Novel approaches to evaluating compositional heterogeneity: a case study using grazing exclosures in alpine meadow communities

by

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Abstract

Despite a long history, accurately quantifying biological diversity remains a priority for ecologists and the continuing development of novel tools and approaches has identified areas that require further investigation. Currently, the quantification of evolutionary diversity (phylogenetic diversity) is receiving intense and critical interest, but few have attempted to quantify among sample phylogenetic variation (beta diversity) and fewer still have measured the influence of grazing on the phylogenetic diversity of plant communities. Novel partitions of beta diversity, which quantify the independent influence of richness differences and species replacement, may better clarify how heterogeneity is structured within a system, but such metrics have not yet been developed for phylogenetic diversity or applied to grazing investigations. Furthermore, it has recently been re-emphasized that, when measuring within-community heterogeneity, the only appropriate approaches that facilitate the concurrent measurement of partitioned beta diversity are 'multiple site beta diversity' metrics. To date 'multiple site' heterogeneity metrics do not exist for phylogenetic diversity. Drawing on previously published derivations of pairwise beta diversity partitions and their phylogenetic analogs, I developed novel multiple site beta diversity tools for taxonomic and phylogenetic diversity that may better quantify community heterogeneity and suggest how these new tools may be useful for the practicing community ecologist. Using long term grazing exclosures, I combined novel beta diversity tools with paired plots across the exclosure fence and appropriate null models to test the influence of grazing on herbaceous alpine plant community heterogeneity. I show that (i) taxonomic and phylogenetic diversity provide differing results, (ii) that grazing influences within community heterogeneity of herbaceous plant communities, but that the response may be site dependent, and (iii) that richness and replacement metrics of beta diversity exhibit different responses to grazing. Novel metrics of partitioned taxonomic and phylogenetic beta diversity therefore provide useful insight into the structuring of herbaceous alpine plant communities. As such, within-community heterogeneity as measured by 'multiple site beta diversity' is an important attribute of any ecosystem and efforts aimed at quantifying and preserving biodiversity for ecosystem management or conservation should include it in their goals.

Preface

Together with the guidance of my supervisor, Dr. Jason Pither and committee members Dr. John Klironomos and Dr. Lauchlan Fraser, I conducted the field work, collected the data, developed the methods in Chapter 2, conducted the analyses outlined in Chapter 3 and wrote this thesis. Some of the work described herein was conducted as part of the Herbaceous Plant Diversity Network (Herb-Net), a group of plant biodiversity researchers from around the world led by committee member Dr. Fraser at Thompson Rivers University. The Herb-Net has agreed upon a sampling design which was followed in the field (see methods). The plant species and biomass data were therefore submitted to Dr. Fraser to be included as part of a global meta-experiment investigating the relationship between community productivity and species richness. My participation in the global meta-experiment does not hinder the publication or novelty of the work described herein, nor does it constitute a conflict of interest.

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α	Alpha diversity is the number of species (i.e. species richness) of a given sample, in this case one 1 x 1 meter quadrat.
β	Beta diversity is the variation in species composition among two (or more) samples.
β_{CC}	The taxonomic multiple site analog of Jaccard's dissimilarity, as denoted in Chapter 2.
β_{-3M}	The multiple site analog of Carvalho et al.'s (2013) replacement component of taxonomic beta diversity as denoted in Chapter 2.
β_{RICH}	The multiple site analog of Carvalho et al.'s (2013) richness component of taxonomic beta diversity as denoted in Chapter 2.
$P\beta_{CC}$	The phylogenetic multiple site analog of Jaccard's dissimilarity, as denoted in Chapter 2.
$P\beta_{-3M}$	The multiple site analog of Carvalho et al.'s (2013) replacement component of phylogenetic beta diversity as denoted in Chapter 2.
$P\beta_{RICH}$	The multiple site analog of Carvalho et al.'s (2013) richness component of phylogenetic beta diversity as denoted in Chapter 2.
γ	Gamma diversity is the species richness of an entire site (or region, also known as the species pool)

List of Abbreviations

MNTD	Mean nearest taxon distance is the average of the phylogenetic distance (branch length) joining each species with its nearest neighbor. This metric is a measure of tip level clustering that is relatively independent of deeper level phylogenetic relationships.
MPD	Mean pairwise distance is the average of the phylogenetic branch length joining all pairs of species in a given community. This metric is represents a tree wide assessment of the phylogenetic clustering of all species in a given community.
PD	Phylogenetic diversity is the sum of the phylogenetic branch lengths joining all species of a given community.

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Chapter 1: Introduction

1.1 General introduction

A central goal of ecological research is the description and quantification of biological diversity (biodiversity). Given the ever increasing rate of habitat loss and associated species extinction, the importance of biodiversity quantification and protection has never been greater; a fact highlighted by the recent formation of the Intergovernmental Panel on Biodiversity and Ecosystem Services (IPBES, 2011). Studies of biodiversity in terms of conservation prioritization and the quantification and preservation of ecosystem services have therefore increased.

Despite its seemingly simple name, biodiversity is difficult to define and even more difficult to quantify (Magurran & McGill 2011). In the simplest of terms it is the pattern of variation in identity of living organisms across space and time; however such patterns have been regularly found to vary with the ecosystem under investigation, the number of species present, the productivity of the region / location, the group of species being investigated (plants, animals, microbes etc.), and the area of the sample under investigation. Furthermore, the inclusion of genetic information and / or historical processes such as dispersal and evolution are altering previously quantified diversity patterns. Being clear about how biodiversity is defined is therefore a critical step towards its measurement (Magurran & McGill 2011).

Traditional investigations of biodiversity have focused on species level diversity, but increasingly, this approach is being criticized as overly simplistic. At one extreme, advances in genetic techniques are revealing cryptic diversity not visible through morphological identification (e.g. Smith et al. 2008), and at the other, historical and evolutionary research is shedding light on the influence of broader taxonomic resolution on observed diversity patterns. In particular, quantification of phylogenetic diversity – which is a measure of the evolutionary diversity of observed species – is receiving increasing interest (Vamosi et al. 2009; Cavender-Bares et al. 2009). Applying the growing variety of diversity research avenues (including taxonomic, phylogenetic and functional diversity) will strengthen our knowledge of the processes that structure communities, allow for investigations of competing theories about community

assembly and composition, and strengthen conservation and reserve planning efforts. Efforts aimed at accurately quantifying diversity, and its pattern, are of utmost importance if ecosystem's ability to adapt to global change is to be retained (Faith 1992; Faith 1994; Cavender-Bares et al. 2009; Devictor et al. 2010).

1.2 Beta-diversity and heterogeneity

THE PARTITIONING OF TAXONOMIC DIVERSITY

The idea of measuring beta diversity dates to the middle of the 20th century when Whittaker (1960, 1972) proposed the partitioning of species richness patterns into multiple components relating primarily to spatial scale and comparisons within and among those scales. Whittaker (1960, 1972) proposed the partitioning of diversity in several components; the most commonly referred to include alpha (the species richness of a sampling unit), gamma (the sum total species richness of all sampling units) and beta, which quantified the relationship between alpha and gamma, thereby describing the heterogeneity of the region for which gamma was representative. Whittaker proposed a multiplicative partition of diversity, denoting:

Equation 1.1 $$\gamma = \bar{\alpha}\beta \,,$$

wherein beta results from the division of regional richness (gamma) by the mean (denoted by the bar) sample species richness (alpha). The multiplicative partition of diversity relates most closely to those metrics that attempt to deduce patterns of turnover (replacement of species) and richness (species gain or loss) between pairs of communities (Veech et al. 2002). Recent work has highlighted the importance of measuring both turnover and richness based portions of beta diversity among sites / samples (e.g. Azeria et al. 2011; Baeten et al. 2012).

Around the same time that Whittaker (1960, 1972) was developing his methods, two others used an additive partitioning of diversity, but did not use Whittaker's (1960, 1972) intuitive alpha, beta, and gamma notation (MacArthur et al. 1966; Levins 1968; Lande 1996; see Veech et al. 2002). As noted by

Lande (1996) and Veech et al. (2002), both MacArthur et al. (1966) and Levins (1968) used an additive partition of diversity that Lande (1996) denoted as:

Equation 1.2 $$\gamma = \bar{\alpha} + \beta \ ,$$

where the individual values follow Whittaker's (1960, 1972) notation. The additive partition of species diversity has gained support because it retains the same units (average species richness for presence / absence data, average diversity for Simpson's or Shannon's index) for all three measures of biodiversity (e.g. Lande 1996; Veech et al. 2002).

BETA DIVERSITY

While investigations of alpha and gamma diversity (i.e. richness patterns) generate interesting results, beta diversity has the potential to better test predictions about the processes structuring communities. In part this is due to its consideration of specific species rather than simple overall sums. More importantly however, beta diversity is thought to help researchers investigate the relative influences of niche based environmental filtering, competition and facilitation, or predation (deterministic processes) and those influences that include chance or variable temporal events like dispersal limitation and random birth or death events (stochastic processes; Stegen & Hurlbert 2011). Anderson et al. (2011) further highlight that beta diversity comes in two general forms which they define as turnover, (i.e. along a gradient) and variation (i.e. among a set of sample units). In the former, research is directed toward testing how the given gradient (or interactions among multiple gradients) influences the (dis)similarity of communities along it, while in the latter, beta diversity acts as a more general measure of how the local scale diversity (sample unit) relates to the available species pool (Anderson et al. 2011).

Beta diversity and its patterns, regardless of the diversity partitioning approach or the goal of the investigation (e.g. turnover or variation *sensu* Anderson et al. 2011), have received increased attention since the publication of Hubbell's (2001) neutral theory which suggests that observed communities are primarily determined by stochastic events (Tuomisto & Ruokolainen 2006). Beta diversity research has increased due to interest in showing that environmental niches are an important determinant of species

communities. As noted by Veech et al. (2002) the idea of beta diversity has therefore often focused on turnover investigations (along gradients). Indeed, one of the main purposes of studying beta diversity is to investigate correlations between changing communities and environmental or spatial factors (Whittaker 1960, 1972; Anderson et al. 2011), thereby determining the relative influences of distance and environment on community shifts. However, in addition to testing theoretical predictions and investigating the processes structuring communities, new approaches for determining changes in beta diversity are being continuously developed (e.g. Baselga 2008, 2010; Bennie et al. 2010).

NEW APPROACHES TO MEASURING BETA DIVERSITY

One new approach to more accurately quantifying beta diversity is its further partitioning into its turnover and nestedness-resultant (richness based) components (*sensu* Baselga 2010). Baselga (2010) broke the classic Sørensen (1948) metric of beta diversity into turnover and nestedness as follows:

Equation 1.3 $$\beta_{sør} = \beta_{sim} + \beta_{sne} ,$$

where $\beta_{sør}$ indicates the classic beta diversity measure developed by Sørensen (1948), β_{sim} indicates the classic Simpson diversity index (Simpson 1949) or the richness independent turnover, and β_{sne} indicates the nestedness-resultant dissimilarity, which is the change in communities due to adding or losing species (i.e. a richness effect). Baselga (2010) clearly demonstrates that breaking beta diversity into these two components sheds more light on the processes structuring beetle communities along a latitudinal gradient in central Europe. More recently, Baselga (2012) extended his partitioning approach to Jaccard's dissimilarity, denoting:

Equation 1.4 $$\beta_{jac} = \beta_{jtu} + \beta_{jne},$$

where β_{jac} indicates the dissimilarity beta diversity measure developed by Jaccard (1901), β_{jtu} indicates the richness independent turnover, and β_{jne} indicates the nestedness-resultant dissimilarity of Jaccard's dissimilarity.

In addition to Baselga's (2010, 2012) own work, others have demonstrated the importance of partitioning beta diversity into nestedness and turnover components (e.g. Azeria et al. 2012; Baeten et al. 2012; Leprieur et al. 2012). For example, Baselga's (2010, 2012) approach has recently been shown to more clearly elucidate patterns of plant community homogenization over the course of three decades (Baeten et al. 2012). Baeten et al. (2012) found that although $\beta_{sør}$ remained the same in the year 2009 as it did in 1979, β_{sim} and β_{sne} changed, with β_{sim} (turnover) decreasing and, given their additive nature, β_{sne} (nestedness) increasing. Baeten et al. (2012) suggest that overall the 2009 species composition is a subset of that found in 1979. Importantly, Baeten et al. (2012) were studying the homogenization of a system independent of a traditional environmental gradient. The work of Baeten et al. (2012; and that of Azeria et al. 2012) was, however restricted to taxonomic measures of diversity (i.e. species richness) which may not capture the ways in which homogenization is influencing ecosystem function (functional diversity), or the community's potential ability to adapt to a changing world (phylogenetic diversity, Webb et al. 2002, Graham and Fine 2008).

Since the publication of Baselga's (2010, 2012) partition of beta diversity, several groups have challenged it, suggesting that the nestedness resultant dissimilarity does not capture nestedness *sensu stricto* (Almeida-Neto et al. 2012) because it does not measure the ordered loss (or gain) of species, while Carvalho et al. (2012, 2013) and Podani and Schmera (2011) propose decomposing beta (as measured by Jaccard dissimilarity) into replacement and richness fractions. Baselga (2010, 2012) however did not attempt to quantify strict sense nestedness (as contended by Almeida-Neto et al. 2012), and attempted to avoid conflict by naming it nestedness-resultant dissimilarity. However, in addition to strong theoretical arguments, Carvalho et al. (2013) show convincingly how Baslega's (2012) partition may fail in certain circumstances. Carvalho et al. (2013) show that in cases of maximum species loss, β_{sne} and β_{jne} are lower than when species loss is moderate, exhibiting a hump shaped pattern with increasing species loss. Therefore, studies based on Baselga's partition may benefit from repeated analysis using more robust partitions, such as that proposed recently by Carvalho et al. (2013).

NULL MODELS AND BETA DIVERSITY

Quantifying the correct patterns of beta diversity is the first step, and as has been shown, is an increasingly complicated endeavor. However, in order to determine if observed patterns are indicative of structuring, or just occur by chance, authors have recommended the use of randomized communities, based on a given pool of available species (Veech et al. 2002; Chase 2010; Chase et al. 2011). In particular, when comparing beta diversity among various treatments or environments, observed patterns may be confounded by variation in alpha or gamma diversity, upon which beta diversity depends (Chase et al. 2011). Randomizing communities under given species pools (null models) can be used to determine the relative influence of any treatment of interest on the structuring of communities (Chase et al. 2011). Furthermore, Chase (2010) has shown that using null models when studying beta diversity can clarify the relative importance of deterministic (e.g. niche based) and stochastic (e.g. dispersal limitation, ecological drift) processes for the heterogeneity of observed communities. Recently, Azeria et al. (2012) extended Chase's (2010) null model approaches to Baselga's (2010, 2012) partition of beta diversity. An important initial finding of Azeria et al. (2012) was that null model randomizations should be based on a fixed-fixed algorithm, in which species occurrence rates (i.e. the number of times/samples in which a species occurs in the region of interest) and the number of species in each community (i.e. community richness) are fixed because both the nestedness-resultant and turnover (Simpson's diversity) components can be influenced by species frequency patterns (Azeria et al. 2012). Applying appropriate null models, Azeria et al. (2012) showed that nestedness-resultant and turnover components of beta diversity of forest saproxylic beetle communities were driven by different environmental factors (β_{sne}: burn severity, tree size; β_{sim}: tree species). Clearly the application of partitioned beta diversity metrics with appropriate null models has the potential to yield important results about the processes structuring biodiversity.

APPLYING NOVEL APPROACHES TO NON-TAXONOMIC METRICS OF BETA DIVERSITY

Despite the relative novelty of Baselga's (2010, 2012) beta diversity partitioning approach, it has already been extended to another measure of beta diversity. Leprieur et al. (2012) recently published an example that combines the beta partitioning proposed by Baselga (2010, 2012) with the growing field of

phylogenetic ecology (see section 1.3 or Vamosi et al. 2009 for a recent review). Leprieur et al. (2012) developed the beta partitioning approach for two popular measures of phylogenetic beta diversity, PhyloSor (Bryant et al. 2008) and UniFrac (Luzopone and Knight 2005), which are based on the Sørensen and Jaccard similarity indices, respectively. The extension to PhyloSor and UniFrac was simple since the deconstruction of beta diversity proposed by Baselga (2010, 2012) itself uses the Sørensen and Jaccard indices. Using an example from coral reef fish, Leprieur et al. (2012) show how comparing phylogenetic beta diversity and taxonomic beta diversity can shed further light on the processes structuring communities of organisms. Importantly, Leprieur et al. (2012) follow both Chase et al. (2011) and Azeria et al. (2012) in using null models to determine if observed patterns of phylogenetic diversity deviate from the null expectation.

WITHIN COMMUNITY BETA DIVERSITY

Despite the far reaching importance of taxonomic beta diversity and its analogous investigations with other diversity measures (e.g. phylogenetic), one area of research remains limited in scope: beta diversity within a similar environment and in particular, beta diversity within a contiguous community (but see Baeten et al. 2012). As originally proposed, measuring beta diversity within a given community runs counter to its purpose of measurement along a gradient (Whittaker 1960, 1972), but as acknowledged by Whittaker himself (Veech et al. 2002), beta diversity can be extended to the general case of dissimilarity of samples, regardless of their position in spatial or environmental space. Building on this idea, I propose that just as a given community has some expected alpha diversity based on its local environment and evolutionary history, so too does it have a predictable beta diversity among samples of a given size (area) within that location.

To date, studies looking at beta diversity within common environments have been restricted primarily to those investigating biotic homogenization under human influence, that is temporal beta diversity (Schwartz et al. 2006; Olden 2006; Tobias & Monika 2011; Trentanovi et al. 2013) or the success of restoration (e.g. Martin et al. 2005) or protection efforts (Rooney et al. 2004; Baeten et al. 2012). In some cases, studies investigating biotic homogenization have extended to include other measures of diversity

including functional (Tobias & Monika 2011) and phylogenetic beta diversity (Winter et al. 2009). One of the main goals of conservation and restoration ecology is to preserve or restore a given level of diversity. This goal necessarily implicates more than simply richness values and among ecosystem variability. It should also as studied by Martin et al. (2005), seek to conserve within community heterogeneity as this feature may have both within and among trophic level effects on diversity (Dumont et al. 2009; Pellissier et al. 2013) and ecosystem function (Cadotte et al. 2009; Cadotte 2013).

Much of the work on beta diversity within the same environment (as noted above) has however been conducted at the regional (e.g. Schwartz et al. 2006: California counties; Trentanovi et al. 2013: within a treatment, across plots) or landscape scale (Winter et al. 2009: all of Europe) and does not investigate variation within a given community (but see Martin et al. 2005; Baeten et al. 2012). While such large scales may be appropriate for determining the larger environmental characteristics that limit species co-occurrence, it does not adequately address biotic processes such as colonization, competition / facilitation, or herbivory; particularly that of smaller organisms like insects (Parker et al. 2012) that occur within a plant community. Furthermore, regional scale taxonomic patterns are particularly insufficient for studying local scale community phylogenetic patterns (Parker et al. 2012). Therefore, studying within community heterogeneity remains an important, if under-explored avenue of diversity research. Fortunately there are several ways to quantify within-community heterogeneity and beta diversity may be one of the simplest approaches.

MULTIPLE SITE BETA DIVERSITY

Despite the fact that Baselga et al. (2007; Baselga 2012, 2013) and others (Harrison et al. 1992; Williams 1996; Diserud & Ødegaard 2007) have all proposed multiple site dissimilarity metrics, the overwhelming method of choice for quantifying heterogeneity is by averaging pairwise dissimilarity (Baselga 2013). Averaging methods include (i) permutational analysis of variance (PERMANOVA) and multivariate dispersion (PERMDISP: Anderson et al. 2006, 2011) as applied by Myers et al. (2012) and Azeria et al. (2012) among others, (ii) the traditional additive and multiplicative measures of beta diversity (e.g. Martin et al. 2005), and (iii) the direct averaging of dissimilarity metrics (e.g. Jaccard dissimilarity,

Trentanovi et al. 2013). As Baselga (2013, p.124) clearly states, when the research question is "how heterogeneous the species composition is among several assemblages, we are addressing an attribute of the whole pool of units." As such "…it is an attribute of the pool" (region) rather than the sampling unit and should be quantified using multiple site dissimilarity metrics (Baselga 2013). It is particularly concerning that the use of averaging approaches continue when they have been shown to mask patterns of co-occurrence across multiple sites (i.e. > two), and that this has been known for more than five years (see Diserud & Ødegaard 2007; Baselga et al. 2007). In addition, multiple site diversity metrics have not been developed for the most recent partition of beta diversity (e.g. Carvalho et al. 2013) despite the demonstration that Caravalho et al.'s (2013) partition is more robust than Baselga's (2010, 2012). This is surprising given that Carvalho et al. (2013) among others (Podani & Schmera 2011; Almeida-Neto et al. 2012) are expressly criticizing Baselga's (2010, 2012) approach wherein multiple site measures are presented. Finally, despite the extension of Baselga's (2010, 2012) partition of pairwise beta diversity to phylogenetic beta diversity (see Leprieur et al. 2012), Carvalho et al.'s (2013) partition has not yet been applied to multiple site phylogenetic beta diversity.

1.3 Phylogenetic Diversity

INTRODUCTION

Interest in the phylogenetic diversity of organismal communities has its roots in conservation biology (Faith 1992; Faith 1994; Clarke & Warwick 1998), wherein the preservation of biodiversity is often paramount, but for which the quantification of that biodiversity was and remains difficult (Faith 1992). Faith (1992) highlighted the importance of conservation efforts that maximize taxonomic diversity, due to the need to preserve the ability of ecological communities to adapt to a changing world. As such, quantifying the relative distinctiveness of representative species in a given community is of high importance. To clarify, traditional methods often refer to species diversity and treat each species as equally important; two closely related species in the same genera and functional group – perhaps two grasses – would rank as importantly as a species – perhaps a large woody tree – that impedes their

colonization. Clearly this approach is inadequate. A potential solution comes in the form of community phylogenetics (Faith 1992; Faith 1994; Bryant et al. 2008; Cavender-Bares et al. 2009).

Community phylogenetics is the study of the phylogenetic diversity of all species in a given community. Such research seeks to quantify the evolutionary distinctiveness of the species present, under the premise that evolutionary diversity may be more important than species diversity. Primarily, community phylogenetic inquiry has – to date – been directed at attempting to describe community assembly and structuring processes (e.g. Webb et al. 2002; Swenson et al. 2006). More recently however, the potential for diversity applications of phylogenetic study have been applied to community ecological theory (Maherali & Klironomos 2007; Morlon et al. 2011). From a practical perspective, quantifying the relative distinctiveness of the species present (both functionally and evolutionarily), will enable weighting of species incidence and abundance by their diversity in traits and evolutionary potential to better conserve an ecosystem's ability to accommodate environmental change. The potentially significant impact of phylogenetic information on community ecology and biodiversity research has resulted in wide ranging applications of phylogenetic diversity concepts, particularly to community ecology (Webb et al. 2002; Cavender-Bares et al. 2009).

QUANTIFICATION OF PHYLOGENETIC DIVERSITY

In the past decade, and chiefly since the publication of Webb *et al*. (2002), the importance of phylogenetic diversity has been recognized not only for conservation purposes but also for its potential effect on community assembly and structure. Attempts to quantify community phylogenetic diversity have therefore increased (e.g. Cavender-Bares et al. 2006; Swenson et al. 2006).

Initially, Faith proposed a simple metric of phylogenetic diversity (PD; Faith 1992). Faith (1992, 1994) reasoned that phylogenetic information might contribute to the general ecological problem of quantifying biodiversity, noting that if traits are conserved, phylogenetic diversity is a proxy for trait diversity. Faith's PD is a simple metric; it is the total length of all branches joining together all species of a given community on a phylogenetic tree with their common ancestor (Faith 1992). Faith based his metric on cladistics and assigned branch lengths to taxonomic levels (e.g. family, genus). Noting that such a

simplistic measure did not take species abundance into account, Clarke and Warwick (1998) proposed a novel metric: Taxonomic Distinctiveness or 'Δ', which is the expected path length (or PD) between any two randomly chosen individuals within a plot. Recognizing that not all datasets or methods allow for abundance sampling, they also introduce Δ* which relies on incidence only and is the expected path length between individual species (Clarke & Warwick 1998). However, these metrics were limited because they were applied to hierarchical taxonomic classification, not actual evolutionary differences.

Phylogenetic distance is meant to approximate the evolutionary distance between species; thus, basing this distance on cladistic trees where each branch length is 'one' does not account for varying evolutionary rates or divergence times among species. More recent studies have therefore employed knowledge about divergence times gleaned from the fossil record to quantify PD (e.g. Slingsby and Verboom 2006; Swenson et al. 2006; Hardy and Senterre 2007). Commonly, mean pairwise distance (MPD) and mean minimum pairwise distance (MMPD; also called mean nearest neighbour distance by Kembel and Hubbell 2006) are considered as raw PD values (Webb et al. 2002; Kembel & Hubbell 2006; Swenson et al. 2006). Mean pairwise distance is the average PD of every species pair in the same plot based on divergence times, representing a tree-wide metric of phylo-relatedness (Webb 2000; Swenson et al. 2006). Mean minimum pairwise distance is the average PD between each species and its nearest neighbour on the phylogenetic tree within the same plot and is considered a terminal metric of PD (Webb 2000; Webb et al. 2002; Swenson et al. 2006). In a notable example, Slingsby and Verboom (2006) took PD quantification methods a step further and generated a molecular clock for the species of sedge that they encountered and used it to estimate divergence times. They then applied these divergence times in place of a path length derived from taxonomy or the fossil record (Slingsby & Verboom 2006).

Hardy and Senterre (2007) proposed new metrics for quantifying phylogenetic diversity that are based on similar indices for genetic (allelic) diversity across space. They introduced methods that rely on abundance data (analogous to Wright's F_{ST} in genetics) and others that rely only on incidence (presence/absence; Hardy and Senterre 2007; Graham and Fine 2008). Such metrics quantify the phylogenetic distance between each pair of distinct species, as quantified by the approximate age of the

most recent common ancestor divided by the age of the common ancestor of all community members in the tree. As such, taxonomic distinctiveness values range from zero to one, with more phylogenetically diverse communities closer to one and less diverse closer to zero. The distinctiveness of all samples taken together is therefore always one. Based on such metrics one can quantify the PD of observed communities, but interpreting these values with respect to ecological or evolutionary processes requires statistical testing.

To determine the significance of observed PD pattern, observed PD values have usually been compared against randomly generated null expectations (e.g. Cavender-Bares et al. 2006, 2009; Kembel and Hubbell 2006; Swenson et al. 2006). Generation of the null expectation typically follows one of two paths: (1) species are shuffled across the tips of the generated phylogenetic tree numerous times (commonly 1000) and the observed communities are retained (Kembel & Hubbell 2006; Swenson et al. 2006; Hardy & Senterre 2007), or (2) the species presence in communities are shuffled (2a) across all quadrats while maintaining the richness of each quadrat or (2b) the richness is again maintained, but also the occurrence rate of species across all quadrats is maintained (i.e. the number of times a species is encountered is maintained) (Kembel & Hubbell 2006). Phylogenetic diversity is calculated based on each of the null trees/communities and compared against the observed values using indices of relatedness. Two popular indices are the Net Relatedness Index (NRI), which is denoted according to:

Equation 1.5

$$NRI = -\left(\frac{MPD - MPD_{NULL}}{sdMPD_{NULL}}\right),$$

where MPD_{NULL} is the average MPD generated by the null model and $sdMPD_{NULL}$ is the respective standard deviation, and the Nearest Taxon Index, which is denoted:

Equation 1.6

$$NTI = -\left(\frac{MMPD - MMPD_{NULL}}{sdMMPD_{NULL}}\right),$$

where – in accordance with the above NRI function – the true value (MMPD) is compared to the null model values ($MMPD_{NULL}$, $sdMMPD_{NULL}$; Webb 2000; Webb et al. 2002; Kembel and Hubbell 2006).

For both NRI and NTI, positive values indicate phylogenetic clustering of member species, while negative values indicate overdispersion (Webb 2000).

Clearly there are diverse methods for quantifying the phylogenetic diversity of communities. Metrics such as the NRI and NTI (Kembel & Hubbell 2006; Swenson et al. 2006) or those proposed by Hardy and Senterre (2007) enable investigation of the phylogenetic structure of communities; i.e. are species within a given assemblage more closely or distantly related than expected by chance? The quantification of community phylogenetic structure and its potential for revealing the processes that lead to the observed structure have made up the majority of phylogenetic studies to date.

PHYLOGENETIC STRUCTURING IN PLANT COMMUNITIES

Efforts aimed at relating phylogenetic diversity patterns to ecological process have increased rapidly since the publication of Webb et al. (2002). Primarily, such studies have sought to quantify phylogenetic structuring in communities (Graham & Fine 2008; Mayfield & Levine 2010). It is argued that significant community phylogenetic pattern occurs due to the interaction of evolutionary (trait conservatism) and ecological processes (habitat filtering and / or competitive exclusion; see below) (Slingsby & Verboom 2006; Gerhold et al. 2008; Cavender-Bares et al. 2009). Quantifying such metrics is therefore crucial to understanding the impacts of the changing world on plant communities (Cavender-Bares et al. 2009). Furthermore, describing phylogenetic diversity applies our increasing knowledge of evolutionary history and divergence times among species to community ecology (Hardy & Senterre 2007). Phylogenetic investigation therefore provides a proxy for interspecific similarity of biogeography and ecology if niche conservatism occurs (Hardy & Senterre 2007). However, inferring process from pattern is notoriously difficult and risky; it has been noted that spatial and taxonomic scale are highly relevant (Cavender-Bares et al. 2006; Swenson et al. 2006), and that if neutral theory – wherein niches do not exist and do not effect community structure (Hubbell 2001) – were to hold, structural conclusions of phylogenetic inquiry could be meaningless.

Despite these concerns, research into the phylogenetic structuring of communities has increased rapidly. Phylogenetic structuring is interpreted as being higher (overdispersion, *sensu* Webb et al. 2002; evenness,

sensu Vamosi et al. 2009) or lower (clustering; *sensu* Webb et al. 2002) than expected phylogenetic diversity, or random pattern depending on the influence of interacting evolutionary and ecological processes (Table 1.1; Webb et al. 2002). Most such studies are observational, whereby natural systems are observed, the phylogenetic diversity quantified, and the relationships of present species analyzed. For example, Swenson et al. (2006) found a negative trend towards dispersion at finer taxonomic scales (species), but marginal clustering at higher taxonomic scales (Family). In addition, the spatial structuring of phylogenetic diversity did not change until discontinuous regions were included, which lead to clustering, as expected (Swenson et al. 2006). As such, both taxonomic and spatial scaling can have an influence on the observed phylogenetic signal (Swenson et al. 2006; Hardy & Senterre 2007). Furthermore, the available species pool size can influence observed phylogenetic structuring (Swenson et al. 2006).

Table 1.1 Predicted community structuring under different assumptions of evolutionary niche / trait conservatism and ecological forces (*adapted from Webb et al. 2002)*.

	Ecological traits are phylogenetically:	
	Conserved	**Convergent**
Dominant ecological force:		
Habitat Filtering (phenotypic attraction)	Clustered	Overdispersed
Competitive Exclusion (phenotypic repulsion)	Overdispersed	Random

The rapid expansion of the field has resulted in criticism (Mayfield & Levine 2010) and calls for experimental study of community phylogenetics (Vamosi et al. 2009). In one such study, Cadotte et al. (2009) found that phylogenetic diversity was the second best predictor of productivity, only marginally less successful than the presence of a nitrogen fixer (which has obvious benefits to any plant community), in a nitrogen limited system. Therefore, quantifying phylogenetic diversity could be important for ecosystem management and conservation because phylogenetic diversity improves community function as measured by productivity. However, none of the phenotypic traits measured by Cadotte et al. (2009) exhibited strong correlation with phylogenetic relatedness (phylogenetic signal). Nonetheless, given the

strong association between productivity and phylogenetic diversity, there must be some traits, not measured, that contribute to productive success (Cadotte et al. 2009). In another experimental study Maherali and Klironomos (2007) showed that important functional traits were conserved within phylogenetic lineages of mycorrhizal fungi and that these functional traits influenced the structure of fungal (arbuscular mycorrhizal fungi) communities. Phylogenetic diversity is therefore an important structuring feature of ecological communities. Despite such encouraging results, debate about the merits of phylogenetic inquiry is ongoing (Vamosi et al. 2009; Mayfield & Levine 2010). As is openly acknowledged (e.g. Swenson et al. 2006; Hardy and Senterre 2007; Cavender-Bares et al. 2009), the field relies heavily on assumptions about niche/trait conservatism within taxonomic clades.

NICHE CONSERVATISM AND COMMUNITY PHYLOGENETICS

One of the primary concerns about the field of community phylogenetics is its foundational assumption: that niches and / or traits are conserved within taxonomic clades of closely related species (Hardy & Senterre 2007; Gerhold et al. 2008). However it is possible – given potentially rapid evolution – for closely related species to not share similar traits, resulting in phylogenetic diversity measures underestimating functional diversity. Conversely, homoplasy (or convergent evolution) – the presence of similar functional traits arising independently – may result in high phylogenetic diversity, but low functional diversity. Despite such possibilities, niche conservatism has been shown to be a general pattern among higher plants (Prinzing et al. 2001). This is of critical importance if community phylogenetics and phylogentic diversity pattern are to be applied to theoretical study and practical decision making. In spite of widespread efforts aimed at its quantification, consensus about patterns relating to phylogenetic diversity and its relevance to community ecology remains elusive (Mayfield & Levine 2010).

CRITICISM OF PHYLOGENETIC INQUIRY

In their cautionary review of community phylogenetics, Mayfield and Levine (2010) structure their argument on two assumptions of the field, namely, (i) an organism's niche is determined by its phylogenetic history, and (ii) that niche differences are important for co-existence of species. As such,

most of the concerns surrounding the application of community phylogenetics are directed at the assumptions of niche conservatism, and the subsequent environmental filtering (cluster together due to their pre-adaptation to a given environment) and / or competitive exclusion among closely related species (Table 1.1). Of additional importance is the argument of neutral theory (Hubbell 2001) which suggests that communities assemble randomly with respect to traits; that is, niches, conserved or not, do not play a role in community assembly. Mayfield and Levine (2010) argue that contrary to working assumptions, community phylogenetics cannot be used to reveal the separate effects of filtering and competitive exclusion, because the interactions are not independent. Applying classic niche theory, it is primarily environmental filtering that limits a species from occurring at a given location, after which competition may further limit species co-occurrence. Therefore, community phylogenetics may only (given niche conservatism) determine the relative strength of these processes for structuring the observed community (Mayfield & Levine 2010). In addition, species with similar niches, but both having weak competitive ability are likely to co-occur, and similarly, species with sharp niche differentiation and high competitive ability may also co-occur (See Figure 1 in Mayfield and Levine 2010). Finally, somewhat more nuanced assumptions must be considered. Mayfield and Levine (2010) identify two of these, namely, (1) that local interactions must moderate phylogenetic structuring (Prinzing et al. 2008), and (2) negative interactions must result in species level exclusion, not character or trait displacement within species (phenotypic plasticity). Because of the great potential for phenotypic plasticity in many plant species, trait similarity does not necessarily equate to competitive exclusion.

Mayfield and Levine (2010) also take issue with the methods used to assess the significance of such interactions, primarily the null model (e.g. Cavender-Bares et al. 2006; Swenson et al. 2006; Chave et al. 2007), arguing that competitive exclusion equates to environmental filtering, and that biotic and abiotic processes should not be separated out as may be the case in null modeling. As such, competitive exclusion may not leave a consistent signal in phylogenies (Mayfield & Levine 2010). Vamosi et al. (2009) also note the potential faults associated with null modeling. In particular, most null models do not control for dispersal limitation when randomly shuffling species. This is important because dispersal has been shown to be an important factor for diversity patterning at the species level (Rosindell & Cornell

2007; Shen et al. 2009). To date most community phylogenetic studies have also ignored positive biotic interactions (e.g. facilitation, but see Valiente-Banuet & Verdú 2007). Studies investigating the effects of biologically relevant processes on observed phylogenetic diversity pattern are therefore warranted.

PHYLO BETA DIVERSITY

As noted in section 1.2, traditional beta diversity (the turnover of species across geographic space) is an important community trait that can help investigate the factors that structure communities (e.g. environmental gradients, habitat heterogeneity) and the relationships between local and regional diversity (Graham & Fine 2008). Since phylogenetic diversity has been proposed as a measure of community structuring and seeks to quantify the impact of evolution on observed communities, a metric of its turnover in space adds a temporal (divergence times) aspect to beta diversity investigation (Graham & Fine 2008). Species diversity, for example, treats even closely related species as equally important without respect for how evolutionarily or functionally divergent they may be. When taken together with phylogenetic community structure, phylogenetic beta diversity can clarify the relative importance of specialization and dispersal (Fine & Kembel 2011). Phylogenetic beta diversity may therefore be an important aspect of biodiversity investigation.

Phylogenetic beta diversity has been defined as "the phylogenetic distance (branch lengths) between samples of individual organisms between any two sites …" (Graham & Fine 2008), and if all encountered species are equally related – a so-called star phylogeny – phylogenetic beta diversity will be proportional to species beta diversity. Phylogenetic beta diversity has been used to investigate how historical processes (Kubota et al. 2011), conserved traits and mutualisms (Bryant et al. 2008), and community structure and dispersal limitation (Fine & Kembel 2011) lead to observed diversity pattern across space. Bryant et al. (2008) quantify the inverse of phylogenetic beta -diversity following Sørensen's similarity index, a popular index of beta diversity based on presence/absence data (i.e. not abundance data) denoted as:

Equation 1.7

$$S\text{ør}_{ij} = \frac{S_{ij}}{\frac{1}{2}(S_i + S_j)},$$

where S_{ij} is the shared species richness (number of shared species), and S_i and S_j are the species richness values for each plot being compared. Similarly then, Bryant et al. (2008) denote the following for phylogenetic beta diversity:

Equation 1.8

$$PhyloSør_{ij} = \frac{BL_{ij}}{\frac{1}{2}(BL_i + BL_j)}$$

where BL_i and BL_j are the rooted branch lengths of communities *i* and *j* and BL_{ij} is the shared branch length of the two communities. Due to the similarity of these equations, the change in taxonomic beta diversity in space can be directly compared to the change in phylogenetic beta diversity in space, providing a temporal or evolutionary aspect to beta diversity quantification. Other models of phylogenetic beta diversity include using the NRI and NTI metrics across samples and plots (Fine & Kembel 2011) or UniFrac (Lozupone & Knight 2005) which measures the fraction of unshared branch lengths (PD) between any two community pairs (e.g. Kubota et al. 2011) and is analogous to Jaccard dissimilarity. Assuming niche conservatism by related species, comparing phylogenetic and taxonomic beta diversity may shed light on the processes structuring changing communities across a gradient (Bryant et al. 2008; Graham & Fine 2008; Fine & Kembel 2011).

The results of comparing phylogenetic beta diversity and taxonomic beta diversity can determine which lineages are leading to turnover patterns between regions and help clarify *in situ* diversification and / or extirpation which currently drive patterns of diversity and composition (Graham & Fine 2008). For example, when phylogenetic turnover closely matches species turnover, this indicates the presence of local endemics with deep phylogenetic relationships; i.e. they diverged a long time ago (Bryant et al. 2008; Graham & Fine 2008; Sander & Wardell-Johnson 2011). Conversely, closely related species that differ between sites will result in lower phylogenetic turnover than species turnover. Sander and Johnson (2011) showed – within the Southwest Australian Floristic Region (SWAFR) using PhyloSør – that phylogenetic turnover was closely related to species turnover and deduced that this indicates the presence of "many locally endemic and phylogenetically relict taxa." Furthermore they note that such clustered

phylogenetic diversity increases the risk of such communities to diversity loss with global change (Sander & Wardell-Johnson 2011).

SPECIES POOLS AND PHYLOGENETIC DIVERSITY

It has been highlighted recently that quantifying diversity patterning without taking the available species pool into account masks patterns or suggests significant patterns that are expected by chance (Lessard et al. 2012). To date however, relatively few studies have investigated the potential impact of species pool differences on phylogenetic diversity explicitly. It is commonly acknowledged however, that when including evolutionarily distinct or environmentally heterogeneous communities, PD will increase (Swenson et al. 2006), in much the same way as the steepening of the species area relationship at large scales (Williamson et al. 2001; Fridley et al. 2005; Palmer 2007). In one study, Gerhold et al. (2008) predicted that large species pools would be indicated by high phylogenetic distinctiveness (*sensu* Clarke and Warwick 1998) of local communities in continuous systems, a pattern they termed the *'Niche conservatism hypothesis of species pools.'* In their study of European herb-layer plant communities Gerhold et al. (2008) found support for this hypothesis, wherein large species pools indeed exhibited higher phylogenetic distinctiveness. Kraft et al. (2007) investigated the effect of sampling completeness with respect to the overall species pool and in the context of community phylogenetic structure found that significant structural results were most likely when local communities had an intermediate richness (30-60%) of the regional species pool. Species pools therefore can relate to phylogenetic signals in herbaceous plant communities, but the extent to which it affects phylogenetic diversity-area relationships is unclear. Furthermore, taking into account the appropriate available species pool will determine the effectiveness of null modeling based on these species pools.

TESTING PATTERNS OF PHYLOGENETIC DIVERSITY

As has been demonstrated, phylogenetic diversity patterns are primarily tested using null model approaches. However, clarifying how phylogenetic diversity is influenced by factors both within and outside the trophic level of interest may require experimental approaches. Cadotte et al. (2009) used

experimental plant communities and examined how phylogenetic diversity influenced functional traits. They found that it was a significant predictor of community productivity, only slightly less important than the presence of a nitrogen fixing species. However they could not find any phylogenetic signal in traits that they measured indicating that perhaps an unmeasured, phylogentically conserved trait, was responsible for the influence on productivity (Cadotte et al. 2009). In a follow up study, this time with plant communities of up to four species specifically set into groups of increasing phylogenetic diversity, Cadotte (2013) again found that phylogenetic diversity was positively related to community productivity. However, these experimental setups are ideal situations, and may not reflect all of the characteristics found in nature. Therefore, 'natural experiments' may shed more light on the way in which phylogenetic diversity structures, or is structured by certain environments and plant communities. One of the longest standing types of natural, ecological experiments is the grazing exclosure. Patterns of plant communities under various grazing regimes, or indeed grazing exclusion have been a central paradigm of plant ecology for decades.

1.4 Grazing and plant biodiversity

Disturbance has been regularly identified as an important mechanism for the maintenance of biodiversity (Svensson et al. 2012). For example, important community ecological theories (e.g. Intermediate Disturbance Hypothesis) suggest that without moderate levels of disturbance, many communities would be much less diverse (Connell 1978; Svensson et al. 2012; but see Fox 2013). Research and theory suggests that moderate disturbance (i) can create new opportunities for colonization, (ii) increases habitat heterogeneity, and can therefore (iii) influence competition and local extinction rates among community members (Olff and Ritchie 1998; Frank 2005). When quantified by area and / or overall biomass, the two most significant sources of plant community disturbance are fire and grazing (Huntly 1991; Díaz et al. 2007). Of these two, grazing (as a human mediated influence) provides feasible opportunities for testing competing ecological theory through experiments. For example, it is reasonably straightforward to exclude large herbivores and to then observe the response of plant communities through time. However, studies on the relationship between grazing and plant species diversity (primarily species richness and / or

evenness) are filled with conflicting results and discussion of site-specific contingencies. In general, the overall direction and magnitude of grazing's influence on plant communities appears to be dependent on (i) the productivity of the system under investigation and the specific traits (e.g. functional, life history) of the present plant species, (ii) the strategies and size of the grazers (e.g. large ungulates vs. lagomorphs), and (iii) the evolutionary history of grazing in the system (Olff and Ritchie 1998; Díaz et al. 2007).

PRODUCTIVITY AND PLANT TRAITS

It is widely recognized that productivity can influence biodiversity patterning in plant communities. For example, limited availability of light in highly productive systems may exclude weaker competitors and / or small statured species that are present in the regional pool (Bakker et al. 2006), while at lower productivity only a smaller subset of available plant species may colonize. It has been suggested that moderate levels of herbivory may allow light to reach smaller species, while limiting the success of larger, more dominant species (without extirpating them), thereby increasing species richness (Bakker et al. 2006). At low productivity however, herbivores feed on any available species, likely further limiting the number of species that can both colonize and survive under grazing pressure at these sites. Adding to the complexity of grazed systems are the widespread, interacting effects of plant traits (functional traits, life history, growth habit, height) on diversity patterning. Given the potential for interplay between herbivore and plant characteristics, it is somewhat surprising to find consistent impacts of grazing on plant traits at the global scale (e.g. Díaz et al. 2007). In general, Díaz et al. (2007) found that annuals increase in both diversity and abundance while perennials decrease. In terms of richness the annual / perennial effect was strongest in humid, highly productive systems. Díaz et al. (2007) suggest that the increase in annual species may drive the overall increases in richness observed under grazing in productive systems. Díaz et al. (2007) also showed that globally, grazing tended to lead to a decrease in tussock forming graminoids with a corresponding increase in stoloniferous and rosette forming forb species; a result supported by the subsequent empirical work of Burns et al. (2009). Evidently plant traits are influenced by, but also have an effect on plant community responses to grazing (Díaz et al. 2007).

HERBIVORE TRAITS AND STRATEGIES

While the traits of plant community members may influence the observed pattern, they are themselves selected for (or against) by the herbivore community. Importantly, varying herbivore traits may be as significant as varying plant traits for community assembly of plants. For example, large herbivores influence dominance patterns by creating gaps in the canopy, trampling and turning over soil and providing nutrient deposition that increase heterogeneity and facilitate colonization (Adler et al. 2001; Deléglise et al. 2011), and correspondingly have been found to increase diversity in productive systems (but be neutral or even negative in low productivity systems; e.g. Bakker et al. 2006). Furthermore, large grazers (e.g. most rangeland livestock) are relatively unselective herbivores, defoliating most species, while smaller herbivores tend to be selective and target certain species or parts of plants (e.g. seeds; Olff and Ritchie 1998). In contrast however, herbivores may also decrease species diversity, increasing homogeneity of the plant community through improved seed dispersal (in fur, dung or hooves; Olff and Ritchie 1998; Frank 2005). Such plant community responses to grazing are therefore often scale dependent, as the local scale for a large ungulate is likely to be much larger than that of a small, seed feeding rodent (Olff and Ritchie 1998). For example, in high productivity systems, larger herbivores have strong influences on diversity (Bakker et al. 2006; Burns et al. 2009), while more selective, small herbivores tend to have limited effect at the scales commonly studied in community ecology (i.e. 1 m^2; Bakker et al. 2006; Díaz et al. 2007). Komac et al. (2011) also found that at the regional scale (i.e. among habitat patches) grazing increased heterogeneity, while at the local scale (within patch), grazing had a homogenizing effect. Given the potentially positive impacts of herbivory in productive systems (in terms of plant alpha diversity), grazing livestock have even been suggested as an important conservation measure (Faria et al. 2012). While the influence of grazing herbivores on plant communities is obviously significant, general patterns of direction and magnitude remain unclear and are contingent upon multiple, often interacting, factors including spatial and / or temporal scale, productivity, plant traits, and the evolutionary history of grazing.

HISTORY AND INTENSITY OF GRAZING

Since plant communities are in part a product of a region's evolutionary history (Taylor et al. 1990; Zobel 1992), it is not surprising that their response to grazing is dependent on the intensity and evolutionary history of grazing in the community under study. Moderate livestock grazing tends to increase plant species diversity (increased richness), while intense grazing, perhaps unsurprisingly, limits diversity as nearly all individuals are eaten and the soil is heavily trampled such that only highly tolerant or unpalatable species remain (Milchunas et al. 1988; Carmona et al. 2012). Intense grazing can therefore lead to a sharp decline in taxonomic and functional diversity (Carmona et al. 2012). Furthermore, variation in intensity throughout history may have led to diversification in the regional pool through time (Cingolani et al. 2005). In fact, Díaz et al. (2007) identified evolutionary history of grazing as an important covariate in the trait based responses of plant communities. For example, the increase in annual species richness under grazing appeared to be primarily driven by increases in annuals in systems with a short history of grazing, whereas in systems with a long history, the observed increase in annual species was not significant (Díaz et al. 2007). Information on the evolutionary history and intensity of grazing of any study system will therefore be crucial to placing observed patterns in context.

GRAZING AND PHYLOGENETIC DIVERSITY PATTERNING

An extensive body of work has investigated the effects of large herbivore grazing on plant species diversity and functional traits. However, few studies have attempted to quantify its influence on phylogenetic diversity (but see Yessoufou et al. 2013). If, as described above, certain functional and / or species groups are strongly favoured in the presence of large herbivores (e.g. annuals, short statured species, unpalatable species in unproductive systems), and if such traits are phylogenetically conserved (Prinzing et al. 2001), the general increase in species richness found in grazed systems may not translate into increased phylogenetic diversity, as specific clades will be favoured, leading to relatively low PD (Yessoufou et al 2013). However, if grazing is moderate (and productivity high enough) such that it increases heterogeneity (i.e. patches of dominant species remain while grazing generates opportunity for smaller statured / less competitive species elsewhere), then phylogenetic diversity patterns should follow

the corresponding increase in species richness. Given the demonstrated importance of evolutionary history for describing the influence of grazing on plant traits (Díaz et al. 2007) and the ability of phylogenetic diversity to capture a signature of history in current diversity patterns (Graham and Fine 2008), further investigation of the relationship between grazing and phylogenetic diversity is warranted.

1.5 Research Outline and Objectives

The rapid and ongoing advancement of methodologies for measuring and studying diversity patterns has led to intriguing findings and better descriptions of the way in which communities are structured and their diversity maintained. However, the rate at which new metrics are proposed and modified, and the continued development of alternative measures of diversity has left gaps in the diversity toolbox. Furthermore, new metrics of diversity and their partitions have not yet been applied to many systems, including grazed plant communities. The widespread use of rangelands as a grazing resource in North America suggests that studies investigating all of the impacts of livestock on plant, and indeed all trophic levels are warranted. However, to date, these studies have been primarily restricted to traditional measures of diversity like species richness. Recent works have applied functional and trait based measures of diversity (e.g. Carmona et al. 2012) to grazing systems, but relatively few have studied phylogenetic diversity (e.g. Yessoufou et al. 2013).

In addition, beta diversity has been often used to measure heterogeneity (Anderson et al. 2011), but recent work highlighting the shortfalls of averaging pairwise dissimilarities has not been adequately addressed. Furthermore, the tools for measuring multiple site beta diversity have not been extended to the most robust partitions of beta diversity, or to alternative measures of diversity. Studies that have used robust measures of average beta diversity (e.g. Whittaker's multiplicative beta; Whittaker 1960, 1972) are not able to investigate patterns of partitioned beta diversity wherein the influence of species turnover (i.e. replacement) and richness (i.e. species loss or gain) components can be investigated independently. As has been demonstrated, these measures often yield differing and informative results not available from the traditional measures. Therefore, the purpose of my research was to further develop the beta diversity toolbox to include the most recent partitions of beta diversity for both taxonomic and phylogenetic

measures, and to study how grazing by large herbivores influences within-community beta diversity, using two alpine meadow systems as case studies. Given that patterns of within-community beta diversity have rarely been quantified, and that the rangeland grazing of alpine meadows by livestock (primarily cattle) is widespread in British Columbia, I sought to establish the impact of cattle grazing on alpine meadow heterogeneity. Specifically, my objectives were to:

1) develop a multiple site beta diversity metric for the recently proposed partition of Jaccard's Dissimilarity (Carvalho et al. 2013),
2) extend the existing partitions of pairwise phylogenetic beta diversity to the novel partition of Jaccard's dissimilarity and to then develop phylogenetic multiple site beta diversity metrics,
3) to quantify the influence of cattle grazing on taxonomic heterogeneity of alpine plant communities as measured by the novel multiple site partition developed in objective 1, and
4) to quantify the influence of cattle grazing on phylogenetic heterogeneity of alpine plant communities as measured by the novel multiple site metrics developed in objective 2.

With newly developed tools for quantifying both taxonomic and phylogenetic heterogeneity, I tested the following predictions:

1. Grazing will increase taxonomic alpha diversity at the quadrat level if biomass is moderate or high (e.g. Bakker et al. 2006).
2. Grazing will increase phylogenetic alpha diversity as measured by MPD and MNTD (Campbell et al. 2009, 2013).
3. Grazing will have a homogenizing effect on within-community taxonomic heterogeneity (Komac et al. 2011).

4. By preferring certain lineages (over those that are non-palatable or toxic) grazing will generate decreased variation in phylogenetic diversity among sampling plots reflecting their homogenizing influence.

To date limited work has investigated the influence of disturbance on phylogenetic beta diversity. However, it is reasonable to suspect that if species (taxonomic) turnover among samples is reduced, that phylogenetic heterogeneity should also decrease. Furthermore, the impact of grazing on herbaceous plant communities has not been investigated with respect to partitioning approaches for quantifying beta diversity, and in particular has not been conducted using the most robust approaches (i.e. Carvalho et al. 2013). It is therefore possible that although grazing cattle reduce heterogeneity at the local scale, this may be a result of influences on alpha diversity, i.e. richness effects. Applying null models may account for richness differences and allow robust tests of beta diversity across the treatment (e.g. Myers et al. 2012). Furthermore, novel partitions of beta diversity specifically seek to quantify the richness and replacement portions of beta diversity independently (Baselga 2010, 2012; Carvalho et al. 2013). Combining null models with beta partitioning approaches will better clarify how communities are being assembled (e.g. Azeria et al. 2012).

Herein I begin by further developing existing measures of biotic heterogeneity (i.e. multiple site beta diversity) to the novel partition of beta diversity proposed by Carvalho et al. (2013) and extend these partitions to an alternative measure of diversity, i.e. phylogenetic diversity in Chapter 2. I provide full mathematical derivations for these formulae and provide R (R Development Core Team 2013) code for their calculation in Appendix E. I then apply the novel partition of taxonomic multiple site beta diversity to the two grazing sites studied herein. When considering alpha diversity I show (i) that grazing did not have any consistent influence at low or moderate productivity sites and (ii) that grazing had no influence on phylogenetic alpha diversity as measured by MPD or MNTD. I compared observed values of multiple site heterogeneity and the difference in those observed values to the null expectation based on three different null models. I show that heterogeneity does indeed vary with the grazing treatment, but that patterns differ for phylogenetic and taxonomic beta diversity, supporting their complementarity in

biodiversity investigations. Furthermore, the grazing influence on heterogeneity differs strongly at the two sites. Taken together, these results highlight that grazing influences the amount of evolutionary diversity available for adaptation to increasing pressure on natural communities, as may be occurring under climate change. In conclusion I discuss the broader results and implications of this work for plant community ecology and conservation. I also highlight some important assumptions and limitations that may limit the generality of the patterns I describe herein. Finally, I suggest (i) ways to improve this study, and (ii) more general directions that research, based on the novel metrics developed in Chapters 2 and 3, may help to further clarify the processes structuring all ecological communities.

Chapter 2: Novel partitions and metrics of multiple site beta diversity

2.1 Introduction

Beta diversity, the change in species composition from one sample to another, has been a rapidly developing field of research, particularly since the publication of Hubbel's (2001) neutral theory (Tuomisto & Ruokolainen 2006). Although originally proposed by Whittaker (1962, 1970) as a multiple site metric ($\beta = \gamma/\alpha$; where alpha is the average species richness across all samples), it has primarily been calculated in a pairwise manner, using familiar dissimilarity metrics like Sørensen or Jaccard dissimilarity for presence / absence data (Tuomisto 2010; Anderson et al. 2011). These pairwise metrics are usually measured along some form of gradient, often environmental, and correlation tests (e.g. Mantel tests; Anderson et al. 2011; Pellissier et al. 2013) are used to determine if species turnover follows environmental difference. Another recent focus is the importance of partitioning the simpler beta diversity measures (e.g. Sørensen) into its richness independent turnover (replacement) and nestedness (richness differences) components. The best method to quantify the turnover and nestedness components is a topic of vigorous debate (e.g. Baselga 2010; Podani & Schmera 2011; Almeida-Neto et al. 2012; Baselga 2012; Carvalho et al. 2013). Furthermore, it has recently been demonstrated that averaging beta diversity values to estimate heterogeneity in a region of interest can yield misleading results (Diserud & Ødegaard 2007; Baselga et al. 2007; Baselga 2013).

BETA DIVERSITY AND WITHIN COMMUNITY HETEROGENEITY

Recently, substantial research interest has begun to look at beta diversity as a way of studying biotic homogeneity. Such research often looks across time at the anthropogenic influence on biodiversity through the lens of alien species introductions and endemic species extinctions (e.g. Rooney et al. 2004; Martin et al. 2005; Trentanovi et al. 2013) and primarily finds a homogenizing influence of humans on plant species diversity (e.g. Rooney et al. 2004; Schwartz et al. 2006). These studies are, however, primarily concerned with beta diversity across time, calculated as temporal dissimilarity in the same

sample. One notable study however looked at the success of preservation efforts in returning an agricultural field to its natural heterogeneity values, measured within a single site (Martin et al. 2005).

Martin et al. (2005) measured alpha, beta, and gamma diversity in a remnant plot of similar environmental conditions and compared observed 'natural' diversity values to those found in the restored / preserved landscape. Martin et al. (2005) found that within community beta diversity remained lower in the preserved area than in the natural system, but measured overall heterogeneity by the additive model of beta diversity (MacArthur et al. 1966; Levins 1968; Lande 1996). I believe Martin et al.'s (2005) approach of quantifying beta diversity in an environmentally homogenous site to be an important departure from conventional beta diversity research, i.e. analyzing beta diversity along gradients, looking for correlations to deduce process from pattern. I support their (Martin et al. 2005) notion that within-habitat beta diversity is an important characteristic of that habitat, in much the same way that alpha diversity, species evenness ("diversity") and gamma diversity are. However, the relatively simplistic additive measure of beta diversity employed by Martin et al. (2005) has come under scrutiny, with debate surrounding which of the additive or multiplicative measures are more appropriate. Several authors have argued convincingly for the multiplicative partition (e.g. Baselga et al. 2012).

While the multiplicative (and indeed the additive, Lande 1996) partition of diversity proposed by Whittaker (1960, 1972) constitutes a multiple site metric, it is blind to the independent patterns of turnover and richness within the given region. As such, research directed at biotic heterogeneity (homogenization) has followed the intuitive notion of averaging pairwise dissimilarity values to get a better picture of beta diversity or variation in biotic communities (Baselga 2012, 2013). However, several recent studies have shown that average pairwise beta diversity is a less than ideal measure of heterogeneity in a region (Diserud and Ødegaard 2007; Baselga et al. 2007; Baselga 2010, 2012).

MULTIPLE SITE BETA DIVERSITY

Diserud and Ødegaard (2007) and Baselga et al. (2007) note that averaging pairwise beta diversity values to estimate heterogeneity is misleading because it discards information where a species is shared among

three or more sites and does not acknowledge adequately that pairwise measures are not independent. Efforts to deal with the non-independence of pairwise beta diversity measures (e.g. permutational analysis of variance or PERMANOVA) are ongoing, but are incomplete (Anderson et al. 2011). The overall averaging of conflicting patterns may then lead to a neutral pattern of beta diversity (Baselga et al. 2007; Baselga 2013). To address this concern, Diserud and Ødegaard (2007) first proposed a metric of multiple site dissimilarity based on the Sørensen index of similarity. Baselga et al. (2007) however noted that since the Diserud and Ødegaard (2007) metric was based on Sørensen similarity, it also retained the Sørensen metric's susceptibility to richness differences (Baselga et al. 2007). As has been noted elsewhere (e.g. Harrison et al. 1992), Baselga et al. (2007) noted that multiple site metric based on Sørensen's similarity could not reliably determine if differences were due to richness differences (nestedness) or actual species turnover. Baselga et al. (2007) therefore proposed a multiple site similarity metric based on Simpson's Index and denote M_{sim}, as

2.1 $$M_{sim} = \frac{\sum_i s_i - s_T}{[\sum_{i<j} \min(b_{ij}, b_{ji})] + [\sum_i s_i - s_T]}$$

which can detect changes in composition while being independent of changing richness values. Baselga (2010) then extended M_{sim} to the Jaccard and Sørensen dissimilarity indices of beta diversity by changing M_{sim} to its corresponding dissimilarity metric that captures the turnover component of the Sørensen index of dissimilarity (Baselga 2010). Following his partition of beta diversity into turnover and nestedness-resultant dissimilarity, Baselga (2010) developed multiple site indices for the metrics β_{SOR}, β_{SIM}, and β_{SNE}, (Sørensen dissimilarity; see Derivation of Formulae and Table 2) and β_{JAC}, β_{JTU}, and β_{JNE} (Jaccard dissimilarity; see Derivation of Formulae and Table 2).

NEW PAIRWISE BETA DIVERSITY PARTITIONS

Relatively recently, Baselga (2010) proposed the further partition of Sørensen beta diversity into two components, the turnover component (i.e. richness independent change in composition as measured by the Simpson index) and the nestedness-resultant dissimilarity, which is the difference of the Sørensen and Simpson indices. Baselga (2012) also derived similar components for Jaccard's pairwise dissimilarity.

Importantly, several studies, including Baselga's own work have found differing patterns in the turnover and nestedness components of beta diversity (e.g. Baselga 2010; Azeria et al. 2011; Baeten et al. 2012). However, Baselga's partition is not without controversy.

A vigorous debate has followed Baselga's partition of pairwise beta diversity into turnover and nestedness resultant dissimilarity, lead primarily by Almeida-Neto et al. (2008, 2012), Podani and Schmera (2011) and Carvalho et al. (2012, 2013). Most of the arguments against Baselga's partition centre on the nestedness portion of the partition. Recently, Carvalho et al. (2013) argued convincingly, using simulations, that Baselga's partition of pairwise dissimilarity was incorrect, as the nestedness-resultant dissimilarity was found to decrease as species loss increased (see section 1.3 also) and proposed their own partition of β_{jac} into β_{rich} and β_{-3} (Table 2.1). Importantly, multiple site metrics for Carvalho et al.'s (2013) partition have not yet been derived. Furthermore, other measures of diversity (e.g. phylogenetic or functional) have not yet been fully applied to these new partitions.

PHYLOGENETIC BETA DIVERSITY PARTITIONING

Recently, Leprieur et al. (2012) applied Baselga's partition of beta diversity to phylogenetic diversity. Following Bryant et al.'s (2008) PhyloSor metric for Sørensen dissimilarity and Luzopone and Knight's (2005) UniFrac metric for Jaccard dissimilarity, Leprieur et al. (2012) derived the turnover components of both PhyloSor and UniFrac. They then deduced that the nestedness resultant dissimilarity was the difference between the overall metric (e.g. Sørensen) and the turnover component. Furthermore, Leprieur et al. (2012) provide the phylogenetic analogs for the familiar '*a*', '*b*', and '*c*' parts of beta diversity, where '*a*' is the number of species shared by the communities being compared, '*b*' is the number of species unique to sample *i* and '*c*' is the number of species unique to sample *j*. Despite this useful step forward, Leprieur et al. (2012) fail to provide the multiple site analogs of Baselga's multiple site beta diversity. In addition, Carvalho et al.'s (2013) partition was perhaps not yet available for derivation at the time of the publication of Leprieur et al. (2012).

Table 2.1 Partitioned, pairwise, taxonomic beta diversity metrics including the partition of Baselga (2010, 2012) and Carvalho et al. (2013). Note that both β_{jac} and β_{cc} correspond to Jaccard dissimilarity and are therefore the same.

Family	Measure	Notation	Formula	Reference
Sørensen (Baselga)	Sørensen dissimilarity	β_{sor}	$\frac{b+c}{2a+b+c}$	Baselga (2010,2012)
	Simpson dissimilarity = turnover of Sørensen	β_{sim}	$\frac{\min(b,c)}{a+\min(b,c)}$	Simpson (1943), Lennon et al. (2001), Baselga (2010, 2012), Carvalho et al. (2013)
	Nestedness resultant dissimilarity of Sørensen	β_{sne}	$\frac{\lvert b-c\rvert}{2a+b+c}$ x $\frac{a}{a+\min(b,c)}$	Baselga (2010, 2012), Carvalho et al. (2013)
Jaccard (Baselga)	Jaccard dissimilarity	$\beta_{jac\ (cc)}$	$\frac{b+c}{a+b+c}$	Jaccard (1912), Colwell & Coddington (1994), Baselga (2012), Carvalho et al. (2013)
	Turnover of Jaccard	β_{jtu}	2 x $\frac{\min(b,c)}{a+2\min(b,c)}$	Baselga (2010, 2012)
	Nestedness resultant dissimilarity of Jaccard	β_{jne}	$\frac{\lvert b-c\rvert}{a+b+c}$ x $\frac{a}{a+2\min(b,c)}$	"
Jaccard (Carvalho)	Jaccard dissimilarity	$\beta_{cc\ (jac)}$	$\frac{b+c}{a+b+c}$	Jaccard (1912), Colwell & Coddington (1994), Schmera & Podani (2011), Baselga (2012), Carvalho et al. (2013)
	Replacement component of Jaccard dissimilarity	β_{-3}	2 x $\frac{\min(b,c)}{a+b+c}$	Williams 1996, Cardoso et al. (2009), Carvalho et al. (2012, 2013)
	Richness component of Jaccard dissimilarity	β_{rich}	$\frac{\lvert b-c\rvert}{a+b+c}$	Schmera & Podani (2011), Carvalho et al. (2012, 2013)

Note: Table modified from Baselga (2012) and Carvalho et al. (2013)

OBJECTIVES

Therefore, there exists a gap in the available tools for studying homo/heterogeneity via beta diversity. It is well established that the partitioning of beta diversity provides information about patterns not visible from conventional beta diversity metrics (e.g. Azeria et al. 2012; Baeten et al. 2012; Baselga 2012, 2013). However Baselga's tools have been called into question and alternative methods for partitioning pairwise beta diversity have been proposed (e.g. Carvalho et al. 2013). Despite the obvious extension to multiple site metrics, these alternative partitions have not been extended to multiple site beta diversity. Furthermore, multiple site beta diversity metrics have not been developed for phylogenetic diversity. Here, I contribute to the beta diversity toolbox by providing functions for calculating (1) the pairwise phylogenetic beta diversity of Carvalho et al.'s (2013) partition and the multiple site phylogenetic beta diversity analogs for (2) Baselga's partition of Sørensen dissimilarity, (3) Baselga's partition of Jaccard dissimilarity, and (4) Carvalho et al.'s (2013) partition of Jaccard dissimilarity.

2.2 Derivation of Formulae

PAIRWISE TAXONOMIC BETA DIVERSITY

Recently, Baselga (2010, 2012, 2013) published his partition of beta diversity into turnover and nestedness-resultant dissimilarity. Carvalho et al. (2013) countered Baselga's proposal with their own partition of beta diversity into replacement (β_{-3}) and richness (β_{rich}) components. All three of these partitions are additive, wherein the turnover and nestedness/richness componenets sum together to equal the overall measure (Jaccard or Sørensen). Here, I display them using the familiar '*a*', '*b*', and '*c*' notation of beta diversity (Lennon et al. 2001), wherein '*a*' is the number of species shared between the i^{th} and j^{th} samples, '*b*' is the number of species unique to to sample *i*, and '*c*' is the number of species unique to sample *j*. These formulae are given in Table 2.1, which has been adapted from Carvalho et al. (2013) and Baselga (2012).

In deriving the multiple site dissimilarity metrics, Baselga (2007, 2012) showed that, since it is inconsequential which site of a pairing is *i* or *j*, the multiple site analog of '*b*' could be approximated by the sum of minimum values of '*b'* or '*c'* for all pairs of *i* and *j*. Following Baselga (2012) I denote b_{multi}:

2.2 $$b_{multi} = \sum_{i<j} \min\left(b_{ij}, b_{ji}\right)$$

The multiple site analog of '*c*' is then the sum of the maximum value of *b* or *c* for all pairs of *i* and *j*. Again following Baselga (2012) I denote c_{multi}:

2.3 $$c_{multi} = \sum_{i<j} \max(b_{ij}, b_{ji})$$

Baselga (2007, 2012) derived '*a*' by summing the species richness of all samples (*i* to *j*) and subtracting the total number of species found (i.e. gamma diversity), denoted here by:

2.4 $$a_{multi} = \sum_i S_i - S_T$$

Where S_T is the total species richness of all samples (regional richness or gamma diversity) and the sum of S_i is the sum of the richness of all samples (regardless of identity).

Substituting the above definitions of 'a_{multi}', 'b_{multi}', and 'c_{multi}' into the pairwise metrics makes the deduction of the β_{multi} formulae straight forward. The resulting formulae are given in Table 2.2 and have been copied from Baselga (2012). I then substituted equations *2.2*, *2.3*, and *2.4* into Carvalho et al.'s (2013) partition to generate the β_{multi} values for their Jaccard based metrics and following Baselga's (2012) approach, distinguish the β_{multi} notation from the pairwise notation by using upper-case subscripts (i.e. β_{CC}, β_{-3M}, and β_{RICH}) as noted in Table 2.2. It is worth emphasizing that subtracting equation *2.2* (b_{multi}) from equation *2.3* (c_{multi}) is equivalent to $|b - c|$ as noted for the pairwise metrics β_{rich} and β_{jne}, since it is always (maximum of *b* and *c*) – (minimum of *b* and *c*).

Table 2.2 Partitioned multiple site taxonomic beta diversity metrics including the partition of Baselga (2010, 2012) and Carvalho et al. (2013).

Family	Measure	Notation	Formula	Ref.
Sørensen (Baselga)	Sørensen dissimilarity	β_{SOR}	$\frac{[\sum_{i<j}\min(b_{ij},b_{ji})]+[\sum_{i<j}\max(b_{ij},b_{ji})]}{2[\sum_i S_i - S_t]+[\sum_{i<j}\min(b_{ij},b_{ji})]+[\sum_{i<j}\max(b_{ij},b_{ji})]}$	Baselga (2010, 2012)
	Simpson dissimilarity (Turnover: Sørensen)	β_{SIM}	$\frac{[\sum_{i<j}\min(b_{ij},b_{ji})]}{[\sum_i S_i - S_t]+[\sum_{i<j}\min(b_{ij},b_{ji})]}$	"
	Nestedness-resultant (Sørensen)	β_{SNE}	$\frac{[\sum_{i<j}\max(b_{ij},b_{ji})]-[\sum_{i<j}\min(b_{ij},b_{ji})]}{2[\sum_i S_i - S_t]+[\sum_{i<j}\min(b_{ij},b_{ji})]+[\sum_{i<j}\max(b_{ij},b_{ji})]} \times \frac{[\sum_i S_i - S_t]}{[\sum_i S_i - S_t]+[\sum_{i<j}\min(b_{ij},b_{ji})]}$	"
Jaccard (Baselga)	Jaccard dissimilarity	$\beta_{JAC\,(CC)}$	$\frac{[\sum_{i<j}\min(b_{ij},b_{ji})]+[\sum_{i<j}\max(b_{ij},b_{ji})]}{[\sum_i S_i - S_t]+[\sum_{i<j}\min(b_{ij},b_{ji})]+[\sum_{i<j}\max(b_{ij},b_{ji})]}$	Baselga (2012)
	Turnover (Jaccard)	β_{JTU}	$\frac{2[\sum_{i<j}\min(b_{ij},b_{ji})]}{[\sum_i S_i - S_t]+2[\sum_{i<j}\min(b_{ij},b_{ji})]}$	"
	Nestedness resultant (Jaccard)	β_{JNE}	$\frac{[\sum_{i<j}\max(b_{ij},b_{ji})]-[\sum_{i<j}\min(b_{ij},b_{ji})]}{[\sum_i S_i - S_t]+[\sum_{i<j}\min(b_{ij},b_{ji})]+[\sum_{i<j}\max(b_{ij},b_{ji})]} \times \frac{[\sum_i S_i - S_t]}{[\sum_i S_i - S_t]+2[\sum_{i<j}\min(b_{ij},b_{ji})]}$	"
Jaccard (Carvalho)	Jaccard dissimilarity	$\beta_{CC\,(JAC)}$	$\frac{[\sum_{i<j}\min(b_{ij},b_{ji})]+[\sum_{i<j}\max(b_{ij},b_{ji})]}{[\sum_i S_i - S_t]+[\sum_{i<j}\min(b_{ij},b_{ji})]+[\sum_{i<j}\max(b_{ij},b_{ji})]}$	This paper*
	Replacement component (Jaccard)	β_{3M}	$\frac{2[\sum_{i<j}\min(b_{ij},b_{ji})]}{[\sum_i S_i - S_t]+[\sum_{i<j}\min(b_{ij},b_{ji})]+[\sum_{i<j}\max(b_{ij},b_{ji})]}$	"
	Richness component (Jaccard)	β_{RICH}	$\frac{[\sum_{i<j}\max(b_{ij},b_{ji})]-[\sum_{i<j}\min(b_{ij},b_{ji})]}{[\sum_i S_i - S_t]+[\sum_{i<j}\min(b_{ij},b_{ji})]+[\sum_{i<j}\max(b_{ij},b_{ji})]}$	"

* modified from Carvalho et al. (2013) and Baselga (2012)

Phylogenetic diversity has received increasing interest as an alternative measure of diversity (e.g. Swenson et al. 2006, 2013; Bryant et al. 2008; Stegen & Hurlbert 2011), and has recently been shown to influence not only plant community function (e.g. Cadotte 2013), but also to influence the diversity of other trophic levels (e.g. insect herbivores, Pellissier et al. 2013). Therefore, quantifying phylogenetic beta diversity is another important characteristic in the structuring of communities. Bryant et al. (2008) developed the PhyloSor metric as a measure of phylogenetic beta diversity. Based on the Sørensen similarity index, Bryant et al. (2008) substituted phylogenetic tree branch lengths for species richness in the '*a'*, '*b'* and '*c*' framework, such that:

2.5 $$PhyloSor = \frac{BL_{ij}}{(BL_i + BL_j)\frac{1}{2}}$$

where BL_{ij} is the branch lengths common to both samples *i* and *j* (a), and BL_i (a+b) and BL_j (a+c) are the total branch lengths of samples *i* and *j* (Bryant et al. 2008). Denoted as a dissimilarity metric, $PhyloSor_{dis}$ can be written as:

2.6 $$PhyloSor_{dis} = \frac{BL_i + BL_j}{2BL_{ij} + BL_i + BL_j}$$

Luzopone and Knight (2005) developed a similar metric for the Jaccard dissimilarity entitled 'UniFrac' (short for unique fraction metric), which, following the notation of Bryant et al. (2008), I present as:

2.7 $$UniFrac = \frac{BL_i + BL_j}{BL_{ij} + BL_i + BL_j}$$

Leprieur et al. (2012) recognized the importance of marrying these phylogenetic beta diversity measures to the recently developed partition of Baselga (2010, 2012) and further developed the '*a'*, '*b'* and '*c*' framework. The notation of Leprieur et al. (2012) departs from that of Bryant et al. (2008) significantly such that it benefits from further explanation. Notably, the novel notation fits well with existing tools for calculating phylogenetic diversity in the package '*picante*' (Kembel et al. 2011) for the commonly used statistical programming language R (R Core Development Team 2013). Calculating unique phylogenetic

diversity metrics would have required developing new tools within the existing phylogenetic diversity functions. Leprieur et al. (2012) manage to avoid doing this by using elegantly simple algebra on the existing phylogenetic diversity functions. As such, Leprieur et al. (2012) denote a_{phylo} as:

2.8 $$a_{phylo} = PD_j + PD_i - PD_{Tot}$$

where PD_i is the phylogenetic diversity of the i^{th} sample (the sum of branch lengths joining all member species in the i^{th} sample), PD_j is the phylogenetic diversity of the j^{th} sample, and PD_{Tot} is the phylogenetic diversity of the combined community (i.e. the branch length joining all unique species in the i^{th} and j^{th} samples). To clarify, this derivation of a_{phylo} makes sense because $PD_j = a + c$, $PD_i = a + b$, and $PD_{Tot} = a + b + c$. Therefore, the portions b and c are subtracted out and $2a - a = a$, the desired value. In keeping with this derivation and notation, Leprieur et al. (2012) define b_{phylo} as:

2.9 $$b_{phylo} = PD_{Tot} - PD_j$$

and c_{phylo} as:

2.10 $$c_{phylo} = PD_{Tot} - PD_i$$

Where b_{phylo} is the phylogenetic branch length unique to the i^{th} sample and c_{phylo} is the phylogenetic branch length unique to the j^{th} sample. Note that in the original derivation by Leprieur et al. (2012) the authors used j and k to denote the samples being calculated. I depart from their notation to match the notation proposed by Baselga (2012) in his derivation of multiple site dissimilarity, which uses i and j to denote the samples being compared.

Substituting their derivations of the 'a_{phylo}', 'b_{phylo}' and 'c_{phylo}' framework, Leprieur et al. (2012) denote Bryant et al.'s (2008) PhyloSor and Luzopone and Knight's (2005) UniFrac as shown in Table 2.3. Leprieur et al. (2012) then proceeded to derive Baselga's (2012) partition for the two pairwise phylogenetic beta diversity measures (Table 2.3). I then follow Leprieur et al.'s (2012) lead and substitute their 'a_{phylo}', 'b_{phylo}' and 'c_{phylo}' values into the partition proposed by Carvalho et al. (2013) to generate the

functions for Phylo-β_{-3} and Phylo-β_{rich} and repeat the UniFrac function for Phylo-β_{cc} because it is the Jaccard dissimilarity as is UniFrac.

Table 2.3 Partitioned pairwise phylogenetic beta diversity metrics, including the partitions of Baselga (2010, 2012) and Carvalho et al. (2013). The derivation of phylogenetic metrics for Carvalho et al.'s (2013) partition is novel here.

Family	Measure	Notation	Formula	Reference
Sørensen (Baselga)	PhyloSor	$P\beta_{Sor}$	$\frac{2PD_{Tot} - PD_j - PD_i}{PD_j + PD_i}$	Bryant et al. (2008), Leprieur et al. (2012)
	$PhyloSor_{turn}$	$P\beta_{turn}$	$\frac{\min(PD_{Tot} - PD_j, PD_{Tot} - PD_i)}{PD_j + PD_i - PD_{Tot} + \min(PD_{Tot} - PD_j, PD_{Tot} - PD_i)}$	Leprieur et al. (2012)
	$PhyloSor_{PD}$	$P\beta_{pd}$	$\frac{\lvert(PD_{Tot} - PD_i) - (PD_{Tot} - PD_j)\rvert}{PD_j + PD_i}$ **X** $\frac{PD_j + PD_i - PD_{Tot}}{PD_j + PD_i - PD_{Tot} + \min(PD_{Tot} - PD_j, PD_{Tot} - PD_i)}$	Leprieur et al. (2012)
Jaccard (Baselga)	UniFrac	$P\beta_{unifrac\ (cc)}$	$\frac{2PD_{Tot} - PD_j - PD_i}{PD_{Tot}}$	Luzopone and Knight (2005), Leprieur et al. (2012)
	Turnover of Jaccard	$P\beta_{UFturn}$	$\frac{2\min(PD_{Tot} - PD_j, PD_{Tot} - PD_i)}{PD_j + PD_i - PD_{Tot} + 2\min(PD_{Tot} - PD_j, PD_{Tot} - PD_i)}$	Leprieur et al. (2012)
	Nestedness resultant dissimilarity of Jaccard	$P\beta_{UFpd}$	$\frac{\lvert(PD_{Tot} - PD_i) - (PD_{Tot} - PD_j)\rvert}{PD_{Tot}}$ **X** $\frac{PD_j + PD_i - PD_{Tot}}{PD_j + PD_i - PD_{Tot} + 2\min(PD_{Tot} - PD_j, PD_{Tot} - PD_i)}$	Leprieur et al. (2012)
Jaccard (Carvalho)	UniFrac dissimilarity	$P\beta_{cc\ (unifrac)}$	$\frac{2PD_{Tot} - PD_j - PD_i}{PD_{Tot}}$	Luzopone and Knight (2005), Leprieur et al. (2012)
	Replacement component of UniFrac dissimilarity	$P\beta_{-3}$	$\frac{2\min(PD_{Tot} - PD_j, PD_{Tot} - PD_i)}{PD_{Tot}}$	This paper*
	PD component of UniFrac dissimilarity	$P\beta_{rich}$	$\frac{\lvert(PD_{Tot} - PD_i) - (PD_{Tot} - PD_j)\rvert}{PD_{Tot}}$	This paper*

*Phylogenetic beta pair metrics were modified from Leprieur et al. (2012) and Baselga and Orme (2012) and based on Carvalho et al. (2013

To date, no metrics have been developed for multiple site phylogenetic beta diversity that I am aware of. I hereby combined the multiple site beta diversity metrics developed above (for Carvalho et al.'s (2013) partition) and by Baselga (2007, 2012) with the phylogenetic diversity metrics developed by Leprieur et al. (2012) to develop a full suite of partitioned, multiple-site, phylogenetic beta diversity measures (Table 2.4). To clarify, I reiterate how the taxonomic multiple site variables in Table 2.2 relate to the phylogenetic multiple site analogs found in Table 2.4, using β_{SOR} as an example below. Recall that which community corresponds to the *b* or *c* portion of these metrics is irrelevant and that in the multiple site analogs, they are represented by the sum of the minimum unique species (or branch lengths) and the sum of the maximum unique species (or branch lengths). Since the basal comparisons are always among a pair of sites, the minimum and maximum unique diversity measures always capture both *b* and *c*. Therefore:

2.2 $$b_{multi} = \sum_{i<j} \min\left(b_{ij}, b_{ji}\right)$$

relates to:

2.11 $$b_{PHYLO} = \sum_{i<j} \min\left(PD_{Tot} - PD_j, PD_{Tot} - PD_i\right),$$

2.3 $$c_{multi} = \sum_{i<j} \max(b_{ij}, b_{ji})$$

relates to:

2.12 $$c_{PHYLO} = \sum_{i<j} \max\left(PD_{Tot} - PD_j, PD_{Tot} - PD_i\right),$$

and

2.4 $$a_{multi} = \sum_i S_i - S_T$$

relates to:

2.13 $$a_{PHYLO} = \sum_i PD_i - PD_{SITE}$$

where PD_{SITE} is the Phylogenetic diversity of all species captured in all samples being compared to make up the multiple site beta diversity metric. Then, given that the traditional Sørensen dissimilarity is:

2.14 $$\beta_{sor} = \frac{b+c}{2a+b+c},$$

and that the multiple site function for Sørensen dissimilarity is:

2.15 $$\beta_{SOR} = \frac{\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]+\left[\sum_{i<j}\max(b_{ij},b_{ji})\right]}{2\left[\sum_i S_i - S_t\right]+\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]+\left[\sum_{i<j}\max(b_{ij},b_{ji})\right]},$$

I substitute the above b_{PHYLO}, c_{PHYLO}, and a_{PHYLO}, to get the phylogenetic multiple site dissimilarity, denoted as:

2.16 $$P\beta_{SOR} = \frac{\left[\sum_{i<j}\min(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]+\left[\sum_{i<j}\max(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]}{2\left[\sum_i PD_i - PD_{SITE}\right]+\left[\sum_{i<j}\min(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]+\left[\sum_{i<j}\max(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]}$$

Following a similar approach I derived the multiple site, phylogenetic beta diversity metrics for Jaccard dissimilarity and for the three partitions of beta diversity, Baselga's (2012) partition of Sørensen and Jaccard dissimilarity and Carvalho et al.'s (2013) partition of Jaccard's dissimilarity as indicated in Table 2.4.

2.3 Discussion and Conclusion

NOVEL CONTRIBUTION

Herein I have provided a small but necessary methodological step forward towards a stronger understanding of how beta diversity might be quantified. I have extended previously developed multiple site methods (see Baselga 2007, 2012) to novel partitions of taxonomic (see Cardoso et al. 2009; Schmera & Podani 2011; Carvalho et al. 2013) and phylogenetic beta diversity (e.g. Leprieur et al. 2012). Given that it has recently been shown that averaging pairwise beta diversity measures may be misleading and inaccurate, the development of appropriate multiple site metrics for stronger partitions of beta diversity (Carvalho et al. 2013) and the extension of these partitions to alternative diversity measures like phylogenetic diversity provides a valuable metric for researchers and managers alike.

Studies of biotic heterogeneity will benefit strongly from appropriate multiple site metrics of beta diversity. It has been well established that phylogenetic diversity adds further understanding to the biological diversity of a given system. Far from being a surrogate for functional diversity as once hoped (e.g. Faith 1992, 1994) phylogenetic diversity adds a further layer of information that could be crucial from a conservation and restoration perspective. Martin et al. (2005) showed that restoration efforts were not succeeding in returning taxonomic beta diversity to the levels observed in neighbouring unaltered habitat. However, this study used the relatively simplistic additive partition of diversity (MacArthur et al. 1966; Levins 1968; Lande 1996) to calculate beta diversity as the difference between site level species richness and the average richness of a sample. Studies such as Martin et al. (2005) may find the multiple site beta diversity approaches developed here, and by Baselga (2007, 2012), useful in further understanding the influence of restoration efforts on biotic heterogeneity.

Furthermore, applying phylogenetic diversity metrics to studies such as that of Martin et al. (2005) may help determine how phylogenetic diversity is influenced by restoration efforts and give a better idea of the patchiness of not only species, but lineages of species under various conditions. Fittingly, phylogenetic beta diversity has been applied in studies of biotic homogenization where changes in community level heterogeneity through time are quantified (e.g. Winter et al. 2009; Tobias and Monika 2012). Winter et al. (2009) quantified biotic heterogeneity within a region and compared it at two different times, but the region of investigation was all of Europe, and the time scales thousands of years. Contrary to the efforts of Winter et al. (2009), it is likely that the greatest utility of the multiple site taxonomic and phylogenetic beta diversity metrics will be at the local scale where species and indeed individuals interact with each other and other trophic levels to generate heterogeneity independent of environmental variation.

Table 2.4. Partitioned multiple site phylogenetic beta diversity metrics for the partition of Baselga (2010, 2012), and Carvalho et al. (2013). All functions presented here are represent novel extensions of Leprieur et al.'s (2012) derivation of partitioned, pairwise phylogenetic beta diversity based on the partition taxonomic beta diversity of Baselga (2010, 2012).

Family	Measure	Notation	Formula	References
Sørensen (Baselga)	Sørensen dissimilarity	$P\beta_{SOR}$	$\frac{\left[\sum_{i<j}\min(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]+\left[\sum_{i<j}\max(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]}{2\left[\sum_i PD_i - PD_{SITE}\right]+\left[\sum_{i<j}\min(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]+\left[\sum_{i<j}\max(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]}$	This paper*
	Simpson dissimilarity (turnover: Sørensen)	$P\beta_{SIM}$	$\frac{\left[\sum_{i<j}\min(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]}{\left[\sum_i PD_i - PD_{SITE}\right]+\left[\sum_{i<j}\min(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]}$	"
	Nestedness-resultant (Sørensen)	$P\beta_{SNE}$	$\frac{\left[\sum_{i<j}\max(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]-\left[\sum_{i<j}\min(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]}{2\left[\sum_i PD_i - PD_{SITE}\right]+\left[\sum_{i<j}\min(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]+\left[\sum_{i<j}\max(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]}$ **X** $\frac{\left[\sum_i PD_i - PD_{SITE}\right]}{\left[\sum_i PD_i - PD_{SITE}\right]+\left[\sum_{i<j}\min(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]}$	"
Jaccard (Baslega)	Jaccard dissimilarity	$P\beta_{JAC\ (CC)}$	$\frac{\left[\sum_{i<j}\min(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]+\left[\sum_{i<j}\max(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]}{\left[\sum_i PD_i - PD_{SITE}\right]+\left[\sum_{i<j}\min(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]+\left[\sum_{i<j}\max(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]}$	This paper*
	Turnover (Jaccard)	$P\beta_{JTU}$	$\frac{2\left[\sum_{i<j}\min(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]}{\left[\sum_i PD_i - PD_{SITE}\right]+2\left[\sum_{i<j}\min(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]}$	"
	Nestedness-resultant (Jaccard)	$P\beta_{JNE}$	$\frac{\left[\sum_{i<j}\max(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]-\left[\sum_{i<j}\min(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]}{\left[\sum_i PD_i - PD_{SITE}\right]+\left[\sum_{i<j}\min(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]+\left[\sum_{i<j}\max(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]}$ **X** $\frac{\left[\sum_i PD_i - PD_{SITE}\right]}{\left[\sum_i PD_i - PD_{SITE}\right]+2\left[\sum_{i<j}\min(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]}$	"
Jaccard (Carvalho)	Jaccard dissimilarity	$P\beta_{CC\ (JAC)}$	$\frac{\left[\sum_{i<j}\min(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]+\left[\sum_{i<j}\max(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]}{\left[\sum_i PD_i - PD_{SITE}\right]+\left[\sum_{i<j}\min(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]+\left[\sum_{i<j}\max(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]}$	This Paper*
	Replacement component (Jaccard)	$P\beta_{3M}$	$\frac{2\left[\sum_{i<j}\min(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]}{\left[\sum_i PD_i - PD_{SITE}\right]+\left[\sum_{i<j}\min(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]+\left[\sum_{i<j}\max(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]}$	"
	Richness component (Jaccard)	$P\beta_{RICH}$	$\frac{\left[\sum_{i<j}\max(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]-\left[\sum_{i<j}\min(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]}{\left[\sum_i PD_i - PD_{SITE}\right]+\left[\sum_{i<j}\min(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]+\left[\sum_{i<j}\max(PD_{Tot}-PD_j, PD_{Tot}-PD_i)\right]}$	"

*Phylogenetic multiple site beta metrics developed from Leprieur et al. (2012), Baselga (2007, 2010, 2012), and Carvalho et al. (2013)

In addition to further exploring biotic heterogeneity as an important feature of ecosystems and habitats everywhere using the provided metrics, there is an obvious and substantial gap: multiple site metrics have not been extended to functional diversity. Clearly, this is the next step to providing a full suite of tools to the practicing ecologist for studying multiple site beta diversity in any system. The complementarity of taxonomic, functional, and phylogenetic diversity metrics will yield the best possible picture of the ways in which individuals and species interact to generate the astounding biological diversity in all systems.

Chapter 3: Cattle grazing influences taxonomic and phylogenetic biotic heterogeneity in high elevation rangelands

3.1 Introduction

Quantifying biological diversity is one of the greatest challenges facing ecologists today. Fundamental steps have been made over the last century including the important contributions of Whittaker (1960, 1972) who proposed the partitioning of diversity into alpha (local species richness), beta (the difference in two local communities) and gamma (the species richness of the region in question). This intuitive partition of diversity has been widely applied in the ecological literature and has spawned multiple alternative measures of beta diversity. It has been regularly emphasized that beta diversity provides a useful tool for determining the factors that lead to community structuring and diversity patterning (Veech et al. 2002; Anderson et al. 2006; Jost 2007; Tuomisto 2010a, b; Anderson et al. 2011). Despite its importance, there remains considerable confusion and discourse about the best way to measure beta diversity (Veech et al. 2002; Jost 2007; Tuomisto 2010a, b; Anderson et al. 2011). Some of this confusion may stem from Whittaker's own work, wherein beta diversity was defined both as a pairwise metric along a known environmental gradient and as an overall measure of heterogeneity for multiple samples (Whittaker 1960, 1972).

More recently, research has identified that, regardless of how it is measured, beta diversity itself is made up of two further components: replacement (or turnover) and nestedness (or richness) (Harrison et al. 1992; Lennon et al. 2001; Baselga 2010). This partitioning approach recognizes that differences between two communities can arise from (i) species replacement, which is richness independent where a species in 'community a' is replaced by a novel species in 'community b', and by (ii) changes in the number of species present (a richness effect) where species are added or eliminated in 'community b'. Efforts aimed at robustly quantifying these two independent components of beta diversity have recently led to vigorous debate (Baselga 2010; Podani & Schmera 2011; Almeida-Neto et al. 2012; Carvalho et al. 2012; Baselga 2012; Carvalho et al. 2013). Baselga (2010) first proposed the partition of Sørensen 's dissimilarity (Sørensen 1948) into the richness independent Simpson's index (Simpson 1949) as a metric of turnover

and their difference as the nestedness-resultant metric (Baselga 2010). Baselga (2010) showed that spatial turnover was much higher in southern Europe than northern Europe, despite comparable overall beta diversity values (resulting in lower nestedness effects in Southern Europe), for long horned beetles (Cerambycidae; Baselga 2010). Therefore, this partitioning approach was able to capture patterns not clear from the broad sense dissimilarity index (Baselga 2010). More recently, and following criticism of his approach (Podani & Schmera 2011; Almeida-Neto et al. 2012; Carvalho et al. 2012), Baselga (2012) also partitioned the Jaccard index of dissimilarity (Jaccard 1912) into nestedness and turnover components. Importantly, independent work applying Baselga's (2012) partition have documented patterns that would not have been apparent under the overall (Jaccard or Sørensen dissimilarity) metrics (e.g. Azeria et al. 2011; Baeten et al. 2012). Furthermore, Leprieur et al. (2012) recently extended Baselga's partitioning approach to Phylogenetic diversity, basing their derivations on the PhyloSor (Bryan et al. 2008) and UniFrac (Luzopone and Knight 2005) metrics for Sørensen and Jaccard phylogenetic dissimilarity respectively. Therefore, partitioning beta diversity into its turnover (replacement) and nestedness (richness) components yields a clearer picture of pairwise diversity patterns. It has however been demonstrated that pairwise metrics of beta diversity are not appropriate for measuring overall heterogeneity (Diserud & Ødegaard 2007; Baselga et al. 2007).

Concurrent to the development of the partitioning approaches for pairwise beta diversity, Baselga et al. (2007; Baselga 2010, 2012, 2013) reiterated what had been demonstrated by Diserud and Odegaard (2007): that averaging pairwise dissimilarities is an inappropriate way to quantify overall heterogeneity because it does not account for co-occurrence of species among more than two plots (Diserud & Ødegaard 2007; Baselga et al. 2007; Baselga 2013). Baselga et al. (2007) therefore developed a novel multiple-site analog of Simpson's similarity index, and further extended it to the partition of Sørensen (Baselga 2010) and Jaccard dissimilarity (Baselga 2012). As such, Baselga (2010, 2012, 2013) developed multiple-site analogs of his pairwise partition of beta diversity and demonstrated how the partitioned components of overall heterogeneity also capture patterns not apparent with their overall counterparts (Baselga 2012, 2013).

Most recently however, Carvalho et al. (2013) have demonstrated that Baselga's (2010, 2012) partition of pair-wise beta diversity is not robust to increasing species loss, which should lead to increasing nestedness-resultant dissimilarity. Instead, Carvalho et al. (2013) show that Baselga's (2010, 2012) nestedness-resultant dissimilarity exhibits a hump backed relationship with increasing species loss, with highest beta diversity values obtained at moderate values of species loss. Carvalho et al. (2013) provide their own partition of beta diversity based on Jaccard's dissimilarity and demonstrate that it is not susceptible to the concerns demonstrated for Baselga's (2010, 212) partition. However, they do not propose multiple-site metrics for their novel partition. Furthermore, the pioneering work of Leprieur et al. (2012) for Baselga's partition of pairwise beta diversity has not been extended to Carvalho et al.'s (2013) partition, nor have multiple site metrics been developed for any of the phylogenetic heterogeneity partitions. I therefore provide a multiple site metric for Carvalho et al.'s (2013) partition and develop phylogenetic heterogeneity metrics for all three partitions of multiple site heterogeneity in Chapter 2. The development of such tools provides a simple way to quantify heterogeneity both among many communities and within multiple samples of the same community. While pairwise metrics have been applied regularly, quantifying the heterogeneity within a given community remains an under-appreciated attribute of ecosystems that has important implications for management and conservation goals.

Management and conservation efforts have been primarily focused on preserving diversity alpha diversity (richness, evenness) and occasionally on among community beta diversity, but a further important characteristic of any system is how diversity varies within a given location or habitat. One approach to measuring within community beta diversity applies a temporal definition of beta diversity, i.e. the change in community composition over decades, by investigating 'biotic homogenization' (Rooney et al. 2004). Such studies correlate the variation in community composition over time with changes in anthropogenic variables (e.g. anthropogenic land cover / use, invasive species; e.g. Rooney et al. 2004; Martin et al. 2005; Trentanovi et al. 2013). Despite measuring beta diversity within the same location, this approach does not attempt to measure within-community heterogeneity. From a conservation or management perspective however, one of the main goals is to preserve existing, or restore previous levels and patterns

of diversity (Thorpe & Stanley 2011). Despite restoration and maintenance of diversity being a primary goal, and the use of larger scale beta diversity approaches to reserve planning (Wiersma & Urban 2005), quantifying within site beta diversity as a characteristic diversity measure remains rarely investigated (but see Martin et al. 2005 for a notable example).

Martin et al. (2005) were interested in the success of conservation efforts in restoring natural biodiversity levels of tall grass prairie in Ohio USA. They quantified an additive partition of diversity, including alpha, beta and gamma. As such, they used mean alpha and overall gamma to approximate the amount that heterogeneity contributed to overall species richness (Martin et al. 2005). Martin et al. (2005) found that beta diversity was higher in restored communities than in unrestored communities and suggested that this may have been due to larger clumps of individual species in the restored community (i.e. lower mean alpha = increased beta). This is a simplistic yet useful approach that can help describe the overall beta diversity of a system, but it is not able to capture the influence of the nested and turnover components of heterogeneity (Baselga 2012, 2013). As Baselga (2012) has shown, methods that average over a site miss much of the detail that partitioned multiple-site metrics can capture. Therefore comparing within-community beta diversity among treatments (as demonstrated by Martin et al. 2005) under novel partitioning approaches may help clarify what is driving the observed differences in heterogeneity observed.

While studying biotic heterogeneity within herbaceous communities is clearly interesting, there is some question as to whether it really matters, i.e. does spatial variation in plant communities matter functionally or to other trophic levels? I contend that the heterogeneity of a herbaceous community could be a highly important characteristic not just within plant communities, but also across trophic levels. For example, studies have regularly shown that insect diversity is strongly related to plant diversity (e.g. Pöyry et al. 2006; Dumont et al. 2009) and maybe dependent on the fine scale physical and spatial structuring of plant communities (e.g. Dennis et al. 1998). The impacts of plant species and structural diversity have even been found to influence vertebrate success (e.g. sparrows, Sutter & Ritchison 2005), though this may be due to an interaction with plant and insect diversity. Furthermore, when considering

among community variation, variation in both taxonomic and phylogenetic plant diversity have been found to be strongly correlated to phylogenetic turnover in Lepidopteran herbivore communities along climatic gradients (Pellissier et al. 2013). It stands to reason then that within-community heterogeneity (or beta diversity) of plants may have similar influences on the phylogenetic diversity of multiple trophic levels, though this has yet to be quantified explicitly. Furthermore, disturbance mechanisms that modify plant communities and their physical, taxonomic and phylogenetic structure may therefore have influences among trophic levels.

One management system where the monitoring of heterogeneity is likely to be important is in natural or rangeland grazing systems. To date, the relationship between grazing regimes and plant communities has been a fundamental field of inquiry in plant ecology, both as a natural characteristic (e.g. wild herbivores, elephants, bison) and as a human induced influence (e.g. cattle, sheep, semi natural grasslands in Europe; see Díaz et al. 2007). Importantly, the response of plant communities to various types and intensities of grazing is dependent on multiple factors, including plant traits like stature, and palatability and the level of biomass production of the overall plant community (Díaz et al. 2007). For example, highly productive sites are often dominated by a few highly competitive species, in congruence with the hump-backed relationship between productivity and species richness (Al-Mufti et al. 1977). In such a scenario, the presence of an unselective, large grazer (e.g. cattle) often results in higher species richness, or alpha diversity, at the sampling spatial scale, as the grazer reduces the dominance effects of the larger plant species (e.g. Bakker et al. 2006), though this is not always the case (Adler et al. 2001). When looking at a given community, most studies investigating such grazing-diversity relationships have focused on this simple level of diversity, i.e. species richness and evenness, despite the presence of multiple other metrics of species communities that take species identity into account and therefore, often shed more light on the processes structuring communities than simple richness.

Recently however, grazing investigations have begun to incorporate beta diversity, investigating changes in grazed plant communities along some type of environmental gradient (e.g. Komac et al. 2010; Golodets et al. 2011; Carmona et al. 2012; Lezama et al. 2013). Such studies generally seek to quantify

how the given environmental gradient (moisture availability, soil depth, temperature, elevation) or their interactions influence community composition, and if the observed influence varies with grazing and grazing intensity or not. For example, Carmona et al. (2012) incorporated both taxonomic and trait level diversity patterns into their investigation of grazing and plant diversity. When investigating beta diversity Carmona et al. (2012) used a modified version of the additive partition of diversity (Lande 1996) denoting $\beta=(\gamma\text{-mean }\alpha)*100/\gamma$, as suggested by de Bello et al. (2010) to quantify beta diversity across all of their sites. In all cases they tested whether moisture availability, year of measurement, and grazing intensity influenced the observed diversity patterns. They found that patterns of taxonomic and functional diversity (both alpha and beta diversity) differed with respect to the influence of the environmental variables, but that they converged in the most extreme scenario (i.e. high grazing pressure, dry site, in a dry year). Clearly, measuring multiple classes of diversity can shed more light on how factors like grazing influence plant communities. However, the samples within a site were on average 106 m apart (minimum = 45 m), increasing the potential for fine scale environmental variation within a site to contribute to any observed patterns of diversity (Carmona et al. 2012). Komac et al. (2011) used the strict sense additive definition of beta diversity ($\gamma = \alpha + \beta$; Lande 1996). They found that at coarse scale (among patches) grazing resulted in increased heterogeneity, while at fine scale (within patches) grazing homogenized plant communities.

Clearly then, beta diversity in general is receiving increasing interest in grazing and plant diversity systems (as investigated by Komac et al. 2011 and Carmona et al. 2012). However, these studies were conducted in Europe where it is likely that the meadow and grassland plant communities have evolved under human influence, including grazing and cutting, for at least the last 500 years (Montserrat & Fillat 1990; Komac et al. 2011). Grassland and meadow communities, and in particular those in high elevation in the western portion of North America, have only been subjected to anthropogenic grazing pressure since roughly 1860 (Fraser 2009) and therefore are unlikely to have fully adapted to this novel characteristic. Therefore, investigating biotic heterogeneity and diversity patterns in grazing systems of North America may yield contrasting patterns to those observed in Europe and Africa (e.g. Yessoufou et

al. 2013). Furthermore, the evolutionary history of grazing in a system is known to have strong influences on the impact of grazers on plant diversity patterns (Díaz et al. 2007), and is likely a driver of evolutionary processes leading to plant speciation. Likewise, the demonstrated influence of phylogenetic diversity on productivity (Cadotte et al. 2009; Cadotte 2013) and other trophic levels (Pellissier et al. 2013) warrants investigation of the relationship between grazing and plant community phylogenetic diversity, a field that to date has received little investigation (but see Yessoufou et al. 2013 for a recent phylogenetic structuring study).

Most importantly however, all studies I encountered that aim to quantify the influence of grazing on beta diversity have used some form of averaging to calculate their diversity metrics. Primarily this has been through the use of Whittaker's (1960, 1972) multiplicative beta diversity (e.g. Lezama et al. 2013) or the additive partition (Lande 1996) of beta diversity (e.g. Komac et al. 2011; Carmona et al. 2012), although average pairwise distance measures like Sørensen's dissimilarity have been used as well (e.g. Lezama et al. 2013). It has been shown that averaging pairwise distance measures (e.g. Jaccard, Sørensen) is unable to account for species shared among more than two sites (Diserud and Odegaard 2007; Baselga et al. 2007; Baselga 2013). Furthermore, although the original beta diversity (i.e. multiplicative) of Whittaker (1960, 1972) relates well to the overall multiple site dissimilarity metrics (i.e. multiple site Jaccard or Sørensen), it is unable to distinguish between beta diversity derived from turnover or richness patterns. Given that recent studies have shown that partitioning beta diversity into its turnover and richness components can yield much different results than when looking at raw beta diversity values (e.g Azeria et al. 2012.; Baeten et al. 2012; Baselga 2012; Leprieur et al. 2012) an investigation of within-community heterogeneity, which partitions both phylogenetic and taxonomic metrics into their richness and replacement components is needed.

OBJECTIVES

I sought to quantify the influence of cattle grazing on taxonomic and phylogenetic plant community heterogeneity within sub-alpine meadow communities in southern British Columbia. I aimed to determine the biotic heterogeneity of grazed and ungrazed plant communities due to non-environmental influences,

such as dispersal mechanisms, the influence and spatial distribution of disturbance, and biotic interactions. Specifically, I ask if, (i) in keeping with previous grazing-diversity studies (e.g. Bakker et al. 2006), the presence of cattle influences alpha diversity, (ii) if patterns of within community heterogeneity are influenced by grazing and (iii) how grazing influences the turnover and richness components of within community heterogeneity. Using recently developed tools for measuring partitioned heterogeneity (i.e. multiple site beta diversity, see Chapter 2) and three null models based on separate definitions of the available species pool (Lessard et al. 2012), I extend my investigation to both taxonomic and phylogenetic diversity measures. I show that both alpha and gamma diversity are influenced by grazing, but that these patterns differ within each site. Furthermore, phylogenetic and taxonomic heterogeneity exhibit similar observed patterns of heterogeneity, regardless of treatment. The influence of grazing however differed for taxonomic and phylogenetic measures and by site.

3.2 Methods

SITE DESCRIPTION

This research was conducted in two rangeland pastures in southern British Columbia, Canada, at Hunter's Range (approximate centroid of plots: 50.665085° N, -118.934921° E, elevation ~2000 m a.s.l.), and on Apex Mountain (approximate centroid of plots: 49.358435° N, -119.917191° E, elevation ~2000 m a.s.l.). The sites are approximately 160 km apart and are located adjacent to the Okanagan Valley in BC. Both sites fall into the Engelmann Spruce-Subalpine Fir (ESSF) and Alpine-Tundra (AT) zones of BC's biogeoclimatic ecosystem classification (BEC) system (British Columbia Ministry of Forests, Lands, and Natural Resource Operations 2008) and are characterized by stands of coniferous trees interspersed by forb dominated meadows. Snow melt occurs during May and June and snow returns in November. Mean annual temperature at Hunter's Range is 0.1 °C and at Apex Mountain is 1.5 °C, while mean annual precipitation at the two sites is 864 mm and 641 mm (interpolated from nearby weather stations, ClimateWNA, Wang et al. 2012), for Hunter's Range (hereafter "Hunter's") and Apex Mountain (hereafter "Apex"), respectively.

I took advantage of pre-existing exclosure fences that were erected in 1994 (Hunter's Range) and 1998 (Apex) by the British Columbia Ministry of Forests, Lands and Natural Resource Operations (R. Tucker, *pers. comm*.). The exclosures were initially set up to monitor the influence of cattle grazing on plant communities, though monitoring work had not been conducted for several years at the time of this study (R. Tucker, *pers. comm*.). The fences generate roughly rectangular exclosures of approximately 2.0 ha at Apex and 0.5 ha at Hunter's (Figure 3.1). The Apex site exhibits an average slope of roughly 10°, while the Hunter's site has an average slope of < 5°. Grazing at both sites is characterized by managers with the BC Ministry of Forests, Lands and Natural Resource Operations (MFLNRO) using Animal Unit Months (AUM). Animal Unit Months are defined in BC as the amount of forage needed to sustain one 450 kg cow (~ 13 kg day^{-1}). Hunter's has had approximately 694 AUM of grazing per year on 1142 ha (0.607 AUM / ha). Apex has had approximately 310 AUM per year since the exclosures were established on a pasture of 3300 ha (0.098 AUM / ha). Cattle are released into the Hunter's pasture in July and removed in September, while cattle are released in August and removed at the end of September at Apex (MFLNRO).

The two sites differed visibly in their general vegetation characteristics, both inside and outside the grazing exclosures. Within the exclosure, Hunter's was characterized by dense forb communities approaching 1 m tall with Sitka valerian (*Valeriana sitchensis*), various sedges (e.g. *Carex illota*, *Carex magellanica*), alpine lupine (*Lupinus arcticus*) and Indian hellebore (*Veratrum viride*) commonly encountered. Outside the exclosure was a patch work of closely cropped grasses (e.g *Agrostis stolonifera, Phleum alpinum, Poa arctica*) between clumps of larger forbs, including alpine lupine (*Lupinus arcticus*), western (or white) pasque-flower (*Pulsatilla occidentalis*) and Indian hellebore (*Veratrum viride*; Figure 3.2).

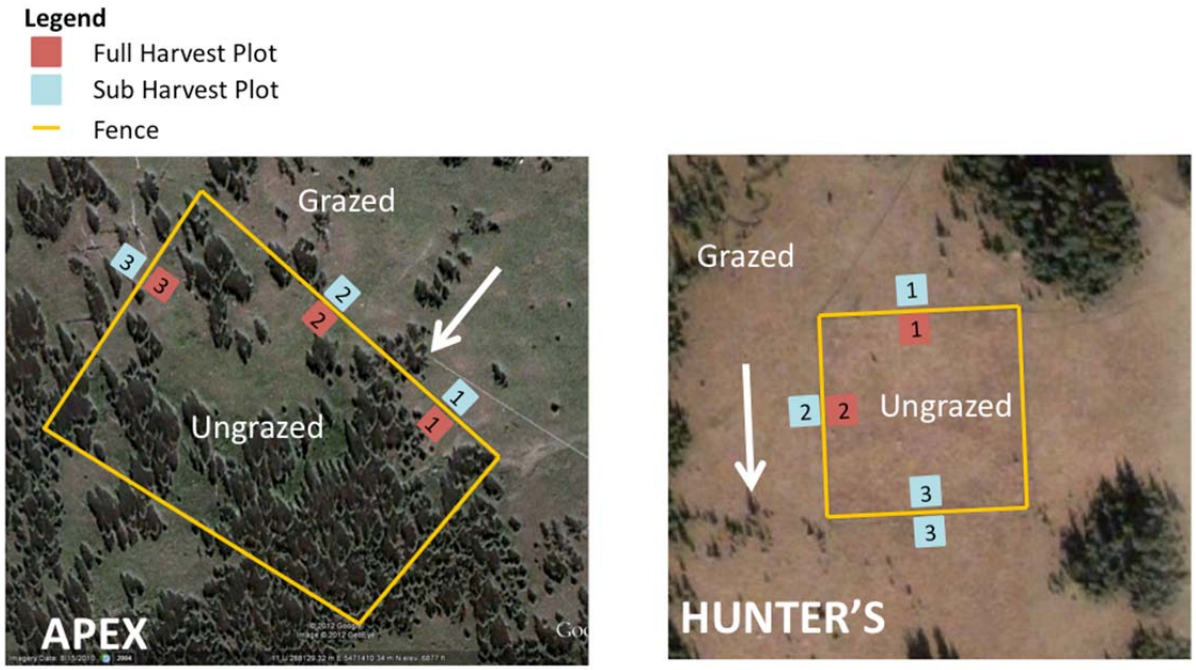

Figure 3.1 The field sites where the research was conducted. Blue plots indicate those were a subsample of quadrats (eight) was harvested for biomass analysis, while red plots were fully harvested (64 quadrats). Note the parkland vegetation structure, characterized by stands of coniferous trees interspersed by forb meadows. White arrows indicate the direction of overall slope, ~10° at Apex and ~5° at Hunter's. The Apex exclosure is approximately 150 m x 75 m, while the Hunter's exclosure is approximately 75 m x 75 m.

Vegetation structure at Apex did not differ so markedly across the treatment. In grazed plots, plants were smaller and there was less standing dead biomass. Grasses appeared to be more common in ungrazed plots (e.g. *Deschampsia elongata*, Appendix A), while grazed plots featured more dominant forbs (e.g. *Lupinus arcticus*). Both inside and outside the exclosure, small statured forbs (e.g. *Collinsia parviflora*, *Microsteris gracilis* var. *humilior*, *Polygonum minimum*) were regularly encountered. Interestingly, exotic species were not common. At Apex the exotic community included *Achillea millefolium*, *Taraxacum officinale*, and *Trifolium pratense*. Exotic species encountered at Hunter's included *Trifolium repens* and *Agrostis stolonifera*. At both sites, the exotic species were more commonly encountered in grazed plots than in ungrazed plots (Appendix A).

Figure 3.2 The vegetative characteristics of the Hunter's Range site showing dense tall forb stands inside the exclosure (left) and a patchwork of cropped grass and large forbs outside (right).

EXPERIMENTAL DESIGN

At each site, three replicate pairs of square grazed and ungrazed 64 m^2 plots were established perpendicular to the adjacent fence (Figures 3.2 and 3.3). Each eight by eight meter plot was set two meters back from the fence to avoid immediate edge effects, particularly on the grazed side where repeated cattle travel had generated well-worn paths at both sites (e.g. Figure 3.2). Each plot was divided into 64 one by one meter quadrats and were situated where they fit at Apex (tree cover prohibited random placement) and at the centre of three randomly chosen sides at Hunter's (Figure 3.1 and 3.3). It is important to emphasize that in using this paired design, I am attempting to minimize environmental heterogeneity within each grazed and ungrazed comparison (pair) while attempting to capture the heterogeneity of the site to assess the generality of my findings for each site. For this work I treat each pair as independent within each site.

Importantly, my gridded design enables investigations of spatial pattern at scales relevant to herbaceous plant individual and species interactions. By using contiguous quadrats I exhaustively sample a single area, minimizing the influence of fine-scale environmental heterogeneity on observed biotic heterogeneity

that may have been encountered by sampling randomly positioned or widely spaced quadrats across the exclosure (e.g. Brudvig 2010). Furthermore, my design provides the opportunity for accurate investigations of spatial structure at scales relevant to the member plant species, including mechanisms of facilitation, light competition, dispersal and competition for soil resources.

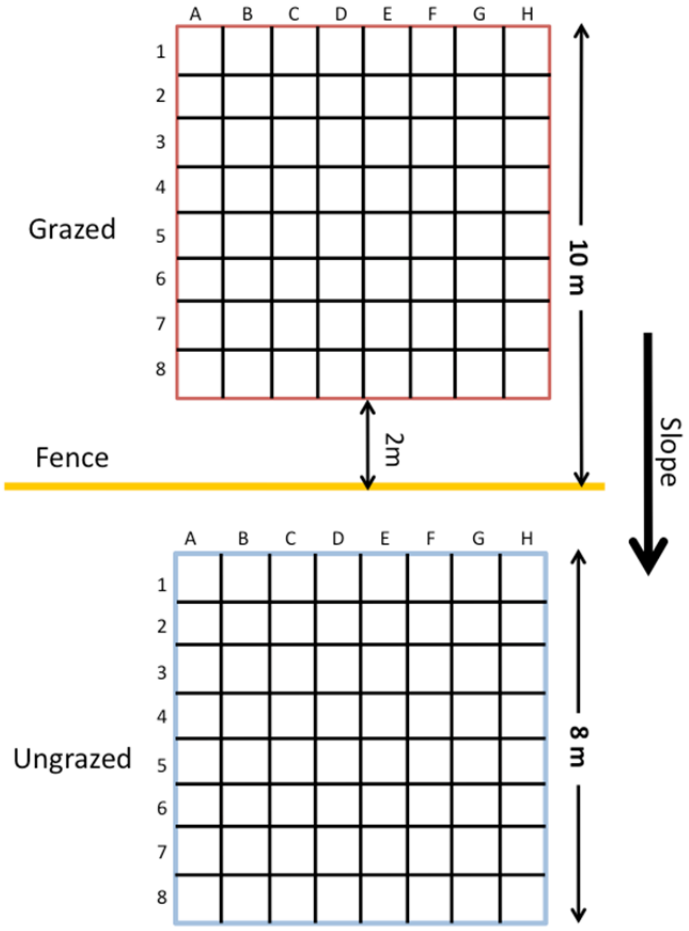

Figure 3.3 An example of the experimental design of one pair of sampling plots. Apex 3 and Hunter's 2 were set up differently, with the fence running parallel to the numbered rows in order to maintain quadrat A1 in the upslope left corner, while Hunter's 3 had the grazed and ungrazed in opposite positions (see Figure 3.1).

In each quadrat within each plot (n = 768), all vascular plant species were identified. Identification followed the Flora of the Pacific Northwest (Hitchcock and Cronquist 1976), with nomenclature updated following the United States Department of Agriculture (USDA) PLANTS database (http://plants.usda.gov/java/, *Last accessed:* July 17, 2013). Voucher specimens for each species were

collected and pressed, and are stored in the herbarium at the Biodiversity and Landscape Ecology Research Facility at the University of British Columbia's Okanagan Campus, Kelowna, BC, Canada (contact: JP).

PHYLOGENETIC TREE CONSTRUCTION

Phylogenetic trees were generated for each site (i.e. Apex and Hunter's) using a super- (or mega-) tree approach with the online tool, *Phylomatic* v. 3.0 (http://phylodiversity.net/phylomatic/, *Last accessed* 17 July, 2013), which is part of the *Phylocom* v. 4.3 (Webb et al. 2008) software package. This approach has been used widely in the community phylogenetics literature (e.g. Swenson et al. 2006; Cavender-Bares et al. 2009). The *Phylocom* approach uses a super-tree backbone which is based on the Angiosperm Phylogeny Group's third family level phylogeny for all flowering plants (APG III 2009). It places all species of the provided community matrix on the overall tree and then 'prunes' the tree, removing lineages not present in the community matrix (Webb & Donoghue 2005; Webb et al. 2008). Within present lineages, *Phylomatic* divides member species at the genus level, but when more than two species from a given family or genus are present, multiple branches from the same node, or polytomies, arise (Webb & Donoghue 2005). In a widely used approach (e.g. Forest et al. 2007), I resolved polytomies using published molecular phylogenies (see Appendix D for published phylogenies used). A three species polytomy in the Genus *Carex* could not be resolved at either site. Furthermore, one reported grass species was not adequately preserved and therefore could not be identified resulting in a polytomy at the family Poaceae for the Hunter's phylogenetic tree. Nodes in the tree were dated using the branch length adjustment (*bladj*) algorithm in *Phylocom*, which bases node ages on Wikström et al. (2001). Undated nodes are averaged between known nodes such that all are evenly spaced between known nodes or present time (Webb et al. 2008). The completed phylogenies are shown in Figures 3.4 (Apex) and 3.5 (Hunter's).

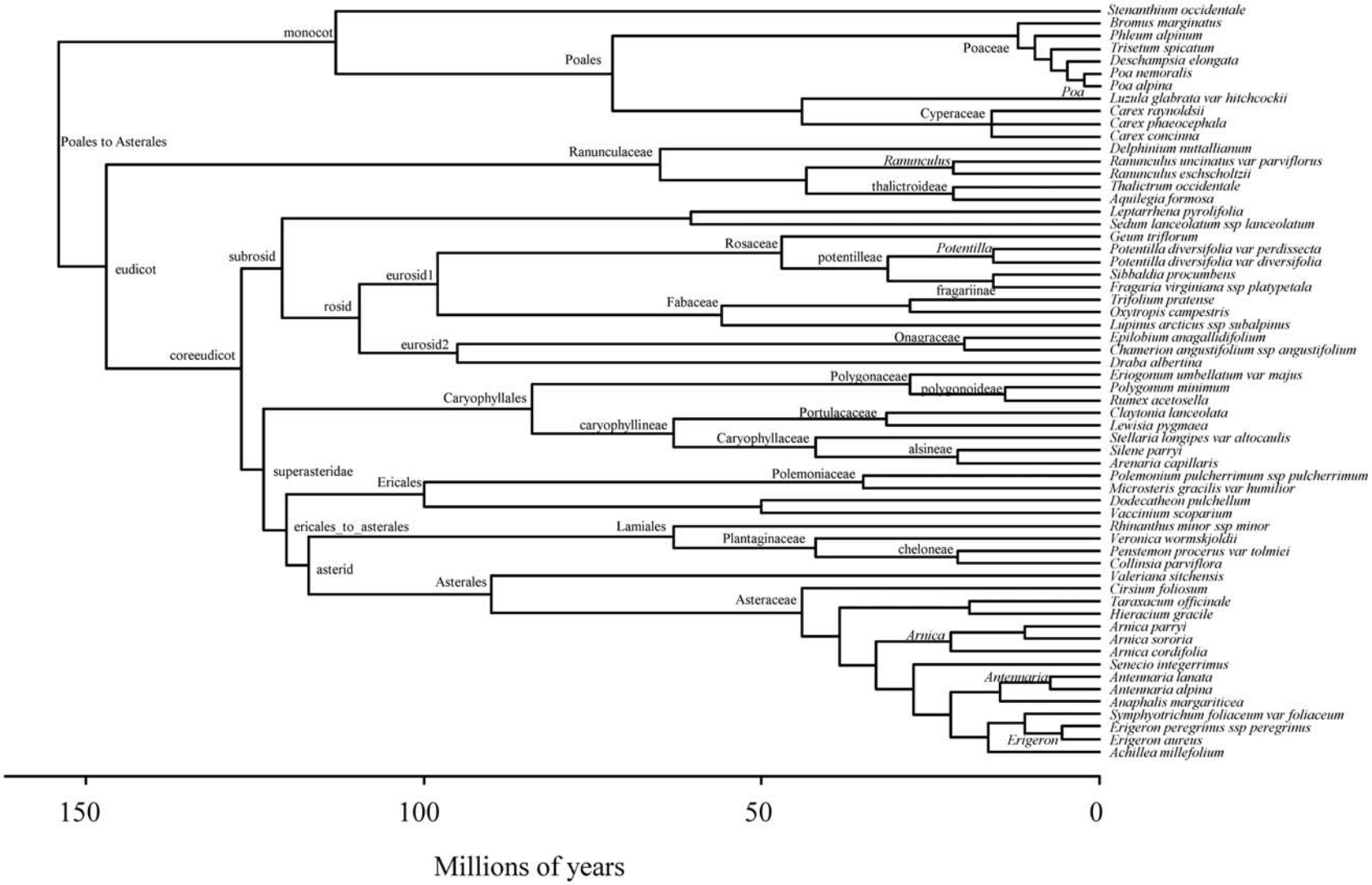

Figure 3.4 The phylogenetic tree for species encountered at Apex Mountain. Note the unresolved polytomy at Cyperaceae, this node age is actually set to the estimated first divergence within Carex.

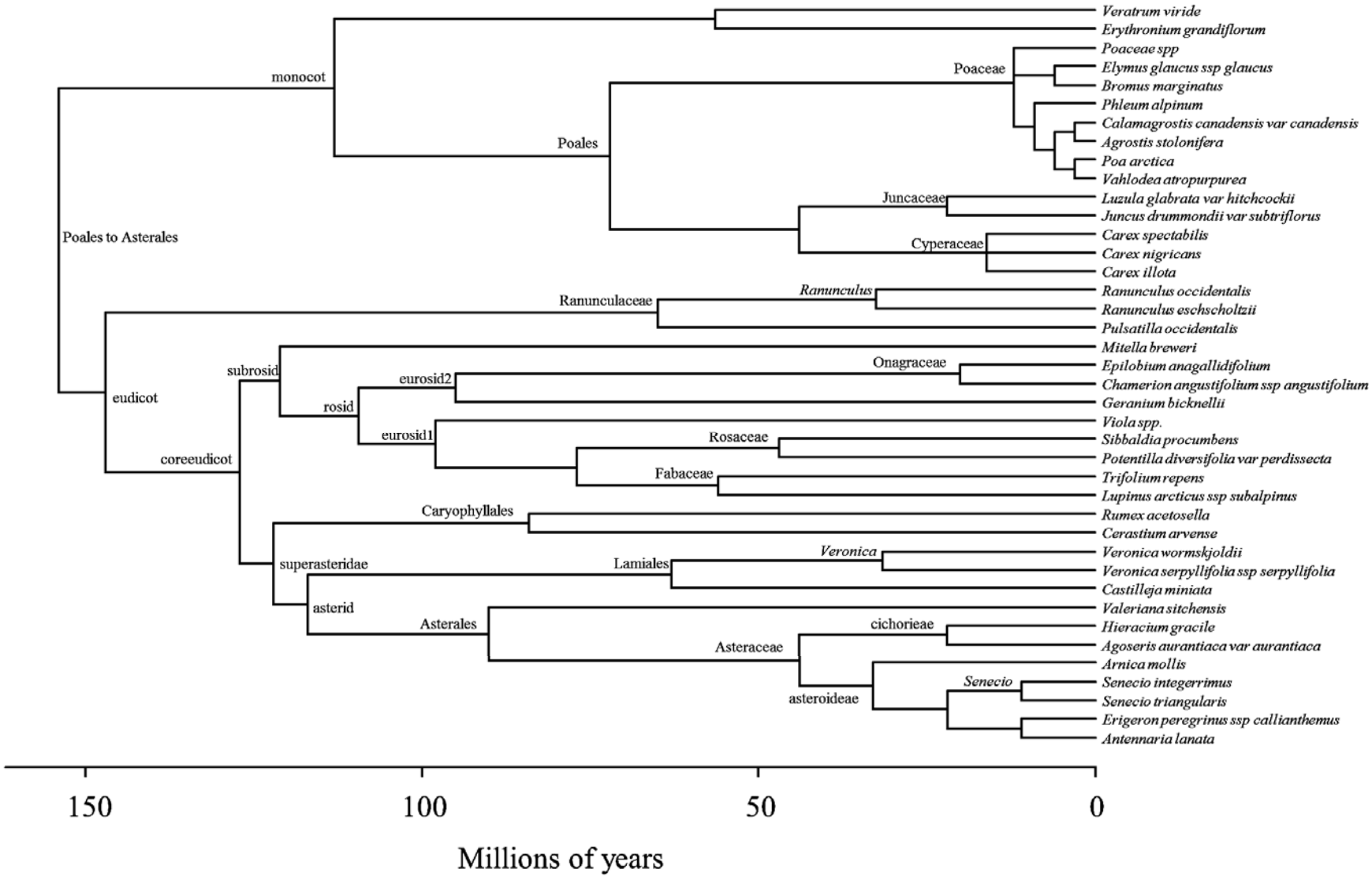

Figure 3.5 The phylogenetic tree for all species encountered at Hunter's Range. Note the unresolved polytomies at Cyperaceae (dated to the divergence of *Carex*) and within Poaceae due to an unidentifiable species.

GENERAL DIVERSITY PATTERNS

Here, alpha and gamma diversity refer to the quadrat (alpha) and site level (gamma) species richness (Whittaker 1962, 1970). Thus, the difference between taxonomic alpha and gamma diversity is an issue of scale alone. I measured taxonomic gamma diversity separately for grazed and ungrazed treatments since some species may be excluded by the presence or absence of grazing. Phylogenetic diversity (PD), as originally proposed by Faith (1992), is the sum of the branch lengths joining all member species of a given community. I calculated PD based on the dated tree developed above for each quadrat, treatment and site. However, raw alpha PD is often tightly correlated with species richness (Webb et al. 2002; Kembel et al. 2010). I therefore quantified both the mean pairwise distance (MPD), which is the average of all pairwise branch lengths of species pairs within a given community, and the mean nearest taxon distance (MNTD), which is the average phylogenetic distance between each species and its nearest neighbor within the given community, as richness independent measures of PD (Webb et al. 2002). Mean pairwise distance is considered a tree wide measure of alpha PD while MNTD is considered a tip level measure (Webb et al. 2002). Both MPD and MNTD are widely used as metrics of phylogenetic alpha diversity (e.g. Cadotte et al. 2009; Winter et al. 2009; Pellissier et al. 2013; Cadotte 2013). I calculated gamma PD by calculating MPD and MNTD on the tree for each site, and on a tree pruned to those species occurring within each treatment, at each site; i.e. $gamma_{site}$ and $gamma_{treatment}$.

WITHIN-COMMUNITY HETEROGENEITY

There is extensive confusion in the current literature about the definition of beta diversity, even among the two original definitions: multiplicative ($\beta = \gamma/\alpha$) or additive ($\beta = \gamma-\alpha$), wherein alpha is the mean species richness of all samples (Whittaker 1960; MacArthur et al. 1966; Levins 1968; Whittaker 1972; Lande 1996; Tuomisto 2010a; Anderson et al. 2011). Therefore, in an effort to be explicit about my definition of beta diversity I define it as the multiple site dissimilarity (beta diversity) calculated from all possible quadrat pairs within each eight by eight meter plot (n = 2016). I quantified within plot beta diversity using the multiple-site Jaccard metric (β_{JAC}) proposed by Baselga (2010, 2012, 2013). Furthermore, I partitioned the Jaccard metric into its turnover and richness dissimilarities following the

partition approach of Carvalho et al. (2013), who denote the pairwise β_{jac} as β_{cc}. I follow the naming structure of Carvalho et al. (2013) to avoid confusion with Baselga's (2010, 2012, 2013) multiple site beta diversity partition and derived the multiple site analogs of Carvalho et al.'s (2013) partition in Chapter 2. I denote the partition as:

Equation 3.1 $$\beta_{CC} = \beta_{-3M} + \beta_{RICH} ,$$

where, following Baselga's (2010, 2012, 2013) lead I denote the multiple site analogs of partitioned pairwise beta diversity using uppercase subscripts where the Jaccard dissimilarity (β_{CC}) is the sum of the turnover (β_{-3M}) and richness (β_{RICH}) components.

Following my approach for taxonomic beta diversity, I calculated phylogenetic heterogeneity using the partitioned, multiple site phylogenetic beta diversity of Jaccard's dissimilarity based on the partition of Carvalho et al. (2013). The pairwise PhyloSor and UniFrac metrics of phylogenetic beta diversity were recently partitioned under Baselga's (2010, 2012) approach (Leprieur et al. 2012), but to date, Carvalho et al.'s (2013) partition has not been extended to phylogenetic beta diversity. Furthermore, multiple site metrics had not been developed for any of the phylogenetic diversity measures applied herein. I developed code for Carvalho et al.'s (2013) partition based on the functions provided by Leprieur et al. (2012) for Baselga's (2010, 2012) partition of Jaccard dissimilarity and provide my adaptation in Chapter 2. I denote the partition of multiple-site phylogenetic beta diversity as:

Equation 3.2 $$P\beta_{CC} = P\beta_{-3M} + P\beta_{RICH}$$

where the 'P' simply denotes 'phylogenetic'.

BIOMASS

As part of a separate, collaborative study, I obtained plot-scale estimates of productivity by harvesting above-ground biomass within quadrats. Litter (standing senesced material and that on the ground) and live biomass were measured separately. Harvesting was conducted at peak-biomass, defined as the majority of plant species exhibiting seed set or flowering. As such, sampling occurred on 2-5 August,

2012 at Apex and 6-9 August, 2012 at Hunter's. All biomass was stored in a dry greenhouse (*The Greenery*, Kelowna, BC) for three weeks prior to being oven dried at 80° C for 48 hours and weighed using a top loading balance. Productivity of communities has been shown to affect beta diversity (Chase 2010) and may therefore be an important predictor of community heterogeneity.

STATISTICAL ANALYSIS

General diversity patterns

The sampling design, which was constrained by logistical impediments, did not provide sufficient replication for analysis of the grazing treatment using a mixed-effects model framework. Nevertheless, to provide context to the main findings of interest, I present qualitative assessments of alpha and gamma diversity patterns across the treatment, pairs, and sites. Furthermore, I tested for an influence of grazing on alpha diversity by calculating the difference in mean quadrat level species richness within each pair and conducting a one sample t-test on the three differences at each site (N = 3). Note that all statistical analyses were conducted in R (R Development Core Team 2013) using the *picante* (Kembel et al. 2010), *vegan* (Oksanen et al. 2013), and *betapart* (Baselga et al. 2013) packages.

Within-community heterogeneity

To test for an influence of grazing on heterogeneity, I calculated the difference in observed multiple site beta diversity for each of the multiple site metrics within each pair of plots ($\beta_{diff} = \beta_{grazed} - \beta_{ungrazed}$). However, the observed heterogeneity values do not facilitate robust statistical tests of the observed patterns, particularly when richness differences are present across the treatment of interest. Recently, null models have been re-emphasized and demonstrated to be an appropriate way to test if patterns of community composition deviate from the expectation when excluding the process of interest (see Chase 2010; Chase et al. 2011; Lessard et al. 2012) and have been shown to appropriately quantify beta diversity, independent of richness differences across differing regions of treatments (Chase et al. 2011; Myers et al. 2012). Limited deviation from the null expectation indicates that observed pattern is a result of species pool attributes (Lessard et al. 2012). Recently, Lessard et al. (2012) proposed null models, applied to geographically replicated experiments, as an ideal tool to resolve the many contingencies

(Lawton 1999) in community ecology. They emphasize that the species pool is a critical feature in determining the response of communities to a factor of interest. Appropriate null models depend heavily on (i) the definition of the species pool from which they draw the species to make up the null communities, and (ii) on the randomization procedure by which they assign the species to each null community (Chase 2010; Lessard et al. 2012). Furthermore, they argue that both stochastic (e.g. dispersal probabilities) and deterministic (e.g. environmental affinities, niches) processes need to be considered in delimiting the species pool (Lessard et al. 2012). Using explicitly defined species pools can reveal what factors are influencing the observed patterns. In particular, defining pools under experimental treatments may generate a clearer picture of the treatment's influence on community assembly.

I therefore applied a randomization approach to test if my observed values deviate from those expected based on three species pools, (i) within the pair (i.e. adjacent grazed and ungrazed plots, $n_{quadrats} = 128$), (ii) within the treatment (i.e. all three grids in a treatment at each site, $n_{quadrats} = 192$), and (iii) within a site (i.e. all six grids at each site, $n_{quadrats} = 384$) as shown in Figure 3.6. In a beta diversity study that incorporated partitioned beta diversity, Azeria et al. (2012) showed that the best null model is one that preserves both sample richness (i.e. the number of species in each sample) and the occurrence rates of each species across all samples in the randomization (the number of times a species occurs in all samples); a so-called Fixed-Fixed model; I followed this approach here. I generated 999 randomizations of the site by species matrices under each species pool and on each of the resulting null communities I repeated my six beta diversity measures; i.e. both partitioned taxonomic and phylogenetic multiple-site beta diversity (note that taxonomic alpha values do not change under null models applied here). These 999 randomizations of each plot under each null model represent the distribution of expected values for my diversity measures against which my observed values can be compared. To test if my results differed significantly from chance, I compared my observed beta and $beta_{diff}$ values to the mean beta and mean $beta_{diff\text{-}null}$ calculated from the 999 randomizations of my observed plant communities using the standardized effect size, as described below.

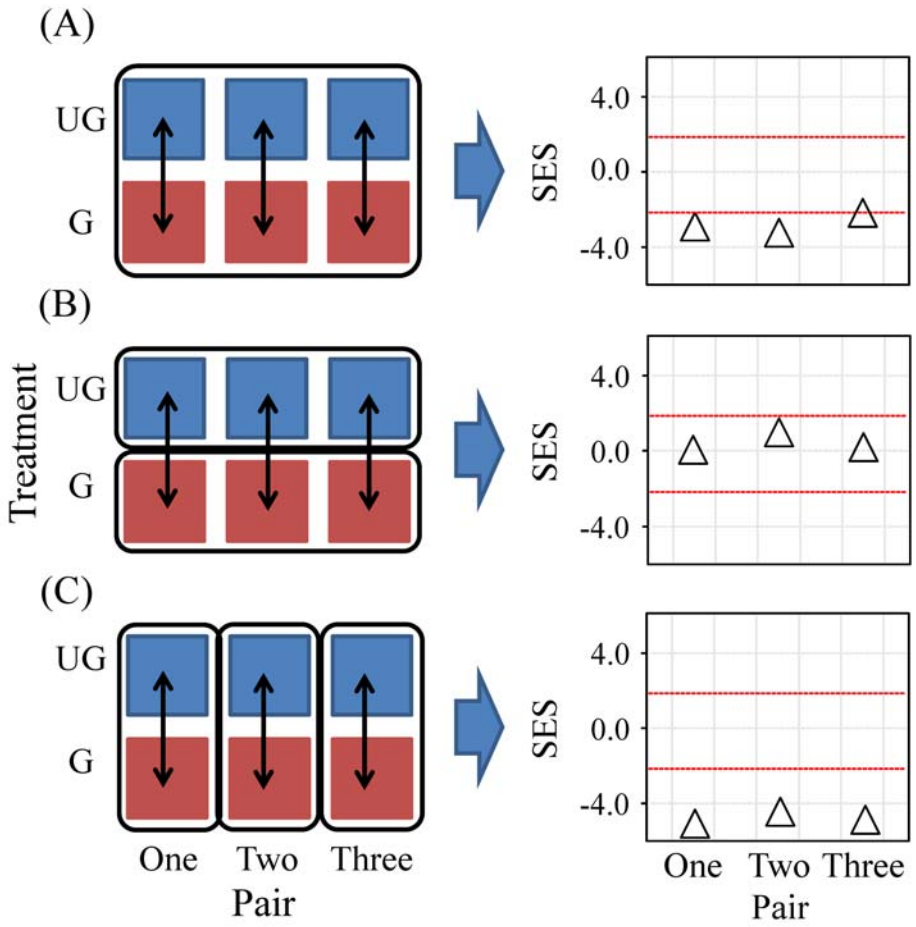

Figure 3.6 Schematic figure describing the null models applied [site (A), treatment (B) and pair (C)] and the associated predictions for the standard effect size of differences (along the black arrows: grazed - ungrazed) in heterogeneity within a grazed and ungrazed pair. Blue squares indicate ungrazed eight by eight meter grids (UG) while red squares represent grazed (G) grids which are each split into 64 one by one meter quadrats. In the null modeling approach, species occurrences are randomized within each black square (in A, B, and C) maintaining occurrence rates (within the black square) and quadrat level richness. I predict that the pair level null model will best capture the influence of grazing and therefore exhibit the strongest deviations (SES value) from the expectation. Based on Komac et al. (2011), I predict that grazing will homogenize the existing heterogeneity, as indicated by negative SES_{diff} values. The site level null model will follow the paired results, but be moderated in their deviation from the expectation by including more environmental heterogeneity. Note that this schematic only represents one site, while herein we explore these patterns at two sites.

The standard approach for comparing null model (expected) results to the observed values is through the standard effect size (SES; e.g. Kembel et al. 2010; Leprieur et al. 2012; Myers et al. 2012), which is an extension of the familiar z-score for testing if an individual deviates significantly from the population mean. The SES is calculated as:

Equation 3.1

$$SES = \frac{X_{obs} - \overline{X_{exp}}}{sd_{exp}},$$

where X_{obs} is the observed value, X_{exp} the expected value (note the bar over X_{exp} indicating that it is the mean of all randomized X), and sd_{exp} is the standard deviation of the expected values. As such, SES values > |1.96| (i.e. more than 1.96 standard deviations from the expected mean) are considered to be significantly different from values expected by chance. When testing $beta_{diff}$, SES values greater than |1.96| indicate the difference is greater than expected by chance. In the case of $beta_{diff}$, the sign of the SES score relates to which treatment is greater, in this case grazed or ungrazed, than expected by chance (Figure 3.7).

Comparing the results of the within and among treatment level randomizations (i.e. the pair and treatment level null models) will determine if grazing is influencing the biotic heterogeneity, as measured by multiple site beta diversity, in these high elevation meadows. For example, if SES values for the pair level null model are significant, but the SES values based on the within treatment level null model are not, I may deduce that the treatment is having an influence on the measured outcome. The site level null model will determine if grazing has a site wide influence, or if it is specifically restricted to within the pairs. If the patterns are restricted to within the pairs, this may indicate that there is environmental and biotic heterogeneity among the pairs that overcomes the influence of grazing on the observed heterogeneity. I predict that the observed communities will be more similar to the null communities randomized within a treatment than those randomized across the grazing treatment (pair or site level null model) if grazing is influencing multiple site beta diversity patterns.

Factors influencing diversity

To assess the effect of grazing on biomass, I conducted one sample t-tests on the differences in biomass at each site separately, treating each pair of plots as a replicate, thus N = 3. Because sample sizes for biomass varied across the treatment (see results), I randomly sampled quadrats from the ungrazed plots to the same sample size as the paired grazed plot (generally n = 8) 999 times. Note that I also randomly sampled plot Apex One Grazed (A1G) 999 times to n = 8 as biomass was collected in 12 quadrats in this

plot. Thus mean biomass comparisons were always conducted on equal sample sizes. I calculated the difference as the mean ungrazed biomass – the mean of 999 mean grazed biomass values. I tested if the difference in biomass across all three pairs deviated significantly from zero at each site.

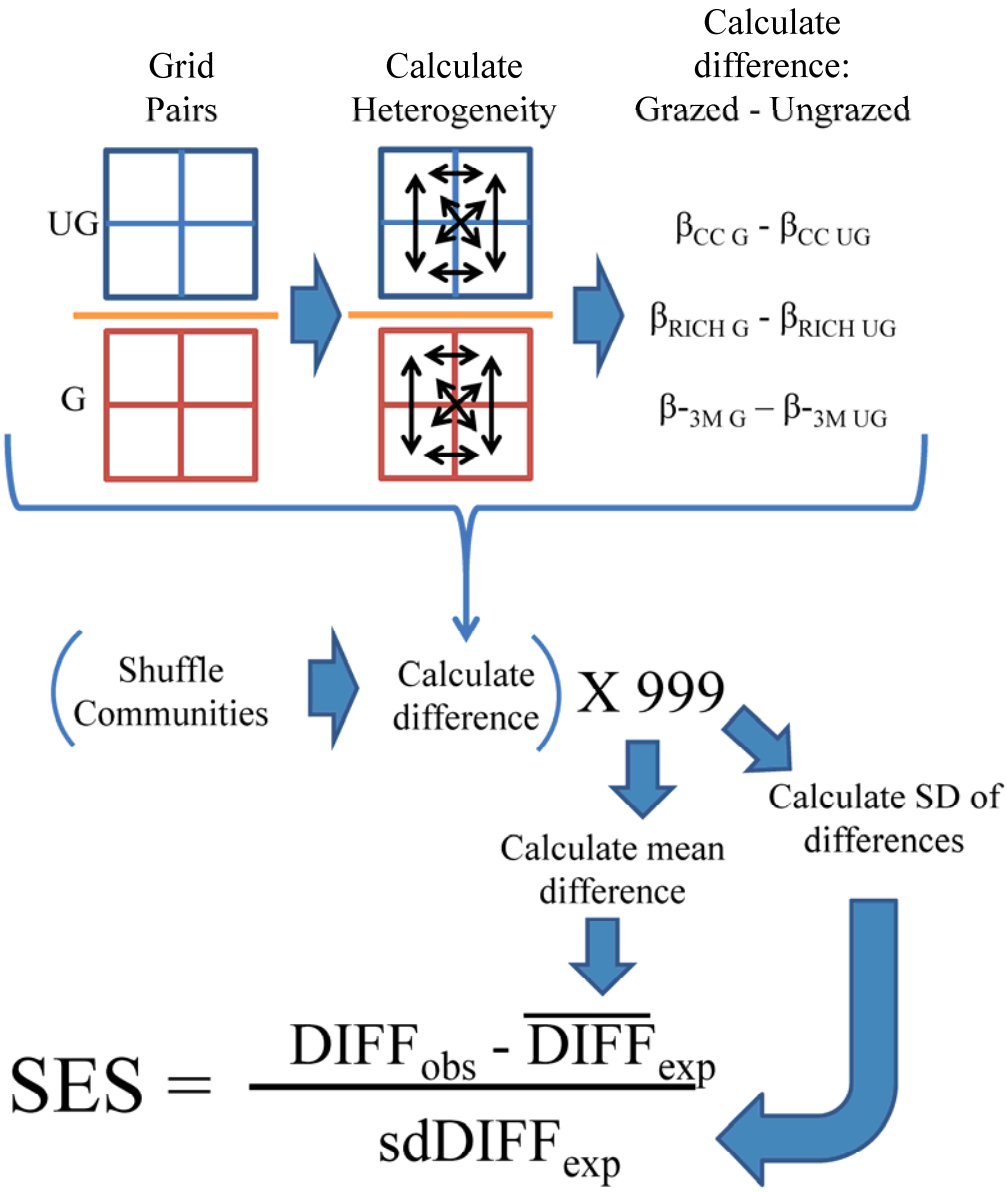

Figure 3.7 A demonstration of the process for calculating standard effect sizes from differences in heterogeneity expected for each pair under each null model (See Figure 3.6). For more details see the main text on pages 63-64.

3.3 Results

GENERAL DIVERSITY PATTERNS

Alpha diversity

Taxonomic alpha diversity did not differ consistently among sites or across the grazing treatment within sites (Figure 3.8). There is some indication that grazing may have increased richness at Apex (Figure 3.8, left panel), though at pair one the difference is negligible. One sample t-tests of the difference in mean quadrat level species richness were insignificant for both sites (Apex: $t = 1.71$, df = 2, $p = 0.23$; Hunter's: $t = 1.18$, df = 2, $p = 0.36$). Phylogenetic alpha diversity showed interesting, but inconsistent patterns. As predicted, raw phylogenetic diversity (PD; Figure 3.9A) closely matched the patterns observed for species richness (Figure 3.8), with only a slight difference observed for pair one at Apex. However, when applying the derived measures of alpha PD (MPD, Figure 3.9B, and MNTD, Figure 3.9C) different patterns emerge. Mean pairwise distance (MPD) was nearly always greater at Hunter's Range than at Apex (except Apex Two, ungrazed; Figure 3.9B). Furthermore, MPD values across and within pairs were much less variable at Hunter's than at Apex. Mean pairwise distance appears to slightly decrease with grazing in all pairs at Apex, while MPD does not consistently vary at Hunter's Range. Interestingly, site level patterns of MNTD do not follow those patterns observed with MPD (Figure 3.9C). There is more overlap in MNTD values among Apex and Hunter's and the variability within each site appears similar. These conflicting patterns between MPD and MNTD support the complementarity of these metrics (Webb et al. 2002). As with biomass comparisons, robust statistical tests of quadrat level values within each plot were inhibited by the sample design.

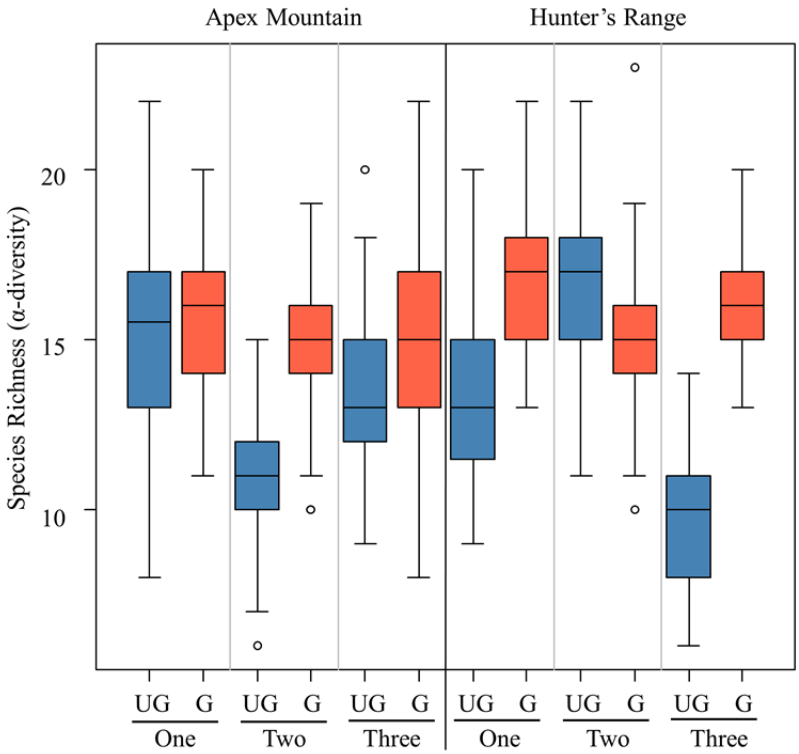

Figure 3.8 Taxonomic alpha diversity (species richness in 1 m^2 quadrats; A) is not different among sites or consistently across treatments within communities. In all cases, each boxplot represents 64 measures of alpha diversity in ungrazed (UG) and grazed (G) plots.

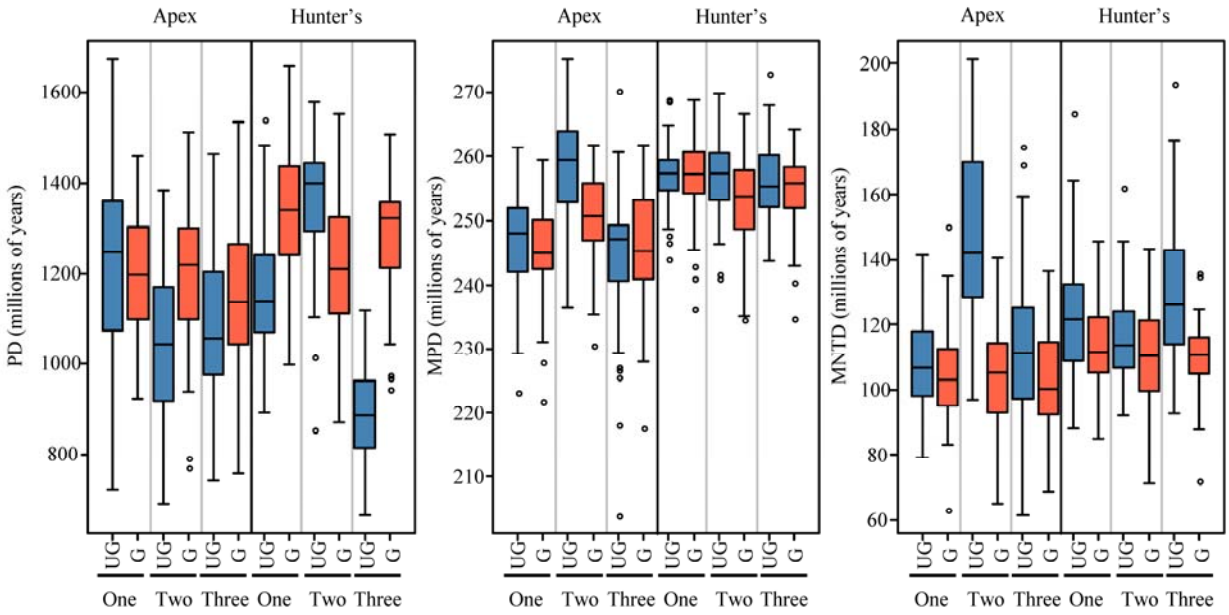

Figure 3.9 Phylogenetic alpha diversity, measured as raw PD (A), mean pairwise distance (MPD; B) and mean nearest taxon distance (MNTD; C), shows inconsistent patterns. In all cases, each boxplot represents 64 measures of alpha diversity in ungrazed (UG) and grazed (G) plots.

Gamma diversity

Species richness at each site (i.e. gamma diversity) was higher at Apex (52 species) than at Hunter's Range (40 species; Table 3.2). The sites shared less than 20% of species (14 species shared). In both cases the shared species accounted for more phylogenetic diversity (PD) than expected based on the overall PD of each site (Apex: PD/sp = 52.4, expected shared = 733.9my; Hunter's: PD/sp = 58.6, expected shared = 820.4). When broken down by treatment within each site, ungrazed plots had higher richness but did not always have higher PD. Despite higher richness encountered over all ungrazed plots at Apex, PD decreased slightly, indicating that the six novel species at Apex are likely to be more closely related than the four they replace.

Table 3.1 Gamma (γ) diversity is higher at Apex for both taxonomic and phylogenetic diversity, though overlap of species pools is low (14 of 78 total species = 17.9%). Treatment level gamma diversity was, in general, higher in the ungrazed plots, except where phylogenetic diversity is lower in the ungrazed plots at Apex, despite increased richness. Taxonomic diversity is measured as number of species while phylogenetic diversity is in millions of years. MPD and MNTD values refer to the overall metric in the column to the left of them (i.e. Diversity, Shared and Unique).

Sample	Diversity	MPD	MNTD	Shared	MPD	MNTD	Unique	MPD	MNTD
Taxonomic γ									
Apex	52			14			38		
Hunter's	40			14			26		
Phylogenetic γ									
Apex	2726	251.5	60.79	1192.5	255.6	106.31	1533.5	251.6	69.26
Hunter's	2344	255.5	72.25	1192.5	255.6	106.31	1151.5	254.4	93.27
APEX									
Taxonomic									
grazed γ	46			42			4		
ungrazed γ	48			42			6		
Phylogenetic									
grazed γ	2570.6	249.5	56.8	2350	247.2	66.8	220.6	258.4	233.3
ungrazed γ	2505.5	249.7	70.5	2350	247.2	66.8	155.5	291.0	267.5
HUNTER'S									
Taxonomic									
grazed γ	32			30			2		
ungrazed γ	38			30			8		
Phylogenetic									
grazed γ	1992.5	254.0	76.5	1761	250.7	71.9	231.5	254.0	254.0
ungrazed γ	2344	254.0	81.8	1761	250.7	71.9	583	257.7	153.0

Looking at the derived phylogenetic gamma values (MPD, MNTD) I found that Hunter's had higher values despite having less overall diversity, perhaps due to carrying similar lineages with fewer species when compared to Apex (Table 3.2). The MNTD was greater in ungrazed plots at each site individually, while MPD did not change appreciably at either site under grazing (Table 3.2). Values of MPD and MNTD for unique species by treatment within communities are heavily influenced by the low diversity of unique species (e.g. two unique species in grazed plots at Apex). It is however interesting to note that the unique species are distantly related as this is the only case where MNTD values approach or exceed those obtained for MPD (Table 3.1).

WITHIN COMMUNITY HETEROGENEITY (BETA DIVERSITY)

Observed differences in multiple site beta diversity metrics show limited consistency at the site level for both the turnover (β_{-3M}) and the richness component (β_{RICH}; Figure 3.10) of beta diversity. The overall metric (β_{CC}) is relatively consistent at Apex, but exhibits variability at Hunter's Range. Negative difference values of both β_{CC} and $P\beta_{CC}$ (i.e. ungrazed is greater than grazed) are obtained at Apex, but positive difference values (i.e. grazed is greater than ungrazed) are obtained at Hunter's Range (except β_{CC} at H3; Figure 3.10A), though these values are close to zero (Figure 3.10). Furthermore, at Hunter's, the pattern of differences of all three beta values is consistent, with positive differences in turnover, and negative differences in richness for both taxonomic and phylogenetic diversity. At Apex however, the order is opposite in pairs A1 and A3, and the spread is narrowest for A2 (Figure 3.10). Both of these patterns are consistent across taxonomic and phylogenetic diversity. Finally, it is also interesting to note that the most extreme differences were obtained at H1 for taxonomic metrics, but were found at A1 for the phylogenetic metric. Within the Hunter's site, the spread of taxonomic metrics was greatest at H1, but was greatest at H3 for phylogenetic metrics, despite H3 exhibiting the narrowest spread of taxonomic metrics.

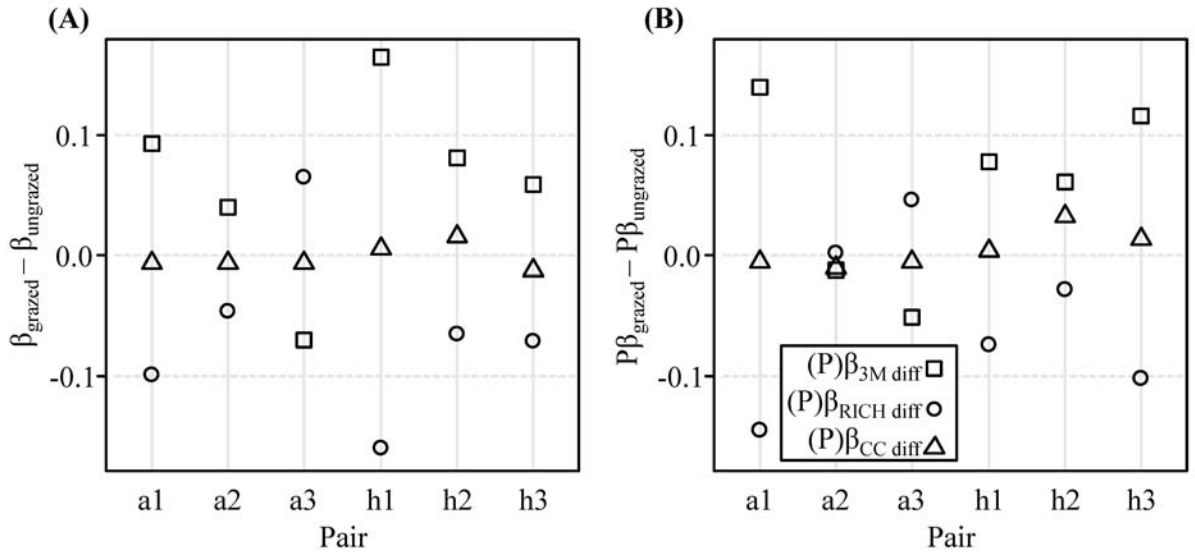

Figure 3.10 Observed differences in partitioned taxonomic (A) and phylogenetic (B) multiple site beta diversity values for each plot. Note that the legend in panel B applies to both panels; the (P) denotes phylogenetic for panel B.

When considering taxonomic metrics of heterogeneity, different species pools indicate that grazing is having an influence on patterns of assembly. For example, at the treatment level null model (Figure 3.11B) I found limited consistency in the direction of difference (positive or negative), and as predicted, many differences that did not deviate from that expected. Within the pair and site level null models however, patterns appear. For example, at Hunter's Range all differences deviated significantly, and, within a metric, in the same direction (Figure 3.11C). β_{CC} and β_{-3M} were always positive (observed difference greater than expected) while β_{RICH} was always negative (Figure 3.9A and C). In addition, pairs H2 and H3 exhibit insignificant differences from random in the treatment level null model, but are strongly significant under the pair level null model (Figure 3.11B and C). Contrary to Hunter's Range, Apex exhibits no consistent pattern within a given null model, but within each pair the pattern is the same across all the null models (Figure 3.11). That is, when significant, the values are in the same direction (i.e. positive or negative). Furthermore, the magnitude of the SES values of the differences at Apex remains similar regardless of the null model applied, while they vary considerably at Hunter's.

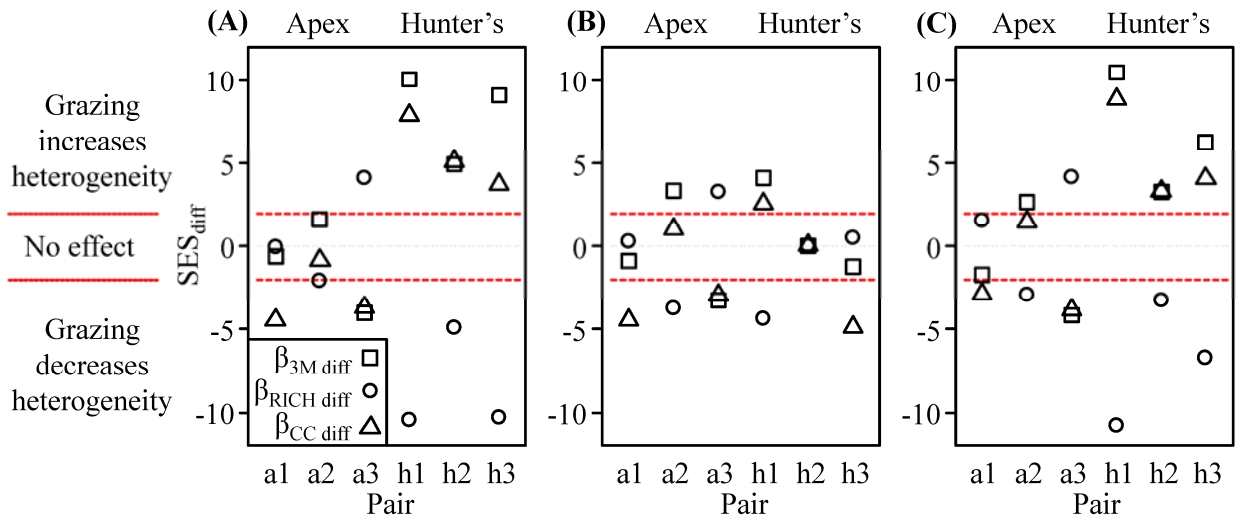

Figure 3.11 Standard effect sizes (SES) of the difference in partitioned multiple site taxonomic beta diversity values of β_{RICH}, β_{-3M} and β_{CC} (β_{JAC}) for each plot in each of three null models: site, treatment and pair (A, B and C, respectively). Dashed redlines indicate SES = ±1.96. Points beyond these lines deviate significantly from the expectation under the given null model.

In terms of phylogenetic heterogeneity, values were generally less extreme than observed for taxonomic heterogeneity. Standard effect sizes were again largely insignificant under the treatment level null model (Figure 3.12B) with four of six pairs (two at each site) being insignificant for all metrics. Furthermore, pair H3 also exhibited insignificant difference values for the richness (β_{RICH}) and turnover (β_{-3M}) components, but pair A1 was significant for all components. Interestingly, these results are contrasted strongly with those found under the pair level null model, particularly at Hunter's Range (Figure 3.12C) where β_{RICH} at H1 and β_{RICH} and β_{3M} at H2 were the only insignificant differences from the expectation. At Apex all metrics of beta diversity were insignificant under the pair level null model. The site level null model results of the differences tend to follow the pair level null model, though the values are often more extreme (Figure 3.12).

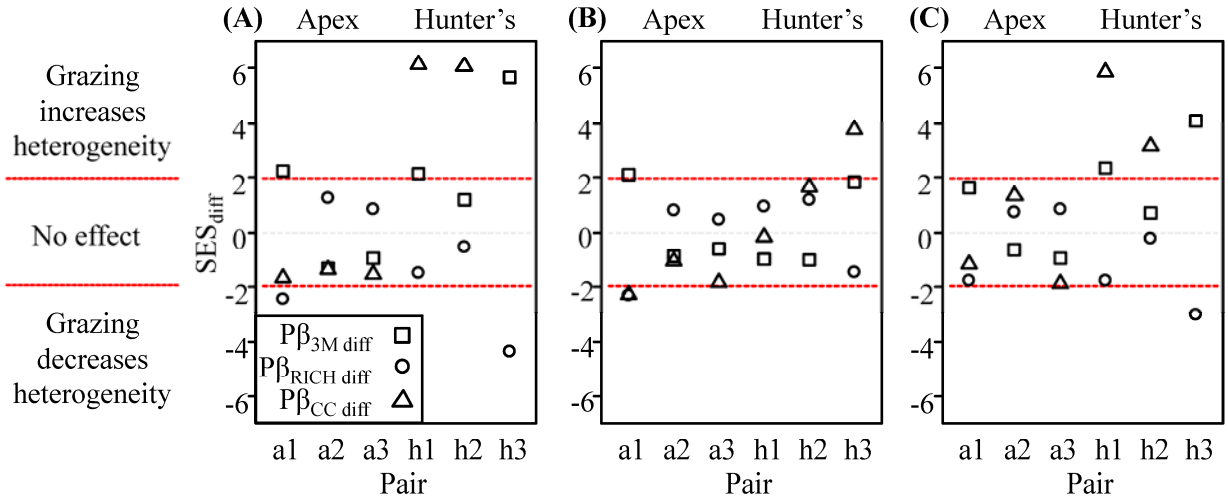

Figure 3.12 Standard effect sizes (SES) of the difference in partitioned multiple site phylogenetic beta diversity values of $P\beta_{RICH}$, $P\beta_{-3M}$ and $P\beta_{CC}$ ($P\beta_{JAC}$) for each plot in each of three null models: site, treatment and pair (A, B and C, respectively). Dashed redlines indicate SES = ±1.96. Points beyond these lines deviate significantly from the expectation under the given null model. Note: Outliers for the differences in β_{-3M} of the site and pair null models were excluded at pair H3 ($P\beta_{-3M}$ site = 13.6, $P\beta_{-3M}$ pair = 12.8) to more clearly show the patterns of the other pairs.

FACTORS INFLUENCING DIVERSITY

My sampling design inhibited robust statistical tests of the relationships between site, treatment and quadrat level biomass due to non-independence of individual quadrats (random effect within the treatment) and the way the treatment (or fixed) effect is nested within multiple random (site and pair) effects. Nonetheless, site and grazing treatment appear to influence above ground biomass per m^2 (Figure 3.13, Table 3.2). Average biomass is always higher in ungrazed plots and live and total biomass are always larger at Hunter's than at Apex. Litter biomass was in general higher at Hunter's as well (except h2g; Table 3.2). Time and logistical constraints did not permit harvesting of entire plots at each site. Therefore the sample sizes within each classification and plot vary with n = 192 in the ungrazed treatment at Apex, n = 28 in the grazed treatment at Apex, n = 136 in the ungrazed treatment at Hunter's and n = 24 in the grazed treatment at Hunter's (Table 3.2). Conservative one sample t-tests of the mean difference in quadrat level biomass found that total biomass differed significantly across the grazing treatment at Apex ($t = 7.36$, df = 2, p=0.018), while at Hunter's was marginally insignificant ($t = 3.50$, df = 2, p = 0.073), though the mean difference was 221.9 g.

Table 3.2 Mean (and standard deviation) live, litter and total biomass per m^2 in each eight by eight meter plot.

Plot	n	Live (g)		Litter (g)		Total (g)	
a1u	64	122.72	(25.54)	32.85	(18.83)	155.57	(36.05)
a1g	12	96.23	(21.24)	10.69	(6.22)	106.92	(24.78)
a2u	64	118.73	(29.39)	39.87	(31.95)	158.60	(54.61)
a2g	8	114.04	(28.66)	6.46	(3.38)	120.50	(28.33)
a3u	64	85.01	(25.17)	19.35	(22.29)	104.36	(35.17)
a3g	8	68.85	(20.42)	4.90	(3.014)	73.75	(21.73)
h1u	64	430.24	(67.51)	86.38	(45.66)	516.63	(96.31)
h1g	8	209.56	(104.65)	15.25	(25.12)	224.81	(128.11)
h2u	64	243.34	(56.10)	48.64	(29.73)	291.98	(60.58)
h2g	8	158.93	(58.01)	38.51	(20.92)	197.44	(57.09)
h3u	8	463.61	(76.16)	124.21	(32.85)	587.83	(88.97)
h3g	8	250.55	(67.36)	57.94	(26.92)	308.49	(75.66)

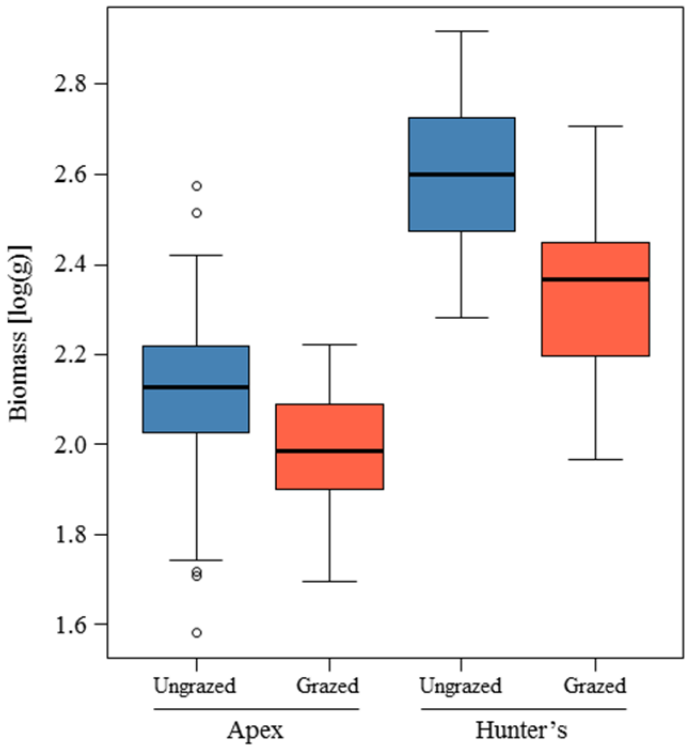

Figure 3.13 Biomass (log(g)) per square meter (live and litter combined) was higher at Hunter's Range than Apex Mountain and was higher in ungrazed (UG) plots than grazed (G) plots at both sites. $N_{Apex\text{-}ungrazed}$=192, $N_{Apex\text{-}grazed}$=28, $N_{Hunter's\text{-}ungrazed}$=136, and $N_{Hunter's\text{-}grazed}$=24.

3.4 Discussion

GENERAL DIVERSITY PATTERNS

Contrary to previous work (e.g. Pykälä 2004; Bakker et al. 2006), I found no consistent influence of grazing on species richness at either site, despite the varying productivity of the two sites. Work has previously shown that, especially in sites with higher productivity, grazing increases local species richness (Olff & Ritchie 1998; Bakker et al. 2006; Díaz et al. 2007). Few studies have considered the effect of grazing on phylogenetic diversity (but see Campbell et al. 2010, 2013; Yessoufou et al. 2013), and herein I found little influence of grazing on raw PD (which closely follows species richness, Figures 3.8 and 3.9) or on MPD or MNTD. Interestingly however, both MPD and MNTD appear to exhibit at least a weak site effect. In both cases, mean values are, in general higher at Hunter's than at Apex, but this pattern is much stronger for MPD. The difference in the strength of this site level response indicates that differences in PD among the sites is driven by tree wide phylogenetic pattern, rather than individual species relationships (Webb et al. 2002). As noted previously however, the sampling design applied inhibited analysis under a mixed-effects model framework that would more robustly test these patterns. Previous work by Campbell et al. (2010; 2013) applied a different metric of phylogenetic diversity, average taxonomic distinctiveness (ATD) as proposed by Clarke & Warwick (1998) to quantify the influence of sheep herbivory on desert rangelands. They found that PD (as measured by ATD) was highest under moderate grazing pressure, though they do not test if this relationship is significant (Campbell et al. 2010). In a similar study conducted in Mexico, Campbell et al. (2013) found no influence of sheep stocking rate on ATD. In neither study do Campbell et al. (2010; 2013) test for variation in PD (i.e. phylogenetic heterogeneity) among samples. I therefore contend that my application of the more widely applied phylogenetic diversity metrics developed by Faith (1992, 1994) and expanded by Webb et al. (2000, 2002) is novel, and suggest that future rangeland management studies may benefit from studying richness independent metrics of phylogenetic alpha diversity like MPD and MNTD (see also Yessoufou et al. 2013).

When considering taxonomic gamma diversity, it appears as though grazing again has limited impact, though there are several species unique to each treatment at each site (Table 3.1, Appendix A). At both site, species richness was higher across all ungrazed plots than across all grazed plots, though the difference is minimal. Turning to phylogenetic gamma diversity I found that raw PD increased at Hunter's (following species richness), but decreased at Apex, despite a concurrent increase in richness. This pattern at Apex suggests the novel species were closely related to existing species in the community, while the species that were lost were more phylogenetically distinct. When considering the more appropriate derived phylogenetic gamma values (MPD, MNTD) I found that MPD did not change at either site, but MNTD was higher across the ungrazed plots. Site level phylogenetic gamma diversity (MPD and MNTD) metrics indicate that Hunter's had higher values despite having lower raw PD, perhaps due to carrying similar lineages with fewer species when compared to Apex.

WITHIN-COMMUNITY HETEROGENEITY

Beta diversity has regularly been invoked as an important feature for determining which processes are leading to the patterns of community structuring (e.g. Swenson 2011; Leprieur et al. 2012; Myers et al. 2012). While the influence of grazing on the spatial heterogeneity of plant communities has been under investigation for some time (e.g. McNaughton 1983; Adler et al. 2001), and others have investigated the influence of grazing on beta diversity specifically (e.g. Carmona et al. 2012), this is the first study to apply an appropriate multiple site beta diversity measure to this question. In another novel step, I extended this investigation to multiple site phylogenetic diversity and found that taxonomic and phylogenetic heterogeneity exhibit similar and site specific responses to grazing.

Observed differences in heterogeneity across the grazing treatment generate inconsistent patterns at Apex for both taxonomic and phylogenetic heterogeneity. In both cases, replacement is higher in grazed plots in pairs A1 and A2 but lower in A3, while the richness component exhibits the opposite pattern (Figure 3.10). Furthermore, pair A1 exhibits the most extreme differences and A2 the least deviation, with phylogenetic measures of heterogeneity barely differing across the treatment (Figure 3.10B), while A3 displays moderate spread. These results are strongly contrasted by those observed for Hunter's, wherein

the patterns of partitioned beta diversity are consistent across all pairs. At Hunter's the replacement component is always higher in grazed plots while the richness component is always lower (Figure 3.10). Importantly, at both sites and for both taxonomic and phylogenetic heterogeneity metrics, the overall measure (i.e. Jaccard dissimilarity or β_{CC}) deviated least from zero. In fact, at Apex it was consistently only slightly negative, while at Hunter's its pattern was inconsistent, but always closer to zero than either of the partitioned components. This result highlights the importance of investigating not only the overall measures of dissimilarity, but also the two independent factors that contribute to it, replacement and richness. Considering only the standard, overall metrics of dissimilarity (in this case Jaccard) I may mistakenly have concluded that there was a limited effect of grazing on heterogeneity. Finally, it is also interesting to note that the most extreme differences were obtained at H1 for taxonomic metrics, but were found at A1 for the phylogenetic metric. Within the Hunter's site, the spread of taxonomic metrics was greatest at H1, but was greatest at H3 for phylogenetic metrics, despite H3 exhibiting the narrowest spread of taxonomic metrics. Both of these results indicate that the taxonomic and phylogenetic heterogeneity measures are capturing independent community heterogeneity patterns. While the observed differences in heterogeneity have generated interesting patterns, it is now well known that they may be expected based on the available species pool (γ diversity) or differences in species richness (α diversity; Chase et al. 2011; Myers et al. 2012; Lessard et al. 2012).

We therefore applied null models under three separate definitions of the species pool: (i) all species within each pair, (ii) all species within a treatment at each site and (iii) all species within a site to test if the observed patterns deviate from those expected by chance, and to more accurately test for an influence of grazing on heterogeneity. Here I focus on comparisons between the within treatment and within pair null models because the site level null models tended to closely follow the pair level differences for both taxonomic and phylogenetic heterogeneity (Figure 3.11 and 3.12). The similarity of the site and pair level null model results indicates that the individual pairs are doing a reasonable job of capturing the differences in available species (pools) based on cattle grazing.

For taxonomic heterogeneity, strong site level patterns emerge (Figure 3.11, Table 3.3). While deviation from the expectation (i.e. SES values) under the treatment level null model are inconsistent and often insignificant at both sites, under the pair level null model, Hunter's pairs exhibit strong, consistent deviations from the expectation. Apex on the other hand exhibits similar patterns to those found under the treatment level null model. Given that the observed differences in heterogeneity for multiple site Jaccard dissimilarity were near zero and that the SES values are strongly positive at Hunter's, the null expectation when considering cross-treatment species pools is that heterogeneity would be greater in ungrazed communities at Hunter's. This is clearly not the case as the observed values indicate limited differences in multiple site heterogeneity (Figure 3.11). Given that the observed difference of multiple site Jaccard dissimilarity is approximately zero and that the SES values are strongly positive, the expected difference in heterogeneity (grazed – ungrazed) must be negative (recall the SES values are observed – mean expected divided by the standard deviation of the expected values; see Figure 3.7). If the expected difference is negative, then expected ungrazed heterogeneity is necessarily greater than grazed heterogeneity. Since this is not the case, as observed differences are near zero, we can conclude that ungrazed heterogeneity is not greater than grazed heterogeneity at Hunter's Range, indicating that cattle are increasing the heterogeneity under the available species pools. These findings provide considerable support for the prediction that cattle grazing does in fact influence within community heterogeneity. However, my results strongly contrast with my prediction of reduced heterogeneity as cattle have increased the taxonomic heterogeneity of the plant community at Hunter's Range.

Similar results were obtained when considering phylogenetic heterogeneity, though important differences occur (Table 3.3). Under the treatment null model there is even less deviation from the expectation over all pairs. Furthermore, the patterns at Apex are less consistent within each site, that is, the sign of the differences for each component and overall value are not the same in each pair under any null model. Finally, although Hunter's again exhibits some strong deviation from the null expectation under the pair and site level null model, the richness component does not deviate from the expectation in pairs H1 or H2 and the turnover component does not vary from the expectation in pair H2. Despite these inconsistencies,

multiple site Jaccard dissimilarity again deviates strongly and positively for phylogenetic heterogeneity, as does the turnover component for pairs H1 and H3. These results contrast with the taxonomic null models which suggested that the turnover component deviated more strongly than the overall metric. The fact that patterns differ under the taxonomic and phylogenetic metrics of heterogeneity indicates that they are providing independent, additional information on how grazing is influencing within-community heterogeneity. Clearly then, significant patterns are emerging, but the results are contingent upon the site. Adler et al. (2001) noticed that a site specific contingent phenomenon was common in the literature on grazing and diversity studies and attempted to construct a framework for predicting when grazing would reduce the heterogeneity of vegetation.

Table 3.3 Summary of the influence of grazing on within community taxonomic and phylogenetic heterogeneity at each sampled pair of plots under each of three null models. '0' indicates no effect, '+' indicates an increase and '-' indicates a decrease in the given measure of heterogeneity (β_{CC}, β_{-3M}, or β_{RICH}) under the influence of grazing.

	Site Null Model			Treatment Null Model			Pair Null Model		
Pair	β_{CC}	β_{-3M}	β_{RICH}	β_{CC}	β_{-3M}	β_{RICH}	β_{CC}	β_{-3M}	β_{RICH}
TAXONOMIC									
Apex 1	-	0	0	-	0	0	-	0	0
Apex 2	0	0	-	0	+	-	0	+	-
Apex 3	-	-	+	-	-	+	-	-	+
Hunter's 1	+	+	-	+	+	-	+	+	-
Hunter's 2	+	+	-	0	0	0	+	+	-
Hunter's 3	+	+	-	-	0	0	+	+	-
PHYLOGENETIC									
Apex 1	0	+	-	-	+	-	0	0	0
Apex 2	0	0	0	0	0	0	0	0	0
Apex 3	0	0	0	0	0	0	0	0	0
Hunter's 1	+	+	0	0	0	0	+	+	0
Hunter's 2	+	0	0	0	0	0	+	0	0
Hunter's 3	+	+	-	+	0	0	+	+	-

Adler et al. (2001) predict that increases in spatial heterogeneity should be indicative of a patchy grazing structure, while decreases in heterogeneity should result from selective or homogeneous grazing across the site. Given that grazing appears to increase heterogeneity at Hunter's (Figures 3.8 and 3.9) it is possible that these results are driven by a patchy approach to grazing by the cattle. Importantly, Adler et al. (2001) stress that studies of heterogeneity involving grazing will be better served if they also measure

the heterogeneity of the grazing approach. I did not attempt to quantify the patterns of grazing herein and note that there were large differences in the grazing pressure across the two sites (0.10 AUM / ha at Apex and 0.61 AUM/ ha at Hunter's) though this is likely a reflection of available forage as biomass was much higher at Hunter's than Apex. However, it remains likely that cattle behaviour and not just vegetative 'behaviour' may be a driving factor in the response of communities to grazing.

SPECIES SELECTION BY CATTLE

It is possible that species selection by grazing cattle may lead to the observed patterns, though this has not been investigated fully. For example, the patchiness of plant communities in the grazed plots at Hunter's was primarily structured by hellebore (*Veratrum viride*), lupine (*Lupinus arcticus*) and pasque-flower (*Pulsatilla occidentalis*). False hellebore is a known toxic plant to both humans (Jaffe et al. 1990) and livestock. It is also relatively large (1 m in height) and exhibited dominance within the ungrazed plots (no species under it) but sheltered many smaller species in the grazed plots. Although alpine lupine is not considered toxic, other members of the genus *Lupinus* are and it is possible that cattle are actively avoiding consuming lupines. Lupine was widespread in the grazed plots at Apex as well, but was less common in ungrazed plots (Appendix A). Western pasque flower, as with many species of the Ranunculaceae, is also known to be toxic when consumed in large quantities. All three of these species are relatively large and may have contributed to sheltering smaller species from cattle grazing in grazed plots. At Apex, another Ranunculaceae species was regularly encountered in grazed plots (*Thalictrum occidentale*, 44 quadrats) but was encountered only once in ungrazed plots (Appendix A). The presence of a family with known toxicity (Ranunculaceae) at both sites may have contributed to the significant phylogenetic heterogeneity patterns observed across the pairs. Since these species were often more common in the grazed plots than in the ungrazed plots, the presence of an entire lineage that expresses this pattern would have substantial influence on the phylogenetic heterogeneity of the system. Repeating my analyses while excluding Ranunculaceae species may help clarify the influence of these species on the phylogenetic pattern shown.

The environment at the two sites investigated is different from many of the previous grazing and heterogeneity studies in that it is not a grassland, but an alpine forb meadow. Previous studies conducted at high elevation describe their systems as grasslands (Deléglise et al. 2011; Komac et al. 2011; Carmona et al. 2012). Clearly cattle exhibit preferences for certain species, as previous work highlights that they prefer to graze on grass in grasslands (e.g. McLean & Willms 1977; Willms et al. 1980; Ralphs & Pfister 1992), however, Ralphs and Pfister (1992) also found that in high mountain rangelands cattle selected forbs in proportion to or exceeding their availability in alpine meadows. Such a strategy may explain the increasing occurrence rates of grass species in grazed plots relative to ungrazed plots at Hunter's range. Considering that alpha diversity did not appear to vary consistently with treatment or site, species-insensitive beta diversity metrics (e.g. additive or multiplicative partitions) and those that do not account for the combining influences of richness and replacement may mask the patterns with which these cattle induced shifts in vegetation alter biotic heterogeneity.

PREVIOUS STUDIES OF BIOTIC HETEROGENEITY (I.E. USING BETA DIVERSITY)

Given the relative novelty of the beta diversity partitioning approaches and in particular the partition applied herein (Carvalho et al. 2013) I compared my results to those found in other biotic heterogeneity studies where traditional beta diversity metrics were the measure of heterogeneity. Most commonly, studies have applied the additive (Martin et al. 2005; Komac et al. 2011; Carmona et al. 2012) or multiplicative (Lezama et al. 2013) partitions of diversity. As has been highlighted previously, neither of these methods is able to account for the separate influences of turnover (replacement) and richness (species loss or gain) across multiple samples. Martin et al. (2005) studied a restored grassland and compared its diversity values to those in a remnant, natural patch. They found that beta diversity was higher in the restored patch, but that alpha diversity measures were lower. This pattern is expected under the additive measure of beta diversity applied and this study would likely benefit from applying null models which can account for differences in alpha diversity to better quantify beta diversity, and therefore the success of restoration efforts. Using approaches such as those outlined here may be a valuable approach where the goal of restoration is to restore all levels of diversity to disturbed ecosystems. When

considering grazing specifically, Komac et al. (2011) show that grazing homogenized plant communities at local scales, while increasing heterogeneity at the among patch scale. They suggest that at larger scales grazing has a heterogeneous effect because it can create gaps and therefore opportunities for colonization, whereas at small scales it disrupts the spatial structuring of the community, leading to a reduction in niche complementarity. My sampling design did not facilitate the investigation of larger scale heterogeneity but, in contrast to Komac et al. (2011) I found increased levels of heterogeneity due to grazing at fine scale at Hunter's Range. However, no significant pattern emerged at Apex Mountain. The increased heterogeneity at Hunter's may have been due to an interaction between plant palatability and their facilitation of palatable species present in their understory.

In an approach similar to mine, Carmona et al. (2012) state that while the influence of grazing on taxonomic diversity patterning is worthy of investigation, a clearer picture may be obtained by extending studies to novel measures of diversity. Carmona et al. (2012) investigate taxonomic and functional diversity in concert and aim to show how taxonomic and functional diversity are influenced by grazing along a gradient of moisture availability and grazing intensity. Carmona et al. (2012) defined beta diversity following de Bello et al. (2010) as $\beta = (\gamma - \text{mean } \alpha)*100/\gamma$ and argue that this approach quantifies the proportion of between site diversity with respect to overall diversity. They further measured beta diversity among grazing intensities where both taxonomic and functional beta diversity were influenced by grazing level and habitat (dry vs. moist). They found that functional homogeneity increased with grazing intensity and that taxonomic homogeneity only increased at dry sites. These findings somewhat support my findings at Apex since it is a dry site (relative to Hunter's) it may have experienced a reduced heterogenizing influence of grazing than Hunter's Range did. They also demonstrated differing patterns of functional and taxonomic diversity metrics, and highlight the need for further studies to incorporate multiple diversity metrics as I do here.

Lezama et al. (2013) studied the influence of grazing on vegetation structure across a productivity gradient. They found that the influence of grazing on beta (in addition to alpha and gamma) increased with productivity. However in contrast to my study, they found reduced heterogeneity with increasing

productivity under grazing. This may be explained by the coarse scale at which they compared beta diversity or by the grazing approach of cattle in those regions (Lezama et al. 2013). In contrast to the results of Lezama et al. (2013), Frank (2005) found a humped relationship between productivity and the influence of grazing on heterogeneity (but not on beta diversity itself). Frank (2005) found that heterogeneity increased under grazing at intermediate productivity, peaking around 275 g / m^2 but decreased at high and low levels of productivity. These results (Frank 2005) support my findings as heterogeneity was increased by grazing at the moderately productive site (Hunter's: mean grazed biomass / m^2 = 243.6 g, n = 24) while grazing exerted no change in heterogeneity at the lower productivity site (Apex: mean ungrazed biomass / m^2 = 139 g, n = 28). Furthermore, my results only appeared in the grazing effect (i.e. the difference in heterogeneity within a pair), not in the straight comparison of grazed plots and ungrazed plots as found by Frank (see Figure 3 in Frank 2005). However, it is difficult to directly compare my results to those of Frank (2005), Lezama et al. (2013), or indeed other studies of grazing and beta diversity because no grazing studies have, to my knowledge, applied null models. It is therefore unclear whether the patterns they find are entirely expected under chance alone (due to differences in alpha or gamma diversity) or if they are indicative of a significant grazing influence. Nonetheless, it appears as though there may be an interacting effect of community productivity and grazing that could lead to the observed influences of grazing on heterogeneity.

PHYLOGENETIC HETEROGENEITY

Given the novelty of Leprieur et al.'s (2012) derivation of partitioned phylogenetic beta diversity it is unsurprising to find that it hasn't been more widely applied. At the time of this work it has only been cited three times (as calculated by Google Scholar); Baselga (2013) and Dapporto et al. (2013) refer to it while further developing methods, while Qian et al. (2013) note it in passing while suggesting that it may not apply to the broad scale of their investigation (state and province level beta diversity) and apply the dissimilarity metrics of PhyloSor (Bryant et al. 2008) and UniFrac (Luzopone and Knight 2005) alone. My results of phylogenetic heterogeneity follow those found for taxonomic diversity, but exhibit less deviation from the null expectation than taxonomic measures. Additionally, when testing for possible

drivers of heterogeneity, such as patchiness as measured by increased heterogeneity with distance, and function, as measured by difference in biomass with beta diversity, I find differing patterns (Appendix C). Taxonomic metrics of beta diversity nearly all deviate from the null expectation (Appendix B) while the partitioned phylogenetic values are regularly indifferent from random. Therefore future work investigating heterogeneity will benefit from applying multiple metrics of diversity, including taxonomic and phylogenetic beta diversity.

3.5 Conclusion

Previous work has attempted to quantify the influence of grazing on heterogeneity (e.g. Golodets et al. 2011, Carmona et al. 2012, Lezama et al. 2013), however, I believe this is the first to use multiple site beta diversity as a measure of within-community heterogeneity. Baselga (2013) has recently reiterated that quantifying overall heterogeneity using average pairwise dissimilarities (including PERMANOVA and dispersion based approaches) masks the patterns of species which co-occur among more than two samples. Furthermore, these approaches do not generally consider the independent factors of richness and replacement and I could find no studies investigating the influence of grazing on phylogenetic heterogeneity.

Herein I have shown how grazing can have conflicting impacts on both taxonomic and phylogenetic plant community beta diversity, depending on the characteristics of the site. At Hunter's Range I found an increase in heterogeneity under the influence of grazing which I speculate is driven by a reduction in overall dominance combined with a facilitative effect of large, unpalatable species protecting smaller statured and palatable species. At Apex, I found no consistency in the differences in heterogeneity, a result supported by previous work which found a homogenizing effect of grazing on taxonomic and functional diversity at drier sites (Carmona et al. 2012). Most importantly, and in support of Diserud and Odegaard (2007) and Baselga (2013), I have demonstrated that multiple site metrics may better capture the overall heterogeneity of a site. Furthermore, I apply appropriate randomization techniques which provide a richness independent way to better quantify the influence of experimental treatments on heterogeneity (beta diversity; Lessard et al. 2012). Studies following my approach might improve upon

my methods by developing multiple site functional diversity metrics and by increasing replication at each site and across a broader array of sites to better test the generality of the results I obtained. However, I believe that my results provide a strong first step in quantifying within community heterogeneity and maintain that, in addition to traditional measures of richness (gamma and alpha diversity), conservation and restoration efforts consider not just broad sense beta diversity (as measured by the multiplicative and additive partitions of diversity) but also attempt to consider the turnover and richness components of beta diversity as these can exhibit contrasting patterns to those obtained for the broad scale measures (e.g. Baeten et al. 2012).

Chapter 4: Conclusion

4.1 General Discussion

Herein I sought to emphasize the importance of applying alternative measures of diversity to more fully understand patterns of plant community assembly. Throughout the introduction I provide a background on diversity quantification, the relatively recent expansion of phylogenetic diversity research and the influence of grazing on diversity patterns. In particular I addressed some of the novel approaches to quantifying (i.e. novel partitions) and comparing (null models) beta diversity. Based on the literature review, I recognized a number of gaps that I sought to fill with my research.

First, to my knowledge, no one has yet extended multiple site dissimilarity measures of beta diversity to the most robust partition of beta diversity to date (Carvalho et al. 2013). Considering that the adaptation is straightforward when applying the 'a' 'b', and 'c' notation of unique ('a' and 'b') shared ('c') species among two samples, and that Baselga (2010, 2012) regularly includes the multiple site metrics in his derivations of his partition, it is surprising to find that the partition of Carvalho et al. (2013) has not yet been extended to the multiple site framework. While a relatively simple derivation, adding this tool here fills a hole in the existing suite of tools for studying taxonomic heterogeneity through beta diversity.

Second, I not only extend the existing toolbox by providing a multiple site analog of Carvalho et al.'s (2013) pairwise taxonomic beta diversity, but I expand upon the work of Baselga (2012, 2013), Leprieur et al. (2012) and Carvalho et al. (2013) in providing the phylogenetic diversity analogs for both the pairwise and multiple site metrics for Carvalho et al.'s (2013) partition (Chapter 2). It has recently been emphasized that studying all facets of diversity, including taxonomic, functional and phylogenetic will yield the best picture of diversity patterning and processes (Stegen & Hurlbert 2011). In the hope that these new tools will be more broadly applied, I supply the R code for calculating all four types (taxonomic and phylogenetic, pairwise and multiple site) of Carvalho et al.'s (2013) partition in a single place (Appendix E). While others have attempted to compile beta diversity functions in one authoritative location (e.g. MBI, Chen 2013), this is the first to bring together multiple site and pairwise metrics. Chen

(2013) further notes that multiple site metrics will soon be added to the MBI R package, but does not refer to the development of phylogenetic metrics of beta diversity.

Finally, I applied the novel partitions of taxonomic and phylogenetic multiple site diversity developed in Chapter 2 to better quantify the influence of grazing on biotic heterogeneity. I found that heterogeneity increased at Hunter's Range under grazing while showing inconsistent results at Apex Mountain. Since Hunter's Range was more productive than Apex Mountain, these results support existing work (Frank 2005), which found that productivity is an important factor that may interact with cattle behaviour leading to increases in heterogeneity at moderate productivity, but increases homogeneity or limited change at high and low productivity respectively. The tools developed in Chapter 2 therefore appear to capture a similar pattern and this finding lends support to their application in biodiversity investigations. In particular, the novel tools applied in this study provide a simple way to estimate heterogeneity of a given system as they require only presence / absence data, and can readily be applied to standard site by species matrices of any size. Furthermore, I have shown how testing their results using null models controls for any potential influence of alpha diversity and critically, can be used to test for an influence of any treatment of interest by excluding it from the applied randomization technique. The combination of null models and multiple site heterogeneity approaches for both taxonomic and phylogenetic diversity therefore provide a robust and simple way to experimentally test natural communities under any influence of interest.

4.2 Assumptions and limitations

Despite the encouraging results obtained from the novel approaches applied, there are factors which may limit the broader impact of the work described in this thesis. First and foremost is that the methods applied, while intriguing, have not been formally tested for their robustness. However, they are based on and derived directly from methods which to date have been demonstrated to be robust under many circumstances (Leprieur et al. 2012; Baselga 2012, 2013; Carvalho et al. 2013). It is possible however, that there are problems with the methods proposed in specific unknown cases. As Carvalho et al. (2013) showed when investigating Baselga's widely accepted partition (e.g. Azeria et al. 2012; Leprieur et al.

2012), novel metrics should be subject to strong scrutiny prior to basing decisions upon their results. I therefore caution against widespread application of this approach until further tests on the methods are completed. In addition, I have not explicitly compared my results to the pairwise metrics that have been developed by Baselga (2010, 2012) and Carvalho et al. (2013) to confirm Baselga's (2007, 2013) and Diserud and Odegaard's (2007) contention that averaging pairwise dissimilarities does not appropriately capture partitioned beta diversity. Preliminary results of pairwise beta diversity values however do indicate contrasting patterns to those observed when applying multiple site beta diversity metrics (data not shown) and these results support the findings of Baselga (2013). For example, averaged pairwise beta diversity found more consistent patterns at Apex (data not shown), while I show more consistent patterns at Hunter's range.

Secondly, the work herein defines species pools based on the species encountered within each sampling plot. There are other species in the pool of the site, that were not encountered while sampling, and these species were not included in the randomizations of the communities. Furthermore, authors have recently proposed the idea of 'dark diversity' for species pools (Pärtel et al. 2011) where they argue that species pool definitions should include those species that could occur in a given location, but at the time of sampling do not. Given that null model results are so heavily dependent on the definition of the available species (Lessard et al. 2012), it is important to consider all possible definitions of the species pool when studying community level heterogeneity patterns. Other studies (e.g. Chase 2010; Chase et al. 2011) using null models to study community structuring applied equiprobable null models based on the Raup-Crick metric of beta diversity and it has been shown that such models can lead to differing results (e.g. Azeria et al. 2012). Though I did not specifically test the influence of different modeling types here, Azeria et al. (2012) demonstrate that the fixed-fixed null model appears to be the best approach.

Third, I was unable to collect adequate trait data to assess functional diversity. Large trait databases exist for many plant species, but these are largely restricted to Europe (e.g. LEDA: Kleyer et al. 2008; TRY: Kattge et al. 2011). While many of the same genera are present in North America, species specific measurements are required for trait diversity and functional diversity investigations. Logistical constraints

limited my measurement of plant traits for the species I encountered. A comprehensive trait database for North American plant species will facilitate stronger approximations of functional land trait diversity in studies such as this.

Finally, and perhaps most importantly, the broader generality of the patterns of heterogeneity under the influence of grazing cannot be established. When considering the sampling design applied herein, it is apparent that when the question of interest is the landscape scale influences, the sample size is two, i.e. the two sites. I attempt to overcome this lack of replication by considering each site an independent study and therefore have a replication of three pairs at each site. While such replication is enough to begin to establish trends it is but a bare minimum. Increased replication, both within each of the sites and among more sites spanning the environmental variation even within alpine environments may overcome this shortfall.

4.3 Future research directions

Despite the limitations outlined above, this study has demonstrated not only the validity of novel approaches, but also the ways in which grazing can influence plant community heterogeneity. I contend that my results demonstrate support for continuing to study beta diversity as an important value of all ecosystems, much in the same way that species richness is considered at either the alpha (sample) level or the gamma (regional) level. Given that grazing can have contrasting and significant impacts on heterogeneity, even when influences on richness appear minimal (Chapter 3) it behooves conservation and rangeland managers to study not only species counts, but how the local communities vary across the site of investigation.

To improve upon the work conducted herein, further replication within communities and regions is necessary. As has been stressed by Lessard et al. (2012) and others, replicated local experiments (such as that conducted herein) across broader geographical gradients, and tested using appropriate null models are likely to be the best way to further clarify the processes which lead to patterns of species diversity. Therefore, setting up larger exclosures (Lezama et al. 2013) and / or multiple smaller exclosures within

similar regions will enable better replication of this study. Furthermore, this approach increases the chance that small variations in environmental characteristics will be picked up to better assess the generality of the results obtained. For example, I was only able to place three pairs at the Apex site due to restrictions on plot locations and the presence of tree cover. As such, I may have sampled in more heterogeneous locations than it appeared, which may have led to inconsistencies at this site. Alternatively, the small size of the Hunter's site and its overall lack of tree cover may have minimized variation among the pairs resulting in more consistent patterns. Therefore, increased replication would enable researchers to better assess the generality of patterns observed herein.

Perhaps one of the most straight forward and immediately beneficial approaches based on this work would be to apply the techniques developed herein to existing data sets that have sampled in contiguous designs, or used a sampling design where multiple subsamples occur within a given plot. Using existing datasets limits the considerable investment in field surveys and takes advantage of, and therefore increases the return on, previous investments of both time and finances. I encourage other groups to test the methods herein on their existing datasets to get a better picture of the generality of the results I obtained.

Furthermore, it is important to validate the methods being used. Clearly I have not fully tested the metrics developed in Chapter 2. I recommend following previous examples for testing the robustness of the developed metrics to communities with known properties of phylogenetic and taxonomic beta diversity. This can be achieved by generating phylogenetic trees with known structure to generate predictable patterns of phylogenetic diversity. For example, Leprieur et al. (2012) show that their phylogenetic analogs of Baselga's (2010, 2012) partition of beta diversity are robust metrics using regional trees generated under a proportional-to-distinguishable arrangement (PDA model) and a Yule model, representing unbalanced and balanced tree structure respectively. In doing so they show that tree structure had limited effect on their partitioned phylogenetic beta diversity values as correlation between the tested phylogenetic beta values from each tree was very high (Leprieur et al. 2012). When testing and comparing their partition to that of Baselga (2010, 2012), Carvalho et al. (2013) used communities with

ever increasing values of species loss to show that Baselga's nestedness-resultant dissimilarity metric failed to increase monotonically, but instead exhibited a hump shaped curve. A promising approach then may be to test both taxonomic and phylogenetic diversity measures in concert by placing communities of species with known heterogeneity properties on phylogenetic trees of known structure.

Finally, multiple site heterogeneity metrics have not yet been developed for functional diversity. It has been argued that studying functional diversity will be the best way to truly quantify the influence of disturbance on communities of species (Mouillot et al. 2013) and the list of studies investigating the responses of functional diversity to influences like grazing is increasing (e.g. Carmona et al. 2012). In order to best describe the influences of disturbance factors like grazing on heterogeneity, it will be important to include taxonomic, functional and phylogenetic diversity (e.g. Bernard-Verdier et al. 2013). Importantly, this is not the daunting task it once was. The increasing availability of modifiable, open source computer code (e.g. Leprieur et al. 2012; Baselga & Orme 2012; Carvalho et al. 2013), diversity tools (e.g. phyloGenerator: Pearse & Purvis 2013), trait datasets (e.g. LEDA: Kleyer et al. 2008), and continuing advancements in computing power will facilitate the inclusion of all three metrics of diversity. A synthesis of the responses at the taxonomic, phylogenetic and functional levels will generate the best picture of the processes that lead to the incredible patterns of diversity observed around the world.

There is therefore ample opportunity to expand on the field of biotic heterogeneity. Conservation and management based studies will further demonstrate the importance of considering heterogeneity in preparing for climate change, while robust tests of methods based on communities with known properties and phylogenetic trees with known structure will continue to develop the rapidly advancing field of biotic heterogeneity.

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Appendix A – Species Occurrence Rates

Table S1.1 Occurrence rates of each species encountered by the number of quadrats in which they were found. Interesting patterns emerge in the Poaceae and the generally toxic (to grazers) Ranunculaceae.

Family	Species	Apex Grazed	Apex Ungrazed	Hunter's Grazed	Hunter's Ungrazed
Asteraceae	*Symphyotrichum foliaceum var foliaceum*	187	186	0	0
Asteraceae	*Erigeron aureus*	38	78	0	0
Asteraceae	*Arnica parryi*	53	73	0	0
Asteraceae	*Taraxacum officinale*	137	15	0	0
Asteraceae	*Anaphalis margaritacea*	3	43	0	0
Asteraceae	*Achillea millefolium*	191	152	0	0
Asteraceae	*Hieracium gracile*	3	7	85	60
Asteraceae	*Erigeron peregrinus ssp peregrinus*	88	38	0	0
Asteraceae	*Antennaria lanata*	1	2	8	5
Asteraceae	*Arenaria capillaris*	29	18	0	0
Asteraceae	*Senecio integerrimus*	114	85	1	1
Asteraceae	*Cirsium foliosum*	20	5	0	0
Asteraceae	*Antennaria alpina*	24	5	0	0
Asteraceae	*Arnica mollis*	0	0	192	152
Asteraceae	*Senecio triangularis*	0	0	156	165
Asteraceae	*Erigeron peregrinus ssp callianthemus*	0	0	129	179
Asteraceae	*Agoseris aurantiaca var aurantiaca*	0	0	15	7
Brassicaceae	*Draba albertina*	12	31	0	0
Caryophyllaceae	*Stellaria longipes var altocaulis*	41	38	0	0
Caryophyllaceae	*Silene parryi*	3	0	0	0
Caryophyllaceae	*Cerastium arvense*	0	0	2	0
Crassulaceae	*Sedum lanceolatum ssp lanceolatum*	142	96	0	0
Cyperaceae	*Carex phaeocephala*	124	80	0	0
Cyperaceae	*Carex raynoldsii*	10	6	0	0
Cyperaceae	*Carex concinna*	4	10	0	0
Cyperaceae	*Carex spectabilis*	0	0	173	189
Cyperaceae	*Carex illota*	0	0	189	125
Cyperaceae	*Carex nigricans*	0	0	8	2
Ericaceae	*Vaccinium scoparium*	10	4	0	0
Fabaceae	*Lupinus arcticus ssp subalpinus*	150	106	144	184
Fabaceae	*Trifolium pratense*	1	0	0	0
Fabaceae	*Trifolium repens*	0	0	6	0
Geraniaceae	*Geranium bicknellii*	0	0	7	0
Juncaceae	*Luzula glabrata var hitchcockii*	1	3	77	65
Juncaceae	*Juncus drummondii var subtriflorus*	0	0	97	75
Liliaceae	*Veratrum viride*	0	0	104	82
Liliaceae	*Erythronium grandiflorum*	0	0	98	177
Montiaceae	*Claytonia lanceolata*	3	4	0	0
Onagraceae	*Epilobium anagallidifolium*	57	128	15	0
Onagraceae	*Chamerion angustifolium ssp angustifolium*	15	0	0	13
Orobanchaceae	*Rhinanthus minor ssp minor*	0	24	0	0
Orobanchaceae	*Castilleja miniata*	0	0	15	38
Plantaginaceae	*Collinsia parviflora*	72	73	0	0

Table S1.1 (cont'd) Occurrence rates of each species encountered by the number of quadrats in which they were found. Interesting patterns emerge in the Poaceae and the generally toxic (to grazers) Ranunculaceae.

Family	Species	Apex Grazed	Apex Ungrazed	Hunter's Grazed	Hunter's Ungrazed
Plantaginaceae	*Veronica wormskjoldii*	2	9	157	70
Plantaginaceae	*Penstemon procerus var tolmiei*	2	0	0	0
Plantaginaceae	*Veronica serpyllifolia ssp serpyllifolia*	0	0	4	0
Poaceae	*Bromus marginatus*	128	146	22	5
Poaceae	*Deschampsia elongata*	187	136	0	0
Poaceae	*Phleum alpinum*	101	94	190	92
Poaceae	*Trisetum spicatum*	112	97	0	0
Poaceae	*Poa nemoralis*	0	18	0	0
Poaceae	*Poa alpina*	14	2	0	0
Poaceae	*Agrostis stolonifera*	0	0	116	26
Poaceae	*Vahlodea atropurpurea*	0	0	122	102
Poaceae	*Calamagrostis canadensis var canadensis*	0	0	43	53
Poaceae	*Elymus glaucus ssp glaucus*	0	0	2	0
Poaceae	*Poa arctica*	0	0	66	12
Poaceae	*Poaceae spp*	0	0	3	0
Polemoniaceae	*Microsteris gracilis var humilior*	190	189	0	0
Polemoniaceae	*Polemonium pulcherrimum ssp pulcherrimum*	41	7	0	0
Polygonaceae	*Polygonum minimum*	97	127	0	0
Polygonaceae	*Eriogonum umbellatum var majus*	10	28	0	0
Polygonaceae	*Rumex acetosella*	0	0	0	2
Portulacaceae	*Lewisia pygmaea*	23	13	0	0
Ranunculaceae	*Delphinium nuttallianum*	0	3	0	0
Ranunculaceae	*Ranunculus uncinatus var parviflorus*	66	91	0	0
Ranunculaceae	*Thalictrum occidentale*	44	1	0	0
Ranunculaceae	*Ranunculus eschscholtzii*	10	0	105	31
Ranunculaceae	*Pulsatilla occidentalis*	0	0	65	45
Ranunculaceae	*Ranunculus occidentalis*	0	0	2	2
Rosaceae	*Potentilla diversifolia var diversifolia*	115	149	0	0
Rosaceae	*Fragaria virginiana ssp platypetala*	140	79	0	0
Rosaceae	*Sibbaldia procumbens*	58	13	154	65
Rosaceae	*Geum triflorum*	10	1	0	0
Rosaceae	*Potentilla diversifolia var perdissecta*	18	0	26	0
Saxifragaceae	*Mitella breweri*	0	0	164	175
Valerianaceae	*Valeriana sitchensis*	0	5	163	191
Violaceae	*Viola sp*	0	0	133	141

Appendix B – Observed plot level, taxonomic and phylogenetic multiple site dissimilarity values and their standard effect sizes under three null models

Overall turnover (i.e. species replacement) is the primary force shaping taxonomic and phylogenetic beta diversity patterns in each plot (except Phylogenetic in H2U; Figure S3.1). This pattern does not appear influenced by grazing in a consistent direction overall, though grazed and ungrazed values for β_{-3M} and β_{RICH} are never the same within a given pair. Furthermore, the importance of taxonomic and phylogenetic turnover (β_{-3M}) always increases with grazing at Hunter's, resulting in a corresponding decrease in richness importance (β_{RICH}). Patterns of response to grazing for observed partitioned within-community beta diversity are inconsistent at Apex.

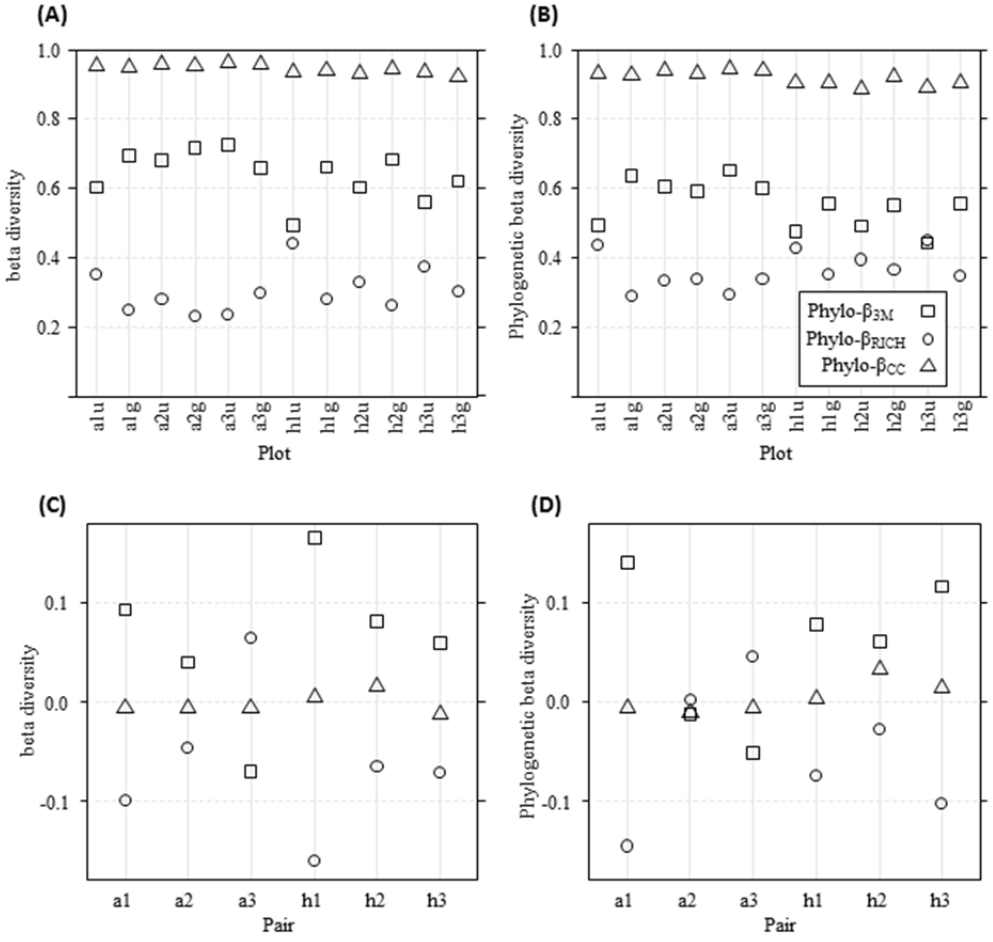

Figure S2.1 Observed partitioned taxonomic (A) and phylogenetic (B) multiple site beta diversity values for each plot and their differences in each pair (C and D respectively). Note that the legend in panel B applies to all four panels. Panels C and D appear in the main text as Figure 3.10 A and B.

Within each plot I found that nearly all plots deviated significantly from expected regardless of the null model applied (SES > |1.96|, red lines in Figure S3.2A, B and C). Only one plot (A3U) was not different from the expected based on the treatment level null model and two plots (H1G and H2G) did not differ from expected based on the pair level null model. Furthermore, SES values obtained from the treatment null model are often more extreme than the SES values obtained from the pair level null model. Such results suggest that variation in biotic heterogeneity is at least as great among plots within a treatment as it is among pairs of plots across the grazing treatment. Looking at the dissimilarity values over all plots, it is clear however that there are some consistencies. For example, the turnover and overall metrics are always negative (or insignificant, H2G, paired null model) demonstrating that observed values are greater (i.e. more dissimilar) than expected by chance. While the within plot SES values have begun to suggest some interesting findings, the real question is how the grazing treatment influences heterogeneity.

Overall phylogenetic SES values are less extreme than those calculated for taxonomic beta diversity with many more insignificant values present. As with taxonomic diversity within each plot, phylogenetic heterogeneity patterns were largely consistent within the treatment level randomizations. In all significant cases, the SES β_{CC} and β_{-3M} was negative, while β_{RICH} was always positive (Figure S3.3A, B, and C). As with the taxonomic metrics A3U again exhibited insignificance within the treatment level null model, but also many others, including both of the partitioned values in A3G, the richness values in H1U, β_{RICH} in A1G, H1G and H2U, and β_{-3M} in A1G, H1U and H2U (Figure S3.3B). In the pair level null model of phylogenetic beta diversity, interesting patterns again emerge, particularly at Hunter's Range. At Hunter's all grazed plots are insignificant for all metrics, i.e. the observed patterns of beta diversity did not deviate from those expected when randomized within the pair. In contrast, ungrazed plots at Hunter's tended to deviate from the expected phylogenetic heterogeneity based on the pair level null model (except β_{-3M} and β_{RICH} in H2U; Figure 3.10C). At Apex, the pair level null model did not yield consistent patterns of SES values. A3U again was insignificant for all metrics, but others were also insignificant. For example, A1G was insignificant for all nestedness-resultant and richness metrics.

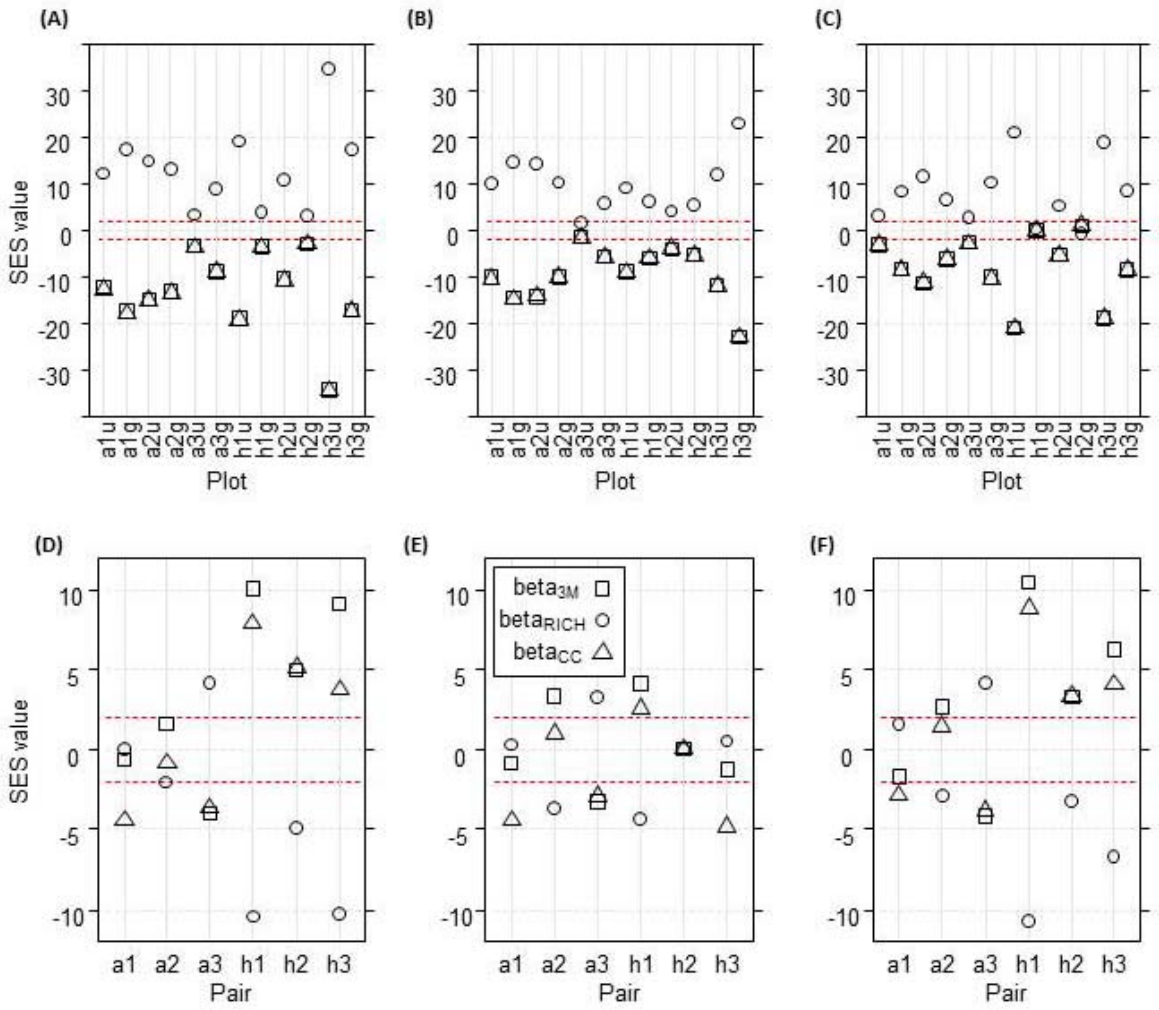

Figure S2.2 Standard effect sizes (SES) of partitioned multiple site taxonomic beta diversity values of β_{RICH}, β_{-3M} and β_{CC} (β_{JAC}) for each plot in each of three null models: site, treatment and pair (A, B and C, respectively), and the difference in SES across each pair of plots, by each null model (D, E and F, respectively). Dashed redlines indicate SES = ±1.96. Points beyond these lines deviate significantly from the expectation under the given null model. *Note:* Outliers for the differences in β_{-3M} of the site and pair null models were excluded at pair H3 (β_{-3M} site = 13.6, β_{-3M} pair = 12.8) to more clearly show the patterns of the other pairs. Panels D, E and F appear in the main text as Figure 3.11 A, B, and C.

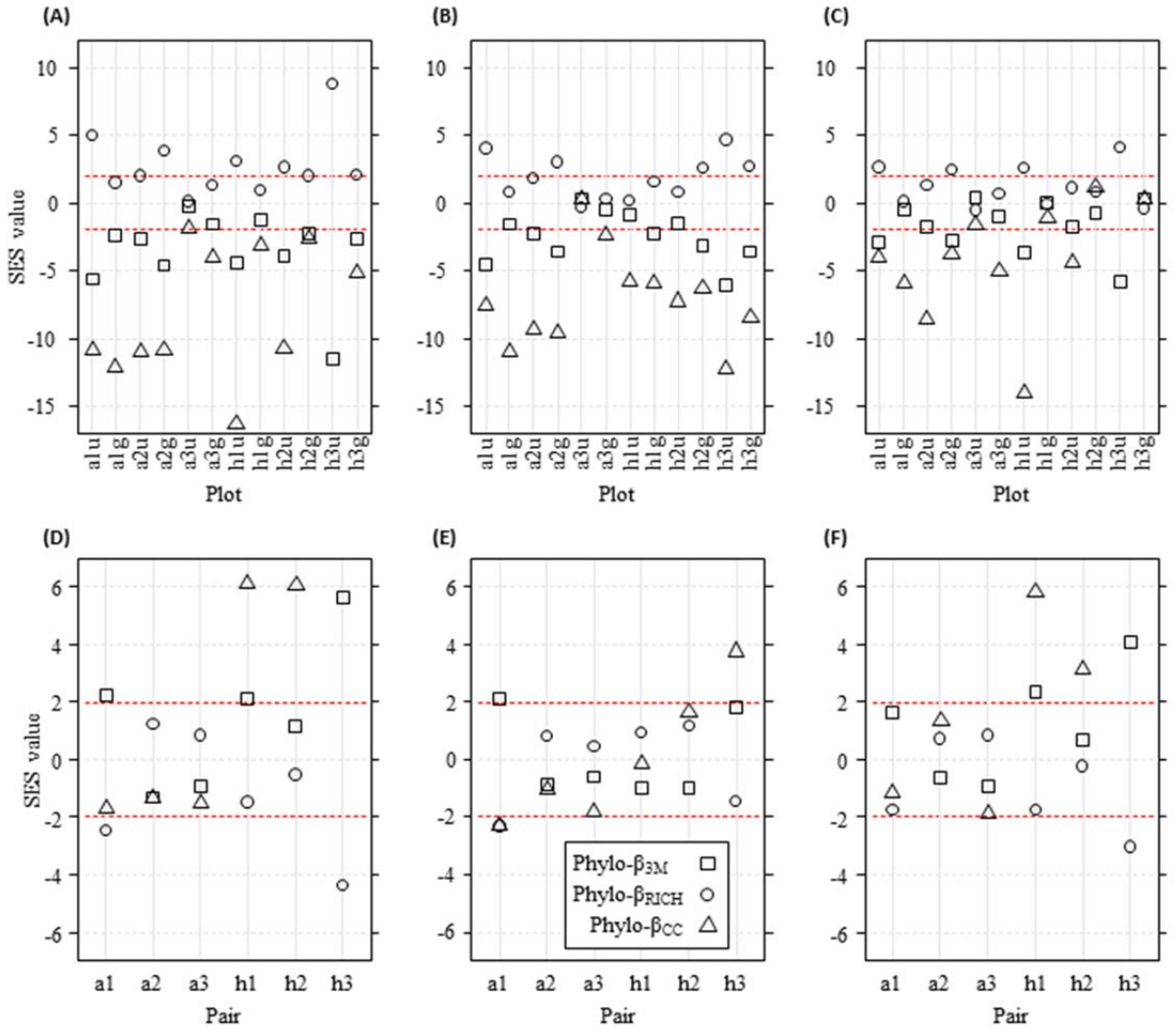

Figure S2.3 Standard effect sizes (SES) of partitioned multiple site phylogenetic beta diversity values of β_{RICH}, β_{-3M} and β_{CC} (β_{JAC}) for each plot in each of three null models: site, treatment and pair (A, B and C, respectively), and the difference in SES across each pair of plots, by each null model (D, E and F, respectively). Dashed redlines indicate SES = ±1.96. Points beyond these lines deviate significantly from the expectation under the given null model. Note: Outliers for the differences in β_{-3M} of the site and pair null models were excluded at pair H3 (β_{-3M} site = 13.6, β_{-3M} pair = 12.8) to more clearly show the patterns of the other pairs. Panels D, E and F appear in the main text as Figure 3.12 A, B, and C.

Below I provide the values obtained for all three partitions (Baselga's Sørensen and Jaccard, Carvalho et al.'s (2013) Jaccard). The values in the tables for Carvlho et al.'s (2013) partition correspond to Figures S2.2 and S2.3.

Table S2.1 Observed taxonomic and phylogenetic multiple site beta diversity values for each plot. Plot names indicate site (A or H), pair number (1, 2 or 3), and ungrazed or grazed (U or G), as mapped in Figure 3.3. Note that only the partitioned values (β_{-3M} and β_{RICH}) are given for Carvalho et al.'s (2013) partition because $\beta_{JAC} = \beta_{CC}$.

Plot	β_{SIM}	β_{SNE}	β_{SOR}	β_{JTU}	β_{JTE}	β_{JAC}	β_{-3M}	β_{RICH}
Taxonomic								
A1U	0.868786	0.044116	0.912902	0.929786	0.0246817	0.954468	0.602945	0.351523
A1G	0.869690	0.031252	0.900943	0.930304	0.0175863	0.947890	0.695562	0.252328
A2U	0.892869	0.028733	0.921601	0.943403	0.0157987	0.959201	0.680060	0.279142
A2G	0.883388	0.025926	0.909315	0.938084	0.0144197	0.952504	0.719612	0.232892
A3U	0.908430	0.020802	0.929239	0.952018	0.0112997	0.963318	0.727818	0.235500
A3G	0.884645	0.033182	0.917827	0.938792	0.0183610	0.957153	0.657176	0.299977
H1U	0.795056	0.084843	0.879899	0.885828	0.0502844	0.936113	0.495684	0.440429
H1G	0.848871	0.040000	0.888871	0.918259	0.0229075	0.941166	0.660922	0.280244
H2U	0.816519	0.056351	0.872869	0.898993	0.0331270	0.932120	0.604153	0.327967
H2G	0.867845	0.032972	0.900817	0.929247	0.0185737	0.947821	0.685306	0.262515
H3U	0.814872	0.065252	0.880125	0.897994	0.0382467	0.936241	0.561295	0.374946
H3G	0.803417	0.055448	0.858865	0.890994	0.0330804	0.924075	0.620601	0.303474
Phylogenetic								
A1U	0.784054	0.088334	0.872388	0.878958	0.0528878	0.931845	0.494909	0.436936
A1G	0.811738	0.051037	0.862776	0.896088	0.0302455	0.926333	0.635265	0.291068
A2U	0.835948	0.051743	0.887691	0.910644	0.0298603	0.940505	0.606331	0.334174
A2G	0.809022	0.059998	0.869019	0.894430	0.03549	0.929920	0.593746	0.336174
A3U	0.859064	0.039477	0.898542	0.924190	0.0223699	0.946560	0.651482	0.295078
A3G	0.835174	0.053086	0.888259	0.910185	0.0306386	0.940824	0.599694	0.341129
H1U	0.713548	0.111033	0.824581	0.832831	0.0710267	0.903858	0.478978	0.424880
H1G	0.750725	0.080034	0.830759	0.857616	0.0499406	0.907557	0.556810	0.350747
H2U	0.684155	0.111826	0.795982	0.812461	0.0739418	0.886403	0.492128	0.394275
H2G	0.774296	0.076496	0.850791	0.872792	0.0465891	0.919381	0.553138	0.366244
H3U	0.669947	0.133670	0.803617	0.802357	0.0887598	0.891117	0.442025	0.449092
H3G	0.745800	0.080429	0.826229	0.854393	0.0504536	0.904847	0.558341	0.346506

Table S2.2 Pair level differences ($beta_{grazed}$ - $beta_{ungrazed}$) in observed multiple site beta diversity.

Pair	β_{SIM}	β_{SNE}	β_{SOR}	β_{JTU}	β_{JTE}	β_{JAC}	β_{-3M}	β_{RICH}
Taxonomic								
A1	0.000904	-0.01286	-0.01196	0.000517	-0.00710	-0.006578	0.092617	-0.0992
A2	-0.009481	-0.00281	-0.012287	-0.005319	-0.00138	-0.006698	0.039553	-0.04625
A3	-0.023786	0.012381	-0.011405	-0.013226	0.007061	-0.006165	-0.07064	0.064477
H1	0.053816	-0.04484	0.008972	0.032431	-0.02738	0.005054	0.165238	-0.16018
H2	0.051326	-0.02338	0.027947	0.030254	-0.01455	0.015701	0.081153	-0.06545
H3	-0.011455	-0.00980	-0.02126	-0.007	-0.00517	-0.012166	0.059306	-0.07147
Phylogenetic								
A1	-0.009612	0.0276848	-0.0372971	-0.0055119	0.0171304	-0.0226423	-0.00551	0.140356
A2	-0.018672	-0.0269263	0.008254	-0.0105848	-0.0162145	0.0056297	-0.01059	-0.01259
A3	-0.010282	-0.0238904	0.0136083	-0.0057363	-0.014005	0.0082687	-0.00574	-0.05179
H1	0.0061783	0.0371773	-0.030999	0.0036992	0.0247853	-0.0210861	0.003699	0.077832
H2	0.0548096	0.0901402	-0.0353306	0.0329782	0.060331	-0.0273528	0.032978	0.061009
H3	0.0226115	0.0758525	-0.053241	0.0137297	0.0520359	-0.0383062	0.013730	0.116316

Table S2.3 **S**tandard effect size (SES) values for all eight taxonomic multiple site beta diversity metrics. SES values presented here were calculated based on 999 randomizations of presence / absence community matrices stratified by *treatment* (occurrences shuffled across all three plots within each treatment, at each site) or by *pair* (occurrences were shuffled within each pair of plots at each site). Italicized values indicate values that exhibit the opposite sign to the majority of values within a metric (e.g. H2G). Boldface values indicate values that did not deviate from expected.

Plot	**SES β_{SIM}**	**SES β_{SNE}**	**SES β_{SOR}**	**SES β_{JTU}**	**SES β_{JTE}**	**SES β_{JAC}**	**SES β_{-3M}**	**SES β_{RICH}**
Treatment								
A1U	-10.97522	11.616648	-10.35824	-11.13811	11.829593	-10.43096	-10.00765	9.949573
A1G	-15.62498	17.401527	-14.71281	-15.92008	17.834147	-14.88328	-14.545	14.468162
A2U	-15.19892	17.053504	-14.09126	-15.43408	17.384922	-14.21682	-14.25582	14.245146
A2G	-10.57732	11.465013	-10.12621	-10.70822	11.648061	-10.20502	-10.14171	10.123424
A3U	**-1.718493**	**1.626082**	**-1.776142**	**-1.720664**	**1.633901**	**-1.777635**	**-1.519536**	**1.477369**
A3G	-5.993954	6.188892	-5.830121	-6.038271	6.246562	-5.852876	-5.716572	5.69423
H1U	-10.01203	10.75271	-9.032263	-10.3055	11.111939	-9.131377	-8.954059	8.926483
H1G	-6.325994	6.620178	-6.117213	-6.398818	6.715368	-6.156509	-6.075483	6.057112
H2U	-4.158503	4.281323	-4.041327	-4.200333	4.332273	-4.061187	-4.033515	4.027368
H2G	-5.512266	5.717208	-5.374814	-5.558675	5.778623	-5.401039	-5.315381	5.296347
H3U	-13.20986	14.902571	-11.75867	-13.65268	15.505732	-11.94198	-11.75635	11.720561
H3G	-25.12261	30.248152	-22.39562	-26.19938	31.925183	-22.93795	-22.79794	22.755882
Pair								
A1U	-3.269634	3.28418	-3.251407	-3.284752	3.304854	-3.258309	-3.117264	3.0981526
A1G	-8.698848	9.2001146	-8.400682	-8.800128	9.3388967	-8.459214	-8.291109	8.2538631
A2U	-11.98346	13.091432	-11.26392	-12.12976	13.287047	-11.34179	-11.46364	11.468436
A2G	-6.531128	6.805284	-6.376946	-6.581249	6.8732807	-6.407312	-6.314228	6.2931866
A3U	-2.931416	2.8604998	-2.975053	-2.938254	2.8746235	-2.979375	-2.693401	2.6473656
A3G	-10.72612	11.335011	-10.25189	-10.83762	11.480418	-10.30829	-10.16129	10.138772
H1U	-24.60497	28.479105	-20.62408	-25.71378	29.975472	-20.99157	-20.97055	20.960419
H1G	**-0.145797**	**0.1299752**	**-0.159117**	**-0.143605**	**0.128034**	**-0.157963**	**-0.139296**	**0.1353386**
H2U	-5.46917	5.6920157	-5.266348	-5.542876	5.7839238	-5.301366	-5.244476	5.2322126
H2G	***0.944554***	***-0.953317***	***0.9372663***	***0.9442204***	***-0.952018***	***0.9371545***	***0.9629495***	***-0.96795***
H3U	-21.19284	24.31233	-18.61594	-21.94979	25.359846	-18.9254	-18.87052	18.849574
H3G	-8.82019	9.3377481	-8.420868	-8.968183	9.5235299	-8.494965	-8.539006	8.5493564

Table S2.4 Standard effect size (SES) values for all eight phylogenetic multiple site beta diversity metrics. SES values presented here were calculated based on 999 randomizations of presence absence community matrices stratified by *treatment* (occurrences shuffled across all three plots within each treatment, at each site) or by *pair* (occurrences were shuffled within each pair of plots at each site). Values > |1.96| indicate that the observed value deviates significantly from the expected based on the given null model. Boldface values indicate values that did not deviate from expected.

Plot	SES $P\beta_{SIM}$	SES $P\beta_{SNE}$	SES $P\beta_{SOR}$	SES $P\beta_{JTU}$	SES $P\beta_{JTE}$	SES $P\beta_{JAC}$	SES $P\beta_{-3M}$	SES $P\beta_{RICH}$
Treatment								
A1U	-8.00819	6.974812	-6.141768	-8.21448	7.301162	-6.185146	-4.95751	4.634562
A1G	-6.47317	2.717032	-9.447105	-6.59481	3.024066	-9.566348	**-1.36131**	**0.70905**
A2U	-8.21746	5.081492	-10.71777	-8.38963	5.408126	-10.83064	-3.01571	2.529091
A2G	-8.73104	5.649572	-10.12349	-8.95035	6.065603	-10.25575	-3.6427	2.990565
A3U	**0.845788**	**-0.91157**	**0.260468**	**0.846283**	**-0.91185**	**0.261384**	**0.898146**	**-0.88984**
A3G	**-1.4017**	**0.680609**	-2.299906	**-1.40359**	**0.730574**	-2.304409	**-0.38023**	**0.245891**
H1U	-3.12434	**1.52902**	-5.70892	-3.18598	**1.788995**	-5.783151	**-0.81257**	**0.22648**
H1G	-4.97273	3.078734	-5.930459	-5.08713	3.386426	-6.008303	-2.14005	**1.509276**
H2U	-4.02706	2.007435	-6.87467	-4.12752	2.347168	-6.978395	**-1.37395**	**0.686153**
H2G	-6.22875	4.513154	-6.540495	-6.38258	4.833307	-6.61339	-3.2196	2.695963
H3U	-10.9179	8.843182	-11.0641	-11.6947	10.04814	-11.40302	-5.61157	4.404415
H3G	-7.87601	5.419414	-8.30279	-8.14914	5.956336	-8.454338	-3.73613	2.861906
Pair								
A1U	-4.4269	3.750313	-3.973091	-4.49379	3.898171	-3.991028	-2.93968	2.707321
A1G	-3.45576	**1.173465**	-5.872104	-3.49067	**1.339863**	-5.91754	**-0.51564**	**0.099882**
A2U	-5.6076	2.966194	-8.533699	-5.68775	3.178549	-8.604226	**-1.72347**	**1.312987**
A2G	-4.16159	3.330741	-3.716156	-4.2138	3.459222	-3.733861	-2.66902	2.423816
A3U	**-0.36491**	**-0.2708**	**-1.573249**	**-0.36228**	**-0.24206**	**-1.574551**	**0.454038**	**-0.53813**
A3G	-3.13244	**1.627669**	-4.968821	-3.15504	**1.739203**	-4.991984	**-0.97567**	**0.723195**
H1U	-9.66123	6.041231	-13.64228	-10.1107	6.844931	-13.95442	-3.65937	2.574986
H1G	**-0.51882**	**0.123009**	**-1.108891**	**-0.51361**	**0.159335**	**-1.109082**	**-0.04309**	**-0.06734**
H2U	-3.5971	2.267579	-4.368014	-3.68171	2.543988	-4.422669	**-1.726**	**1.145463**
H2G	**0.132866**	**0.473855**	**1.207275**	**0.138272**	**0.407899**	**1.205409**	**-0.69233**	**0.836386**
H3U	-17.2705	10.99519	-23.06163	-18.7277	12.99681	-23.96716	-5.85087	4.130276
H3G	**0.425788**	**-0.40434**	**0.264151**	**0.430537**	**-0.41387**	**0.266071**	**0.36276**	**-0.34482**

Table S2.5 Standard effect sizes (SES) for the difference in taxonomic multiple site beta diversity metrics based on the treatment and pair level null models. Positive values indicate that the observed difference was greater than the expected difference. Values > |1.96| indicate that the observed value deviates significantly from the expected based on the given null model. Boldface values indicate values that did not deviate from expected.

Plot	SES β_{SIM}	SES β_{SNE}	SES β_{SOR}	SES β_{JTU}	SES β_{JTE}	SES β_{JAC}	SES β_{-3M}	SES β_{RICH}
Treatment								
A1	-2.128625	**-0.871517**	-4.298259	-2.117819	**-0.87179**	-4.411455	**-0.89061**	**0.3203839**
A2	**1.987676**	-3.5347183	**1.1515314**	**1.896047**	-3.39903	**1.043919**	3.322495	-3.7239443
A3	-3.332531	3.9095144	-2.894796	-3.398427	3.98593	-2.925891	-3.21241	3.2539995
H1	4.779135	-6.7538006	2.5422311	5.106576	-7.12401	2.593293	4.098531	-4.3404208
H2	**0.494676**	**-1.0983305**	**-0.02291**	**0.665521**	**-1.29249**	**0.071264**	**0.020011**	**-0.009464**
H3	-2.636052	**-0.0471408**	-4.609619	-2.791932	**0.153017**	-4.876122	**-1.22264**	0.5138246
Pair								
A1	-2.073805	**1.192976**	-2.828412	-2.069326	**1.20286**	-2.865494	**-1.70861**	**1.52051**
A2	**1.953097**	-2.742423	**1.48538**	**1.905328**	-2.66836	**1.428435**	2.654477	-2.873073
A3	-4.353968	5.148147	-3.794204	-4.441927	5.259614	-3.833882	-4.15663	4.20453
H1	11.14374	-13.655838	8.832692	11.46139	-14.0679	8.857431	10.48283	-10.771383
H2	3.45152	-3.661447	3.271937	3.518953	-3.74705	3.30543	3.25782	-3.24778
H3	5.482914	-7.057967	4.237176	5.373228	-6.88141	4.073553	6.249428	-6.700987

Table S2.6 Standard effect sizes (SES) for the difference in phylogenetic multiple site beta diversity metrics based on the treatment and pair level null models. Values > |1.96| indicate that the observed value deviates significantly from the expected based on the given null model. Boldface values indicate values that did not deviate from expected.

Plot	SES $P\beta_{SIM}$	SES $P\beta_{SNE}$	SES $P\beta_{SOR}$	SES $P\beta_{JTU}$	SES $P\beta_{JTE}$	SES $P\beta_{JAC}$	SES $P\beta_{-3M}$	SES $P\beta_{RICH}$
Treatment								
A1	**1.6719902**	-3.7447211	-3.0446606	**1.7934837**	-3.835609	-3.1402015	2.6575577	-2.8846192
A2	**-1.0973239**	**0.5586959**	**-1.5878289**	**-1.2916733**	**0.741639**	**-1.7734831**	**-0.2603083**	**0.162588**
A3	**-1.6560087**	**1.1358499**	**-1.9236096**	**-1.6598552**	**1.1720461**	**-1.9334624**	**-0.9317372**	**0.8302372**
H1	**-0.3493644**	**0.3886587**	**-0.1412376**	**-0.2313544**	**0.2466856**	**-0.1127351**	**-0.8397725**	**0.8557445**
H2	**0.1387761**	**0.4608997**	**1.2847939**	**0.4737188**	**0.0875567**	**1.5528892**	**-1.0874097**	**1.2760211**
H3	4.2354016	-3.9888232	3.3945662	4.8131483	-4.7867392	3.5625516	**1.7365912**	**-1.36125**
Pair								
A1	**1.0102027**	-2.0659272	**-1.116606**	**1.0804812**	-2.1008096	**-1.14309**	**1.6263791**	**-1.7695773**
A2	**0.2804727**	**0.5276563**	**1.401445**	**0.1924245**	**0.5627585**	**1.335329**	**-0.6214929**	**0.7412691**
A3	**-1.7031377**	**1.2564799**	**-1.854883**	**-1.7298099**	**1.3131216**	**-1.874111**	**-0.9409838**	**0.8389021**
H1	4.9630419	-3.5199172	5.84802	5.06357	-3.830022	5.857566	2.3525343	**-1.7525345**
H2	2.3387548	**-1.3112308**	3.105402	2.4418135	**-1.5715817**	3.159012	**0.6942481**	**-0.2177494**
H3	9.6489497	-6.3702951	12.738176	9.9323726	-7.0699818	12.811156	4.1116332	-3.0018754

Appendix C – Mantel tests between pairwise beta diversity, biomass and distance

METHODS – Chase (2010) and others have previously demonstrated that pairwise beta diversity increases with productivity. I tested for the influence of above ground biomass and Euclidean geographic distance on observed pairwise dissimilarity values within each plot (again partitioned according to Carvalho et al. 2013). I conducted Mantel tests on pairwise dissimilarity (i.e. β_{cc}, β_{-3}, and β_{rich}, see Chapter 2) and Euclidean distance, and pairwise dissimilarity and difference in biomass (for quadrats where biomass was collected) with 999 permutations. Mantel tests are regularly used to correlate distance measures such as pairwise dissimilarity and pairwise Euclidean distances in beta diversity studies across gradients (e.g. Komac et al. 2011, Carmona et al. 2012, Qian et al. 2013). I extend this method to within community heterogeneity here.

RESULTS – Mantel tests of taxonomic and phylogenetic pairwise dissimilarity (beta diversity) and pairwise distance between quadrats yielded strongly significant results for many plots and beta diversity values (Table S4.1). Overall patterns of significance were similar for taxonomic and phylogenetic beta diversity metrics (Table S4.1). Some interesting variation between phylogenetic and taxonomic patterns of significance do however arise. For example, only two plots did not significantly vary (marginally) in terms of β_{cc} with distance (A2U, $p = 0.057$ and H1G, $p = 0.084$), but four plots did not differ for $P\beta_{cc}$ (Table S4.1). In addition, all grazed plots at Apex did not vary in β_{RICH} significantly with distance and no grazed plots significantly varied $P\beta_{rich}$ with distance. Only one plot significantly varied for all three metrics of both taxonomic and phylogentic beta diversity (H1U). In addition to H1U however, A3U and H3G also varied for all three metrics when measured by taxonomic betadiversity. Finally, three plots did not vary for any phylogenetic beta diversity metrics with distance while no plots exhibited this pattern under taxonomic beta diversity (Table S4.1).

Table S3.1 Mantel tests in general show a significant relationship between Euclidean distance and pairwise beta diversity. P-values are given for each plot and beta diversity metric and significant values are indicated in bold face. Euclidean distances range from 1.0 m to 9.90 m within each plot.

Beta metric	a1u	a1g	a2u	a2g	a3u	a3g	h1u	h1g	h2u	h2g	h3u	h3g
Taxonomic												
β_{cc}	**0.001**	**0.001**	0.057	**0.001**	**0.001**	**0.001**	**0.001**	0.084	**0.011**	**0.001**	**0.028**	**0.001**
β_{-3m}	0.412	**0.001**	**0.024**	**0.001**	**0.020**	**0.001**	**0.006**	0.310	0.415	**0.001**	**0.005**	**0.001**
β_{rich}	**0.003**	0.595	0.830	0.655	**0.003**	0.080	**0.001**	**0.049**	**0.003**	0.354	0.926	**0.012**
Phylogenetic												
$P\beta_{cc}$	**0.001**	**0.001**	0.246	**0.001**	**0.006**	**0.001**	**0.001**	0.165	0.433	**0.001**	0.243	**0.001**
$P\beta_{-3m}$	0.856	**0.001**	0.356	**0.001**	0.150	**0.001**	**0.001**	0.142	0.497	**0.001**	**0.003**	**0.012**
$P\beta_{rich}$	**0.001**	0.132	0.419	0.110	**0.044**	0.051	**0.001**	0.626	0.436	0.096	0.999	0.056

When testing if beta diversity varied with biomass differences, comparisons were restricted to those plots for which biomass was measured. Biomass subsampling occurred in all grazed plots and in one ungrazed plot at Hunter's (H3U). Biomass variation and beta diversity values were significantly correlated much less frequently than with Euclidean distance (Table S4.2). Interestingly, patterns of significance under phylogenetic and taxonomic beta diversity were the same at Apex, but were not similar at Hunter's. There does not appear to be any relationship between the grazing treatment and whether or not biomass and phylogenetic diversity are correlated (Table S4.2).

Table S3.2 Results of Mantel tests on the relationship between pairwise beta diversity and pairwise difference in biomass. *P*-values are given for each plot and beta diversity metric. Significant values are indicated in bold. The row titled *n* indicates the number of quadrats for which biomass data was available, beta diversity was calculated only on these same quadrats (i.e. when n=64, n_{pairs}=2016; when n=12, n_{pairs}=66).

Beta metric	a1u	a1g	a2u	a2g	a3u	a3g	h1u	h1g	h2u	h2g	h3u	h3g
n	64	12	64	8	64	8	64	8	64	8	8	8
Taxonomic												
β_{cc}	**0.023**	0.591	**0.001**	0.082	0.387	0.137	**0.001**	0.123	0.850	0.085	0.419	**0.009**
β_{-3m}	0.767	0.493	0.615	**0.044**	0.246	0.289	0.378	0.280	0.987	0.285	0.283	0.695
β_{rich}	**0.004**	0.489	**0.001**	0.923	0.818	0.049	**0.001**	0.342	**0.039**	**0.015**	0.626	**0.022**
Phylogenetic												
$P\beta_{cc}$	**0.008**	0.496	**0.001**	0.170	0.068	0.298	**0.001**	0.521	0.971	0.390	0.707	**0.017**
$P\beta_{-3m}$	0.657	0.307	0.630	**0.021**	0.210	0.483	**0.038**	0.439	0.861	0.863	0.194	0.391
$P\beta_{rich}$	**0.013**	0.734	**0.007**	0.988	0.215	0.180	0.060	0.806	0.850	0.146	0.962	0.067

Appendix D – Published molecular phylogenies used to resolve polytomies

A list, organized by site and plant family, of the publications used to resolve polytomies in the phylogenetic trees generated for each site using Phylocom (Webb et al. 2008) and Phylomatic (Webb & Donoghue 2005). This approach to resolving sub-familial trees is widely applied in the literature (e.g. Forest et al. 2007). For all analyses in this thesis I used separate trees for each site. I therefore present first the resolved polytomies for Apex Mountain (I) and second for Hunter's Range (II). Lineages where poloytomies did not occur are not included here and their relationships are based on the output of Phylomatic (http://phylodiversity.net/phylomatic/ , *Last accessed:* August 19, 2013).

In addition to the citations below, the Angiosperm Phylogeny Website (http://www.mobot.org/MOBOT/research/APweb/ , *Last accessed* August 8, 2013, Stevens 2001) was consulted extensively. Phylogenetic trees were constructed using the Newick format (see: http://evolution.genetics.washington.edu/phylip/newicktree.html , *Last accessed:* August 8, 2013) wherein daughter lineages are enclosed in nested parentheses.

I. Apex Mountain

Asteraceae (Ekenäs et al. 2007; Panero & Funk 2008; Zidorn 2008; Ekenäs et al. 2012)

((((((Achillea_millefolium,((Erigeron_aureus,Erigeron_peregrinus_ssp_peregrinus)Erigeron,Symphyotrichum_foliaceum_var_foliaceum)),(Anaphalis_margaritacea,(Antennaria_alpina,Antennaria_lanata)antennaria)),Senecio_integerrimus),(Arnica_cordifolia,Arnica_sororia)Arnica),(Hieracium_gracile,Taraxacum_officinale)),Cirsium_foliosum)Asteraceae

Caryophyllaceae (Greenberg & Donoghue 2011)

((Arenaria_capillaris,Silene_parryi)alsineae,Stellaria_longipes_var_altocaulis)Caryophyllaceae

Cyperaceae (Starr et al. 2004; Ford et al. 2006; Hipp et al. 2006)

(Carex_concinna,Carex_phaeocephala,Carex_raynoldsii)Cyperaceae*

**None of the hundreds of Carex species in these three publications could further resolve the three species I encountered at Apex Mountain.*

Plantaginaceae (Albach et al. 2005)

((Collinsia_parviflora,Penstemon_procerus_var_tolmiei)cheloneae,Veronica_wormskjoldii)Plantaginaceae

Poaceae (Gillespie & Soreng 2005; Quintanar et al. 2007; GPWGII 2011)

(((((Poa_alpina,Poa_nemoralis)Poa,Deschampsia_elongata),Trisetum_spicatum),Phleum_alpinum),Bromus_marginatus)Poaceae

Polygonaceae (Sanchez et al. 2009)

((Rumex_acetosella,Polygonum_minimum)polygonoideae,Eriogonum_umbellatum_var_majus)Polygonaceae

Ranunculaceae (Ro et al. 1997; Cai et al. 2009)

(((Aquilegia_formosa,Thalictrum_occidentale)thalictroideae,(Ranunculus_eschscholtzii,Ranunculus_uncinatus_var_parviflorus)Ranunculus),Delphinium_nuttallianum)Ranunculaceae

Rosaceae (Potter et al. 2007)

(((Fragaria_virginiana_ssp_platypetala,Sibbaldia_procumbens)fragariinae,(Potentilla_diversifolia_var_diversoflia,Potentilla_diversifolia_var_perdissecta)Potentilla)potentilleae,Geum_triflorum)Rosaceae

II. Hunter's Range

Asteraceae (Ekenäs et al. 2007; Panero & Funk 2008; Zidorn 2008; Ekenäs et al. 2012)

((((Antennaria_lanata,Erigeron_peregrinus_ssp_callianthemus),(Senecio_triangularis,Senecio_integerrimus)Senecio),Arnica_mollis)asteroideae,(Agoseris_aurantiaca_var_aurantiaca,Hieracium_gracile)cichorieae)Asteraceae

Cyperaceae (Starr et al. 2004; Ford et al. 2006; Hipp et al. 2006)

(Carex_illota,Carex_nigricans,Carex_spectabilis)Cyperaceae*

**None of the hundreds of Carex species in these three publications could further resolve the three species I encountered at Hunter's Range.*

Poaceae (Gillespie & Soreng 2005; Quintanar et al. 2007; GPWGII 2011)

((((Vahlodea_atropurpurea,Poa_arctica),(Agrostis_stolonifera,Calamagrostis_canadensis_var_canadensis)),Phleum_alpinum),(Bromus_marginatus,Elymus_glaucus_ssp_glaucus),Poaceae_spp)Poaceae†

†One specimen was not preserved well enough for accurate identification and is listed as Poaceae spp generating a polytomy.

Ranunculaceae (Ro et al. 1997; Cai et al. 2009)

(Pulsatilla_occidentalis,(Ranunculus_eschscholtzii,Ranunculus_occidentalis)Ranunculus)Ranunculaceae

Appendix E – R-code for calculating novel beta diversity metrics

Note that this code expects presence absence site by species matrices where rows indicate unique sites and columns indicate species. It requires two packages which will need to be installed and loaded.

```
# requires:
library(picante);library(betapart);

#########################################################################
###
# Function 1 #
##############

# Functions for calculating Carvalho et al.'s (2013) partition of
pairwise beta diversity (as published by Carvalho et al. 2013)
### Note: I modified their supplied function to generate a list output
identical to that of Baselga and Orme's (2012) betapart package

carv.beta <- function(site.spec){#where site.spec is the site by
species matrix you want to calculate beta diversity on
beta.cc<-function (x)
{
x <- ifelse(x > 0, 1, 0)
d <- tcrossprod(x)
a <- as.dist(d)
S <- diag(d)
N <- length(S)
b <- as.dist(matrix(rep(S, N), nrow = N)) - a
c <- as.dist(matrix(rep(S, each = N), nrow = N)) - a
out = (b+c)/(a+b+c)
out
}
beta.3<-function (x)
{
x <- ifelse(x > 0, 1, 0)
d <- tcrossprod(x)
a <- as.dist(d)
S <- diag(d)
N <- length(S)
b <- as.dist(matrix(rep(S, N), nrow = N)) - a
c <- as.dist(matrix(rep(S, each = N), nrow = N)) - a
out = 2*pmin(b,c)/(a+b+c)
out
}
beta.rich<-function (x)
{
x <- ifelse(x > 0, 1, 0)
d <- tcrossprod(x)
a <- as.dist(d)
S <- diag(d)
N <- length(S)
b <- as.dist(matrix(rep(S, N), nrow = N)) - a
```

```
c <- as.dist(matrix(rep(S, each = N), nrow = N)) - a
out = abs(b-c)/(a+b+c)
out
}
all.carv.beta <-
list(beta.3=beta.3(site.spec),betarich=beta.rich(site.spec),beta.cc=be
ta.cc(site.spec))#generate a list of the distance matrices of each
diversity measure
return(all.carv.beta)#return the list and assign it to named object
}

### call using:
carv.beta(x) # where x is a site by species matrix where rows are
sites and columns are species in presence absence format (i.e. 1 =
present, 0 = absent)

##############################################################################
###
# Function 2 #
##############

# Function for calculating pairwise phylogenetic beta diversity under
the partition of Carvalho et al. (2013), as modified from Leprieur et
al. (2012).

### First, Leprieur et al. (2012) use function pd2 instead of pd as
supplied by Baselga (results do not change, but it is faster
computationally),
#### therefore I supply LEprieur et al.'s (2012) pd2 function here:


pd2 <- function (samp, tree, include.root = TRUE) {
       if (is.null(tree$edge.length)) {
    stop("Tree has no branch lengths, cannot compute pd")
    }
  species <- colnames(samp)
  tree  <- node.age(tree)
  PDout <- apply(samp,1, function(x) {
    present <- species[x > 0]
    treeabsent <- tree$tip.label[which(!(tree$tip.label %in%present))]
    if (length(present) == 0) {
      PD <- 0
      }
    else if (length(present) == 1) {
      if (!is.rooted(tree) || !include.root) {
        warning("Rooted tree and include.root=TRUE argument required
to calculate PD of single-species sampunities. Single species
sampunity assigned PD value of NA.")
        PD <- NA
        }
      else {
        PD <- tree$ages[which(tree$edge[, 2] ==
        which(tree$tip.label == present))]
        }
```

```
      }
    else if (length(treeabsent) == 0) {
      PD <- sum(tree$edge.length)
      }
    else {
      sub.tree <- drop.tip(tree, treeabsent)
      if (include.root) {
        if (!is.rooted(tree)) {
          stop("Rooted tree required to calculate PD with
include.root=TRUE argument")
        }
        sub.tree <- node.age(sub.tree)
        sub.tree.depth <- max(sub.tree$ages)
        orig.tree.depth <- max(tree$ages[which(tree$edge[,2] %in%
which(tree$tip.label %in% present))])
        PD <- sum(sub.tree$edge.length) + (orig.tree.depth -
sub.tree.depth)
        }
      else {
        PD <- sum(sub.tree$edge.length)
        }
      }
    SR <- length(present)
    PDout <- c(PD,SR)
    } )
  PDout <- t(PDout)
  rownames(PDout) <- rownames(samp)
  colnames(PDout) <- c("PD","SR")
  return(PDout)
} # end of function pd2

### Second, I modified the beta.pd.utils function provided by Leprieur
et al. (2012) by adding objects max.pd.obs and pd.site.
#### These modifications support its use with multiple site
phylogenetic beta diversity (See Function 5)

beta.pd.utils <- function(com, tree) { #### generates the object named
betapd elsewhere in the scripts
combin  <-  combn(nrow(com),2)
labcomb <-  apply(combin,2,function(x)
paste(rownames(com)[x],collapse="-"))
pd.obs  <-  pd2(com,tree)[,"PD"]
pd.site <- pd2(as.matrix(t(ifelse(colSums(com)>=1,1,0))),tree)[,"PD"]
# calculates the additive PD of all sites (analogous so S_t) Note that
this is not the total PD of unique species in the plot, i.e. not gamma
PD
com.tot <- t(apply(combin,2,function(x) colSums(com[x,])>0))
pd.obs.tot <- pd2(com.tot,tree)[,"PD"]
sum.pd.obs <- apply(combin,2,function(x) sum(pd.obs[x]))
min.pd.obs <- apply(pd.obs.tot-t(combn(pd.obs,2)),1,min)
max.pd.obs <- apply(pd.obs.tot-t(combn(pd.obs,2)),1,max) # subtracts
the smaller PD values of the pair from PD tot to find the maximum
unique PD of the pair = max(b,c)
dif.pd.obs <- apply(combin,2,function(x) diff(pd.obs[x]))
```

```
return(list(pd.obs=pd.obs,pd.site=pd.site,pd.obs.tot=pd.obs.tot,sum.pd
.obs=sum.pd.obs,min.pd.obs=min.pd.obs,max.pd.obs=max.pd.obs,dif.pd.obs
=dif.pd.obs,labcomb=labcomb,combin=combin))# returns the above objects
as a list
}

### Finally, drawing on the partitioned UniFrac function supplied by
Leprieur et al. (2012)
#### I developed the code for calculating Carvalho et al.'s (2013)
partition of pairwise phylogenetic beta diversity as follows:

betacarv.pd <- function(betapd) {

  Phylo.cc <- (2*betapd$pd.obs.tot-
betapd$sum.pd.obs)/betapd$pd.obs.tot ## analogous to Jaccard's
dissimilarity
  Phylo.3 <- 2*(betapd$min.pd.obs)/betapd$pd.obs.tot ## the species
replacement component (i.e. novel species in the next community)
  Phylo.rich <- abs(betapd$dif.pd.obs)/betapd$pd.obs.tot ## the
richness component

return(as.matrix(data.frame(Phylo.3,Phylo.rich,Phylo.cc,row.names=beta
pd$labcomb))) ## returns a table of the 3 values in the same way
beta.pair does (Baselga and Orme 2012)
}

#### Call using:
betacarv.pd(y) # where y is the output of the beta.pd.utils function
above

##########################################################################
###
# Function 3 #
##############

# Function for calculating multiple site metrics of Carvalho et al.'s
(2013) partition

### My modification of Baselga and Orme's (2012) function 'beta.multi'
to include Carvalho et al.'s (2013) partition,
### Note: You must call the appropriate partition still, default is
carvalho!

beta.multi.carv<-function (x, index.family = "carvalho")
{library(betapart)
    index.family <- match.arg(index.family, c("jaccard", "Sørensen
","carvalho"))
    if (!inherits(x, "betapart")) {
        x <- betapart.core(x)
    }
    maxbibj <- sum(x$max.not.shared[lower.tri(x$max.not.shared)])
    minbibj <- sum(x$min.not.shared[lower.tri(x$min.not.shared)])
    switch(index.family, Sørensen  = {
        beta.sim <- minbibj/(minbibj + x$a)
```

```
        beta.sne <- (x$a/(minbibj + x$a)) * ((maxbibj - minbibj)/((2 *
            x$a) + maxbibj + minbibj))
        beta.sor <- (minbibj + maxbibj)/(minbibj + maxbibj +
            (2 * x$a))
        multi <- list(beta.SIM = beta.sim, beta.SNE = beta.sne,
            beta.SOR = beta.sor)
    }, jaccard = {
        beta.jtu <- (2 * minbibj)/((2 * minbibj) + x$a)
        beta.jne <- (x$a/((2 * minbibj) + x$a)) * ((maxbibj -
            minbibj)/((x$a) + maxbibj + minbibj))
        beta.jac <- (minbibj + maxbibj)/(minbibj + maxbibj +
            x$a)
        multi <- list(beta.JTU = beta.jtu, beta.JNE = beta.jne,
            beta.JAC = beta.jac)
    }, carvalho = {
        beta.3 <- (2 * minbibj)/(minbibj + maxbibj + x$a)
        beta.rich <- ((maxbibj - minbibj)/(minbibj + maxbibj + x$a))
        beta.cc <- (minbibj + maxbibj)/(minbibj + maxbibj + x$a)
        multi <- list(beta.3multi = beta.3, beta.RICH = beta.rich,
            beta.CC = beta.cc)
    })
    return(multi)
}

### Call using:
beta.multi.carv(x, index.family="carvalho") # where x is a site by
species matrix where rows are samples and columns are species, in
presence/absence format, may also call index.family = "jaccard" or
index.family = "Sørensen " to calculate Baselga's partitions.

#########################################################################
###
# Function 4 #
##############

#Function for calculating multiple site phylogenetic beta diversity
for Baselga's (2010, 2012) two partitions and Carvalho et al.'s (2013)
partition

### These all rely on the beta.pd.utils function provided above (See
Function 2)

### calculate Baselga's Sørensen  Beta-Multi metrics for phylogenetic
diversity
betaSOR.pd <- function(betapd) { #where betapd is the output from
beta.pd.utils
       PBDSOR <-
(sum(betapd$min.pd.obs)+sum(betapd$max.pd.obs))/(2*(sum(betapd$pd.obs)
-betapd$pd.site)+sum(betapd$min.pd.obs)+sum(betapd$max.pd.obs))
       PBDSIM <- sum(betapd$min.pd.obs)/((sum(betapd$pd.obs)-
betapd$pd.site)+sum(betapd$min.pd.obs))
       PBDSNE <- ((sum(betapd$max.pd.obs)-
sum(betapd$min.pd.obs))/(2*(sum(betapd$pd.obs)-
betapd$pd.site)+sum(betapd$min.pd.obs)+sum(betapd$max.pd.obs)))*((sum(
```

```
betapd$pd.obs)-betapd$pd.site)/((sum(betapd$pd.obs)-
betapd$pd.site)+sum(betapd$min.pd.obs)))
       return(list(PBDSIM=PBDSIM,PBDSNE=PBDSNE,PBDSOR=PBDSOR))
}

### Call using:
betaSOR.pd(y) # where y is the output of the beta.pd.utils function
(See Function 2 above)

## calculate Baselga's Jaccard Beta-Multi metrics for phylogenetic
diversity
betaJAC.pd <- function(betapd) {
PBDJAC <-
(sum(betapd$min.pd.obs)+sum(betapd$max.pd.obs))/((sum(betapd$pd.obs)-
betapd$pd.site)+sum(betapd$min.pd.obs)+sum(betapd$max.pd.obs))
PBDJTU <- (2*sum(betapd$min.pd.obs))/((sum(betapd$pd.obs)-
betapd$pd.site)+(2*sum(betapd$min.pd.obs)))
PBDJNE <- ((sum(betapd$max.pd.obs)-
sum(betapd$min.pd.obs))/((sum(betapd$pd.obs)-
betapd$pd.site)+sum(betapd$min.pd.obs)+sum(betapd$max.pd.obs)))*((sum(
betapd$pd.obs)-betapd$pd.site)/((sum(betapd$pd.obs)-
betapd$pd.site)+(2*sum(betapd$min.pd.obs))))
return(list(PBDJTU=PBDJTU,PBDJNE=PBDJNE,PBDJAC=PBDJAC))
}

### Call using:
betaJAC.pd(y) # where y is the output of the beta.pd.utils function
(See Function 2 above)

### calculate Carvalho's Jaccard Beta-Multi metrics for phylogenetic
diversity
betaCARV.pd <- function(betapd) {
PBDCC <-
(sum(betapd$min.pd.obs)+sum(betapd$max.pd.obs))/((sum(betapd$pd.obs)-
betapd$pd.site)+sum(betapd$min.pd.obs)+sum(betapd$max.pd.obs))
PBD3M <- (2*sum(betapd$min.pd.obs))/((sum(betapd$pd.obs)-
betapd$pd.site)+sum(betapd$min.pd.obs)+sum(betapd$max.pd.obs))
PBDRICH <- (sum(betapd$max.pd.obs)-
sum(betapd$min.pd.obs))/((sum(betapd$pd.obs)-
betapd$pd.site)+sum(betapd$min.pd.obs)+sum(betapd$max.pd.obs))
return(list(PBD3M=PBD3M,PBDRICH=PBDRICH,PBDCC=PBDCC))
}

### Call using:
betaCARV.pd(y) # where y is the output of the beta.pd.utils function
(See Function 2 above)

##########################################################################
###
```