RDA) (Borcard *et al*., 2011) and variation partitioning (Legendre, 2008; Peres-Neto *et al*., 2006) were used to discern the relative importance of each explanatory variable and subset of variables, respectively, in explaining the variation in the response dataset. In combining both multiple regression and principal component analysis (PCA) to analyze community composition data tables, RDA is a useful tool for any ecologist as it allows the clear visualization of the relationships among environmental parameters and species diversity indices (Borcard *et al*., 2011). Similarly, variation partitioning is considered the method of choice to analyze community composition tables (Legendre, 2008). RDA and variation partitioning do have a weakness in that there is always the potential for collinearity between explanatory variables, which can generate misleading results by rendering unstable the regression coefficients of explanatory variables (Borcard *et al*., 2011; Marini *et al*., 2007). To minimize the chances of this occurring, variation inflation factors (VIFs) were used to detect and

remove any environmental variable that exhibited strong collinearity with another (Borcard *et al.,* 2011); as a result, mean annual temperature (MAT), mean annual precipitation (MAP), and soil organic matter (LOI) were removed from the explanatory data table prior to analysis (Table 4).

Finally, there is always a conundrum to face when wondering whether a statistically significant effect is biologically significant as well (Yoccoz, 1991). We can refer to a "small" statistically significant effect with a p-value of 0.04 for instance, but have no idea whether this "small" statistical effect is also small in a biological sense. To remedy this, when statistical contribution to my R^2_{adj} value was especially low, as it was for total nitrogen, available phosphorus and the C:N ratio during the redundancy analyses, effect sizes were verified using the G*Power© software (Faul *et al.*, 2006, 2009) to determine whether there was any biological significance in the contribution of these variables to my most parsimonious models. Indeed, even when the addition of variable to a model was statistically significant ($p<0.05$), the biological significance was generally low if the relative contribution of variance explained was low. This demonstrated that in my case, biological significance typically follows the relative contribution of each variable or subset to the explained variance of the model: lower contributions had lower effect sizes, and vice versa. It has been suggested that effect sizes, rather than just p-values, be used in all biological journals as they are more reflective of biological significance and appropriate for ecological questions (Nakagawa & Cuthill, 2007).

3.2.1 Other Limitations

Apart from limitations inherent to the methods used, as described in section 3.2, the major constraint to my study was simply the short length of the field season due to the abnormally heavy snowpack that built up during the winter and spring of 2011. For instance, the

Blackcomb Ski Resort, located within my study region near the Singing Pass plots, recorded 150 % more snowfall than average (Whistler Blackcomb, 2012). This forced initial sampling in late July towards the drier, northeastern portion of the transition zone, but nearing the end of the field season in mid-September it was possible to sample the wetter, southwestern sites. One of my prospective sites was still under snow in September and I had to forfeit it, but luckily my sample size was large enough without it to continue with analysis (see power analysis in section 2.2.2). Additionally, by moving my sampling throughout the season from the drier part of the coastal-interior transition zone to the wetter part, I avoided changes in community composition resulting from differences in the amount of time that had elapsed since snowmelt.

This abnormally large snow year could be considered an extreme weather event that is likely to become more common with future climate change (e.g. Gayton, 2008; Min *et al*., 2011). How alpine plant communities will respond will only reveal itself in the long run. However, as a one-time event, I don't believe that this abnormal snow year would have significantly altered the diversity patterns I observed, mainly because alpine systems have evolved the capacity to buffer environmental change, in part because they are dominated by long-lived perennials (Wilson & Nilsson, 2009). This, along with the fact that I sampled each meadow around the same time following snowmelt, should ensure that the diversity sampled was truly representative of the existing plant community.

3.4 Overall Conclusions

To predict how sensitive alpine environments will respond to our changing climate, it is critical to uncover the underlying determinants of the diversity patterns we see today. This study, in association with an overview of relevant literature on the topic (Table 1), has shown that topography and soil are the primary determinants of regional alpine plant diversity, with climate

coming in third place (Table 6). Within these groups, elevation, slope, soil moisture and mean summer temperature are most significant (Tables 5 & 7). Interestingly, in southwestern British Columbia I found that precipitation plays only a small role, even though my study area spanned a precipitation gradient ranging from a low of 747 mm/yr to over 2034 mm/yr. This contradicts recent findings predicting that altered precipitation regimes will have a greater impact on alpine species than temperature-related changes in the years to come (Crimmins *et al.*, 2011; Engler *et al.*, 2011; Pauli *et al*., 2012). In contrast, the stronger influence of temperature, especially for woody species β-diversity, supports findings of shrub expansion in arctic-alpine systems in both experimental and observational studies (Hallinger *et al.*, 2010; Johnson *et al*., 2011; Klanderud & Totland, 2005; Wilson & Nilsson, 2009).

This study has also re-fueled the debate regarding the use of species richness as a proxy for species composition, or diversity, when conducting ecological analyses. My results show that the determinants of richness and β-diversity are relatively similar when examining all species together as a group, but when life forms are examined separately the determinants of richness and β-diversity grow less comparable as the groups grow more species-poor (Tables 5, 6 & 7). This finding contradicts studies by Marini *et al*. (2007) and Rey Benayas & Scheiner (2002), who found that the determinants of overall species richness and diversity were very different in subalpine and alpine ecosystems in Europe. Therefore, the magnitude of this discrepancy may be region-specific, and potentially influenced by the higher anthropogenic impact in European alpine zones.

The lower importance of climate as a determinant of regional alpine plant diversity, especially for forbs, the dominant life form in alpine meadow ecosystems, suggests that these productive environments may be more resilient to on-going changes in atmospheric climate

conditions than previously believed. This theory was suggested by Randin *et al.* (2009) and Scherrer & Körner (2010 & 2011), as highly topographically heterogeneous mountain environments create a patchwork of micro-climates near the ground that can differ significantly from atmospheric climate conditions, and thus offer nearby "escape" habitats for alpine species (Scherrer & Körner, 2010 & 2011).

3.5 Future Directions

This study has created the groundwork for future research by beginning to disentangle the web of abiotic determinants behind present-day alpine plant diversity, in the hope that once we understand how the environment controls diversity in alpine ecosystems, we can better predict how it will respond to future climate change. Moreover, it is the first study of its kind to take place in Canada, and is one of the few conducted in a relatively pristine region that is not heavily impacted by urbanization and agriculture. As such, several questions have emerged that have the potential to fuel future research endeavors with the aim to improve our overall understanding of life in sensitive mountain ecosystems.

(1) At what geographic scale does climate increase in importance to be on par or above soil and topography-related controls of alpine plant diversity?

(2) Which environmental factors are most important in structuring patterns of alpine plant diversity when elevation is controlled?

(3) How do the determinants of alpine plant diversity differ between relatively pristine and anthropogenically disturbed alpine systems?

(4) Do species-poor plant groups or life forms truly experience a greater discrepancy between the determinants of species richness and β-diversity than species-rich groups, or was my study unique in this regard?

By answering these questions, we will improve our state of knowledge in this field, make more accurate predictions of how alpine plant communities will respond to a changing climate, and assess the true level of their resilience to environmental change.

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Appendices

Appendix I – Study Sites and Methods

Plate 1: Alpine meadow study site at Blowdown Pass, British Columbia, Canada (50°21’99.114”N; 122°09’95.73”W).

Plate 2: Alpine meadow study site at Cinnabar Basin, British Columbia, Canada (50°57’81.986”N; 122°4949.96”W).

Plate 3: Alpine meadow study site at Downton Creek, British Columbia, Canada (50°35’00.471”N; 122°16’43.64”W).

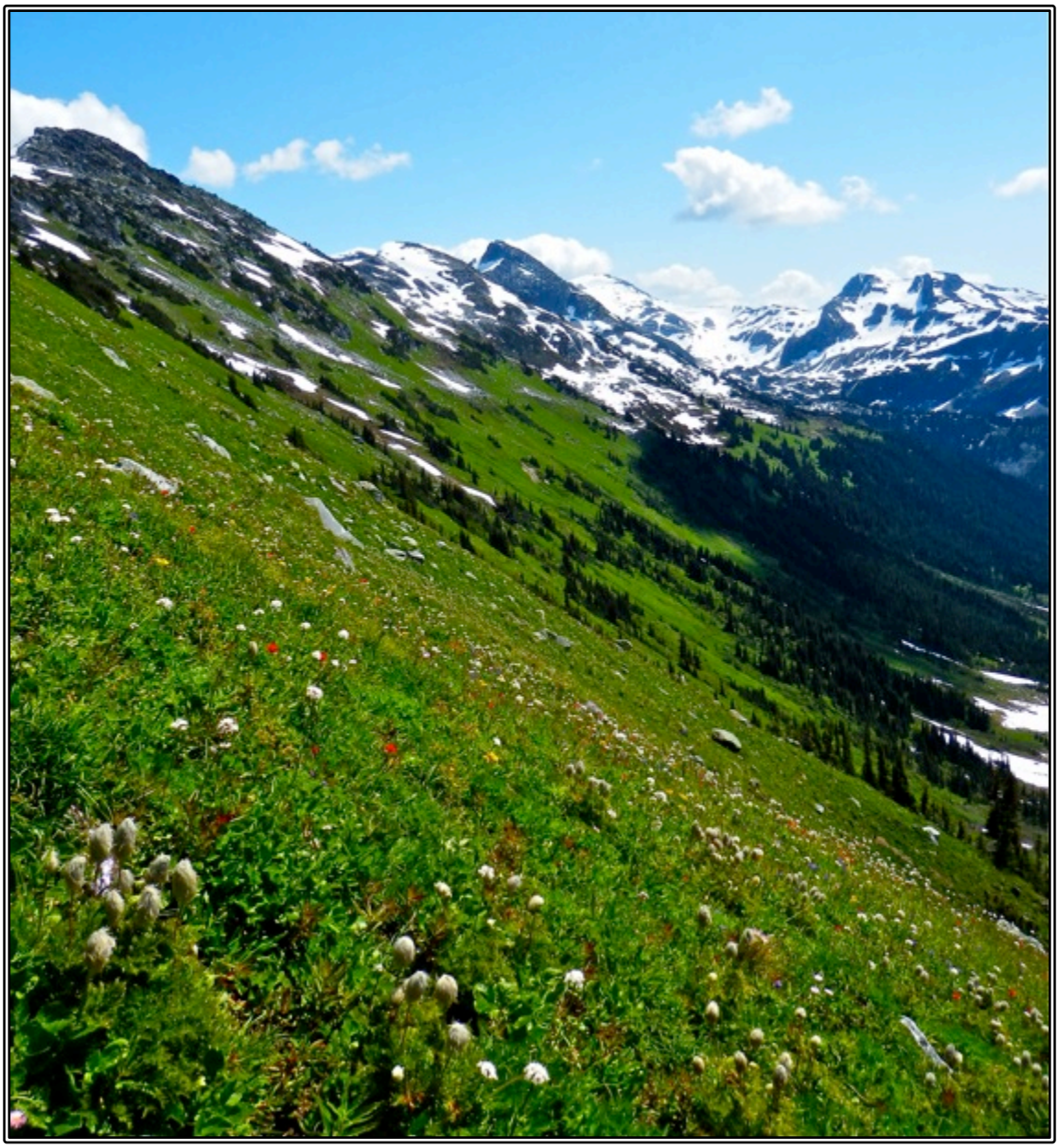

Plate 4: Alpine meadow study site at Marriott Basin, British Columbia, Canada (50°25’93.186”N; 122°27’64.99”W).

Plate 5: Alpine meadow study site at McGillivray Pass, British Columbia, Canada (50°41’24.214”N; 122°34’91.10”W).

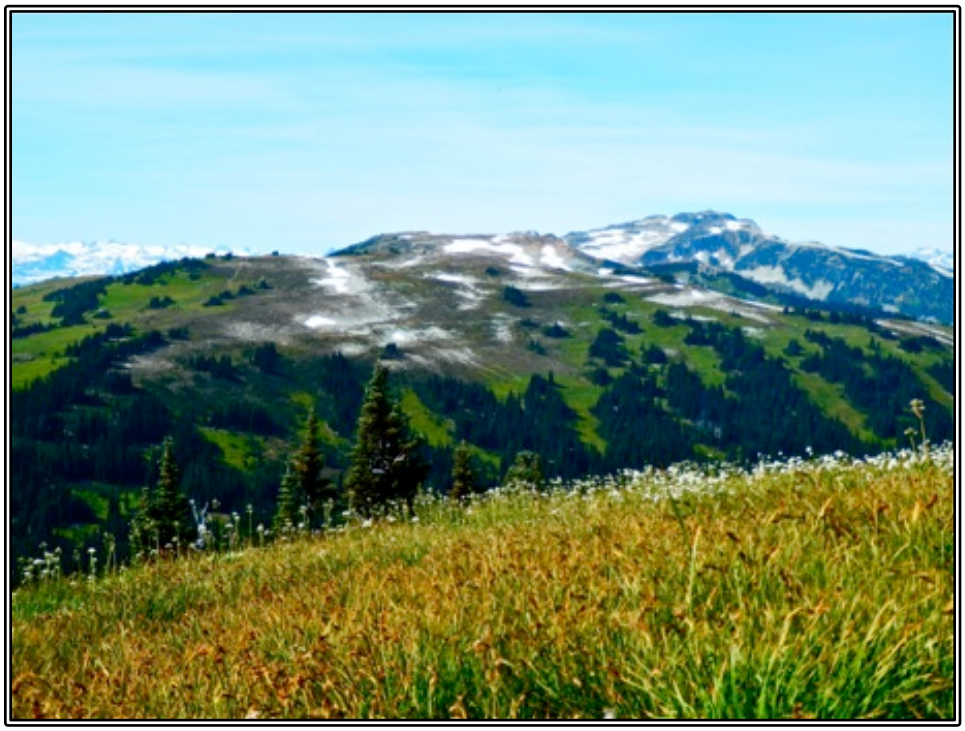

Plate 6: Alpine meadow study site at Singing Pass, British Columbia, Canada (50°01’84.80”N; 122°52’71.54”W).

Plate 7: Alpine meadow study site at Texas Creek, British Columbia, Canada (50°26’12.067”N; 121°59’72.95”W).

Plate 8: Intensive Plot set up at Downton Creek, British Columbia, Canada (50°35’00.471”N122°16’43.64”W). Note 1 m^2 quadrat made of PVC pipe in the left-center of the photo, and the larger plots laid out with orange string.

Table 8: The characteristics and associated values used to develop the 'accessibility' explanatory variable at each site. The range of values for each characteristic is reflective of the range experienced in the field. The resulting access ranking for each site is the sum of their unique values from each category.

Categories	**Values**			
	1	**2**	**3**	**4**
Distance from site to major road (km)	> 21	11-20	1-10	-
Distance from trailhead to Vancouver, BC (km)	> 300	201-300	100-200	-
Length of logging road accessing trailhead (km)	> 20	11-20	0-10	-
Vehicle class (for trailhead access)	4wd (high clearance)	4wd (low clearance)	2wd	-
Trail class	Faint trail	Clear trail	ATV access	Vehicle access
Trail difficulty	Difficult	Moderate	Easy	-
Recreation Type	Hiking	ATV/ Dirtbike	-	-
Grazing	Baseline (wildlife only)	Horses	Cattle	-

Appendix II – Species List

Table 9: Species list from the study region with associated species code and sites. (Sites: BD = Blowdown Creek, CB = Cinnabar Basin, = Downton Creek = DT, Marriott Basin = MB, MC = McGillivray Creek, SP = Singing Pass, TC = Texas Creek).

Species	CODE	Site
Forbs		
Achillea millefolium L.	ACMI	BD, CB, DT, SP, TC
Agoseris aurantiaca (Hook.) Greene	AGAU	CB, DT, MB, MC, SP, TC
Agoseris glauca (Pursh) Raf.	AGGL	CB, SP, TC
Anemone occidentalis (S.Watson) Freyn	ANOC	BD, CB, DT, MB, MC, SP, TC
Antennaria alpina (L.) Gaertn.	ANAL	CB, SP, TC
Antennaria microphylla Rydb.	ANMI	BD, DT
Arabis drummondii A. Gray	ARDR	BD, MB, TC
Arabis lyallii S. Watson	ARLY	BD, CB, SP, TC
Arenaria capillaris Poir.	ARCA	DT
Arnica cordifolia Hook.	ARCO	BD, CB, DT, MB, MC, SP, TC
Arnica diversifolia E. Greene	ARDI	BD, CB, TC
Arnica latifolia Bong.	ARLA	MB
Arnica mollis Hook.	ARMO	CB, MB, MC, TC
Artemisia norvegica Fr.	ARNO	BD, CB, DT, MB, MC, TC
Aster modestus (Lindl.) G. L. Nesom	ASMO	TC
Caltha leptosepala DC.	CALE	MB
Castilleja miniata Douglas ex Hook.	CAMI	BD, CB, MB, SP, TC
Castilleja parviflora Bong. *var. albida* (Pennell) Ownbey	CAPA	MC
Cerastium arvense L.	CEAR	CB
Cerastium beeringianum Cham. & Schltdl.	CEBE	DT, MB, MC
Chamerion angustifolium (L.) Holub	CHAN	BD, CB, DT, MB, MC, SP, TC
Chamerion latifolium (L.) Holub	CHLA	CB
Cirsium edule Nutt.	CIED	MB
Claytonia lanceolata Pall. ex Pursh	CLLA	BD, CB, DT, MB, MC, SP
Delphinium menziesii DC.	DEME	CB, TC
Draba albertina Greene	DRAL	BD, CB, MB, MC
Epilobium anagallidifolium Lam.	EPAN	CB, SP, TC
Erigeron humilis Graham	ERHU	CB, DT
Erigeron peregrinus (Banks ex Pursh) Greene	ERPE	BD, CB, DT, MB, MC, SP, TC
Erythronium grandiflorum Pursh	ERGR	BD, DT, MB, MC, TC
Fragaria virginiana Duchesne	FRVI	TC
Heracleum maximum Bartram	HEMA	MC
Hieracium gracile Hook.	HIGR	SP
Lithophragma parviflorum (Hook.) Nutt. ex Torr. & A. Gray	LIPA	MB
Lupinus arcticus S. Watson	LUAR	CB, MC, TC
Lupinus nootkatensis Donn ex Sims	LUNO	BD, DT, MB, SP
Mimulus lewisii Pursh	MILE	MB
Minuartia rubella (Wahlenb.) Hiern.	MIRU	BD, CB, DT, TC
Mitella pentandra Hook.	MIPE	MB, SP
Myosotis laxa Lehm.	MYLA	CB
Myosotis scorpioides L.	MYSC	TC
Pedicularis bracteosa Benth.	PEBR	BD, CB, DT, MB, MC, SP, TC
Platanthera hyperborea (L.) Lindl.	PLHY	MB

Polemonium pulcherrimum Hook.	POPU	CB
Polemonium viscosum Nutt.	POVI	DT
Polygonum douglasii Greene	PODO	TC
Potentilla diversifolia Lehm.	PODI	BD, CB, DT, SP, TC
Potentilla flabellifolia Hook. ex Torr. & A. Gray	POFL	BD, MB, MC, SP, TC
Ranunculus eschscholtzii Schltdl.	RAES	BD, CB, DT, MB, MC, SP, TC
Saxifraga caespitosa L.	SACA	CB
Saxifraga occidentalis S. Watson	SAOC	CB, MB
Sedum divergens S. Watson	SEDI	MB
Sedum lanceolatum Torr.	SELA	CB, DT, TC
Senecio integerrimus Nutt.	SEIN	BD, CB, DT, MB, MC, TC
Senecio triangularis Hook.	SETR	CB, MB, MC, SP
Silene acaulis (L.) Jacq.	SIAC	CB
Silene douglasii Hook.	SIDO	CB, DT, SP, TC
Solidago multiradiata Aiton	SOMU	BD, CB, DT, MB, SP, TC
Thalictrum occidentale A. Gray	THOC	BD, CB, DT, MB, MC, TC
Tonestus lyallii (A. Gray) A. Nelson	TOLY	TC
Trollius laxus Salisb.	TRLA	DT, MB
Valeriana sitchensis Bong.	VASI	BD, CB, DT, MB, MC, SP, TC
Veratrum viride Aiton	VEVI	MB, MC, SP, TC
Veronica wormskjoldii Roem. & Schult.	VEWO	DT, MB
Viola glabella Nutt.	VIGL	MB
Graminoids		
Agrostis humilis Vasey	AGHU	CB
Bromus sitchensis Trin.	BRSI	TC
Carex hoodii Boott	CAHO	TC
Carex macrochaeta C. A. Mey.	CAMA	MB
Carex nigricans C. A. Mey.	CANI	CB, DT, MC, SP
Carex phaeocephala Piper	CAPH	CB, MB, MC, SP, TC
Carex podocarpa R. Br.	CAPO	MC, SP
Carex rossii Boott	CARO	BD, MB, TC
Carex spectabilis Dewey	CASP	BD, CB, DT, SP, TC
Deschampsia cespitosa (L.) P. Beauv.	DECE	SP, TC
Elymus elymoides (Raf.) Swezey	ELEL	TC
Elymus glaucus Buckley	ELGL	MC
Elymus trachycaulus (Link) Gould ex Shinners	ELTR	CB
Festuca brachyphylla Schult. ex Schult. & Schult. f.	FEBR	CB, DT
Juncus drummondii E. Mey.	JUDR	BD, MB, TC
Luzula arcuata (Wahlenb.) Sw.	LUZA	MB, TC
Luzula hitchcockii Hämet-Ahti	LUHI	BD, CB, DT
Luzula piperi (Coville) M. E. Jones	LUPI	SP
Luzula spicata (L.) DC.	LUSP	BD, CB, DT
Phleum alpinum L.	PHAL	CB, DT, MB, MC, SP, TC
Poa abbreviata R. Br.	POAB	CB, DT
Poa alpina L.	POAL	CB, TC
Poa cusickii Vasey	POCU	BD, DT, MB, MC, SP, TC
Trisetum spicatum (L.) K. Richt.	TRSP	BD, CB, DT, MC, MC, SP, TC
Woody Species		
Cassiope mertensiana (Bong.) G. Don	CAME	DT, MB
Eriogonum umbellatum Torr.	ERUM	BD, CB, TC
Luetkea pectinata (Pursh) Kuntze	LUPE	BD, MB, SP, TC
Orthilia secunda (L.) House	ORSE	MB
Penstemon procerus Douglas ex Graham	PEPR	BD, CB, MB, SP, TC
Phacelia sericea (Graham) A. Gray	PHSE	CB
Phlox diffusa Benth.	PHDI	BD, DT, MB, SP, TC
Phyllodoce empetriformis (Sm.) D. Don	PHEM	DT, TC

Phyllodoce glanduliflora (Hook.) Coville	PHGL	MB
Sibbaldia procumbens L.	SIPR	BD, CB, DT, MB, SP
Vaccinium caespitosum Michx.	VACA	DT
Vaccinium scoparium Leiberg ex Coville	VASC	TC

Appendix III – Plot Variables

Table 1: Geographic location, species richness and environmental parameters recorded at each study plot in southwestern British Columbia. Methods for measuring environmental variables are outlined in Table 4. MAT, MAP & LOI were removed prior to analysis due to high collinearity with other variables (see section 2.2.5). Abbreviations (Lat = Latitude; Long = Longitude; SR = Species Richness; Slo = Slope; Elev = Elevation; SI.S = Sun Index, South; SI.E = Sun Index, East; Acc = Accessibility; MAT = Mean Annual Temperature; MAP = Mean Annual Precipitation; MST = Mean Summer Temperature (May-Sept); MSP = Mean Summer Precipitation (May-Sept); SMo = Soil Moisture; LOI = Soil Organic Matter; N = Total Nitrogen; P = Available Phosphorus; C/N = Total Carbon/Total Nitrogen Ratio).

Plot	Lat (°)	Long (°)	SR	Elev (m)	Slo (°)	SI.S	SI.S	Acc	MAT (°C)	MAP (mm)	MST (°C)	MSP (mm)	pH	SMo (%)	LOI (%)	N (%)	P (mg/ Kg)	C/N
BD1	50°21972	122°09782	19	2127	30	-0.98	0.08	17	-0.2	1013	7.3	279	5.20	14.6	10	0.31	16.4	15.0
BD2	50°21975	122°09845	31	2125	31	0.29	0.28	17	-0.2	1013	7.3	279	5.25	19.9	14	0.53	16.5	13.7
BD3	50°21983	122°09901	23	2122	30	0.70	0.69	17	-0.2	1013	7.3	279	5.29	16.6	11	0.40	20.7	14.7
BD4	50°21989	122°09959	27	2132	31	-0.38	0.14	17	-0.2	1013	7.3	279	5.91	20.7	13	0.48	23.0	14.4
BD5	50°21996	122°10017	23	2141	31	0.19	-0.35	17	-0.2	1013	7.3	279	5.63	19.4	14	0.51	22.2	13.7
BD6	50°22008	122°10069	25	2141	30	-0.47	-0.87	17	-0.2	1013	7.3	279	5.12	17.7	13	0.40	13.0	15.5
BD7	50°22015	122°10128	26	2138	30	-0.47	-0.87	17	-0.2	1013	7.3	279	5.22	18.6	13	0.43	15.5	14.5
CB1	50°57726	122°49392	27	2077	21	-0.16	-0.82	20	-1.4	806	5.8	260	4.67	12.3	9	0.30	115.6	13.4
CB2	50°57762	122°49411	35	2088	25	-0.04	-0.13	20	-1.4	806	5.8	260	5.47	7.1	10	0.39	34.5	13.7
CB3	50°57804	122°49451	24	2086	27	-0.69	0.67	20	-1.4	806	5.8	260	5.23	10.3	12	0.47	18.4	13.7
CB4	50°5783	122°49493	32	2093	26	0.72	-0.26	20	-1.4	806	5.8	260	5.59	7.3	8	0.32	16.0	12.6
CB5	50°57862	122°49528	32	2084	24	0.88	0.21	20	-1.4	806	5.8	260	5.15	10.3	12	0.40	35.5	13.8
CB6	50°57877	122°49583	25	2082	33	0.93	-0.35	20	-1.4	806	5.8	260	5.68	10.5	11	0.42	9.1	12.7
CB7	50°57878	122°49639	29	2106	24	0.90	0.06	20	-1.4	806	5.8	260	5.49	15.2	16	0.59	16.2	13.6
DT1	50°34987	122°16266	23	2127	9	0.39	-0.15	15	-0.3	747	7.2	232	4.87	26.6	15	0.52	9.8	14.6
DT2	50°34985	122°16323	22	2104	10	0.51	0.18	15	-0.3	747	7.2	232	4.87	40.8	18	0.59	12.3	15.8
DT3	50°34984	122°16376	22	2110	9	-0.41	-0.03	15	-0.3	747	7.2	232	4.75	64.6	27	0.90	18.3	15.4
DT4	50°34995	122°16429	27	2116	8	0.20	-0.97	15	-0.3	747	7.2	232	4.66	62.0	28	0.90	9.5	16.0
DT5	50°35018	122°16496	21	2118	7	0.58	-0.31	15	-0.3	747	7.2	232	4.66	46.5	24	0.78	15.6	15.8
DT6	50°35033	122°16554	24	2128	10	0.53	-0.12	15	-0.3	747	7.2	232	4.50	83.3	37	1.25	14.2	15.4
DT7	50°35031	122°16611	27	2128	11	0.48	-0.88	15	-0.3	747	7.2	232	4.59	89.1	36	1.27	30.1	15.0
MB1	50°25978	122°27851	32	2041	36	0.48	-0.87	18	-0.4	1049	6.5	304	4.98	21.7	13	0.54	10.3	13.5

MB2	50°25967	122°27787	23	2041	36	0.60	-0.79	18	-0.4	1049	6.5	304	4.98	19.5	13	0.42	9.3	14.4
MB3	50°25958	122°27729	27	2041	40	-0.59	-0.45	18	-0.4	1049	6.5	304	4.86	16.3	13	0.47	18.5	14.3
MB4	50°25929	122°27625	34	2061	39	-0.90	0.33	18	-0.4	1049	6.5	304	4.97	57.6	20	0.70	7.4	15.7
MB5	50°25913	122°27571	31	2037	40	0.45	-0.60	18	-0.4	1049	6.5	304	5.33	61.1	19	0.73	9.2	13.4
MB6	50°25898	122°27517	23	2041	40	0.66	-0.35	18	-0.4	1049	6.5	304	5.09	20.4	14	0.49	10.2	13.7
MB7	50°2588	122°27469	23	2041	41	0.13	0.10	18	-0.4	1049	6.5	304	5.29	32.7	12	0.51	10.5	12.3
MC1	50°4113	122°34763	19	1991	26	0.54	-0.54	15	-0.3	831	6.7	215	5.02	34.5	16	0.59	23.1	13.0
MC2	50°4121	122°34808	17	2062	26	-0.72	0.26	15	-0.3	831	6.7	215	4.80	36.7	19	0.67	16.7	14.2
MC3	50°41223	122°34864	17	2061	25	0.03	0.13	15	-0.3	831	6.7	215	4.82	44.1	17	0.60	27.1	14.8
MC4	50°41261	122°34903	20	2043	25	-0.13	0.01	15	-0.3	831	6.7	215	4.98	47.6	18	0.65	19.1	13.4
MC5	50°41272	122°34957	17	2067	26	0.45	0.61	15	-0.3	831	6.7	215	5.22	37.9	16	0.61	19.5	13.5
MC6	50°41288	122°35013	22	2061	29	-0.39	-0.54	15	-0.3	831	6.7	215	5.51	29.9	13	0.50	10.2	13.5
MC7	50°41311	122°35069	20	2062	30	-0.58	-0.80	15	-0.3	831	6.7	215	5.21	39.1	16	0.58	19.1	13.9
SP1	50°01793	122°52587	22	1960	23	-0.29	-0.80	18	0.7	2034	7.8	432	4.92	19.8	24	0.81	89.6	15.3
SP2	50°0181	122°52615	20	1960	20	0.54	0.74	18	0.7	2034	7.8	432	4.59	17.7	22	0.75	54.3	15.3
SP3	50°01829	122°52653	23	1966	17	0.35	-0.90	18	0.7	2034	7.8	432	4.54	16.2	15	0.51	17.3	14.4
SP4	50°01849	122°52739	15	1952	16	-0.13	-0.26	18	0.7	2034	7.8	432	4.49	17.8	19	0.67	74.7	15.3
SP5	50°01864	122°52773	25	1944	15	-0.04	-0.65	18	0.7	2034	7.8	432	4.76	20.9	29	1.01	68.5	15.5
SP6	50°01883	122°52807	19	1935	14	0.97	0.22	18	0.7	2034	7.8	432	4.52	14.2	17	0.59	41.6	15.2
SP7	50°01908	122°52834	15	1925	16	0.27	0.11	18	0.7	2034	7.8	432	4.44	16.4	13	0.49	25.6	14.0
TC1	50°26085	121°59839	29	2082	33	0.58	-0.81	13	0	1223	7	346	5.35	8.8	14	0.63	24.2	14.9
TC2	50°26096	121°59799	27	2082	32	0.18	-0.52	13	0	1223	7	346	5.61	6.5	12	0.45	14.1	15.1
TC3	50°26107	121°59763	29	2091	32	0.54	-0.13	13	0	1223	7	346	5.41	10.9	18	0.58	42.2	13.4
TC4	50°2612	121°59719	33	2089	25	0.03	-0.13	13	0	1223	7	346	5.22	7.1	13	0.52	50.5	14.9
TC5	50°26147	121°59637	37	2090	35	0.25	-0.35	13	0	1223	7	346	5.02	8.4	12	0.40	23.4	15.3
TC6	50°26169	121°5962	29	2073	31	0.25	0.31	13	0	1223	7	346	5.10	16.1	21	0.69	33.6	15.0

Appendix IV – Raw Data

Table 1: Untransformed presence-absence matrix (0 = Absent; 1 = Present). The columns list species (full species names are outlined in Table 9), and the rows 100 m^2 plots (sites: BD = Blowdown Creek, CB = Cinnabar Basin, = Downton Creek = DT, Marriott Basin = MB, MC = McGillivray Creek, SP = Singing Pass, TC = Texas Creek).

Life Form	Forbs									
Species Plots	ACMI	AGAU	AGGL	ANAL	ANMI	ANOC	ARCA	ARCO	ARDI	ARDR
BD1	0	0	0	0	1	1	0	0	1	0
BD2	1	0	0	0	1	1	0	0	1	0
BD3	0	0	0	0	0	1	0	0	1	0
BD4	1	0	0	0	0	1	0	1	1	1
BD5	1	0	0	0	0	0	0	0	0	1
BD6	1	0	0	0	0	1	0	0	1	0
BD7	1	0	0	0	0	1	0	0	1	1
CB1	0	1	0	0	0	1	0	1	1	0
CB2	1	1	1	1	0	1	0	1	1	0
CB3	1	1	1	0	0	1	0	0	1	0
CB4	1	0	1	1	0	1	0	0	1	0
CB5	1	1	1	1	0	1	0	0	1	0
CB6	1	1	1	1	0	1	0	0	1	0
CB7	1	1	1	0	0	0	0	0	1	0
DT1	1	0	0	0	1	1	0	1	0	0
DT2	1	0	0	0	1	0	0	0	0	0
DT3	1	0	0	0	0	0	0	0	0	0
DT4	0	1	0	0	0	1	1	1	0	0
DT5	1	0	0	0	1	1	0	0	0	0
DT6	0	1	0	0	0	0	1	1	0	0
DT7	0	0	0	0	0	0	1	1	0	0
MB1	0	1	0	0	0	1	0	1	0	1
MB2	0	1	0	0	0	1	0	1	0	0
MB3	0	1	0	0	0	1	0	1	0	1
MB4	0	1	0	0	0	1	0	1	0	0
MB5	0	1	0	0	0	1	0	1	0	0
MB6	0	1	0	0	0	1	0	1	0	1
MB7	0	1	0	0	0	0	0	1	0	1
MC1	0	0	0	0	0	1	0	1	0	0
MC2	0	1	0	0	0	1	0	1	0	0
MC3	0	1	0	0	0	1	0	1	0	0
MC4	0	0	0	0	0	0	0	1	0	0

MC5	0	1	0	0	0	1	0	1	0	0
MC6	0	1	0	0	0	1	0	1	0	0
MC7	0	1	0	0	0	1	0	1	0	0
SP1	0	1	0	0	0	0	0	0	0	0
SP2	0	1	1	0	0	0	0	0	0	0
SP3	0	1	1	1	0	1	0	0	0	0
SP4	0	1	0	0	0	0	0	1	0	0
SP5	1	1	1	0	0	0	0	1	0	0
SP6	0	0	0	0	0	0	0	1	0	0
SP7	0	0	0	0	0	0	0	1	0	0
TC1	1	0	1	1	0	0	0	0	0	0
TC2	1	0	1	1	0	0	0	0	0	0
TC3	1	0	1	0	0	1	0	0	0	1
TC4	1	0	1	0	0	0	0	0	1	1
TC5	1	0	1	1	0	1	0	1	0	0
TC6	1	1	0	0	0	1	0	1	0	1
Plot Species	ACMI	AGAU	AGGL	ANAL	ANMI	ANOC	ARCA	ARCO	ARDI	ARDR

Life Form	Forbs									
Species Plots	ARLA	ARLY	ARMO	ARNO	ASMO	CALE	CAMI	CAPA	CEAR	CEBE
BD1	0	0	0	1	0	0	0	0	0	0
BD2	0	1	0	1	0	0	1	0	0	0
BD3	0	0	0	1	0	0	1	0	0	0
BD4	0	0	0	1	0	0	1	0	0	0
BD5	0	0	0	1	0	0	0	0	0	0
BD6	0	1	0	1	0	0	1	0	0	0
BD7	0	1	0	1	0	0	1	0	0	0
CB1	0	1	0	1	0	0	0	0	0	0
CB2	0	1	1	1	0	0	0	0	1	0
CB3	0	0	0	1	0	0	1	0	0	0
CB4	0	1	0	1	0	0	0	0	1	0
CB5	0	1	0	1	0	0	0	0	1	0
CB6	0	0	0	1	0	0	0	0	1	0
CB7	0	0	0	1	0	0	0	0	1	0
DT1	0	0	0	1	0	0	0	0	0	0
DT2	0	0	0	1	0	0	0	0	0	1
DT3	0	0	0	1	0	0	0	0	0	1
DT4	0	0	0	1	0	0	0	0	0	0
DT5	0	0	0	1	0	0	0	0	0	0
DT6	0	0	0	1	0	0	0	0	0	0
DT7	0	0	0	1	0	0	0	0	0	1
MB1	1	0	1	1	0	0	0	0	0	1
MB2	1	0	0	1	0	0	0	0	0	1

MB3	1	0	1	1	0	0	0	0	0	1
MB4	0	0	1	1	0	1	1	0	0	1
MB5	1	0	1	1	0	0	1	0	0	1
MB6	0	0	0	1	0	0	0	0	0	1
MB7	0	0	0	1	0	0	0	0	0	1
MC1	0	0	1	0	0	0	0	0	0	0
MC2	0	0	0	1	0	0	0	1	0	0
MC3	0	0	0	0	0	0	0	0	0	0
MC4	0	0	0	1	0	0	0	0	0	0
MC5	0	0	0	1	0	0	0	0	0	0
MC6	0	0	1	1	0	0	0	0	0	0
MC7	0	0	1	1	0	0	0	0	0	1
SP1	0	1	0	0	0	0	1	0	0	0
SP2	0	0	0	0	0	0	1	0	0	0
SP3	0	0	0	0	0	0	1	0	0	0
SP4	0	0	0	0	0	0	0	0	0	0
SP5	0	0	0	0	0	0	1	0	0	0
SP6	0	0	0	0	0	0	0	0	0	0
SP7	0	0	0	0	0	0	0	0	0	0
TC1	0	1	1	0	0	0	1	0	0	0
TC2	0	0	1	0	1	0	1	0	0	0
TC3	0	0	1	0	1	0	0	0	0	0
TC4	0	1	1	0	1	0	1	0	0	0
TC5	0	0	1	1	0	0	1	0	0	0
TC6	0	0	0	1	0	0	0	0	0	0
Plot Species	ARLA	ARLY	ARMO	ARNO	ASMO	CALE	CAMI	CAPA	CEAR	CEBE

Life Form	Forbs									
Species Plots	CHAN	CHLA	CIED	CLLA	DEME	DRAL	EPAN	ERGR	ERHU	ERPE
BD1	0	0	0	1	0	0	0	0	0	1
BD2	1	0	0	1	0	1	0	1	0	1
BD3	1	0	0	1	0	0	0	1	0	1
BD4	1	0	0	1	0	0	0	1	0	1
BD5	1	0	0	1	0	0	0	1	0	1
BD6	0	0	0	1	0	0	0	1	0	1
BD7	1	0	0	1	0	0	0	1	0	1
CB1	0	0	0	1	0	1	1	0	1	1
CB2	0	1	0	0	1	0	0	0	0	1
CB3	1	0	0	0	0	0	0	0	0	1
CB4	0	0	0	0	0	0	0	0	0	1
CB5	0	0	0	0	0	0	0	0	0	1
CB6	1	0	0	0	0	0	0	0	0	1
CB7	1	0	0	1	1	0	0	0	0	1

DT1	0	0	0	1	0	0	0	1	0	1
DT2	1	0	0	1	0	0	0	0	0	1
DT3	0	0	0	1	0	0	0	0	0	1
DT4	0	0	0	1	0	0	0	0	1	1
DT5	0	0	0	1	0	0	0	0	1	1
DT6	0	0	0	1	0	0	0	0	1	1
DT7	0	0	0	1	0	0	0	0	0	1
MB1	1	0	0	1	0	1	0	1	0	1
MB2	0	0	0	1	0	0	0	1	0	1
MB3	0	0	0	1	0	0	0	1	0	1
MB4	0	0	0	1	0	0	0	1	0	1
MB5	1	0	0	1	0	1	0	1	0	1
MB6	1	0	0	1	0	1	0	1	0	1
MB7	1	0	1	1	0	1	0	1	0	1
MC1	1	0	0	1	0	0	0	1	0	1
MC2	0	0	0	1	0	0	0	1	0	1
MC3	0	0	0	1	0	0	0	1	0	1
MC4	0	0	0	1	0	0	0	1	0	1
MC5	0	0	0	1	0	0	0	1	0	1
MC6	0	0	0	1	0	0	0	1	0	1
MC7	0	0	0	1	0	1	0	1	0	1
SP1	1	0	0	0	0	0	1	0	0	1
SP2	0	0	0	0	0	0	0	0	0	1
SP3	0	0	0	1	0	0	0	0	0	1
SP4	1	0	0	1	0	0	0	0	0	1
SP5	0	0	0	1	0	0	0	0	0	1
SP6	0	0	0	1	0	0	0	0	0	1
SP7	0	0	0	1	0	0	0	0	0	1
TC1	1	0	0	0	1	0	0	1	0	1
TC2	1	0	0	0	1	0	0	1	0	1
TC3	1	0	0	0	1	0	0	1	0	1
TC4	1	0	0	0	1	0	1	1	0	1
TC5	1	0	0	0	1	0	0	1	0	1
TC6	0	0	0	0	0	0	0	1	0	1
Plot Species	CHAN	CHLA	CIED	CLLA	DEME	DRAL	EPAN	ERGR	ERHU	ERPE

Life Form	Forbs									
Species Plots	FRVI	HEMA	HIGR	LIPA	LUAR	LUNO	MILE	MIPE	MIRU	MYLA
BD1	0	0	0	0	0	1	0	0	1	0
BD2	0	0	0	0	0	1	0	0	1	0
BD3	0	0	0	0	0	1	0	0	1	0
BD4	0	0	0	0	0	1	0	0	1	0
BD5	0	0	0	0	0	1	0	0	1	0

BD6	0	0	0	0	0	1	0	0	1	0
BD7	0	0	0	0	0	1	0	0	1	0
CB1	0	0	0	0	1	0	0	0	1	0
CB2	0	0	0	0	1	0	0	0	1	1
CB3	0	0	0	0	1	0	0	0	1	0
CB4	0	0	0	0	1	0	0	0	1	1
CB5	0	0	0	0	1	0	0	0	1	1
CB6	0	0	0	0	1	0	0	0	1	1
CB7	0	0	0	0	1	0	0	0	1	1
DT1	0	0	0	0	0	1	0	0	1	0
DT2	0	0	0	0	0	1	0	0	1	0
DT3	0	0	0	0	0	1	0	0	1	0
DT4	0	0	0	0	0	1	0	0	1	0
DT5	0	0	0	0	0	1	0	0	1	0
DT6	0	0	0	0	0	1	0	0	1	0
DT7	0	0	0	0	0	1	0	0	1	0
MB1	0	0	0	0	0	1	0	0	0	0
MB2	0	0	0	0	0	1	0	0	0	0
MB3	0	0	0	0	0	1	0	0	0	0
MB4	0	0	0	0	0	1	0	0	0	0
MB5	0	0	0	0	0	1	1	1	0	0
MB6	0	0	0	0	0	1	0	0	0	0
MB7	0	0	0	1	0	1	0	0	0	0
MC1	0	1	0	0	1	0	0	0	0	0
MC2	0	0	0	0	1	0	0	0	0	0
MC3	0	0	0	0	1	0	0	0	0	0
MC4	0	1	0	0	1	0	0	0	0	0
MC5	0	1	0	0	1	0	0	0	0	0
MC6	0	1	0	0	1	0	0	0	0	0
MC7	0	1	0	0	1	0	0	0	0	0
SP1	0	0	0	0	0	1	0	0	0	0
SP2	0	0	1	0	0	1	0	0	0	0
SP3	0	0	1	0	0	1	0	0	0	0
SP4	0	0	1	0	0	1	0	0	0	0
SP5	0	0	1	0	0	1	0	0	0	0
SP6	0	0	1	0	0	1	0	1	0	0
SP7	0	0	1	0	0	1	0	1	0	0
TC1	1	0	0	0	1	0	0	0	1	0
TC2	1	0	0	0	1	0	0	0	1	0
TC3	0	0	0	0	1	0	0	0	1	0
TC4	0	0	0	0	1	0	0	0	1	0
TC5	0	0	0	0	1	0	0	0	1	0
TC6	0	0	0	0	1	0	0	0	1	0
Plot Species	FRVI	HEMA	HIGR	LIPA	LUAR	LUNO	MILE	MIPE	MIRU	MYLA

Life Form	Forbs									
Species Plots	MYSC	PEBR	PLHY	PODI	PODO	POFL	POPU	POVI	RAES	SACA
BD1	0	0	0	0	0	1	0	0	0	0
BD2	0	1	0	1	0	1	0	0	1	0
BD3	0	1	0	0	0	1	0	0	1	0
BD4	0	0	0	1	0	1	0	0	1	0
BD5	0	1	0	1	0	1	0	0	1	0
BD6	0	1	0	1	0	1	0	0	0	0
BD7	0	1	0	1	0	1	0	0	0	0
CB1	0	1	0	0	0	0	0	0	1	0
CB2	0	1	0	1	0	0	1	0	1	0
CB3	0	0	0	1	0	0	1	0	0	0
CB4	0	0	0	1	0	0	1	0	0	1
CB5	0	1	0	1	0	0	1	0	0	0
CB6	0	1	0	1	0	0	1	0	0	0
CB7	0	0	0	1	0	0	1	0	0	0
DT1	0	0	0	1	0	0	0	0	0	0
DT2	0	1	0	1	0	0	0	1	0	0
DT3	0	0	0	1	0	0	0	0	0	0
DT4	0	1	0	1	0	0	0	0	0	0
DT5	0	1	0	1	0	0	0	0	0	0
DT6	0	1	0	1	0	0	0	0	1	0
DT7	0	1	0	1	0	0	0	1	1	0
MB1	0	1	0	0	0	1	0	0	1	0
MB2	0	1	0	0	0	1	0	0	0	0
MB3	0	1	0	0	0	1	0	0	0	0
MB4	0	1	1	0	0	1	0	0	0	0
MB5	0	1	1	0	0	1	0	0	1	0
MB6	0	1	0	0	0	1	0	0	0	0
MB7	0	1	0	0	0	1	0	0	1	0
MC1	0	1	0	0	0	1	0	0	0	0
MC2	0	1	0	0	0	1	0	0	0	0
MC3	0	1	0	0	0	1	0	0	0	0
MC4	0	1	0	0	0	1	0	0	1	0
MC5	0	1	0	0	0	1	0	0	0	0
MC6	0	1	0	0	0	1	0	0	0	0
MC7	0	1	0	0	0	1	0	0	0	0
SP1	0	1	0	0	0	1	0	0	1	0
SP2	0	1	0	0	0	1	0	0	1	0
SP3	0	1	0	0	0	1	0	0	0	0
SP4	0	0	0	0	0	1	0	0	0	0
SP5	0	1	0	1	0	1	0	0	1	0
SP6	0	1	0	0	0	1	0	0	0	0

SP7	0	0	0	0	0	1	0	0	0	0
TC1	1	0	0	1	0	0	0	0	0	0
TC2	0	0	0	1	0	0	0	0	0	0
TC3	1	1	0	1	0	0	0	0	0	0
TC4	0	1	0	1	0	0	0	0	0	0
TC5	0	1	0	1	1	1	0	0	0	0
TC6	0	1	0	0	0	1	0	0	1	0
Plot Species	MYSC	PEBR	PLHY	PODI	PODO	POFL	POPU	POVI	RAES	SACA

Life Form	Forbs									
Species Plots	SAOC	SEDI	SEIN	SELA	SETR	SIAC	SIDO	SOMU	THOC	TOLY
BD1	0	0	1	0	0	0	0	1	0	0
BD2	0	0	1	0	0	0	0	1	1	0
BD3	0	0	1	0	0	0	0	1	0	0
BD4	0	0	1	0	0	0	0	1	0	0
BD5	0	0	1	0	0	0	0	0	1	0
BD6	0	0	1	0	0	0	0	1	0	0
BD7	0	0	1	0	0	0	0	0	0	0
CB1	0	0	1	1	0	0	1	0	0	0
CB2	0	0	1	1	1	0	1	1	0	0
CB3	0	0	1	0	0	0	1	1	1	0
CB4	1	0	0	1	0	1	1	1	0	0
CB5	1	0	1	1	0	0	1	1	0	0
CB6	0	0	0	0	0	0	1	1	0	0
CB7	1	0	1	1	0	0	1	1	1	0
DT1	0	0	1	1	0	0	1	1	1	0
DT2	0	0	1	1	0	0	1	0	1	0
DT3	0	0	1	1	0	0	1	1	0	0
DT4	0	0	1	1	0	0	0	1	0	0
DT5	0	0	0	1	0	0	0	1	0	0
DT6	0	0	0	1	0	0	0	0	0	0
DT7	0	0	1	1	0	0	1	0	0	0
MB1	0	1	1	0	0	0	0	1	1	0
MB2	0	0	1	0	0	0	0	1	0	0
MB3	0	1	0	0	0	0	0	1	0	0
MB4	1	1	0	0	0	0	0	0	0	0
MB5	0	0	0	0	1	0	0	0	0	0
MB6	0	0	0	0	0	0	0	1	0	0
MB7	0	0	0	0	1	0	0	0	0	0
MC1	0	0	0	0	1	0	0	0	1	0
MC2	0	0	0	0	1	0	0	0	0	0
MC3	0	0	0	0	1	0	0	0	0	0
MC4	0	0	1	0	1	0	0	0	0	0

MC5	0	0	0	0	1	0	0	0	0	0
MC6	0	0	1	0	0	0	0	0	1	0
MC7	0	0	0	0	1	0	0	0	0	0
SP1	0	0	0	0	1	0	1	1	0	0
SP2	0	0	0	0	1	0	1	1	0	0
SP3	0	0	0	0	1	0	1	1	0	0
SP4	0	0	0	0	0	0	0	0	0	0
SP5	0	0	0	0	1	0	1	0	0	0
SP6	0	0	0	0	1	0	1	0	0	0
SP7	0	0	0	0	0	0	0	0	0	0
TC1	0	0	1	0	0	0	1	1	1	0
TC2	0	0	0	0	0	0	1	1	1	0
TC3	0	0	1	0	0	0	1	1	1	0
TC4	0	0	1	1	0	0	1	1	1	0
TC5	0	0	1	0	0	0	1	1	1	1
TC6	0	0	1	0	0	0	1	0	1	0
Plot Species	SAOC	SEDI	SEIN	SELA	SETR	SIAC	SIDO	SOMU	THOC	TOLY

Life Form	Forbs					Graminoids				
Species Plots	TRLA	VASI	VEVI	VEWO	VIGL	AGHU	BRSI	CAHO	CAMA	CANI
BD1	0	0	0	0	0	0	0	0	0	0
BD2	0	1	0	0	0	0	0	0	0	0
BD3	0	1	0	0	0	0	0	0	0	0
BD4	0	1	0	0	0	0	0	0	0	0
BD5	0	1	0	0	0	0	0	0	0	0
BD6	0	1	0	0	0	0	0	0	0	0
BD7	0	1	0	0	0	0	0	0	0	0
CB1	0	1	0	0	0	0	0	0	0	1
CB2	0	1	0	0	0	0	0	0	0	0
CB3	0	0	0	0	0	0	0	0	0	0
CB4	0	0	0	0	0	1	0	0	0	0
CB5	0	0	0	0	0	0	0	0	0	1
CB6	0	0	0	0	0	0	0	0	0	0
CB7	0	0	0	0	0	0	0	0	0	0
DT1	0	1	0	0	0	0	0	0	0	1
DT2	0	0	0	0	0	0	0	0	0	0
DT3	0	0	0	1	0	0	0	0	0	1
DT4	0	0	0	1	0	0	0	0	0	1
DT5	0	0	0	0	0	0	0	0	0	0
DT6	0	1	0	1	0	0	0	0	0	1
DT7	1	1	0	1	0	0	0	0	0	1
MB1	0	1	0	0	0	0	0	0	1	0
MB2	0	1	0	1	0	0	0	0	1	0

MB3	0	1	0	0	0	0	0	0	1	0
MB4	1	1	1	1	0	0	0	0	1	0
MB5	1	1	0	1	0	0	0	0	1	0
MB6	0	1	0	0	0	0	0	0	1	0
MB7	0	1	0	0	1	0	0	0	1	0
MC1	0	1	1	0	0	0	0	0	0	0
MC2	0	1	0	0	0	0	0	0	0	0
MC3	0	1	1	0	0	0	0	0	0	1
MC4	0	1	1	0	0	0	0	0	0	0
MC5	0	1	0	0	0	0	0	0	0	0
MC6	0	1	1	0	0	0	0	0	0	0
MC7	0	1	0	0	0	0	0	0	0	0
SP1	0	1	0	0	0	0	0	0	0	0
SP2	0	1	0	0	0	0	0	0	0	0
SP3	0	1	0	0	0	0	0	0	0	0
SP4	0	1	0	0	0	0	0	0	0	0
SP5	0	1	0	0	0	0	0	0	0	0
SP6	0	1	0	0	0	0	0	0	0	1
SP7	0	1	1	0	0	0	0	0	0	1
TC1	0	0	0	0	0	0	1	1	0	0
TC2	0	0	0	0	0	0	1	1	0	0
TC3	0	1	0	0	0	0	1	1	0	0
TC4	0	0	0	0	0	0	1	1	0	0
TC5	0	1	0	0	0	0	1	1	0	0
TC6	0	1	1	0	0	0	1	0	0	0
Plot Species	TRLA	VASI	VEVI	VEWO	VIGL	AGHU	BRSI	CAHO	CAMA	CANI

Life Form	Graminoids									
Species Plots	CAPH	CAPO	CARO	CASP	DECE	ELEL	ELGL	ELTR	FEBR	JUDR
BD1	0	0	1	0	0	0	0	0	0	1
BD2	0	0	0	1	0	0	0	0	0	1
BD3	0	0	1	0	0	0	0	0	0	1
BD4	0	0	1	1	0	0	0	0	0	1
BD5	0	0	1	0	0	0	0	0	0	1
BD6	0	0	1	1	0	0	0	0	0	1
BD7	0	0	1	1	0	0	0	0	0	1
CB1	1	0	0	1	0	0	0	0	0	0
CB2	1	0	0	0	0	0	0	1	1	0
CB3	1	0	0	0	0	0	0	0	0	0
CB4	1	0	0	1	0	0	0	0	1	0
CB5	1	0	0	1	0	0	0	0	1	0
CB6	1	0	0	0	0	0	0	0	1	0
CB7	1	0	0	1	0	0	0	1	0	0

DT1	0	0	0	1	0	0	0	0	0	0
DT2	0	0	0	1	0	0	0	0	0	0
DT3	0	0	0	1	0	0	0	0	0	0
DT4	0	0	0	1	0	0	0	0	1	0
DT5	0	0	0	1	0	0	0	0	0	0
DT6	0	0	0	0	0	0	0	0	1	0
DT7	0	0	0	1	0	0	0	0	1	0
MB1	1	0	0	0	0	0	0	0	0	1
MB2	1	0	1	0	0	0	0	0	0	0
MB3	1	0	1	0	0	0	0	0	0	1
MB4	1	0	1	0	0	0	0	0	0	1
MB5	1	0	0	0	0	0	0	0	0	1
MB6	0	0	1	0	0	0	0	0	0	0
MB7	0	0	0	0	0	0	0	0	0	0
MC1	1	1	0	0	0	0	1	0	0	0
MC2	0	1	0	0	0	0	0	0	0	0
MC3	0	1	0	0	0	0	0	0	0	0
MC4	1	1	0	0	0	0	1	0	0	0
MC5	0	1	0	0	0	0	0	0	0	0
MC6	1	1	0	0	0	0	1	0	0	0
MC7	0	1	0	0	0	0	1	0	0	0
SP1	0	0	0	1	1	0	0	0	0	0
SP2	0	0	0	1	0	0	0	0	0	0
SP3	1	0	0	1	0	0	0	0	0	0
SP4	0	0	0	1	1	0	0	0	0	0
SP5	1	0	0	1	1	0	0	0	0	0
SP6	0	0	0	1	1	0	0	0	0	0
SP7	0	1	0	0	1	0	0	0	0	0
TC1	1	0	0	0	1	0	0	0	0	1
TC2	1	0	0	0	0	1	0	0	0	1
TC3	1	0	0	0	0	1	0	0	0	0
TC4	1	0	1	0	0	0	0	0	0	1
TC5	1	0	1	0	0	0	0	0	0	1
TC6	1	0	1	1	1	0	0	0	0	0
Plot Species	CAPH	CAPO	CARO	CASP	DECE	ELEL	ELGL	ELTR	FEBR	JUDR

Life Form	Graminoids									Woody Species
Species Plots	LUHI	LUPI	LUSP	LUZA	PHAL	POAB	POAL	POCU	TRSP	CAME
BD1	0	0	1	0	0	0	0	1	1	0
BD2	1	0	1	0	0	0	0	1	1	0
BD3	0	0	0	0	0	0	0	1	1	0
BD4	0	0	1	0	0	0	0	1	1	0
BD5	0	0	0	0	0	0	0	1	1	0

BD6	0	0	0	0	0	0	0	1	1	0
BD7	0	0	0	0	0	0	0	1	1	0
CB1	1	0	0	0	1	1	0	0	1	0
CB2	0	0	0	0	1	1	0	0	1	0
CB3	0	0	0	0	1	1	1	0	1	0
CB4	0	0	1	0	0	1	1	0	1	0
CB5	1	0	1	0	1	1	0	0	1	0
CB6	1	0	0	0	0	1	1	0	1	0
CB7	0	0	0	0	1	1	1	0	1	0
DT1	0	0	0	0	0	0	0	1	1	0
DT2	1	0	0	0	0	0	0	1	1	0
DT3	1	0	1	0	1	0	0	1	1	0
DT4	0	0	1	0	1	0	0	1	0	1
DT5	0	0	1	0	1	1	0	1	0	0
DT6	0	0	1	0	1	0	0	1	1	0
DT7	1	0	0	0	1	0	0	1	0	0
MB1	0	0	0	1	1	0	0	1	1	0
MB2	0	0	0	1	0	0	0	1	1	0
MB3	0	0	0	1	0	0	0	1	1	0
MB4	0	0	0	1	1	0	0	1	1	1
MB5	0	0	0	1	1	0	0	1	1	0
MB6	0	0	0	1	0	0	0	1	1	0
MB7	0	0	0	0	1	0	0	1	0	0
MC1	0	0	0	0	0	0	0	1	0	0
MC2	0	0	0	0	1	0	0	1	1	0
MC3	0	0	0	0	1	0	0	1	1	0
MC4	0	0	0	0	1	0	0	1	1	0
MC5	0	0	0	0	1	0	0	1	1	0
MC6	0	0	0	0	1	0	0	1	1	0
MC7	0	0	0	0	0	0	0	1	1	0
SP1	0	0	0	0	1	0	0	1	1	0
SP2	0	0	0	0	1	0	0	1	1	0
SP3	0	0	0	0	1	0	0	1	1	0
SP4	0	1	0	0	1	0	0	1	0	0
SP5	0	0	0	0	1	0	0	1	1	0
SP6	0	1	0	0	1	0	0	1	0	0
SP7	0	0	0	0	1	0	0	1	1	0
TC1	0	0	0	0	1	0	0	1	1	0
TC2	0	0	0	0	0	0	1	1	1	0
TC3	0	0	0	0	1	0	1	1	1	0
TC4	0	0	0	0	1	0	1	1	1	0
TC5	0	0	0	1	1	0	0	1	1	0
TC6	0	0	0	0	1	0	1	1	1	0
Plot Species	LUHI	LUPI	LUSP	LUZA	PHAL	POAB	POAL	POCU	TRSP	CAME

Life Form	Woody Species										
Species Plots	ERUM	LUPE	ORSE	PEPR	PHDI	PHEM	PHGL	PHSE	SIPR	VACA	VASC
BD1	0	1	0	0	1	0	0	0	1	0	0
BD2	1	0	0	1	1	0	0	0	0	0	0
BD3	1	0	0	1	1	0	0	0	0	0	0
BD4	0	0	0	1	1	0	0	0	0	0	0
BD5	1	0	0	1	1	0	0	0	0	0	0
BD6	0	0	0	1	1	0	0	0	1	0	0
BD7	1	0	0	1	1	0	0	0	0	0	0
CB1	0	0	0	0	0	0	0	0	1	0	0
CB2	0	0	0	1	0	0	0	0	1	0	0
CB3	1	0	0	1	0	0	0	0	0	0	0
CB4	1	0	0	1	0	0	0	1	1	0	0
CB5	1	0	0	0	0	0	0	0	1	0	0
CB6	1	0	0	0	0	0	0	0	0	0	0
CB7	1	0	0	0	0	0	0	0	0	0	0
DT1	0	0	0	0	1	0	0	0	0	1	0
DT2	0	0	0	0	1	0	0	0	0	1	0
DT3	0	0	0	0	1	0	0	0	0	1	0
DT4	0	0	0	0	1	1	0	0	1	1	0
DT5	0	0	0	0	1	0	0	0	1	1	0
DT6	0	0	0	0	1	0	0	0	1	1	0
DT7	0	0	0	0	1	1	0	0	0	1	0
MB1	0	1	0	1	1	0	0	0	0	0	0
MB2	0	0	0	0	1	0	0	0	0	0	0
MB3	0	0	0	1	1	0	0	0	1	0	0
MB4	0	0	1	0	1	0	1	0	1	0	0
MB5	0	0	0	0	0	0	0	0	0	0	0
MB6	0	0	0	1	1	0	0	0	0	0	0
MB7	0	0	0	0	1	0	0	0	0	0	0
MC1	0	0	0	0	0	0	0	0	0	0	0
MC2	0	0	0	0	0	0	0	0	0	0	0
MC3	0	0	0	0	0	0	0	0	0	0	0
MC4	0	0	0	0	0	0	0	0	0	0	0
MC5	0	0	0	0	0	0	0	0	0	0	0
MC6	0	0	0	0	0	0	0	0	0	0	0
MC7	0	0	0	0	0	0	0	0	0	0	0
SP1	0	0	0	1	1	0	0	0	1	0	0
SP2	0	0	0	1	1	0	0	0	1	0	0
SP3	0	0	0	1	1	0	0	0	1	0	0
SP4	0	0	0	0	1	0	0	0	0	0	0
SP5	0	0	0	1	1	0	0	0	1	0	0
SP6	0	1	0	0	1	0	0	0	0	0	0

SP7	0	0	0	0	0	0	0	0	0	0	0
TC1	1	0	0	0	1	0	0	0	0	0	0
TC2	1	0	0	0	1	0	0	0	0	0	0
TC3	0	0	0	0	1	0	0	0	0	0	0
TC4	0	0	0	0	1	0	0	0	0	0	1
TC5	0	1	0	1	1	1	0	0	0	0	0
TC6	0	0	0	0	1	0	0	0	0	0	1
Plot Species	ERUM	LUPE	ORSE	PEPR	PHDI	PHEM	PHGL	PHSE	SIPR	VACA	VASC

Table 12: Untransformed abundance (% cover) matrix. The columns list species (full species names are outlined in Table 9), the rows plots (sites: BD = Blowdown Creek, CB = Cinnabar Basin, = Downton Creek = DT, Marriott Basin = MB, MC = McGillivray Creek, SP = Singing Pass, TC = Texas Creek), and the values represent the average percent cover of each species in each study plot (each value is an average from 4 1 m^2 subplots).

Life Form	Forbs									
Species Plots	ACMI	AGAU	AGGL	ANAL	ANMI	ANOC	ARCO	ARDI	ARDR	ARLA
BD1	0	0	0	0	0	2.75	0	1.75	0	0
BD2	0.5	0	0	0	0	0.125	0	1	0	0
BD3	0	0	0	0	0	0	0	2.25	0	0
BD4	0.25	0	0	0	0	0	0.25	0.25	0.125	0
BD5	0.75	0	0	0	0	0	0	0	0.125	0
BD6	0	0	0	0	0	0.25	0	1.75	0	0
BD7	0	0	0	0	0	0.25	0	0	0.125	0
CB1	0	1.75	0	0	0	15.5	9.75	2.5	0	0
CB2	0.75	2.25	0	0	0	3.5	0.125	5.125	0	0
CB3	5	6	8	0	0	4.75	0	7.75	0	0
CB4	1	0	1.625	2	0	0.125	0	4.5	0	0
CB5	0	0.375	3.75	0	0	2.5	0	0.25	0	0
CB6	6.5	0.5	3	1.25	0	0	0	2.25	0	0
CB7	16.25	5.75	1.375	0	0	0	0	2.5	0	0
DT1	0.625	0	0	0	0	10	2.75	0	0	0
DT2	1	0	0	0	0.25	0	0	0	0	0
DT3	0.875	0	0	0	0	0	0	0	0	0
DT4	0	0.375	0	0	0	0	0.5	0	0	0
DT5	0.25	0	0	0	0.5	0.5	0	0	0	0
DT6	0	0.125	0	0	0	0	0	0	0	0
DT7	0	0	0	0	0	0	1.5	0	0	0
MB1	0	0.5	0	0	0	1.75	1.25	0	0.25	0.25
MB2	0	0.875	0	0	0	10.75	6.75	0	0	0.625
MB3	0	0	0	0	0	11.25	15	0	0	1.25
MB4	0	0.25	0	0	0	2.5	4.25	0	0	0
MB5	0	0	0	0	0	0	3.625	0	0	0

MB6	0	1.5	0	0	0	8.25	18.5	0	0	0
MB7	0	0	0	0	0	0	8.25	0	0	0
MC1	0	0	0	0	0	0	3	0	0	0
MC2	0	0.25	0	0	0	6.5	7.875	0	0	0
MC3	0	0.75	0	0	0	4.75	8	0	0	0
MC4	0	0	0	0	0	0	7.25	0	0	0
MC5	0	1.5	0	0	0	7.25	7.25	0	0	0
MC6	0	0	0	0	0	9.5	6	0	0	0
MC7	0	2	0	0	0	10.75	10.75	0	0	0
SP1	0	2.5	0	0	0	0	0	0	0	0
SP2	0	3	0	0	0	0	0	0	0	0
SP3	0	0.5	0	0	0	4.5	0	0	0	0
SP4	0	0.25	0	0	0	0	0	0	0	0
SP5	0.125	0.625	0	0	0	0	3.5	0	0	0
SP6	0	0	0	0	0	0	4.5	0	0	0
SP7	0	0	0	0	0	0	1	0	0	0
TC1	8.25	0	5.5	0	0	0	0	0	0	0
TC2	1.375	0	0	0.25	0	0	0	0	0	0
TC3	8.5	0	2.75	0	0	3	0	0	0	0
TC4	5.5	0	4.5	0	0	0	0	3	0	0
TC5	0.625	0	1.25	0.5	0	3	2.25	0	0	0
TC6	0.375	2.875	0	0	0	13.25	14	0	0	0
Plot Species	ACMI	AGAU	AGGL	ANAL	ANMI	ANOC	ARCO	ARDI	ARDR	ARLA

Life Form	Forbs									
Species Plots	ARLY	ARMO	ARNO	ASMO	CALE	CAMI	CAPA	CEAR	CEBE	CHAN
BD1	0	0	2	0	0	0	0	0	0	0
BD2	0	0	7.625	0	0	0.375	0	0	0	4.5
BD3	0	0	1.25	0	0	0	0	0	0	1.375
BD4	0	0	5.25	0	0	0	0	0	0	1.5
BD5	0	0	8.75	0	0	0	0	0	0	3.25
BD6	0	0	7.25	0	0	0	0	0	0	0
BD7	0.25	0	10.25	0	0	0.125	0	0	0	0
CB1	0.125	0	4	0	0	0	0	0	0	0
CB2	0.375	0.75	13.75	0	0	0	0	0.5	0	0
CB3	0	0	8.25	0	0	3.25	0	0	0	26.75
CB4	0.375	0	1.75	0	0	0	0	0.75	0	0
CB5	0	0	11.875	0	0	0	0	0.125	0	0
CB6	0	0	8	0	0	0	0	0.125	0	2.75
CB7	0	0	18.5	0	0	0	0	3.5	0	10.5
DT1	0	0	9.25	0	0	0	0	0	0	0
DT2	0	0	2.25	0	0	0	0	0	0	0.25
DT3	0	0	24	0	0	0	0	0	0	0

DT4	0	0	18	0	0	0	0	0	0	0
DT5	0	0	13	0	0	0	0	0	0	0
DT6	0	0	28.75	0	0	0	0	0	0	0
DT7	0	0	31.75	0	0	0	0	0	0.25	0
MB1	0	0	4.5	0	0	0	0	0	0.25	4.75
MB2	0	0	6.5	0	0	0	0	0	1	0
MB3	0	0	8	0	0	0	0	0	1.25	0
MB4	0	0.375	7	0	1.75	0.125	0	0	0.75	0
MB5	0	2.75	3.375	0	0	1	0	0	1	0.25
MB6	0	0	5	0	0	0	0	0	0.625	2.625
MB7	0	0	3	0	0	0	0	0	0.125	7.25
MC1	0	1	0	0	0	0	0	0	0	1.25
MC2	0	0	6.25	0	0	0	0.25	0	0	0
MC3	0	0	0	0	0	0	0	0	0	0
MC4	0	0	7.5	0	0	0	0	0	0	0
MC5	0	0	9	0	0	0	0	0	0	0
MC6	0	0	8	0	0	0	0	0	0	0
MC7	0	0	5.5	0	0	0	0	0	0.25	0
SP1	0	0	0	0	0	2.75	0	0	0	0.125
SP2	0	0	0	0	0	0.5	0	0	0	0
SP3	0	0	0	0	0	0.125	0	0	0	0
SP4	0	0	0	0	0	0	0	0	0	0.25
SP5	0	0	0	0	0	0	0	0	0	0
SP6	0	0	0	0	0	0	0	0	0	0
SP7	0	0	0	0	0	0	0	0	0	0
TC1	0.25	5.125	0	0	0	0.75	0	0	0	3.25
TC2	0	0.625	0	0	0	0.5	0	0	0	0.25
TC3	0	7.75	0	3	0	0	0	0	0	9.75
TC4	0	5.5	0	1	0	1.5	0	0	0	10.125
TC5	0	3	0	0	0	1.5	0	0	0	0
TC6	0	0	2.5	0	0	0	0	0	0	0
Plot Species	ARLY	ARMO	ARNO	ASMO	CALE	CAMI	CAPA	CEAR	CEBE	CHAN

Life Form	Forbs									
Species Plots	CHLA	CIED	CLLA	DEME	DRAL	EPAN	ERGR	ERHU	ERPE	FRVI
BD1	0	0	3.75	0	0	0	0	0	1.5	0
BD2	0	0	1.5	0	0.125	0	4.125	0	1.375	0
BD3	0	0	5.5	0	0	0	6.75	0	3.25	0
BD4	0	0	4.25	0	0	0	4.75	0	2.5	0
BD5	0	0	2.125	0	0	0	3.5	0	2.25	0
BD6	0	0	3	0	0	0	1.25	0	5.5	0
BD7	0	0	3.25	0	0	0	5.25	0	2.75	0
CB1	0	0	8.5	0	0.125	0	0	5.5	2.75	0

CB2	0.5	0	0	1	0	0	0	0	4	0
CB3	0	0	0	0	0	0	0	0	2	0
CB4	0	0	0	0	0	0	0	0	0.375	0
CB5	0	0	0	0	0	0	0	0	2.875	0
CB6	0	0	0	0	0	0	0	0	0	0
CB7	0	0	0.125	0	0	0	0	0	0.125	0
DT1	0	0	2	0	0	0	6.75	0	3.5	0
DT2	0	0	1.625	0	0	0	0	0	2.25	0
DT3	0	0	1.5	0	0	0	0	0	11.5	0
DT4	0	0	0.875	0	0	0	0	1.5	11.5	0
DT5	0	0	3.25	0	0	0	0	0.5	12	0
DT6	0	0	0.75	0	0	0	0	1	10.5	0
DT7	0	0	0.875	0	0	0	0	0	21.5	0
MB1	0	0	0.75	0	0	0	3.25	0	4.25	0
MB2	0	0	0.875	0	0	0	1.75	0	4.25	0
MB3	0	0	0.625	0	0	0	3.5	0	8.75	0
MB4	0	0	0.25	0	0	0	1.5	0	15	0
MB5	0	0	2.125	0	0.25	0	1.5	0	16.625	0
MB6	0	0	4.75	0	0	0	2	0	2	0
MB7	0	0.25	3.75	0	0.25	0	1.25	0	3	0
MC1	0	0	3.5	0	0	0	4.25	0	4.5	0
MC2	0	0	1.5	0	0	0	5.5	0	4.25	0
MC3	0	0	5	0	0	0	6	0	6	0
MC4	0	0	2.5	0	0	0	2	0	4.25	0
MC5	0	0	3.5	0	0	0	7	0	2.25	0
MC6	0	0	1.875	0	0	0	1.75	0	2.125	0
MC7	0	0	2.25	0	0	0	5.25	0	3.5	0
SP1	0	0	0	0	0	0.125	0	0	0.125	0
SP2	0	0	0	0	0	0	0	0	0.375	0
SP3	0	0	0.25	0	0	0	0	0	6	0
SP4	0	0	1.5	0	0	0	0	0	2.75	0
SP5	0	0	0.375	0	0	0	0	0	1.25	0
SP6	0	0	1.5	0	0	0	0	0	6.75	0
SP7	0	0	0.375	0	0	0	0	0	0.5	0
TC1	0	0	0	2	0	0	0.25	0	1.25	5.25
TC2	0	0	0	0.375	0	0	0	0	0.5	5.25
TC3	0	0	0	0.75	0	0	2.25	0	10	0
TC4	0	0	0	0.125	0	1.25	0.25	0	3.75	0
TC5	0	0	0	0.375	0	0	0.875	0	0.375	0
TC6	0	0	0	0	0	0	0.5	0	3.5	0
Plot Species	CHLA	CIED	CLLA	DEME	DRAL	EPAN	ERGR	ERHU	ERPE	FRVI

Life Form	Forbs

Species Plots	HEMA	HIGR	LUAR	LUNO	MIPE	MIRU	MYLA	MYSC	PEBR	PLHY
BD1	0	0	0	2.25	0	8.25	0	0	0	0
BD2	0	0	0	0.875	0	3	0	0	0.75	0
BD3	0	0	0	5.25	0	1.5	0	0	0	0
BD4	0	0	0	3.75	0	3.5	0	0	0	0
BD5	0	0	0	14.75	0	4.75	0	0	0	0
BD6	0	0	0	7.5	0	9	0	0	0.25	0
BD7	0	0	0	14.75	0	8.25	0	0	0.75	0
CB1	0	0	6.25	0	0	1.375	0	0	2.625	0
CB2	0	0	1.125	0	0	12	0	0	0	0
CB3	0	0	8.25	0	0	12.75	0	0	0	0
CB4	0	0	0.75	0	0	27	0.625	0	0	0
CB5	0	0	13.5	0	0	10	0.125	0	0.75	0
CB6	0	0	18.5	0	0	39	0.25	0	0	0
CB7	0	0	14.25	0	0	12.625	0	0	0	0
DT1	0	0	0	0.5	0	1.375	0	0	0	0
DT2	0	0	0	7.75	0	6.25	0	0	0	0
DT3	0	0	0	0.5	0	8.5	0	0	0	0
DT4	0	0	0	2.375	0	6.25	0	0	0	0
DT5	0	0	0	1.5	0	7.25	0	0	0.75	0
DT6	0	0	0	1.625	0	5.75	0	0	5.75	0
DT7	0	0	0	2.25	0	8.75	0	0	2.25	0
MB1	0	0	0	8.5	0	0	0	0	0	0
MB2	0	0	0	13	0	0	0	0	0.25	0
MB3	0	0	0	4.375	0	0	0	0	0	0
MB4	0	0	0	1.625	0	0	0	0	0	0.25
MB5	0	0	0	2.5	0	0	0	0	0.75	0
MB6	0	0	0	4.25	0	0	0	0	0.25	0
MB7	0	0	0	5.125	0	0	0	0	0.625	0
MC1	0	0	2.5	0	0	0	0	0	0.25	0
MC2	0	0	6.75	0	0	0	0	0	0	0
MC3	0	0	4.5	0	0	0	0	0	0.75	0
MC4	6.25	0	6.25	0	0	0	0	0	0.25	0
MC5	0	0	7	0	0	0	0	0	2	0
MC6	0	0	9	0	0	0	0	0	0.75	0
MC7	1	0	5.75	0	0	0	0	0	0.375	0
SP1	0	0	0	7	0	0	0	0	0	0
SP2	0	0.375	0	7.5	0	0	0	0	4.75	0
SP3	0	3	0	7.25	0	0	0	0	0.75	0
SP4	0	0.375	0	1.75	0	0	0	0	0	0
SP5	0	1.25	0	4.25	0	0	0	0	1.5	0
SP6	0	0	0	1.75	1.25	0	0	0	0	0
SP7	0	0.25	0	5	0.25	0	0	0	0	0
TC1	0	0	10.875	0	0	12	0	0	0	0

TC2	0	0	0	0	0	9.75	0	0	0	0
TC3	0	0	1.875	0	0	3.25	0	0.25	0.125	0
TC4	0	0	8.25	0	0	0.75	0	0	0.5	0
TC5	0	0	2.75	0	0	2.25	0	0	0	0
TC6	0	0	11	0	0	0.125	0	0	1.75	0
Plot Species	HEMA	HIGR	LUAR	LUNO	MIPE	MIRU	MYLA	MYSC	PEBR	PLHY

Life Form	Forbs									
Species Plots	PODI	POFL	POPU	POVI	RAES	SAOC	SEDI	SEIN	SELA	SETR
BD1	0	1.625	0	0	0	0	0	0.75	0	0
BD2	0	2.5	0	0	0	0	0	1.25	0	0
BD3	0	0.125	0	0	0	0	0	1	0	0
BD4	0.5	1.75	0	0	0.25	0	0	2.25	0	0
BD5	0	0.75	0	0	0	0	0	3.5	0	0
BD6	0	0.25	0	0	0	0	0	0	0	0
BD7	0.25	0.25	0	0	0	0	0	0.5	0	0
CB1	0	0	0	0	0.375	0	0	0.25	0.125	0
CB2	2.5	0	2.25	0	0	0	0	0.625	0.125	0.5
CB3	3.25	0	0.625	0	0	0	0	2.5	0	0
CB4	7.75	0	1.125	0	0	0	0	0	0.5	0
CB5	4.5	0	0.75	0	0	0.125	0	0.5	0	0
CB6	13	0	4.375	0	0	0	0	0	0	0
CB7	5.5	0	4.375	0	0	0	0	0.125	0	0
DT1	1.25	0	0	0	0	0	0	2.5	0	0
DT2	1.5	0	0	0.125	0	0	0	0.375	0.75	0
DT3	1	0	0	0	0	0	0	1.25	0.125	0
DT4	0.125	0	0	0	0	0	0	0	0.25	0
DT5	0.75	0	0	0	0	0	0	0	0.375	0
DT6	1	0	0	0	0	0	0	0	1	0
DT7	1	0	0	0	0.125	0	0	0.25	0.25	0
MB1	0	3	0	0	0.25	0	0.625	0.25	0	0
MB2	0	1.25	0	0	0	0	0	0	0	0
MB3	0	2	0	0	0	0	0	0	0	0
MB4	0	3.25	0	0	0	0.25	0.25	0	0	0
MB5	0	9.25	0	0	0.625	0	0	0	0	1.875
MB6	0	2.25	0	0	0	0	0	0	0	0
MB7	0	4.875	0	0	1	0	0	0	0	5.5
MC1	0	3.75	0	0	0	0	0	0	0	3.5
MC2	0	8.75	0	0	0	0	0	0	0	3
MC3	0	6.5	0	0	0	0	0	0	0	0.5
MC4	0	1	0	0	0.125	0	0	0.375	0	6.25
MC5	0	4.25	0	0	0	0	0	0	0	2.75
MC6	0	5.75	0	0	0	0	0	0.25	0	0

MC7	0	4.25	0	0	0	0	0	0	0	0
SP1	0	3	0	0	0.125	0	0	0	0	0
SP2	0	11.75	0	0	0.25	0	0	0	0	0
SP3	0	6	0	0	0	0	0	0	0	0.5
SP4	0	10.75	0	0	0	0	0	0	0	0
SP5	0.125	5	0	0	0	0	0	0	0	0
SP6	0	4.5	0	0	0	0	0	0	0	0.125
SP7	0	8.25	0	0	0	0	0	0	0	0
TC1	0.75	0	0	0	0	0	0	1.25	0	0
TC2	1	0	0	0	0	0	0	0	0	0
TC3	0.25	0	0	0	0	0	0	1	0	0
TC4	0	0	0	0	0	0	0	2.125	0.125	0
TC5	0.125	0.125	0	0	0	0	0	0.75	0	0
TC6	0	0	0	0	0.5	0	0	0.5	0	0
Plot Species	PODI	POFL	POPU	POVI	RAES	SAOC	SEDI	SEIN	SELA	SETR

Life Form	Forbs									Gram-inoids
Species Plots	SIDO	SOMU	THOC	TOLY	TRLA	VASI	VEVI	VEWO	VIGL	AGHU
BD1	0	5.75	0	0	0	0	0	0	0	0
BD2	0	1.25	3.5	0	0	13.25	0	0	0	0
BD3	0	2.125	0	0	0	6.125	0	0	0	0
BD4	0	1	0	0	0	18.625	0	0	0	0
BD5	0	0	10.25	0	0	3.75	0	0	0	0
BD6	0	0.25	0	0	0	0	0	0	0	0
BD7	0	0	0	0	0	0.25	0	0	0	0
CB1	0.25	0	0	0	0	0.5	0	0	0	0
CB2	2.5	5.75	0	0	0	15.75	0	0	0	0
CB3	3	12.25	4.375	0	0	0	0	0	0	0
CB4	2	11.75	0	0	0	0	0	0	0	0.25
CB5	2.25	12.5	0	0	0	0	0	0	0	0
CB6	4	27.25	0	0	0	0	0	0	0	0
CB7	3	20.5	20.25	0	0	0	0	0	0	0
DT1	0.125	1	3.75	0	0	7.625	0	0	0	0
DT2	4.25	0	2.5	0	0	0	0	0	0	0
DT3	0.5	2.25	0	0	0	0	0	0.125	0	0
DT4	0	0	0	0	0	0	0	0	0	0
DT5	0	0.5	0	0	0	0	0	0	0	0
DT6	0	0	0	0	0	4.75	0	0	0	0
DT7	0.25	0	0	0	3	2.375	0	0.375	0	0
MB1	0	2.25	0	0	0	22.875	0	0	0	0
MB2	0	1	0	0	0	11	0	0	0	0
MB3	0	0.375	0	0	0	14.25	0	0	0	0
MB4	0	0	0	0	2	8.25	0	0.375	0	0

MB5	0	0	0	0	2.75	12	0	0.875	0	0
MB6	0	0.5	0	0	0	23	0	0	0	0
MB7	0	0	0	0	0	30.5	0	0	2.5	0
MC1	0	0	0.25	0	0	52.5	0	0	0	0
MC2	0	0	0	0	0	28.25	0	0	0	0
MC3	0	0	0	0	0	28.75	1.75	0	0	0
MC4	0	0	0	0	0	18	0	0	0	0
MC5	0	0	0	0	0	42.5	0	0	0	0
MC6	0	0	1.25	0	0	29.5	0	0	0	0
MC7	0	0	0	0	0	25.5	0	0	0	0
SP1	1.5	0.375	0	0	0	8.25	0	0	0	0
SP2	5	0	0	0	0	9.5	0	0	0	0
SP3	0.25	0	0	0	0	17.75	0	0	0	0
SP4	0	0	0	0	0	22	0	0	0	0
SP5	1.875	0	0	0	0	5.5	0	0	0	0
SP6	0.25	0	0	0	0	46	0	0	0	0
SP7	0	0	0	0	0	20.5	0	0	0	0
TC1	3	0.75	30.25	0	0	0	0	0	0	0
TC2	3.75	0.375	9	0	0	0	0	0	0	0
TC3	0	0.25	32.5	0	0	10.75	0	0	0	0
TC4	0.5	0	8	0	0	0	0	0	0	0
TC5	1.75	0	6.75	1	0	5.625	0	0	0	0
TC6	0.5	0	1.25	0	0	23.75	0.125	0	0	0
Plot Species	SIDO	SOMU	THOC	TOLY	TRLA	VASI	VEVI	VEWO	VIGL	AGHU

Life Form	Graminoids									
Species Plots	BRSI	CAHO	CAMA	CANI	CAPH	CAPO	CARO	CASP	DECE	ELEL
BD1	0	0	0	0	0	0	1.625	0	0	0
BD2	0	0	0	0	0	0	0	0.5	0	0
BD3	0	0	0	0	0	0	2.25	0	0	0
BD4	0	0	0	0	0	0	1	3.75	0	0
BD5	0	0	0	0	0	0	0.5	0	0	0
BD6	0	0	0	0	0	0	1.25	7.5	0	0
BD7	0	0	0	0	0	0	1.25	0	0	0
CB1	0	0	0	5.75	0.75	0	0	6.75	0	0
CB2	0	0	0	0	2.5	0	0	0	0	0
CB3	0	0	0	0	5.25	0	0	0	0	0
CB4	0	0	0	0	4.75	0	0	0	0	0
CB5	0	0	0	0	3.25	0	0	18	0	0
CB6	0	0	0	0	9	0	0	0	0	0
CB7	0	0	0	0	28.5	0	0	1	0	0
DT1	0	0	0	0.125	0	0	0	0.75	0	0
DT2	0	0	0	0	0	0	0	0.125	0	0

DT3	0	0	0	0.375	0	0	0	6.5	0	0
DT4	0	0	0	0.375	0	0	0	0.75	0	0
DT5	0	0	0	0	0	0	0	1.125	0	0
DT6	0	0	0	2.125	0	0	0	0	0	0
DT7	0	0	0	0.25	0	0	0	1.4375	0	0
MB1	0	0	6.75	0	0	0	0	0	0	0
MB2	0	0	12.5	0	0	0	0.5	0	0	0
MB3	0	0	2	0	4	0	0.25	0	0	0
MB4	0	0	4	0	0	0	0.25	0	0	0
MB5	0	0	12.25	0	0	0	0	0	0	0
MB6	0	0	10.75	0	0	0	0.25	0	0	0
MB7	0	0	15.25	0	0	0	0	0	0	0
MC1	0	0	0	0	0	28.75	0	0	0	0
MC2	0	0	0	0	0	4.75	0	0	0	0
MC3	0	0	0	5.25	0	13.5	0	0	0	0
MC4	0	0	0	0	0	10	0	0	0	0
MC5	0	0	0	0	0	16	0	0	0	0
MC6	0	0	0	0	1.25	1.25	0	0	0	0
MC7	0	0	0	0	0	4.375	0	0	0	0
SP1	0	0	0	0	0	0	0	64.25	0	0
SP2	0	0	0	0	0	0	0	49.75	0	0
SP3	0	0	0	0	2	0	0	12	0	0
SP4	0	0	0	0	0	0	0	51.5	0	0
SP5	0	0	0	0	0.25	0	0	45.25	0	0
SP6	0	0	0	0	0	0	0	38.5	0.5	0
SP7	0	0	0	2.625	0	29.75	0	0	0.625	0
TC1	6.5	16	0	0	1	0	0	0	0	0
TC2	5.25	4	0	0	1	0	0	0	0	0.25
TC3	13.25	0	0	0	6.5	0	0	0	0	0
TC4	4.75	0	0	0	5.75	0	1.875	0	0	0
TC5	12.25	0	0	0	1.75	0	5.75	0	0	0
TC6	1	0	0	0	3.5	0	0.25	5.5	2	0
Plot Species	BRSI	CAHO	CAMA	CANI	CAPH	CAPO	CARO	CASP	DECE	ELEL

Life Form	Graminoids									
Species Plots	ELGL	ELTR	FEBR	JUDR	LUHI	LUPI	LUSP	LUZA	PHAL	POAB
BD1	0	0	0	14.25	0	0	0	0	0	0
BD2	0	0	0	0.25	2.5	0	0.375	0	0	0
BD3	0	0	0	0	0	0	0	0	0	0
BD4	0	0	0	5.25	0	0	0.125	0	0	0
BD5	0	0	0	0	0	0	0	0	0	0
BD6	0	0	0	6.75	0	0	0	0	0	0
BD7	0	0	0	0	0	0	0	0	0	0

CB1	0	0	0	0	1.125	0	0	0	1	6.5
CB2	0	0	0.25	0	0	0	0	0	0.375	5
CB3	0	0	0	0	0	0	0	0	0.5	7.5
CB4	0	0	0.25	0	0	0	1.25	0	0	3.75
CB5	0	0	1	0	0	0	0	0	0	1.5
CB6	0	0	1.875	0	0.5	0	0	0	0	4
CB7	0	3.75	0	0	0	0	0	0	5	3.25
DT1	0	0	0	0	0	0	0	0	0	0
DT2	0	0	0	0	0.5	0	0	0	0	0
DT3	0	0	0	0	3.75	0	0.5	0	0	0
DT4	0	0	0.375	0	0	0	3.5	0	0.5	0
DT5	0	0	0	0	0	0	0.125	0	0.5	0.125
DT6	0	0	0.125	0	0	0	0.625	0	0.25	0
DT7	0	0	0.125	0	3.25	0	0	0	0.625	0
MB1	0	0	0	0.25	0	0	0	0.75	0.125	0
MB2	0	0	0	0	0	0	0	1.875	0	0
MB3	0	0	0	1	0	0	0	3.5	0	0
MB4	0	0	0	0.5	0	0	0	1.25	0.25	0
MB5	0	0	0	0.75	0	0	0	0.625	0	0
MB6	0	0	0	0	0	0	0	0	0	0
MB7	0	0	0	0	0	0	0	0	0.75	0
MC1	0.5	0	0	0	0	0	0	0	0	0
MC2	0	0	0	0	0	0	0	0	0.125	0
MC3	0	0	0	0	0	0	0	0	0.125	0
MC4	0.125	0	0	0	0	0	0	0	0	0
MC5	0	0	0	0	0	0	0	0	0	0
MC6	0.5	0	0	0	0	0	0	0	0	0
MC7	0	0	0	0	0	0	0	0	0	0
SP1	0	0	0	0	0	0	0	0	5.25	0
SP2	0	0	0	0	0	0	0	0	5.125	0
SP3	0	0	0	0	0	0	0	0	0.125	0
SP4	0	0	0	0	0	0	0	0	0	0
SP5	0	0	0	0	0	0	0	0	1.75	0
SP6	0	0	0	0	0	0.5	0	0	0.25	0
SP7	0	0	0	0	0	0	0	0	0	0
TC1	0	0	0	1	0	0	0	0	0.25	0
TC2	0	0	0	8.25	0	0	0	0	0	0
TC3	0	0	0	0	0	0	0	0	2.125	0
TC4	0	0	0	1.5	0	0	0	0	0.75	0
TC5	0	0	0	0.875	0	0	0	0.125	0.75	0
TC6	0	0	0	0	0	0	0	0	0.25	0
Plot Species	ELGL	ELTR	FEBR	JUDR	LUHI	LUPI	LUSP	LUZA	PHAL	POAB

Life Form	Graminoids	Woody Species

Species Plots	POAL	POCU	TRSP	CAME	ERUM	LUPE	ORSE	PEPR	PHDI	PHEM
BD1	0	0.625	0.625	0	0	0.75	0	0	24.75	0
BD2	0	1.25	0.25	0	4.375	0	0	0.5	19	0
BD3	0	6.5	0.625	0	0.25	0	0	0.625	34	0
BD4	0	1.25	0.625	0	0	0	0	0	27.5	0
BD5	0	2.25	0.375	0	0	0	0	0.125	25.75	0
BD6	0	0.25	0.375	0	0	0	0	0	29.5	0
BD7	0	1.875	0.625	0	0	0	0	0.5	41.75	0
CB1	0	0	0.75	0	0	0	0	0	0	0
CB2	0	0	1.125	0	0	0	0	2.625	0	0
CB3	0.25	0	3.25	0	1.5	0	0	0	0	0
CB4	0	0	0.5	0	1.125	0	0	0.25	0	0
CB5	0	0	1.75	0	0.25	0	0	0	0	0
CB6	0.375	0	5.5	0	5.875	0	0	0	0	0
CB7	1.5	0	6.5	0	0	0	0	0	0	0
DT1	0	4.75	0.125	0	0	0	0	0	39	0
DT2	0	7.5	1.5	0	0	0	0	0	30	0
DT3	0	8	0.25	0	0	0	0	0	15.5	0
DT4	0	0.625	0	0	0	0	0	0	13.5	0.125
DT5	0	2	0	0	0	0	0	0	28.75	0
DT6	0	5.5	1.875	0	0	0	0	0	18.25	0
DT7	0	0.25	0	0	0	0	0	0	9.125	0
MB1	0	1.875	0.375	0	0	0	0	0.25	10.63	0
MB2	0	3.75	0.625	0	0	0	0	0	24.5	0
MB3	0	2	0	0	0	0	0	2	10.75	0
MB4	0	1.25	0	4.75	0	0	0.375	0	7.5	0
MB5	0	0	0.25	0	0	0	0	0	0	0
MB6	0	1.125	0	0	0	0	0	0	3.25	0
MB7	0	0	0	0	0	0	0	0	0	0
MC1	0	0	0	0	0	0	0	0	0	0
MC2	0	5.25	0.75	0	0	0	0	0	0	0
MC3	0	2.25	0	0	0	0	0	0	0	0
MC4	0	1.25	0.5	0	0	0	0	0	0	0
MC5	0	1.5	0.625	0	0	0	0	0	0	0
MC6	0	3.25	0.625	0	0	0	0	0	0	0
MC7	0	4	0.25	0	0	0	0	0	0	0
SP1	0	3	0.75	0	0	0	0	1.25	13	0
SP2	0	3.5	4.5	0	0	0	0	0.25	7.5	0
SP3	0	1.875	0.25	0	0	0	0	0	1.75	0
SP4	0	3	0	0	0	0	0	0	0.25	0
SP5	0	1.25	0.375	0	0	0	0	0	5.25	0
SP6	0	0.75	0	0	0	0	0	0	0	0
SP7	0	0	0.125	0	0	0	0	0	0	0
TC1	0	2.375	0.5	0	3	0	0	0	14.5	0

TC2	0.5	1.875	0.5	0	2.5	0	0	0	48.75	0
TC3	0.25	6.25	1	0	0	0	0	0	3.75	0
TC4	1.625	8.5	0.75	0	0	0	0	0	7.75	0
TC5	0	2.625	0.875	0	0	4	0	2	10.75	2.25
TC6	0.75	0.75	0.625	0	0	0	0	0	3.5	0
Plot Species	POAL	POCU	TRSP	CAME	ERUM	LUPE	ORSE	PEPR	PHDI	PHEM

Life Form	Woody Species			
Species Plots	PHGL	SIPR	VACA	VASC
BD1	0	0.5	0	0
BD2	0	0	0	0
BD3	0	0	0	0
BD4	0	0	0	0
BD5	0	0	0	0
BD6	0	0	0	0
BD7	0	0	0	0
CB1	0	0.375	0	0
CB2	0	0.5	0	0
CB3	0	0	0	0
CB4	0	0	0	0
CB5	0	0.25	0	0
CB6	0	0	0	0
CB7	0	0	0	0
DT1	0	0	4	0
DT2	0	0	26.25	0
DT3	0	0	11	0
DT4	0	0	25	0
DT5	0	0.25	26.75	0
DT6	0	0.25	16	0
DT7	0	0	9.5	0
MB1	0	0	0	0
MB2	0	0	0	0
MB3	0	0	0	0
MB4	17	0	0	0
MB5	0	0	0	0
MB6	0	0	0	0
MB7	0	0	0	0
MC1	0	0	0	0
MC2	0	0	0	0
MC3	0	0	0	0
MC4	0	0	0	0
MC5	0	0	0	0
MC6	0	0	0	0

MC7	0	0	0	0
SP1	0	0.75	0	0
SP2	0	2.5	0	0
SP3	0	0.75	0	0
SP4	0	0	0	0
SP5	0	0.25	0	0
SP6	0	0	0	0
SP7	0	0	0	0
TC1	0	0	0	0
TC2	0	0	0	0
TC3	0	0	0	0
TC4	0	0	0	1.5
TC5	0	0	0	0
TC6	0	0	0	3.75
Plot Species	PHGL	SIPR	VACA	VASC