STOCHASTIC AND DETERMINISTIC ASSEMBLY WITHIN FOREST PLANT
COMMUNITIES OF BRITISH COLUMBIA

by

Elaine Dobie Bambrick

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Abstract

Patterns of beta diversity, the variation in species composition among sites, are often used to gain insights into the processes governing plant community assembly. Deterministic processes including environmental selection and stochastic processes such as stochastic colonization and extinction, and / or priority effects vary in their relative importance for explaining patterns of diversity. Sampling strategies that simultaneously control for variation in the environment as well as gradients in species richness improve our ability to quantify the relative importance of stochastic and deterministic community assembly processes. Using data that control for environmental variation, collected from 809 standardized survey plots across British Columbia, Canada, I show using a null model analysis that controls for species richness gradients, that patterns of beta diversity are no different than expected based on random sampling within 31 site units sampled from the Interior Cedar Hemlock (ICH), Englemann Spruce Subalpine Fir (ESSF), Sub-Boreal Pine and Spruce (SBPS) and Boreal White and Black Spruce (BWBS) zones described by Biogeoclimatic Ecosystem Classification (BEC). I also show that deterministic assembly is revealed when beta diversity is compared to patterns expected under broader definitions of the species pools, but not consistently across plant lifeforms or across categories defined by BEC. I further found that dispersal limitation influences beta diversity and increases in importance from shrubs to herbs to trees. By using a null model approach that enables detection of stochastic assembly, I was also able to show that beta diversity is no different than expected based on random sampling for tree species composition within the subzone / variant level of BEC, which supports an underlying assumption of Bioclimate Envelope Models. I suggest that the high beta diversity within BEC site units is likely attributable to stochastic

assembly processes, which deserve more attention in future research, especially at fine scales of

community organization.

Preface

With guidance from my supervisor, Dr. Jason Pither, I was responsible for the analyses described in Chapter 2, Chapter 3 and Chapter 4 of this thesis. Vegetation plot data were provided by the Ministry of Forests Lands and Natural Resource Operations. I am responsible for the writing of this thesis. This thesis has been reviewed by my supervisor, Dr. Jason Pither as well committee members Dr. Melanie Jones and Dr. Sybille Haeussler.

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Chapter 1: General introduction

Understanding the processes that govern patterns of diversity represents a fundamental objective in ecology (Willis 1926, Whittaker 1960, MacArthur 1965, Shmida and Wilson 1985, Qian 2009). In recent decades, this objective has increasingly been pursued to better inform biodiversity conservation and management decisions (Pimm and Lawton 1998, Aarts and Nienhuis 1999, Margules and Pressey 2000, Legendre et al. 2009). In British Columbia (BC), Canada, maintenance of biodiversity is a key criterion in sustainable forest management and forest certification schemes (Canadian Council of Forest Ministers 2000, FSC Canada 2005, Boutin et al. 2009, Klenner et al. 2009, Steenberg et al. 2011). To provide an ecological foundation for forest management in BC, the Biogeoclimatic Ecosystem Classification (BEC) system was established in the 1970s (Pojar et al. 1987) and continues to inform forest management decisions today (MFLNRO 2012a). In addition to providing an ecological framework for forest management, data collected as part of the BEC system are increasingly being used to assess the potential impacts of climate change on tree and ecosystem distributions (Hamann and Wang 2006, Delong et al. 2010, Hamann and Aitken 2013). Comprising more than 30,000 standardized plots throughout the province (Klinkenberg 2010), BEC data provide an unparalleled opportunity to explore general patterns of vascular plant diversity within and among multiple ecosystem types and across large spatial scales, and to test competing hypotheses about the origins of said patterns. Using a subset of BEC plot data that have been vetted by experts, I address the following four objectives: (i) to describe patterns of alpha, beta, and gamma diversity of vascular plants within BEC ecosystem classes, (ii) to test the hypothesis that beta diversity among sites within BEC site units is no different from that expected under stochastic (random) community assembly, (iii) to test the hypothesis that beta diversity of plant lifeforms (trees,

shrubs and herbs) among sites within BEC site units is no different from that expected under stochastic (random) community assembly, and (iv) to formally test the assumption, adopted in recent climate change research, that locations within a given BEC subzone or variant are of equivalent suitability from the perspective of tree species.

In this first chapter, I describe the theory and previous research that together provide context to the objectives of my thesis. I start by defining alpha, beta, and gamma diversity and discuss how these measures are quantified using examples from the literature. I then provide a brief overview of different ecological processes influencing diversity based on the framework described by Vellend (2010). In introducing ecological processes, I will focus on the difference between stochastic and deterministic processes and why in general, it is important to understand the relative importance of stochastic and deterministic processes in driving diversity patterns. Following the discussion of ecological processes, I shift to describing how beta diversity patterns are used to infer process from pattern. I then describe BEC, and highlight the properties of BEC data that lend it to testing my research objectives. Finally, I provide an overview of my research objectives and predictions that will be described in the remaining chapters.

1.1 Literature review

1.1.1 Alpha, beta, and gamma diversity

Alpha and gamma diversity are both measures of species richness, the primary difference between them being the spatial extent over which they are measured (Jurasinski et al. 2009, Gotelli and Colwell 2011). Alpha diversity is the number of species present at a local site (Whittaker 1960) – for example, the number of species within a plot or along a transect. In studies of plant diversity, the local site is the sampling unit within a defined ecosystem type

(Qian et al. 1998, Lenoir et al. 2010, Pärtel et al. 2011), which ideally represents an area that is

sufficient for capturing the composition of the ecosystem. Gamma diversity is the taxonomic

richness of a defined region or landscape (Whittaker 1960) and while subject to the definition of

the 'region' or 'landscape', it is commonly described as the 'regional species richness' of a

number of community samples (Loreau 2000, Jurasinski et al. 2009, Pärtel et al. 2011).

Both alpha and gamma diversity are sensitive to sampling effort (Gotelli and Colwell 2001,

2011, Veech et al. 2002, Melo et al. 2003, Hortal et al. 2006). This observation coincides with

the species area hypothesis – the larger the area sampled, the more species will be encountered

(Arrhenius 1921). In practice, sampling units at the local scale (transects / quadrats) tend to be

standardized with respect to sampling effort, such that alpha diversity can be directly compared

among units (e.g., Hortal et al. 2006, Normand et al. 2006, Zeleny and Chytrý 2007, Zeleny et al.

2010). The same is generally not true of estimates of gamma diversity, as it is often difficult to

know the degree to which gamma diversity is underestimated for a given region (Gotelli and

Colwell 2011). Multiple approaches have been developed to assess uncertainty in gamma

diversity (Gotelli and Colwell 2001). A first step, and good way to visualize the degree of

underestimation of gamma diversity, is to plot species accumulation curves, which depict

changes in gamma diversity with increasing sampling effort; the higher the slope of the species

accumulation curve, the more under-sampled a given community is (Figure 1). To more

accurately predict species richness, two approaches are commonly used: (i) rarefaction and (ii)

species estimation. Rarefaction generates an expected species accumulation curve by repeatedly

drawing random samples (i.e., species) from a set of N samples (i.e., plots), where N is restricted

to the least sampled community (i.e., the community with the fewest plots) (Gotelli and Colwell

2001). The main criticism of rarefaction is the loss of information that occurs when communities

with more samples (i.e., plots) are limited to the number of samples in the least-sampled

community (Melo et al. 2003). Species estimation on the other hand, estimates gamma diversity

from samples. Species richness estimates correct the observed species richness by adding a term

based on the number of singletons (number of species found only in one plot) or duplicates

(number of species in two plots) (Gotelli and Colwell 2001). For presence-absence data, non-

parametric methods of species estimation including Jackknife and Chao perform best (Melo et al.

2003, Walther and Moore 2005, Hortal et al. 2006). For more thorough discussions on the

different methods of species estimation see Gotelli and Colwell (2001), Melo et al. (2003) and

Hortal et al. (2006).
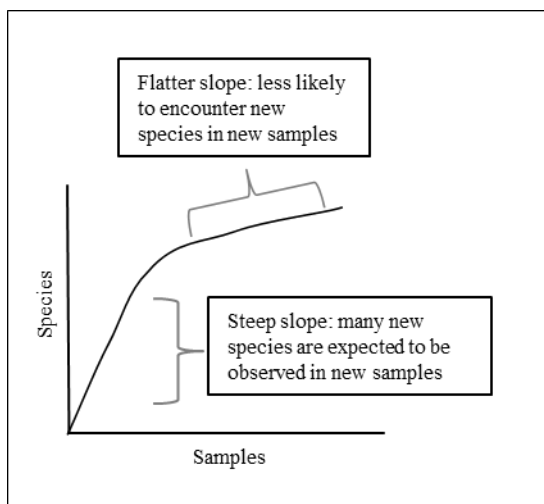
Figure 1: Hypothetical species accumulation curve. The slope of the species accumulation curve remains steep in under-sampled communities and levels off in well-sampled communities.

Whereas gamma and alpha diversity are measures of species richness, beta diversity quantifies

the variation in species richness between local sites. Originally defined by Whittaker (1960), beta

diversity was described as the "extent of change in community composition, or degree of

community differentiation, in relation to complex-gradient of environment, or a pattern of

environments". As summarized by Anderson et al. (2011), beta diversity is used to describe

either *turnover* in richness among sites that are situated along some gradient (Harrison et al. 1992, Qian and Ricklefs 2007) or *variation* in richness among sites within a pre-defined area (Legendre et al. 2005, Chase 2010). In addition to being measured to describe differentiation in community assembly among sites, beta diversity is often studied in order to provide guidance for conservation planning (Pimm and Gittleman 1992, Nekola and White 2002, Tuomisto et al. 2003) because variation in species composition among sites dictates the spatial requirements for conservation (Nekola and White 1999, 2002, Ferrier et al. 2002). In addition to improving understanding of how communities are formed and delineated, ecologists are increasingly conducting detailed analyses of beta diversity to gain insights into the importance of different ecological processes, in particular stochastic versus deterministic assembly (Williams et al. 1999, Moritz et al. 2000, Legendre et al. 2005, Azeria et al. 2011, Chase and Myers 2011, Chase et al. 2011, Kraft et al. 2011), which will be discussed further below.

To calculate beta diversity, a number of measures have been identified in the literature (for reviews see Koleff et al. 2003, Anderson et al. 2011, Jost et al. 2011). Due in part to differences in beta diversity measures, describing general trends is challenging (Koleff et al. 2003, Jost et al. 2011). Because my research uses presence-absence data, abundance-based beta diversity measures will not be discussed. A common incidence-based measure is the Jaccard similarity metric, which measures the similarity in composition between two sites as follows: $\beta_j = a/(a+b+c)$ where a is the number of shared species between two plots and b and c are the number of unique species in plot 1 and 2 respectively (Koleff et al. 2003). Jaccard dissimilarity is then calculated as $1 - \beta_j$; a value of 1 indicates that no species are shared between plots whereas a value of 0 indicates that all species are shared. Other similar measures that compare similarity between pairs of plots include Sorensen and Simpson indexes (Jost et al. 2011).

The main criticism with common beta diversity metrics including the Jaccard dissimilarity metric, is that the different diversity components (alpha, beta and gamma diversity) are not independent (Lande 1996, Lennon et al. 2001, Jost 2007, Azeria et al. 2011) – any change in alpha diversity necessarily changes beta diversity independent of any change in environmental or spatial factors (Chase and Myers 2011). Beta diversity is most often analyzed in relation to environmental and / or spatial factors (Qian et al. 1998, Lenoir et al. 2010, Azeria et al. 2011, Chase et al. 2011) using multiple methods (see reviews by Tuomisto 2010, Anderson et al. 2011), including multiple regressions on distance matrices (Normand et al. 2006, Qian and Ricklefs 2007) and redundancy analyses (Legendre et al. 2009). As my research does not directly analyze beta diversity in relation to environmental gradients, this topic is not discussed further. I do, however, evaluate associations between beta diversity and geographic distance using Mantel tests, which have long been used to gain insights into the potential influence of dispersal limitation on patterns of species composition (e.g., Nekola and White 1999, Tuomisto et al. 2003, Pither and Aarssen 2005). This topic will be discussed further below.

1.1.2 Ecological processes influencing diversity

For most of the last century, the field of community ecology witnessed vigorous debates regarding the importance of local versus regional scale processes (Willis 1926, Hutchinson 1957, MacArthur 1965, Currie 1991, Latham and Ricklefs 1993, Weiher and Keddy 1995, Qian and Ricklefs 2000, Lennon et al. 2000, Blevins and With 2011), and deterministic versus stochastic processes (Clements 1936, Gleason 1939, Chase 2007, Chase et al. 2009). With few clear outcomes emerging from these debates, community ecology was famously qualified as 'a mess' (Lawton 1999). Recently, in an attempt to bring much needed coherence to the field, Vellend (2010) proposed a new framework for considering the problem of community assembly that

focused on four categories of process: speciation, dispersal, selection and drift. Together, these processes describe why particular species are present in a given location and how species diversity is maintained or lost (Vellend 2010).

The origin of species in a given location is described through *speciation*: the ecological and evolutionary process through which new species are formed (Vellend 2010). Speciation is an important explanation of variation in species composition among communities (Eriksson 1993) and is influential to gamma diversity – the suite of species present in a region that are capable of persisting in a given location (Latham and Ricklefs 1993, Qian and Ricklefs 2000, Vellend 2010). High rates of speciation may cause high beta diversity by limiting the range sizes of species or by increasing the number of ecologically equivalent species that occupy a given location (Ricklefs 1987, Qian et al. 2005).

To describe the movement of individuals or propagules across space, *dispersal* further contributes to the presence or absence of species in a given location. Depending on dispersal capabilities, species population size, and size and location of suitable habitats (Cadotte 2006, Moral et al. 2010), dispersal will influence the abilities of species to occupy the full extent of their fundamental niche – the entire range of ecological conditions where the species could persist (Hutchinson 1957). In study systems characterized by spatially restricted dispersal, or "dispersal limitation" (i.e., most plant communities), one expects a negative correlation between geographic distance and species composition similarity (Nekola and White 1999) (discussed further below). The sequence of species arrival can also influence species composition, with advantages often going to early colonists through so-called "priority effects" (Chase 2010, Moral et al. 2010). Mass effects, the process through which species are maintained on unsuitable sites by a continuous influx of propagules, can similarly alter species composition (Kunin 1998,

Zeleny et al. 2010). In short, it is widely agreed that dispersal influences diversity patterns through a variety of pathways (Tilman 1994, Srivastava 1999, Pinto and MacDougall 2010).

Selection describes the fitness differences between individuals (Vellend 2010) that are often mediated by environmental conditions. If selection were the dominant process governing species composition, one would expect dominance by the species with the traits best suited to the local environmental conditions (Ricklefs 2004). Under severe environmental conditions, it has been observed that alpha and beta diversity are low due to environmental filtering that limits species presence (Chase et al. 2009). Opposing the deterministic organization of species under selection, *drift* includes the stochastic colonization and extinction dynamics (birth and death) that alter species composition (Vellend 2010). Under neutral theory (Hubbell 2001), dispersal and drift are hypothesized to be the dominant processes explaining variation in species composition because species are otherwise assumed to be equivalent in their responses to selection. The strength of drift, like other processes, is not uniform in time and space and is more likely to occur simultaneously with other processes (Ricklefs 2004, Vellend 2010). Drift has a random pattern and can therefore result in high beta diversity in otherwise homogenous communities. In theory, loss of species through drift can be balanced by the addition of new species, either through speciation in the long term and immigration (dispersal) in the short term (Bell et al. 2006).

1.1.3 The deterministic versus stochastic assembly debate

Debates about the relative importance of stochastic versus deterministic processes in governing community assembly and diversity patterns began in the early 20th century. Whereas Clements (1936) described plant communities as the predictable outcome of local environmental conditions (selection), Gleason (1939) argued that multiple communities could develop on environmentally similar sites due to chance dispersal events (stochastic), variations in the source

pool of species, and imperfect or incomplete matching between environmental conditions and differentially adapted species. In the middle of the last century, emphasis shifted toward local determinism (MacArthur 1965, Weiher and Keddy 1999, Moore et al. 2001, Shurin and Allen 2001) with the introduction of Hutchinson's (1957) niche concept. Then, at the turn of this century, the debate about the importance of deterministic relative to stochastic processes culminated with the popularization of neutral theories of biodiversity (Bell 2001, Hubbell 2001). Neutral theories effectively dismissed the niche concept (and thus selection) by assuming that all co-occurring individuals were effectively ecologically equivalent. The success with which neutral theories accounted for many ecological patterns fostered increased attention among ecologists to the potential importance of stochastic assembly processes, including dispersal, drift, and speciation.

It is now widely accepted that both deterministic (i.e., selection) and stochastic (i.e., drift) processes are influential in generating patterns of diversity (Alder et al. 2007, Cadotte 2007, Dumbrell et al. 2010, Ofiteru et al. 2010) thanks in part to the long-standing debates about opposing community assembly theories. The focus has now turned to disentangling the respective roles and relative importance of stochastic and deterministic processes (Chase 2007, 2010, Myers and Harms 2009, Chase et al. 2009, Chase and Myers 2011). Many studies now also consider how different ecological factors including disturbance (Chase 2007, Myers and Harms 2011) and productivity (Chase 2010) influence the relative importance of deterministic versus stochastic processes; however, this is not the focus of my research.

1.1.4 Inferring assembly processes through beta diversity patterns

The labelling of ecology as 'a mess' or 'idiosyncratic' (Lawton 1999) is due in part to the unpredictability of processes driving patterns of diversity – there fails to be consistent agreement

on the relative importance of different ecological processes (i.e., speciation, dispersal, selection and drift) (Lessard et al. 2012). Because beta diversity quantifies differentiation in species composition between locations, it is an important tool for understanding processes that drive diversity patterns, in particular the relative importance of stochastic versus deterministic processes (Legendre et al. 2005). Guiding beta diversity research is a set of predictions about how beta diversity relates to environmental dissimilarity or geographic distance among sites (Figure 2). If species are differentially adapted to different environments, deterministic selection is potentially important and beta diversity is predicted to increase with increasing environmental dissimilarity among sites (Tuomisto et al. 2003, Qian and Ricklefs 2011) (Figure 2a). Observing such a pattern does not, however, represent unequivocal evidence of the role of deterministic selection because dispersal limitation can result in a similar pattern (Nekola and White 1999, Hubbell 2001, Soininen et al. 2007) (Figure 2b). Environmental dissimilarity tends to increase with geographic distance (Bell et al. 1993) (Figure 2c) further complicating the interpretation of beta diversity patterns, in particular the relative importance of stochastic (dispersal limitation) and deterministic (selection) processes.
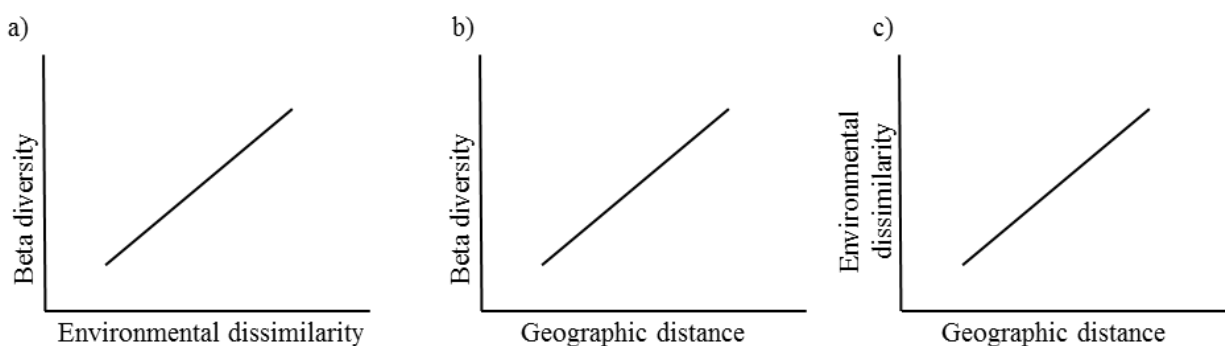
Figure 2: Simplifications of general beta diversity patterns reported in the literature: a) positive relationship between beta diversity and environmental dissimilarity (i.e. environmental 'distance' between sites) and b) positive relationship between beta diversity and geographic distance (more commonly reported as decreasing similarity with increasing geographic distance). c) Common pattern of increasing site-site environmental dissimilarity with increasing site-site geographic distance.

Numerous studies have sought to address the problem of co-variance between environmental dissimilarity and geographic distance by using correlative statistical methods called "variation partitioning methods" (Legendre et al. 2005, Anderson et al. 2006), but the reliability of these methods for inferring the relative importance of stochastic versus deterministic processes have been called into question (Gilbert and Bennett 2010). An alternative approach that has recently yielded some success is to strategically select sites in ways that control for environmental and / or spatial variation (Gilbert and Lechowicz 2004), thus facilitating the disentangling of environment-mediated selection from dispersal selection. It is this approach I use here (discussed further below).

Referring again to Figure 2, if environmental dissimilarity is minimized among sites, and thus the potential influence of deterministic selection is minimized, then speciation, dispersal, and drift are the processes that remain potentially important for explaining variation among sites. Drift, including stochastic colonization and extinction dynamics, is likely influential everywhere (Vellend 2010), but based upon experimental research, has been hypothesized to increase with increasing productivity (Chase 2007), and decreasing habitat area (Orrock and Watling 2010). Speciation would be important if the study spanned evolutionary timescales, or if sampling spanned regions with different historical / biogeographical histories (Vellend 2010). For example, if two sites shared similar local conditions but one site belonged to a biogeographical region in which speciation yielded a more diverse species pool, then the two sites would, all else being equal, exhibit different species composition despite their similar local conditions (Qian and Ricklefs 2000, Qian et al. 2005, Lenoir et al. 2010). The magnitude of beta diversity resulting from speciation will depend in part upon the degree to which the two regions differ in their species pools, which will be governed by their histories; comparing regions with distinctly

different histories (i.e., opposite hemispheres) will result in high beta diversity because of few shared species.

In my research, the role of speciation is assumed to be negligible because the study area experienced the same general glacial history. This assumption is based on the understanding that during the last glaciation period approximately 15,000 years ago, a majority of BC was covered in glaciers, which effectively re-set biodiversity; rather than speciation, current plant biodiversity is the result of migration from ecosystems that already existed to the south, east and north (Hebda 2007, Shafer et al. 2010). While it is recognized that a few glacial refugia existed (e.g., Haida Gwaii and Brooks Peninsula for coastal ecosystems), it is possible that additional unknown refugia were influential to current diversity patterns; however minimal paleoecological data have limited the inferences about the importance of glacial refugia (Shafer et al. 2010). Because speciation is assumed to be negligible, dispersal and drift remain as the potentially influential processes. With environmental variation minimized among sites, the role of geographic dispersal limitation can be assessed by relating beta diversity to inter-site geographic distance (Figure 2b). Importantly, other processes included in the umbrella of dispersal may still be important, but are not directly related to geographic distance alone (i.e., priority effects or mass effects).

Recent advances in the use of null model analyses (randomization procedures) (Azeria et al. 2011, Chase and Myers 2011, Chase et al. 2011, Stegen et al. 2012, Myers et al. 2012) are helping efforts to infer process from beta diversity patterns (Azeria et al. 2011, Chase and Myers 2011, Kraft et al. 2011). Proponents of null model analyses argue that before inferring ecological mechanisms that drive beta diversity, one should determine the degree to which beta diversity deviates from what would be expected based on a random community assembly process (i.e.,

stochastic colonization and extinction in the absence of dispersal limitation) (Kraft et al. 2011).

As an illustration of the utility of null models, Chase et al. (2011) applied the Raup-Crick null

model to two different communities that differed in exposure to disturbances (drought in

experimental ponds and bleaching in coral reefs) and found that communities affected by

drought were more similar whereas communities affected by bleaching were no different than

expected based on random sampling from the regional species pool. Chase (2010) concluded that

in ponds subject to drought, community assembly appeared to be influenced by deterministic

processes (ecological filter) whereas in coral reefs subject to bleaching, community assembly

appeared to be influenced by factors stochastic in nature (no different from random sampling).

In general, the null model analyses currently applied to beta diversity analyses are beneficial in

that they show whether observed beta diversity is higher, lower, or no different than what would

be expected if species were randomly drawn from the species pool (Myers et al. 2012). The

closer observed dissimilarity is to expected dissimilarity (i.e., small deviation from expected), the

more likely that influential community assembly processes lead to random (stochastic) patterns

of species diversity (Azeria et al. 2011, Chase et al. 2011). Negative deviations from expected

composition dissimilarity imply that composition is more similar than expected by chance

(Chase et al. 2011), which can occur when the species pool includes species not suitable in the

focal site (i.e., deterministic processes filter species from the regional species pool resulting in

higher similarity that expected by chance (Chase 2007)). On the other hand, positive deviations

from expected composition dissimilarity imply that communities are more dissimilar than

expected by randomly sampling species from the regional species pool (Kraft et al. 2011, Myers

et al. 2012) due to aggregation among sites within the communities analyzed. For example, a

strong environmental gradient may cause sites to have more different composition than expected

if species were randomly assigned, possibly due to environmental-mediated selection. Notably, by minimizing among-site variation in environmental conditions, one increases confidence in any inferences about the role of stochastic processes.

Another benefit of using null models is that they control for the dependence of beta diversity metrics on alpha and gamma diversity (Chase and Myers 2011, Jost et al. 2011), an underlying criticism of beta diversity metrics. To be truly independent, any diversity component should have no influence over another component (Jost et al. 2011). Null models effectively control for differences in species richness by randomly assembling communities such that for a given alpha and gamma diversity, expected beta diversity is quantified. For example, Myers et al. (2012) controlled for differences in regional species richness between tropical and temperate forest ecosystems and found that despite differences in species richness, beta diversity within each ecosystem type was higher than expected based on random sampling from the species pool.

There are two critical features of null model analyses that are integral to isolating the influence of stochastic from deterministic processes: (i) the species pool from which communities are randomly assembled needs to be well defined (Chase et al. 2011, Lessard et al. 2012), and (ii) the environmental heterogeneity within communities needs to be minimized. Species pools are challenging to quantify (Lessard et al. 2012) and are typically based on lists of observed species from a given community, which do not account for species that could disperse to the focal community but have not been detected (Pärtel et al. 2011). Ideally, one would generate a species pool that accounts for species-specific niches and dispersal probabilities, but rarely does one have the necessary information about species' physiological tolerances and environmental-specific fitness characteristics (Pärtel et al. 1996). The most common recommendation to address concerns over species pool definitions is to repeat the null model analyses with different

definitions of the species pool (Chase et al. 2011, Lessard et al. 2012). In my research, null

models are applied to communities that share similar environmental conditions as described in

the next section. In addition, null model analyses are repeated using multiple species pool

definitions. Null models have only recently begun to be applied to beta diversity analyses, and

some of the properties of their outcomes have yet to be fully explored. In particular, it is unclear

how patterns of species occupancy (i.e., the number of sites occupied by each species) affect null

model expectations.

1.2 Biogeoclimatic Ecosystem Classification

In order to maximize one's ability to detect and quantify the influence stochastic processes have

on beta diversity, it is necessary to simultaneously minimize among-site variation in local abiotic

conditions, and maximize replication within and across areas of different environmental

conditions. I acquired a dataset that approaches this ideal: Biogeoclimatic Ecosystem

Classification (BEC) plot data within the province of British Columbia (BC). Consistent with

community ecology theory in the mid-20th century (Hutchinson 1957, MacArthur 1965), BEC

was founded on the understanding that selection dominates community assembly processes –

plant communities are the products of climate, parent material, organisms, topography and time

(Pojar et al. 1987). Broad variation in climate and soil have been used to describe the array of

ecosystems in BC (Meidinger et al. 1991, MacKinnon et al. 1992, Austin et al. 2008, Delong et

al. 2010). BEC combines vegetation, climatic (zonal) and site (topography and soil)

classifications to organize ecosystems at regional and local levels and by doing so, creates a

framework for ecosystem-based decision-making across the province (MFLNRO 2012a). There

is also a chronological classification that I do not discuss in my research. The province has been

classified into sixteen distinct zones (Figure 3) representing large geographic areas with broad

macroclimates, vegetation communities and soils (McLennan 1999, MFLNRO 2012a).
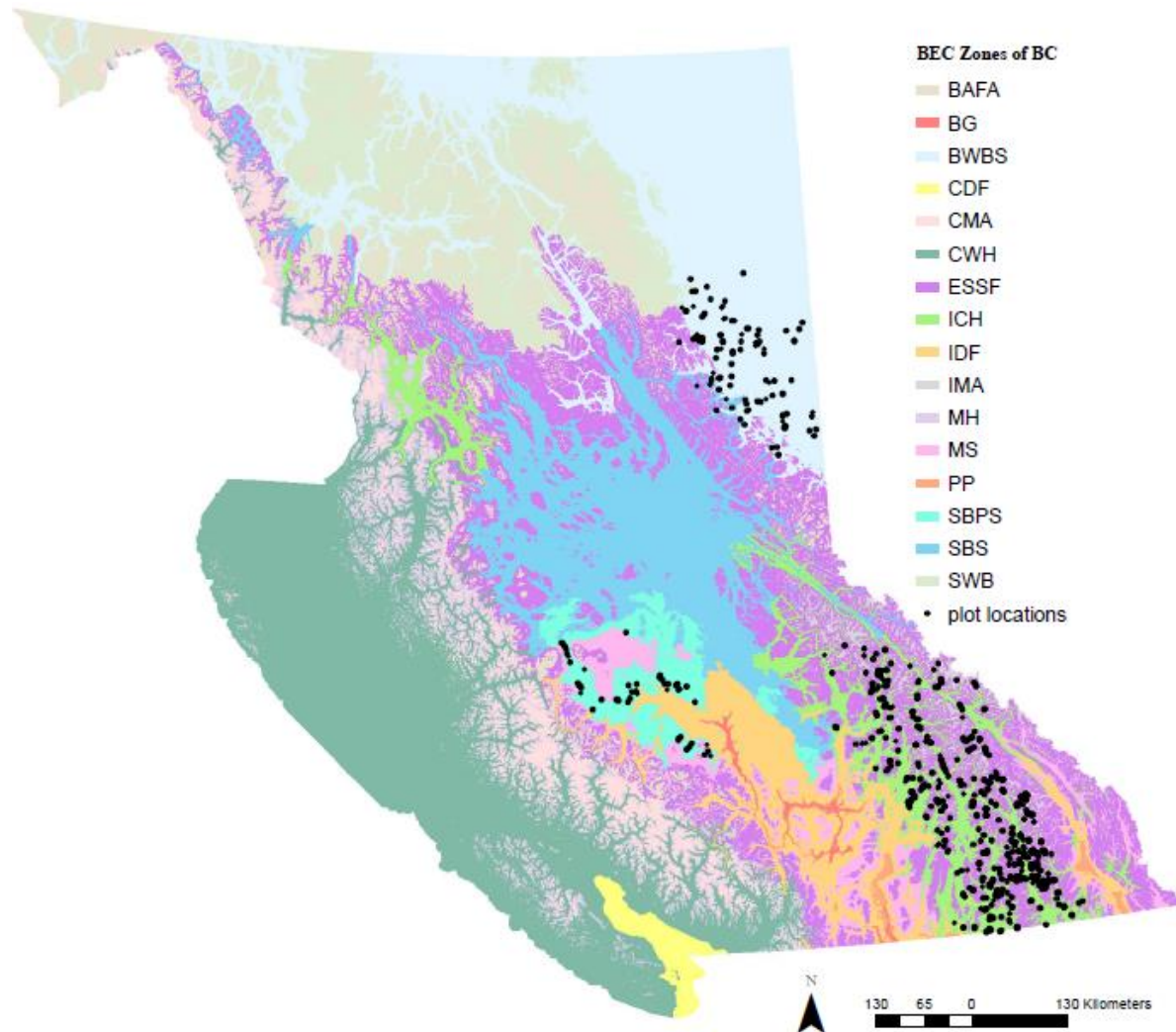
Figure 3: Biogeoclimatic Zones of British Columbia (MFLNRO 2012a)**. Plot locations are shown for the 809 BEC plots used in my research.**

Through climatic and vegetation classification, biogeoclimatic subzones are defined by

similarities in vegetation, soils, and topography on zonal sites, sites that are least influenced by

local topography and soils and that best reflect the regional climate (Pojar et al. 1987, MFLNRO

2012a). Subzones with similar vegetation and climate on zonal sites are grouped to create sixteen

biogeoclimatic zones (McLennan 1999, MFLNRO 2012a) (Figure 3). In some locations,

subzones are delineated into variants, where subtle differences in regional climates (i.e., slightly

drier, colder or snowier than subzone conditions) results in slight differences in plant

communities. Within subzones or variants, areas that are capable of supporting the same climax

plant community are defined as site associations, which are delineated into site series within

subzones or variants of subzones. Site series describe the relative soil moisture and nutrient

conditions within a subzone or variant. While site series have plant species indicative of the

potential vegetation, they largely reference physical site attributes including slope, soil and

relative position in the landscape (Macmillan et al. 2007). For simplification, a site series unique

to a given BEC subzone or variant will hereafter be referred to as a site unit. Nomenclature of

site units is described in Figure 4. At the local level of classification (site unit) there can still be

considerable site variation due to compensating factors (Meidinger et al. 1991). For example,

different combinations of elevation, soil and aspect can result in the same site quality and thus be

classified as the same site unit; however the key is that growing conditions are considered equal

in that vegetation potential is the same within a site unit. The majority of site units described by

BEC refer to mature and older forest types, with limited classifications for younger successional

stages; however, some non-forested ecosystems are described, but fine-scale descriptions vary

depending on ecosystem type (MFLNRO 2012a).
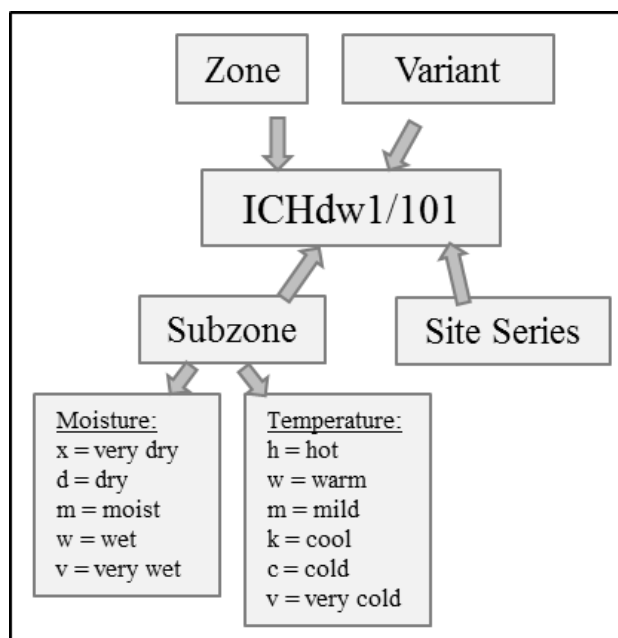
Figure 4: Description of BEC site unit naming. Note that in coastal ecosystems, subzones are described by moisture and continentality (distance to ocean) rather than temperature. The example provided is the 101 site series in the West Kootenay variant of the dry-warm subzone in the Interior Cedar Hemlock zone (ICHdw1/101).

At all levels of classification, there is an inherent reliance on vegetation; in the initial stages of classification, plots are grouped based in part on similar species composition (diagnostic combination of species). As described by Pojar et al. (1987), vegetation is classified into hierarchical categories (Class, Order, Alliance, Association and Subassociation) differentiated by diagnostic species. In BC, few character species (i.e., those species with strong indicator values) have been described and therefore dominant or common species are often used instead. The corresponding environmental variables collected for each plot are analysed to determine whether sites have similar environmental characteristics; readjustment of plots belonging to the same group may be adjusted based on environmental characteristics (Krestov et al. 2000). The reliance on vegetation in the development of BEC raises circularity concerns – sites may be similar in composition due to the classification process rather than underlying environmental similarity. However, for the following reasons, I assume that circularity is of minimal influence in my

research. (1) Although BEC relies on vegetation, implicit consideration is given to site characteristics to ensure that site units are environmentally consistent (Klinka and Chen 2009). (2) Use of site characteristics is especially important in BC given the lack of character species (i.e., indicator species) that would more easily differentiate plant communities (Pojar et al. 1987). (3) Further support for the assumption of environmental similarity within site units is gained through the ability of one to accurately describe a site unit based on site quality (soil moisture and nutrients) independent of a full vegetation analysis (some key indicator species may or may not be used in the assessment) (McLennan 1999).

In total, there are more than 30,000 standardized BEC plots surveyed by the Ministry of Forests Lands and Natural Resource Operations (MFLNRO). Each plot is 400 m^2. For each plot, site and vegetation information is collected following the procedures and protocols described in the *Field Manual for Describing Terrestrial Ecosystems 2nd edition* (MFLNRO and MOE 2010). While the primary purpose of establishing plots is to generate and improve the classification system, there is growing use of BEC plot data for more general ecological research including predicting tree species and ecosystem distributions under current and future climatic conditions (Hamann and Wang 2006, Delong et al. 2010, Rehfeldt and Jaquish 2010, Fitterer et al. 2012). At broad scales (BEC zone/subzone/variant), there is support for relationships between climate and ecosystem types (Hamann and Wang 2006, Delong et al. 2010) and tree species distributions (Hamann and Wang 2006); however such associations are likely to weaken at finer scales and with lesser vegetation (shrubs and herbs) (Pearson and Dawson 2003, Lo et al. 2010a, 2010b).

At the scale of the local site unit, it is recognized that "disturbance, chance, and time" (i.e., dispersal, drift and speciation) are influential to community assembly (Pojar et al. 1987); however, the degree to which these comparatively stochastic processes dominate over

environmental determinism (selection) is poorly understood. BEC plot data are ideal for assessing the importance of stochastic processes because (i) limited environmental variation within site units serves to minimize the potential influence of selection and, (ii) large geographic distances between plots of the same site unit allow for the possible detection of geographic dispersal limitation, and (iii) the plot data are sufficiently replicated over a broad geographic extent (multiple BEC variants, subzones, and zones).

Using a subset of 809 plots (Figure 3), the degree to which beta diversity differs from random community assembly will be evaluated within 31 site units from 8 BEC subzones/variants and 4 BEC zones. Importantly, findings can be applied within a well-understood framework for ecosystem-related decision-making in the province (Macmillan et al. 2007). Further, with land-use change, resource extraction, and climate change all having profound impacts on BC's ecosystems (Gayton 2008, Spittlehouse 2008, Campbell et al. 2009) there is growing recognition of the importance of understanding and explaining the origins of diversity across the landscape, particularly because of the demonstrated links between diversity and ecosystem health and functioning (Duffy 2009).

1.3 Research overview and objectives

Disentangling the relative importance of dispersal, selection, drift and speciation helps ecologists understand why site-to-site variation ("beta diversity") in species composition exists. As discussed earlier, environmental variation leads to high beta diversity through environmental-mediated selection (Whittaker 1960, MacArthur 1965, Weiher and Keddy 1995, Lennon et al. 2000); however it remains challenging to isolate and quantify the more stochastic processes including dispersal and drift that simultaneously influence species composition (Chase 2003, 2010, Fukami 2004, Moral et al. 2010). Through the appropriate use of null models, the goal of

my research is to gain a better understanding of the degree to which local composition is influenced by stochastic processes (Chase and Myers 2011), which is important for achieving a more accurate and complete understanding of the origins of diversity patterns in general.

1.3.1 Alpha, beta, and gamma diversity in BC ecosystems

The first objective of my research is to describe patterns of alpha, beta, and gamma diversity using BEC plot data. There are no specific hypotheses associated with this research objective, as its purpose is to describe current patterns of vascular plant diversity in the subset of BEC plot data being used in this research. In particular, quantifying alpha and gamma diversity will indicate the degree to which species richness varies in the dataset, which has implications for beta diversity. As discussed by Chase and Myers (2011), when alpha diversity is low compared to gamma diversity, beta diversity will necessarily be high in order to account for the variation needed among plots to generate gamma diversity. On the other hand, if gamma diversity is low and alpha diversity is a high proportion of gamma diversity, it is expected that beta diversity will be low. Due to the non-independence of alpha, beta, and gamma diversity (Chase et al. 2011), it was necessary to first quantify each of these diversity components in order to understand how observed beta diversity may be affected by underlying species richness gradients. Null model analyses were then used in part to account for differences in species richness among sites.

1.3.2 The relative importance of stochastic assembly

The second objective of my research is to test the hypothesis that beta diversity among sites within BEC site units is no different from that expected under stochastic community assembly. Given the assumption that there is minimal environmental variation among plots of the same site unit, and given minimal historical / biogeographical differences among plots, dispersal and drift represent the potentially important drivers of beta diversity among sites. If dispersal limitation is

present, as it often is in plant communities (Bell 2001, Hubbell 2001, Myers and Harms 2011),

then a positive correlation between composition dissimilarity and geographic distance is

expected. If dispersal limitation causes near sites to be more similar and clustering of

composition among plots within a site unit, then positive deviation from expected beta diversity

generated by randomly sampling from the regional species pool (Figure 5c) may occur (Chase

and Myers 2011). Where negative deviations occur (Figure 5a), observed dissimilarity is more

similar than expected by chance (Azeria et al. 2011, Chase et al. 2011), which may occur when

some factor consistently filters species from the regional species pool (Chase 2007). When

observed dissimilarity is no different from expected similarity (Figure 5b), the processes

responsible for compositional variation among plots are analogous to randomly sampling species

from the species pool.
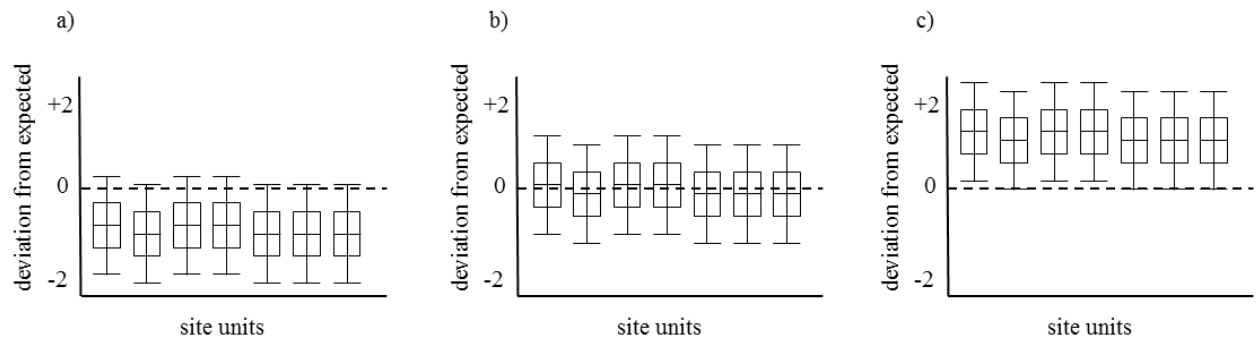
Figure 5: Hypothetical scenarios where a) observed dissimilarity is more similar (negative deviation), b) observed dissimilarity is no different (deviation close to zero) and c) observed dissimilarity is more dissimilar (positive deviation) than expected based on random sampling from the regional species pool.

Importantly, the above predictions are based on the null model analysis used in this research,

which controls for species richness and species occupancy, but does not include ecological

constraints or dispersal probabilities in the randomization procedure; it is assumed that species

are equally suited at all sites and have equal dispersal capabilities. Given that the null model

analysis assumes that all species in the species pool are equally capable of colonizing a focal site,

beta diversity analyses were repeated using multiple species pool definitions as recommended in the literature (Chase et al. 2011, Lessard et al. 2012) to better understand underlying processes. When the regional species pool includes only those species known to be capable of colonizing focal sites (i.e., those species observed within a site unit), it is expected that observed dissimilarity will be no different (Figure 5b) or more dissimilar (Figure 5c) than expected by chance depending on the importance of dispersal limitation or some other factor that caused systematic clustering (grouping of sites with similar species composition in response to some deterministic factor such as soil moisture). On the other hand, if the regional species pool includes multiple species not capable of colonizing the focal sites due to environmental constraints (i.e., environmental selection), it is predicted that observed dissimilarity within a BEC site unit will in fact be more similar than expected by chance (Figure 5a) due to selective filtering of species.

1.3.3 Stochastic assembly of different plant lifeforms (trees, shrubs, herbs)

The third objective of my research is to test the hypothesis that beta diversity of plant lifeforms (trees, shrubs and herbs) among sites within BEC site units is no different from that expected under stochastic community assembly. This hypothesis parallels that of my second research objective with the exception of examining tree, shrub and herb species independently. It is important to understand diversity patterns of trees, shrubs, and herbs independently as they are not equivalent in terms of total species richness, presence in a community, niche breadth or dispersal capabilities (Reilly et al. 2006, Wang et al. 2009, Jayakumar and Nair 2012). Herb species richness in temperate and boreal forests vastly exceeds that of shrub or tree species (Gilliam 2007, Austin et al. 2008). Similarly, both niche breadth and dispersal capabilities of tree species are typically greater for tree rather than shrub or herb species (Reilly et al. 2006,

Jayakumar and Nair 2012). As a result, gamma, alpha, and beta diversity of tree species is typically lower than that of shrub or herb species (e.g., Rey Benayas 1995).

It is still assumed that the environmental similarity within BEC site units controls for selection in all lifeforms, even for herb species, whose ecological niches may be comparatively narrow. Similar to the second research hypothesis, speciation is expected to be negligible given the similar biogeographical history (Hebda 2007) of the study extent. Therefore, dispersal and drift are the remaining processes that are potentially important drivers of beta diversity among sites. Because herb and shrub species are generally more limited in dispersal than tree species (Willson 1993), influence of dispersal limitation is more likely for herb and shrub species and will be evident by a negative relationship between geographic distance and composition similarity or positive deviations from expected in the null model analysis (Figure 5c). If dispersal limitation is non-significant within BEC site units, little deviation from expected dissimilarity is expected in the null model analysis (Figure 5b); this is anticipated to be most true for tree species whose dispersal distances exceed that of shrub or herb species (Jayakumar and Nair 2012). Where dispersal limitation does not explain beta diversity (i.e., high observed beta diversity that is no different than expected based on random sampling from the regional species pool) within BEC site units, drift (colonization and extinction dynamics) is more likely the dominant process driving variation in composition among plots. Similar to the previous research objective, expansion of the regional species pool to include species from different environments could result in higher similarity within BEC site units than expected by chance (Figure 5a) due to systematic species filtering. This is least likely for tree species due to their comparably wide ecological niches.

1.3.4 Stochastic assembly of tree species in BEC subzones/variants

The fourth and final objective of my research is to formally test the assumption, adopted in recent climate change research, that locations within a given BEC subzone/variant are of equivalent suitability from the perspective of tree species. In light of climate change, ecologists strive to understand how species and ecosystems will respond to changing climate conditions. As has been done in BC (Hamann and Wang 2006), climate envelope models are used to generate species distribution models that can be used to predict current and future species ranges. Hamann et al. (2005) used tree species frequency (% cover) extracted from BEC plot data to create species distribution maps of *potential* habitat. Underlying this approach is "the assumption that a species should be able to grow anywhere within a variant in which it is observed" (McLane and Aitken 2012: Appendix A). This assumption corresponds with the testable hypothesis that composition dissimilarity in tree species among plots of the same BEC subzone/variant will be dominated by stochastic processes (i.e., trees are able to establish anywhere within a BEC subzone/variant). Evidence consistent with this hypothesis could be revealed if beta diversity of tree species among plots of the same BEC subzone / variant is no different from that expected based on random sampling from the regional species pool (Figure 5b). Alternatively, if tree species perceive the environmental conditions within a given BEC subzone / variant as heterogeneous, then null model analyses will reveal that beta diversity is higher than expected (due to systematic clustering of species at sites with apparently different environments) based on random sampling from the regional species pool (Figure 5c).

Chapter 2: Quantifying species richness and beta diversity of vascular plant species in a sample of BC ecosystems

2.1 Summary

An underlying goal of ecology is to describe and explain observed patterns of species diversity and to use this understanding to guide ecosystem management and conservation. In British Columbia (BC), Canada, Biogeoclimatic Ecosystem Classification (BEC) describes ecosystems based on the premise that plant communities are defined by climate, organisms, topography, parent material and time as well as the assumption that plant communities develop along a linear successional pathway resulting in predictable climax ecosystems that reflect dominant climatic conditions (Pojar et al. 1987, MFLNRO 2012a). Based on 'polyclimax theory' (Tansley 1935), BEC assumes a direct relationship between plant communities and site conditions, and is largely consistent with the dominant perspectives in community ecology during the mid-20th century (Ricklefs 2004) – that species composition is the result of deterministic relationships between vegetation and local environmental conditions. Despite being founded upon outdated theories (i.e., equilibrium theory and local determinism (Ricklefs 2004, Haeussler 2011)), BEC has established itself as a reliable and commonly used ecosystem classification system (MFLNRO 2012a).

As discussed in the introductory chapter, deterministic processes are important filters on plant community assembly; however, growing evidence suggests that stochastic processes including chance colonization or extinction should also be considered when trying to understand the processes that give rise to patterns of diversity (Cadotte 2007, Vergnon et al. 2009, Vellend 2010, Chase and Myers 2011). For example, a site unit describes a suite of environmental conditions (i.e., a niche) that is suitable for many species, but as Pärtel et al. (2011) describe, uncommon species are rarely observed in all locations of suitable habitat. Dispersal barriers

(Ricklefs 2004), priority effects (Chase 2003, 2010, Moral et al. 2010) and ecological drift (Vellend 2010) can filter species assembly in a given location. As a result, even sites with similar environmental conditions can be occupied by different vegetation and result in high site-to-site variation (beta diversity).

Measuring variation among sites takes careful consideration (Koleff et al. 2003, Anderson et al. 2011) in part due to the lack of independence between alpha, gamma and beta diversity (Jost 2007). When alpha diversity of sites represents a small proportion of gamma diversity, it is expected that beta diversity will be high, regardless of underlying processes that cause alpha diversity to be low (Chase and Myers 2011). Therefore, it is necessary to use methods that control for differences in alpha diversity when quantifying beta diversity of a community (Azeria et al. 2011, Chase and Myers 2011, Chase et al. 2011). If the underlying assumption is correct that similar plant communities will develop on environmentally similar sites, one expects any observed beta diversity in species composition to be the result of stochastic rather than deterministic processes. A corresponding hypothesis is that plots within a site unit will be no different than expected based on random sampling from the regional species pool.

2.2 Methods

2.2.1 Vegetation plot data

I used 809 standardized plots from mature conifer-dominated inland temperate, sub-boreal and boreal forest ecosystems to examine the potential influence that stochastic assembly processes have on beta diversity in plant communities defined by BEC. The 809 plots are classified into 31 site units following the procedures and protocols in the *Field Manual for Describing Terrestrial Ecosystems* (MFLNRO and MOE 2010). I assumed that each site unit represents an area of

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homogenous environmental conditions that has the same vegetation potential (Pojar et al. 1987).

I used site units that are from 8 BEC subzones/variants, which represent samples of 4 BEC zones

(Figure 6). Variants are only defined in suzbones that contain climatic variation and therefore

variants are comparable to subzones when no variants exist as is the case for BWBSmw and

SBPSxc in the dataset (Figure 6). All plot data have "confirmed" classification (deemed by

regional ecologists to be correctly classified and of good quality) and were provided by the

MFLNRO (MFLNRO 2012b). A majority (647) of the plots are from northern temperate forests

(Engelmann-Spruce Subalpine Fir (ESSF) and Interior Cedar Hemlock (ICH)), while 162 plots

are from (sub) boreal (Sub-Boreal Pine Spruce (SBPS)) and boreal (Boreal White and Black

Spruce (BWBS)) ecosystems. Inclusion of samples from the SBPS and BWBS zones expands the

spatial extent of the study (> 800 km) and incorporates clear differences in environmental

conditions (Figure 7). A summary of the site units used in my research is included in Table 1 and

detailed descriptions of the subzones, variants and site units can be found elsewhere (Meidinger

et al. 1991, MFLNRO 2012a).

Zone:

BWBS SBPS ESSF ICH

Subzone:

BWBSmw SBPSxc ESSFwc ESSFwm ICHdw ICHwk

Variant:

ESSFwc4 ESSFwcw ESSFwm2 ESSFwm4 ICHdw1 ICHwk1

Site series:

BWBSmw/101
BWBSmw/103
BWBSmw/104
BWBSmw/111

SBPSxc/01
SBPSxc/02

ESSFwc4/101
ESSFwc4/103
ESSFwc4/110
ESSFwc4/111

ESSFwm2/101
ESSFwm2/103
ESSFwm2/104
ESSFwm2/110

ICHdw1/101
ICHdw1/102
ICHdw1/103
ICHdw1/104
ICHdw1/112

ICHwk1/101
ICHwk1/103
ICHwk1/104
ICHwk1/110
ICHwk1/111

ESSFwcw/101
ESSFwcw/103
ESSFwcw/104
ESSFwcw/110

ESSFwm4/101
ESSFwm4/104
ESSFwm4/110

Figure 6: Hierarchy of BEC plot data used in this research. Subzones are the main units of classification. Subzones used are samples from 4 BEC zones. Not all subzones are delineated into BEC variants (4 of 6 subzones are delineated into variants in the sample of BEC data used in this research). Site series listed have 10 or more BEC plots (site units with fewer than 10 plots were excluded from analyses). Abbreviations defined in Table 1.

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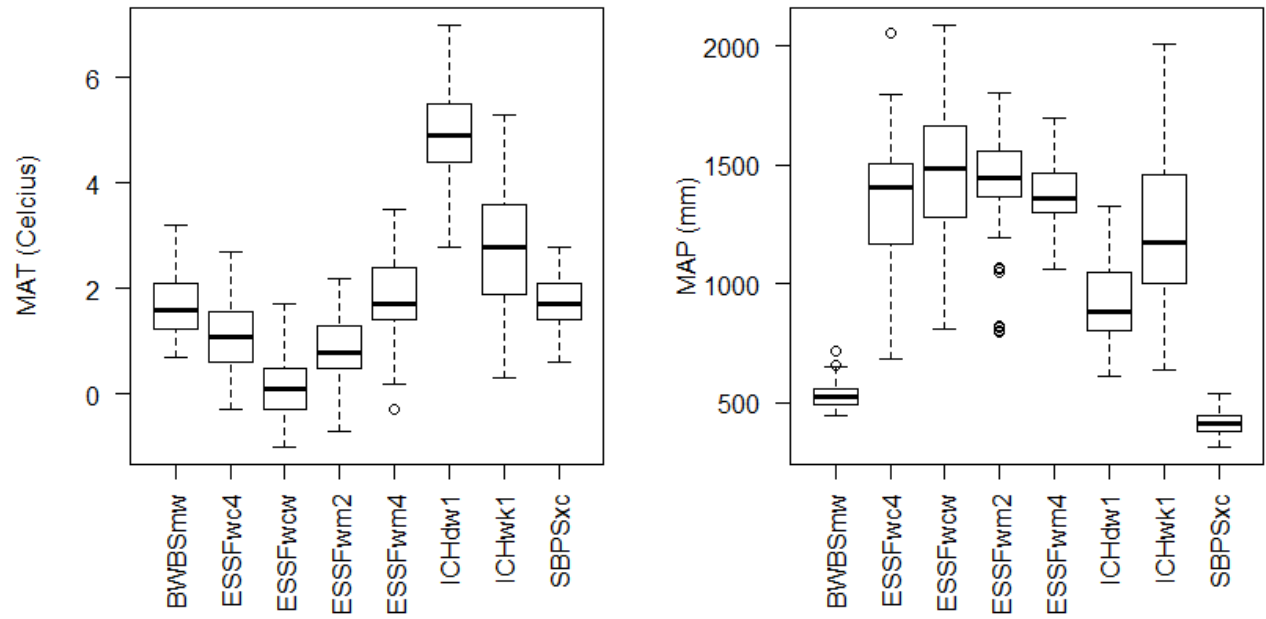
Figure 7: Mean annual temperature (MAT (°C)) and mean annual precipitation (MAP (mm)) for 8 BEC subzones/variants. Climate data extracted from ClimateWNA model (Wang et al. 2012)**.**

Table 1: BEC Site Unit summary of total species richness (gamma diversity). BEC zone, subzone and variant are named in full.

Zone	Subzone	Variant	Site Series	Site Unit Classification	Total no. of species	No. of plots	Tree layer No. of species	Tree layer %	Shrub layer No. of species	Shrub layer %	Herb layer No. of species	Herb layer %
Interior Cedar Hemlock	Dry warm	West Kootenay	102	ICHdw1/102	81	10	9	11.1	26	32.1	46	56.8
			103	ICHdw1/103	147	22	18	12.2	31	21.1	98	66.7
			104	ICHdw1/104	159	60	23	14.5	38	23.9	98	61.6
			101	ICHdw1/101	106	35	17	16	30	28.3	59	55.7
			112	ICHdw1/112	78	13	14	17.9	19	24.4	45	57.7
	Wet cool	Shuswap	103	ICHwk1/103	60	13	10	16.7	22	36.7	28	46.7
			104	ICHwk1/104	98	36	10	10.2	27	27.6	61	62.2
			101	ICHwk1/101	104	55	10	9.6	26	25	68	65.4
			110	ICHwk1/110	103	48	9	8.7	26	25.2	68	66
			111	ICHwk1/111	104	19	11	10.6	21	20.2	72	69.2
Sub Boreal Pine Spruce	Very dry cold		02	SBPSxc/02	74	21	8	10.8	11	14.9	55	74.3
			01	SBPSxc/01	80	32	5	6.2	16	20	59	73.8
Boreal White and Black Spruce	Moist warm		103	BWBSmw/103	102	18	12	11.8	24	23.5	66	64.7
			104	BWBSmw/104	115	29	11	9.6	34	29.6	70	60.9
			101	BWBSmw/101	118	38	12	10.2	25	21.2	81	68.6
			111	BWBSmw/111	139	24	13	9.4	31	22.3	95	68.3
Englemann Spruce Subalpine Fir	Wet mild	Central Purcell low elevation	104	ESSFwm4/104	63	16	9	14.3	21	33.3	33	52.4
			101	ESSFwm4/101	80	20	8	10	22	27.5	50	62.5
			110	ESSFwm4/110	77	19	8	10.4	19	24.7	50	64.9
	Wet mild	Central Purcell	103	ESSFwm2/103	55	14	6	10.9	15	27.3	34	61.8
			104	ESSFwm2/104	35	10	7	20	10	28.6	18	51.4
			101	ESSFwm2/101	82	23	6	7.3	16	19.5	60	73.2
			110	ESSFwm2/110	80	16	3	3.8	14	17.5	63	78.8
	Wet cold	Selkirk	103	ESSFwc4/103	67	29	5	7.5	17	25.4	45	67.2
			101	ESSFwc4/101	72	34	5	6.9	16	22.2	51	70.8
			110	ESSFwc4/110	68	16	3	4.4	15	22.1	50	73.5
			111	ESSFwc4/111	89	20	4	4.5	9	10.1	76	85.4
	Wet cold	Woodland	103	ESSFwcw/103	56	31	4	7.1	12	21.4	40	71.4
			104	ESSFwcw/104	54	39	6	11.1	13	24.1	35	64.8
			101	ESSFwcw/101	89	37	3	3.4	17	19.1	69	77.5
			110	ESSFwcw/110	81	12	2	2.5	9	11.1	70	86.4

In total, 1207 BEC plots were provided by the MFLNRO; however additional data integrity checks and data filtering were completed to generate the final dataset (809 plots). To ensure reasonable replication, only site units with 10 or more plots were used. Site units in the BWBSmw that are dominated by deciduous tree species were not included because the current research focuses on diversity patterns within conifer-dominated forest ecosystems; however a comparison between conifer and deciduous forest types would be interesting to pursue in future research. Elevation records associated with the field plot data were compared with 30 m resolution Digital Elevation Model (DEM) elevation data extracted from the Canadian National Topographic Database (GeoBase 2000) in order to identify plots with questionable georeferencing. Plots were removed if elevation discrepancies between the two elevation sources exceeded 30 m. I assumed that any spatial inaccuracy in plot data would not yield systematic biases in my results. Species coding was compared to the 2009 provincial species code list (Meidinger et al. 2009) and records containing unidentified or generic (e.g., "GRASS") codes were eliminated. Non-vascular species were not included in analyses because of concern over consistency in species identification and data collection (personal communication – Deb MacKillop). In addition, data describing species percent cover were not used in the current analyses due to concerns over inconsistent interpretation; however future analyses should attempt to include percent cover as it is an important aspect of species diversity (Anderson et al. 2011, Jost et al. 2011). From the refined plot data, site-by-environment and presence/absence site-by-species tables were created. Climate variables were added to the site-by-environment table using data extracted from the ClimateWNA program (Wang et al. 2012). Figure 7 illustrates the general climatic characteristics of the 8 subzones / variants used in my study.

2.2.2 Data analysis

2.2.2.1 Species richness (alpha and gamma diversity)

I calculated alpha diversity as the number of species within a plot and mean alpha diversity as the average number of species per plot within a given site unit. I calculated gamma diversity as the total number of species within a site unit. To visually assess the sensitivity of gamma diversity to sampling effort (Gotelli and Colwell 2001, Veech et al. 2002, Melo et al. 2003, Hortal et al. 2006), I generated species accumulation curves using the "accumcomp" function in the *BiodiversityR* package in R (Kindt and Coe 2005). To further predict actual species richness, species estimation was chosen over rarefaction to avoid the loss of information that occurs when plots in more heavily sampled communities are removed during rarefaction (Melo et al. 2003). Because they perform well with incidence data (Walthur and Moore 2005), I calculated first order Jackknife (Jack1) and Chao estimates using the "specpool" function in the package *Vegan* in R (Oksanen et al 2012).

2.2.2.2 Beta diversity

To test the hypothesis that site units are no different than expected based on random sampling from the regional species pool, I used a null model approach to compare observed beta diversity with beta diversity expected from randomly sampling species from the regional species pool. Observed beta diversity was calculated as the dissimilarity between each pair of plots using the presence-absence Jaccard dissimilarity metric where $\beta_j = 1 - a/(a+b+c)$; a equals the number of shared species between two plots, and b and c equal the number of unique species within plot 1 and 2 respectively (Koleff et al. 2003). I ran the null model using the permatfull function in the package *Vegan* in R (Oksanen et al. 2012) similar to the methods of Azeria et al. (2011). The null model randomly draws species from the regional species pool while maintaining the number

of species per plot as well as the species frequency in the regional species pool as recommended

by Azeria et al. (2011) (Figure 8). From 999 randomizations, expected Jaccard dissimilarity was

calculated as the mean pairwise Jaccard dissimilarity of the randomizations. I calculated the

standardized effect size (SES) as the difference between mean observed and mean expected beta

diversity divided by the standard deviation of expected values ($SES = (\ mean\ \beta_j - mean\ \beta_{exp})\ /\ s.d.$

β_{exp}) for all pairs of plots within each site unit (Azeria et al. 2011). I then used the Student's T

Test (t-test) to determine whether mean pairwise SES values within each site unit differed from

zero (significance level of $\alpha = 0.05$). Significant t-test results indicate that observed Jaccard

dissimilarity is different than what is expected based on random sampling of species from the

regional species pool (i.e., pairwise SES value is different from zero). Negative t-test statistic

results indicate that values are less than zero while positive t-test statistic results indicate that

values are greater than zero. As discussed by Chase and Myers (2011), negative SES values

below -1.96 imply that composition is statistically more similar than expected by chance and

positive SES values above 1.96 imply that composition more dissimilar than expected by chance.

I calculated the differences between observed and expected beta diversity for all pairs of plots

within 31 site units. Using a significance level of 0.05, one can expect to observe, on average, a

significant t-test in 1.55 of the 31 site units, purely by chance.
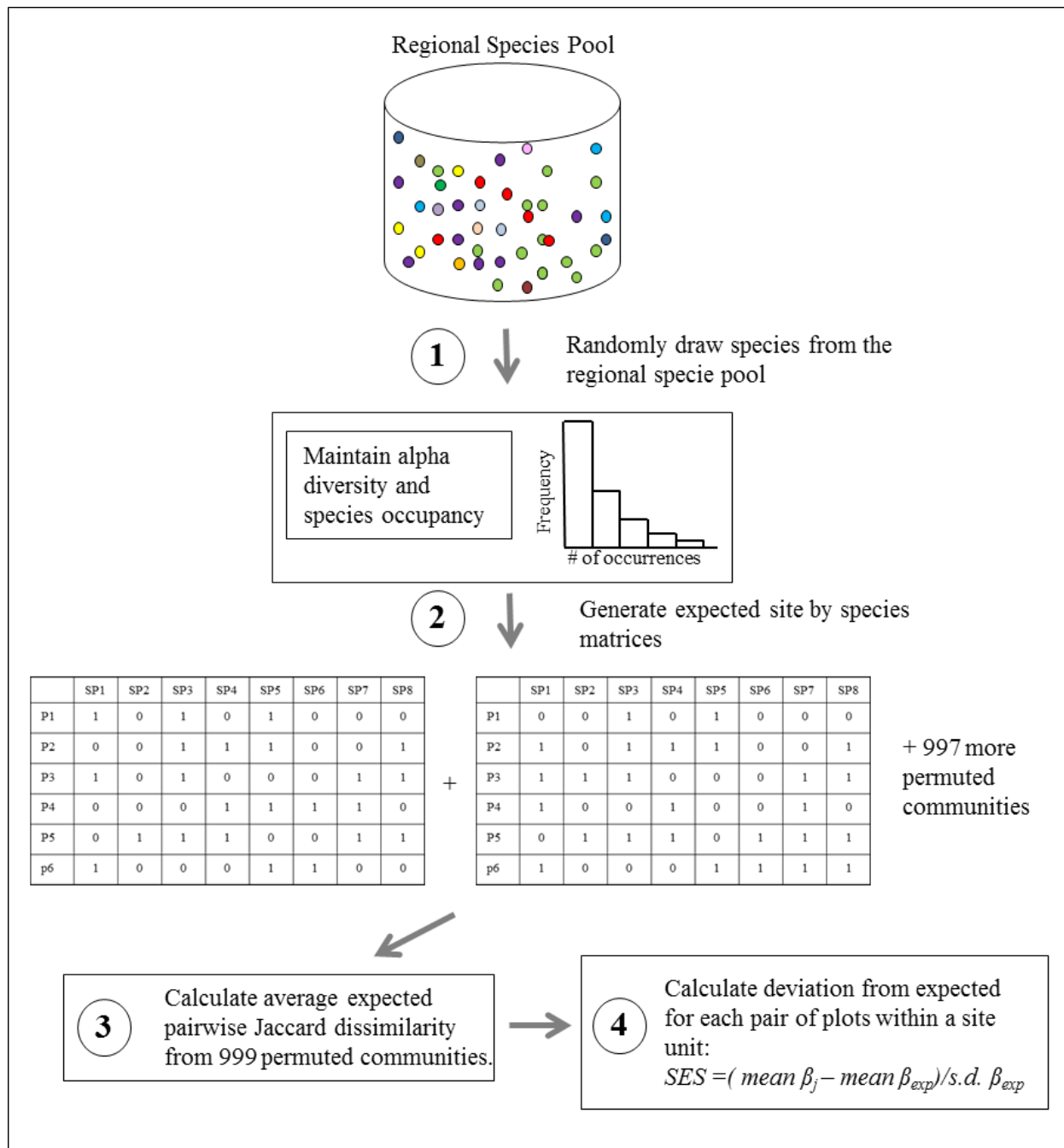
Figure 8: Schematic illustration of the process of the permatfull null model analysis used in this research.

In order to isolate whether dispersal limitation was influencing beta diversity, I used the Mantel test (Mantel 1967) to determine whether pairwise composition similarity was correlated to geographic distance. Specifically, the Mantel test compares the observed correlation (in this case Spearman Rank correlation) to correlation coefficients generated from permuted species

composition and geographic distance matrices, which effectively allowed me to quantify whether or not changes in the species composition similarity matrix (1-Jaccard dissimilarity) corresponded to changes in the geographic distance matrix. Mantel tests have been used for similar analyses in many other studies (e.g., Legendre et al. 2005, Pither and Aarssen 2005, Schulz et al. 2009, Bacaro et al. 2011). The Mantel test calculates a correlation coefficient (Mantel r) that ranges on a scale from -1 to +1, with negative values indicating a negative correlation and positive values indicating a positive correlation. I used 9999 permutations to calculate the p-values at a significance level of $\alpha = 0.05$. Importantly, the Mantel test is useful for testing the relationship along a single gradient, but it is less useful if multiple gradients are included (Anderson et al. 2011). One critique of the Mantel test is lack of statistical power (Legendre and Fortin 2010); the Mantel test is not always able to detect an effect when one is present.

2.2.2.3 Species pool sensitivity analysis

As recommended by Chase et al. (2011) and Lessard et al. (2012), I repeated beta diversity analyses within BEC site units with multiple species pools to assess how results change with different species pool definitions and to test for the influence of environmental selection. There is lack of detailed information regarding species' physiological tolerances and environment-specific fitness characteristics, so I defined species pools within the bounds of BEC as follows: (1) all species observed in the plots within a BEC site unit (i.e., gamma diversity), (2) all species observed within a BEC subzone / variant and (3) all species observed in the dataset. Because BEC subzones/variants include more environmental heterogeneity than site units, environmental selection is likely more influential in generating compositionally similar site units. Similarly, environmental selection is likely even more influential when beta diversity analyses are repeated

with the species pool inclusive of all species in the dataset, as the dataset spans an even larger environmental gradient.

For species pools 2 and 3, I included plots that were previously excluded from the dataset due to under-sampling in the site unit (i.e., fewer than 10 plots in the site unit). As a result, species pools 2 and 3 were built from a site by species matrix that has 938 plots; these plots were included to ensure that as many species as had been observed in a given BEC subzone / variant were included in the regional species pool. For expanded species pools, I built the permuted communities for each site using the additional species that were observed in either the BEC subzone/variant or in all plots. When expected Jaccard dissimilarity was calculated, the site by species matrices were restricted to only those plots in the observed site unit, thereby maintaining the same number of plots in observed and expected communities. Inherent in all three species pool definitions is the assumption that all species observed in the dataset are equally likely to colonize all sites within a site unit for each null model analysis.

2.2.3 Data limitations

It is important to note that the data used in my research comprises a non-random subset of the over 30,000 BEC plots that have been sampled across BC. Sampling is described as subjective without preconceived bias and relies on the judgement of professional ecologists (Pojar et al. 1987). The subset of data that I have used includes plots whose data were verified by experts to be reliable. It is assumed that the plots included in the present analyses represent an unbiased sample of forests within the subzones included in the analyses. Nevertheless, because the subset includes only a small portion of the entire dataset, there are inherent concerns with how I have defined species pools. At the finest scale, the species pool is limited to those species observed in the given site unit. If site units are under sampled, it is possible that additional species are

equally suited to the growing conditions of the site unit, but were not observed in any of the plots. Increasing the species pool to include all species observed in the BEC subzone or variant within which a given site unit is defined, is more likely to capture all species suited to the environmental conditions of the given site unit, but there will also be species that are not suited to local conditions. Further, including all species observed in the dataset overestimates the species pool, as very few species have such wide ecological niches.

Because I did not personally collect the field data, human error could not be estimated. Plot data have been collected over multiple decades by multiple ecologists (MFLNRO 2012a), but to my knowledge the dataset being used is not biased with respect to data quality. Nevertheless, if plots are included that do not include all species present, alpha diversity will be driven down and potentially influence the amount of beta diversity observed between plots. These data limitations apply to the research I completed in Chapters 3 and 4 as well.

2.3 Results

2.3.1 General diversity patterns

In total, 464 vascular plant species were observed across the 809 plots. Of these, 33 were tree, 85 were shrub and 346 were herbaceous species. One hundred and sixty one species (35%) were uncommon, occurring in 2 or fewer plots (Figure 9a). Each of the 31 BEC site units exhibited similar species occupancy distributions (Figure A1 in the appendix). Local species richness (alpha diversity) of plots varied from 5 to 46 species, with most site units showing a range of alpha diversity (Figure 10). Site units within the ESSF had the lowest average alpha diversity (10 species in the 103 and 104 site units in the wet-cold woodland ESSF (ESSFwcw/103 and ESSFwcw/104) and the 104 site unit in the Central Purcell wet-mild ESSF (ESSFwm2/104);

standard deviation = 3.46, 3.04 and 3.70 respectively), while site units within the BWBS and

ICH had the highest average alpha diversity (29 species in the 101 and 111 site units of the

moist-warm BWBS (BWBSmw/101 and BWBSmw/111) and the 103 site units of the West

Kootenay dry-warm ICH (ICHdw1/103); standard deviation = 6.74, 7.22 and 7.72 respectively)

(Figure 10).
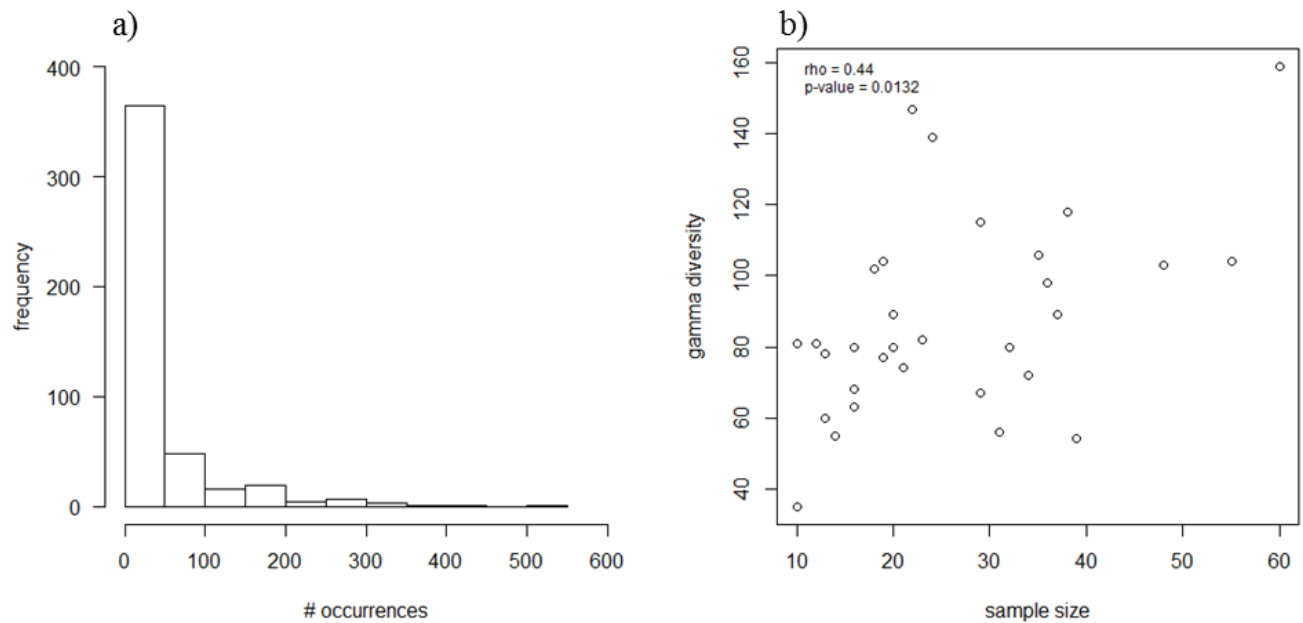
Figure 9. a) Histogram of species occupancy across all 809 plots; most species occur few times. Comparatively few species occur many times. b) relationship between gamma diversity and sample size in 31 site units. A positive relationship exists (Spearman Rank Correlation rho = 0.44, p = 0.0132).
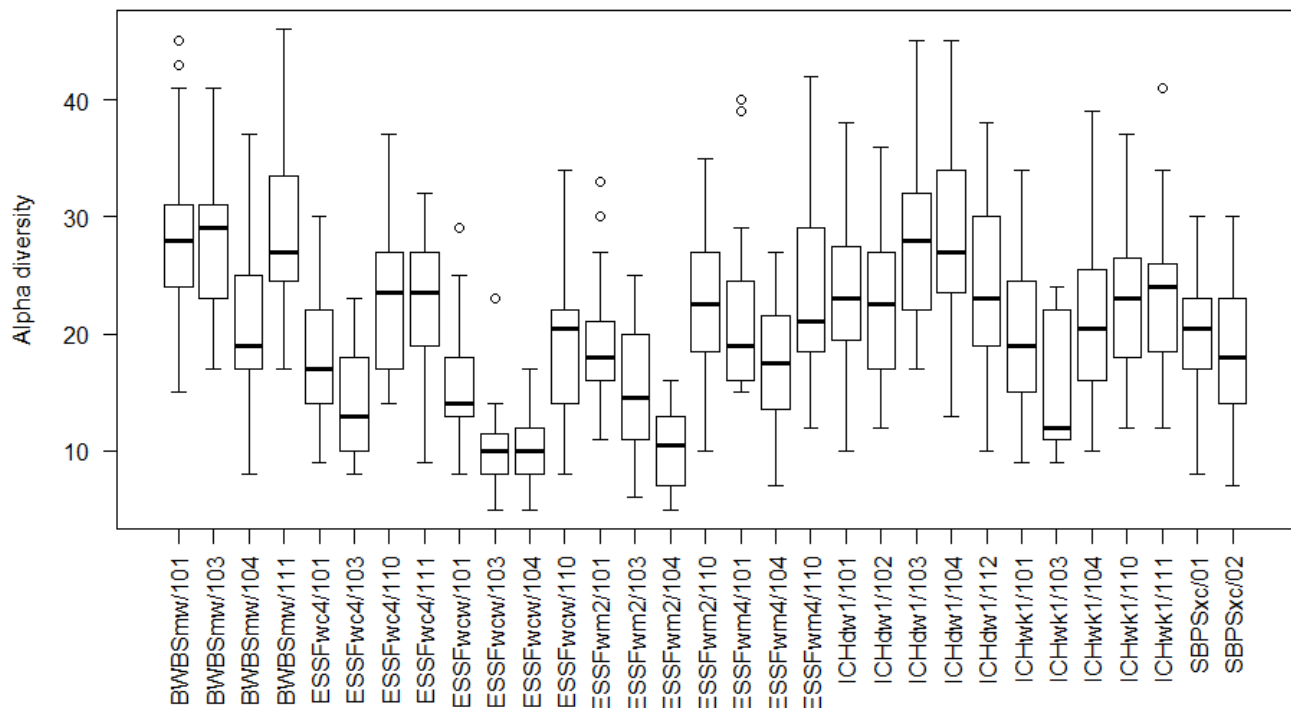
Figure 10: Alpha diversity of 31 site units. Each site unit has 10 or more plots.

I found gamma diversity to be between 31 species in the ESSFwm2/104 and 159 species in the

ICHdw1/103. I found a positive relationship between site unit gamma diversity and sample size

(Figure 9b). Species accumulation curves further show that additional species would be

encountered if more sampling were to occur (Figure 11). Chao species estimates showed an

increase of 10 to 145 species per site unit while Jackknife 1 species estimates showed an increase

of 14 to 63 species (Figure 12). Strong positive linear correlations exist between observed

species richness and species richness estimates (Spearman rank correlation p-values < 0.001).

Because there is variation in magnitude of estimated under-sampling of gamma diversity,

interpretations of results need to be viewed with caution. Based on the Chao estimates, 13 site

units have a shortfall of more than 30% (Table 2).
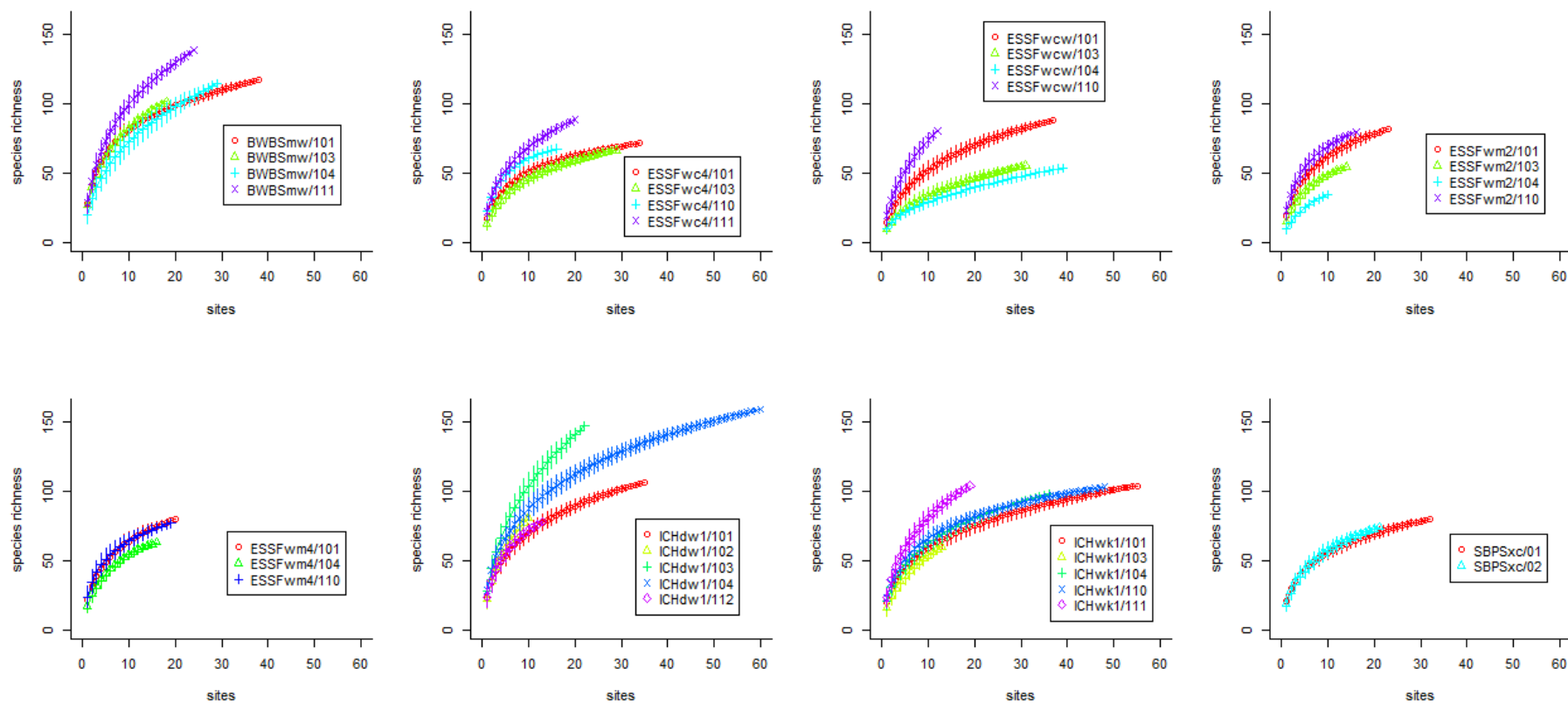
Figure 11: Species accumulation for 31 site units within 8 BEC subzones / variants. Where accumulation curve slopes do not level off, additional species are likely to be encountered should more sampling occur.

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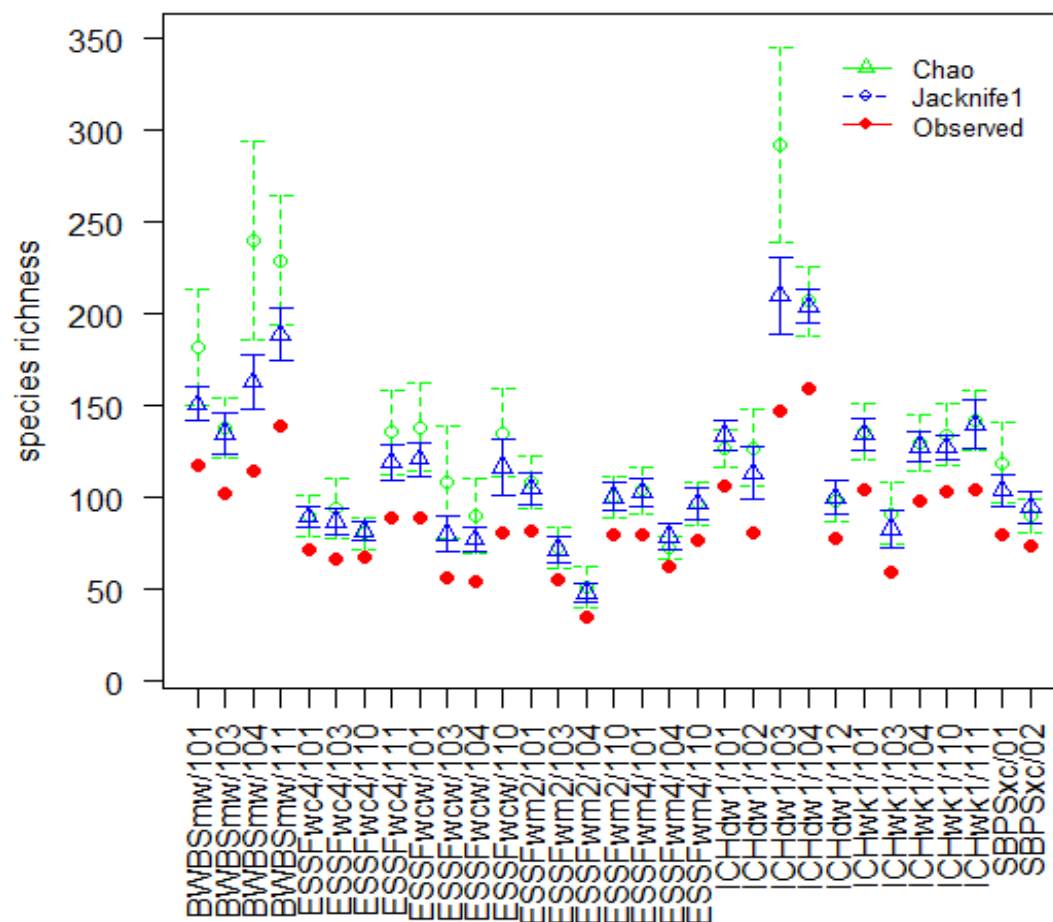
Figure 12. Observed, Chao, and Jackknife 1 species richness estimates for 31 site units (vertical lines represent standard error). Observed species richness shown as solid red circles.

Table 2: Thirteen site units where the percentage of under-sampled species exceeds 30%.

Site unit	Observed species richness	Chao species richness estimate	Percent shortfall (%)
BWBSmw/101	118	182	35
BWBSmw/104	115	240	52
BWBSmw/111	139	229	39
ESSFwc4/111	89	136	34
ESSFwcw/101	89	139	36
ESSFwcw/103	56	108	48
ESSFwcw/104	54	90	40
ESSFwcw/110	81	135	40
ESSFwm2/104	35	51	31
ICHdw1/102	81	127	36
ICHdw1/103	147	292	50
ICHwk1/103	60	91	34
SBPSxc/01	80	119	33

2.3.2 Beta diversity

Beta diversity (Jaccard dissimilarity) was high within all site units (Figure 13); between 59 and 74% of species were unshared between pairs of plots within the 31 site units studied. I observed evidence consistent with a role for dispersal limitation in 15 of 31 site units (Table 3) based on significant Mantel correlations (Figure 14, and Figures A2, A3 and A4 in the Appendix). Despite the apparent variation among site units in the importance of dispersal limitation, the null model results indicate that when the species pool was restricted to the site unit, dissimilarity between pairs of plots within each of the 31 site units was no different than expected based on random sampling from the regional species pool (Figure 15). When the regional species pool was expanded to include all species observed in the BEC variant / subzone, only 1 site unit (the 111 site unit of the Shuswap wet-cool ICH (ICHwk1/111); t-test p-value = 0.261) was no different than expected based on random sampling from the regional species pool (Figure 16). All other site units were more similar than expected based on random sampling from the regional species pool (t-test p-values < 0.05). Interestingly, the 110 site unit in the woodland wet-cool ESSF

(ESSFwcw/110) was significantly different from zero with a positive SES value; suggesting that species composition in the observed community was in fact more dissimilar than expected based on random sampling from the regional species pool (Chase and Myers 2011). When the regional species pool was expanded further to include all species observed in the dataset, mean pairwise SES values were all negative and significantly different from zero (t-test: p-value < 0.05) (Figure 17) indicating that composition was more similar than expected by chance. Despite the inclusion of more samples and species in species pools 2 and 3, species accumulation curves failed to level off and occupancy distributions remained highly skewed (Figures A5 and A6 in the Appendix).
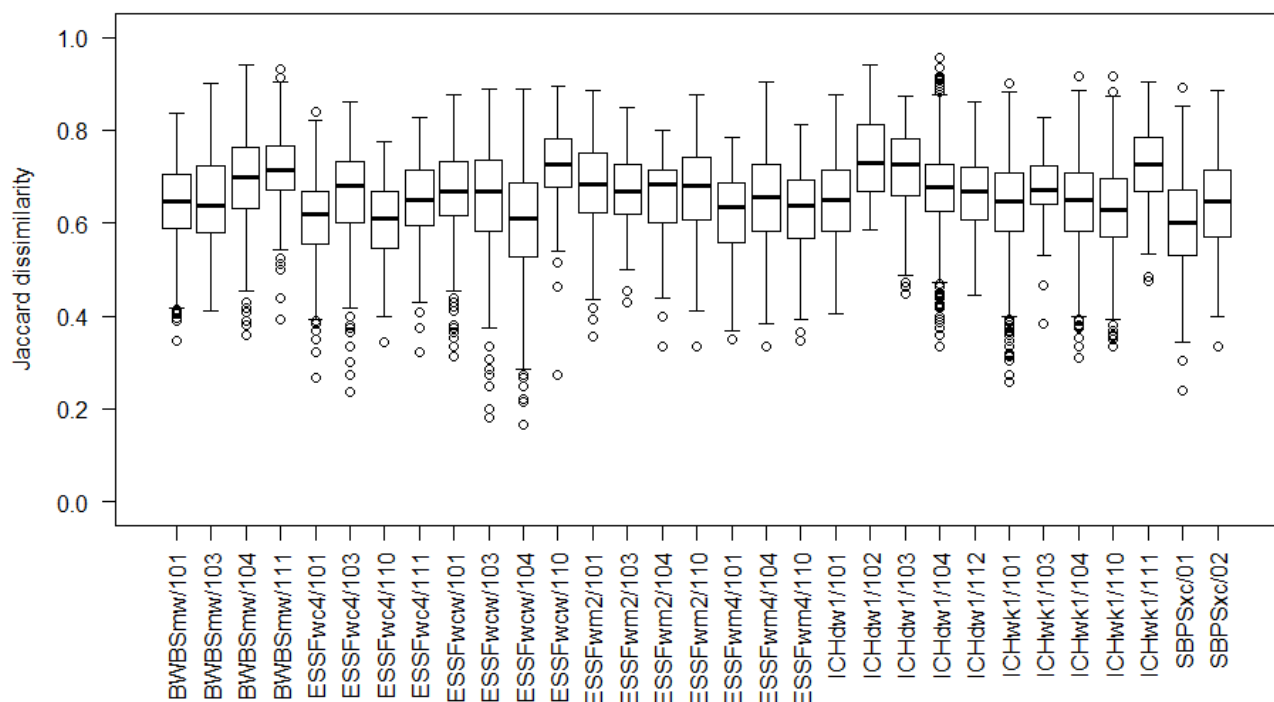
Figure 13: Observed Jaccard dissimilarity within 31 site units. Jaccard dissimilarity ranges from 0 to 1, with 0 being completely similar and 1 being completely dissimilar.

Table 3: Fifteen significant negative Mantel correlations between geographic distance and Jaccard similarity (α = 0.05). Mantel test performed on all 31 site units with 9999 permutations.

Site Unit	statistic	significance
BWBSmw/101	-0.1690761	0.0017
BWBSmw/103	-0.3338318	0.0181
BWBSmw/104	-0.1906109	0.0040
BWBSmw/111	-0.1800788	0.0438
ESSFwc4/110	-0.2349025	0.0105
ESSFwcw/101	-0.1548615	0.0051
ESSFwcw/103	-0.2131539	0.0189
ESSFwcw/104	-0.2072971	0.0024
ESSFwm2/101	-0.2208747	0.0118
ESSFwm2/110	-0.2471458	0.0158
ICHdw1/103	-0.1971284	0.0119
ICHwk1/101	-0.1609189	0.0003
ICHwk1/110	-0.1002068	0.0241
ICHwk1/111	-0.2290618	0.0118
SBPSxc/01	-0.1432826	0.0296
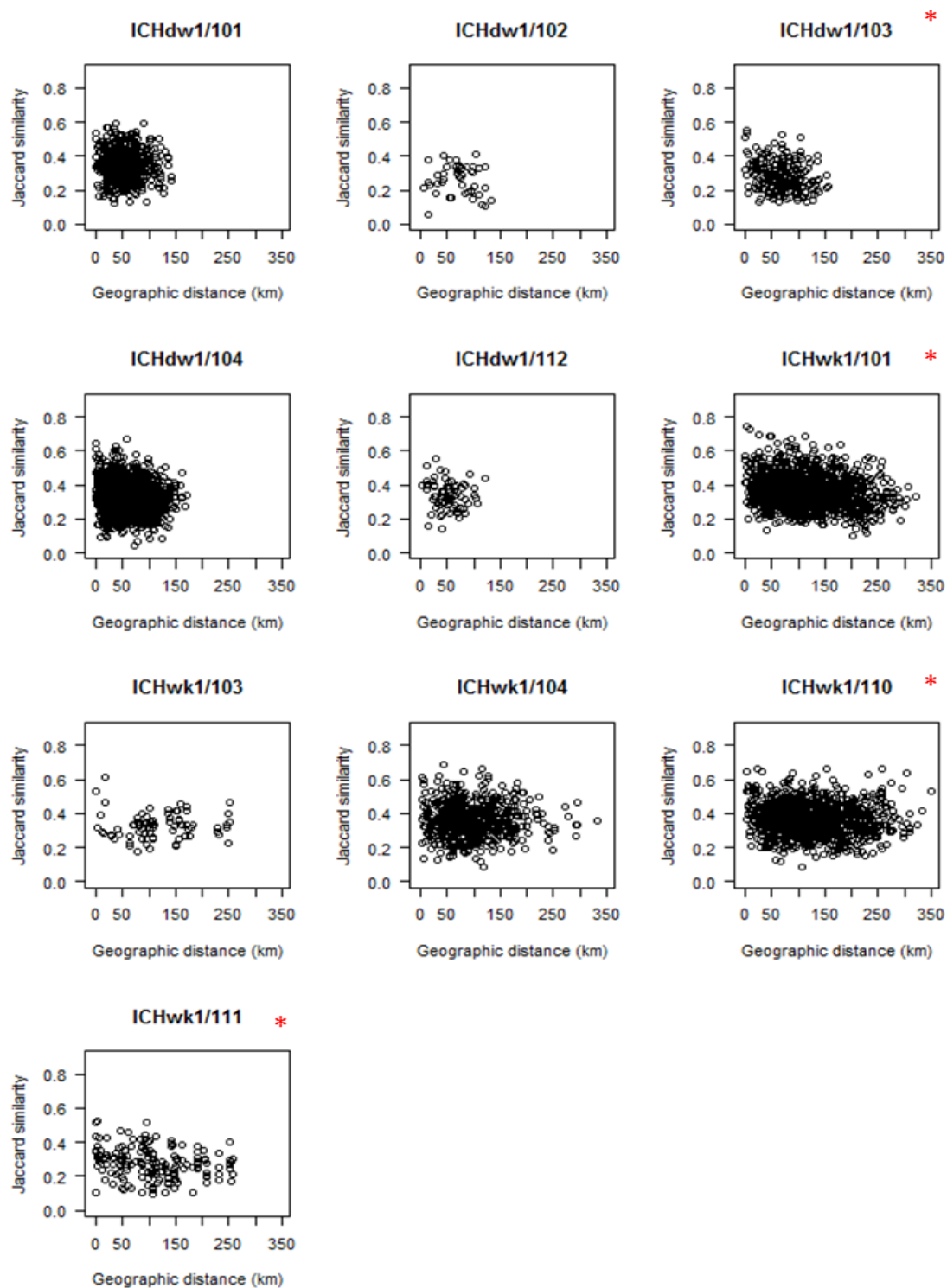
Figure 14: Sample distance-decay plots from 10 site units in the Interior Cedar Hemlock BEC zone. There is significant negative correlation between geographic distance (m) and Jaccard similarity (Mantel r < 0; Mantel p-value < 0.05) in 4 ICH site units (indicated with *). For all other site units see Figures A2, A3, and A4 in the Appendix.
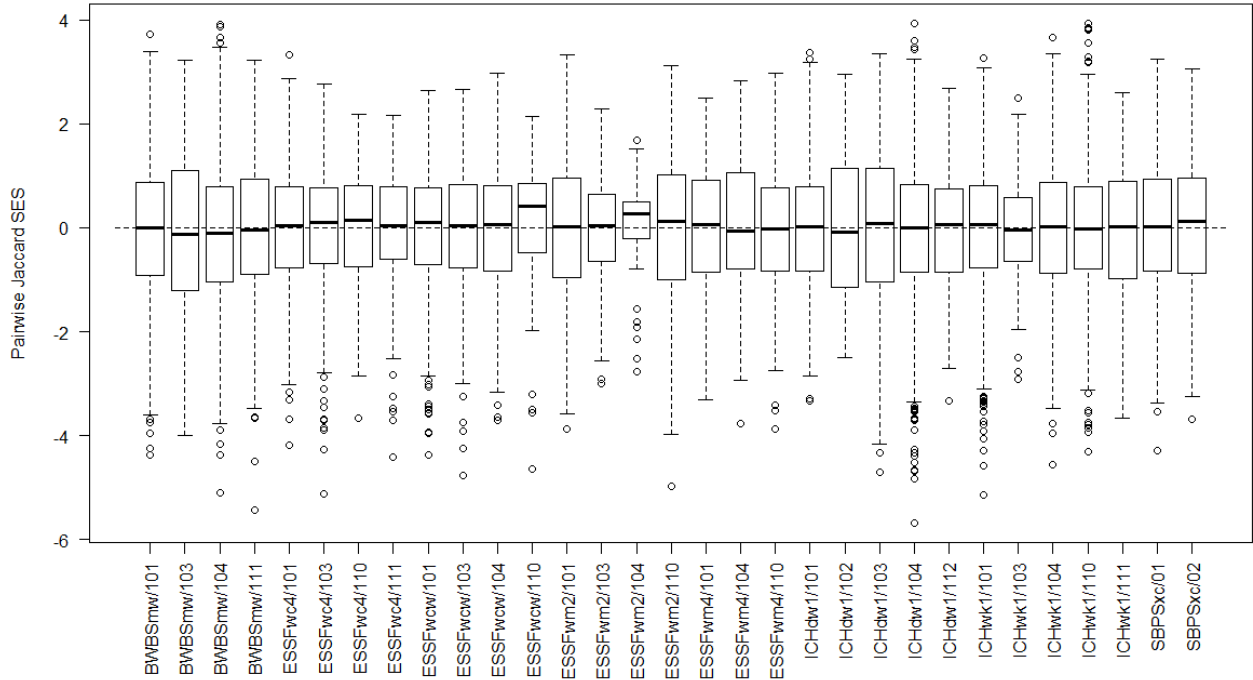
Figure 15: Pairwise Standard Effect Sizes (SES) for 31 site units using Jaccard dissimilarity values. Within each site unit, mean expected SES values are no different from zero (t-test, p-value > 0.05) when regional species pool is restricted to those species observed the site unit.
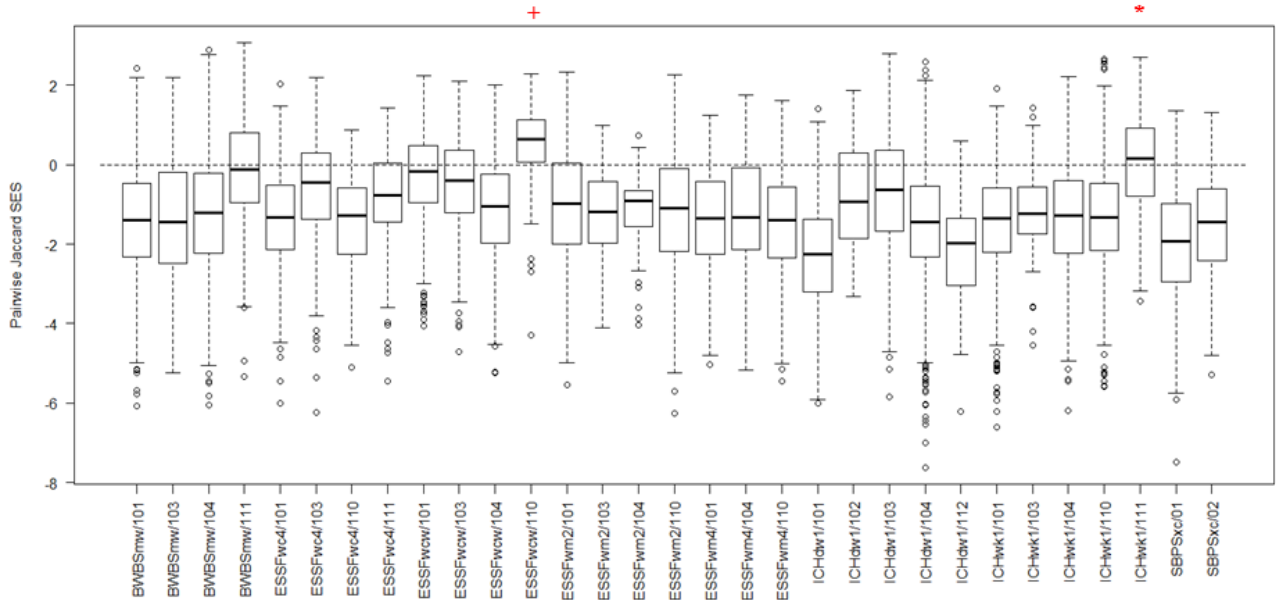
Figure 16: Pairwise Standard Effect Sizes (SES) for 31 site units using Jaccard dissimilarity values. Within each site unit, mean expected SES values are less than zero (negative t-test statistic, p-value < 0.05) for all site units except ICHwk1/111 (t-test, p-value > 0.05) – noted with * in figure. In addition, ESSFwcw/110 was significantly greater than zero (positive t-test statistic, p-value < 0.05) – noted with + in figure. Regional species pool is restricted to those species observed in the BEC subzone/variant.
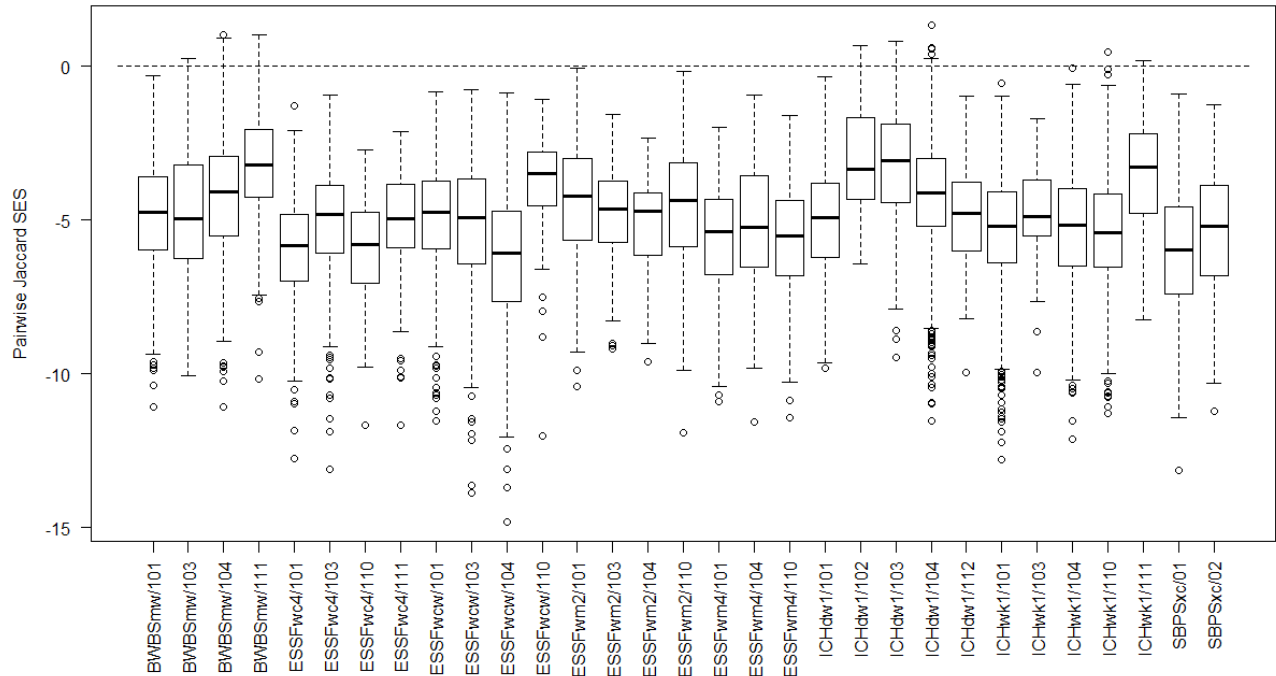
Figure 17: Pairwise Standard Effect Sizes (SES) for 31 site units using Jaccard dissimilarity values. Within each site unit, mean expected SES values are less than zero (negative t-test statistic, p-value < 0.05) for all 31 site units. Regional species pool is restricted to those species observed in the dataset (938 plots).

2.4 Discussion

In addition to quantifying patterns of alpha, beta and gamma diversity within site units, the primary aim of this chapter was test the degree to which patterns of beta diversity within site units differed from expectations based on stochastic community assembly. That is, does observed beta diversity differ from what would be expected if species in the regional species pool colonized sites at random? The results of my null model analyses indicate that beta diversity does not differ from what would be expected when the regional species pool was limited to the species observed within a given site unit. This finding supports the notion of equal vegetation potential within site units – the organization of species within a site unit does not appear to vary in a systematic way but rather is likely governed by community assembly processes such as drift that generate more random diversity patterns. To provide context for this finding, I first provide

results pertaining to alpha diversity and species occupancy patterns. I then discuss beta diversity patterns.

2.4.1 Explaining underlying species richness and occupancy patterns

The finding of a highly skewed species occupancy distribution (Figure A1 in the Appendix) is common, especially for perennial herbaceous species (McGeoch and Gaston 2002, Kammer and Vonlanthen 2009). Increasing the sample plot size could decrease the number of rare species and perhaps generate a more bimodal distribution; however, the observation that species occupancy distributions remain skewed regardless of sampling intensity across site units suggests that the observed species occupancy distribution is not an artefact of sample design (Kammer and Vonlanthen 2009). It is important to note however, that based on species accumulation curves, additional species would be encountered with continued sampling (Gotelli and Colwell 2001). An implication of many rare species (i.e., skewed species occupancy distribution in the regional species pool) is high beta diversity among plots (McGlinn and Hurlbert 2012) (Figure 18) due to the low probability of species being shared among multiple plots. Had species pool 2 or 3 resulted in more bimodal species occupancy distributions, lower beta diversity would have been expected and positive SES values could have been possible.

Increasing dissimilarity between pairs of communities →
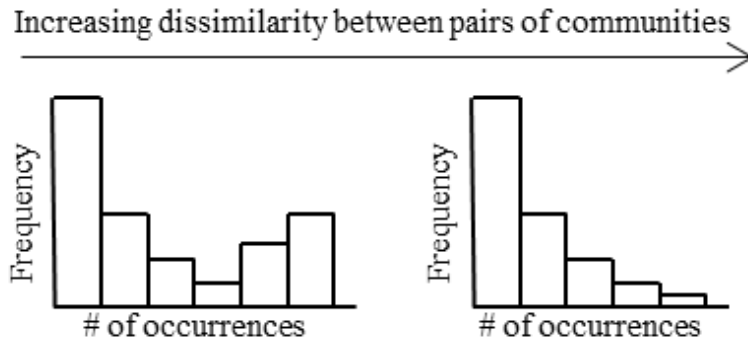
Figure 18: As the relative proportion of rare species increases (i.e., skewed species occupancy distributions contain mostly infrequent species), the dissimilarity increases as well.

With many infrequent species, it is not surprising that I observed that alpha diversity was consistently a low proportion (never more than 55%) of gamma diversity (Srivastava 1999, Loreau 2000). Interestingly, the proportion remained consistent, evident by the positive relationship between alpha and gamma diversity (Figure 19). Proportionally low alpha diversity relative to gamma diversity implies that while local site conditions are suitable for species observed in the community, they are potentially not capable of supporting all suited species observed across the community (i.e., within the site unit). Alternatively, all species do not have the dispersal capacity to reach each site. Given the assumption that vegetation within site units is capable of growing anywhere within the site unit, it is assumed that many species have equivalent ecological niches. This assumption is supported by Pojar et al. (1987) who state that few plant species in BC have narrow ecological niches (i.e., few are 'character' species).
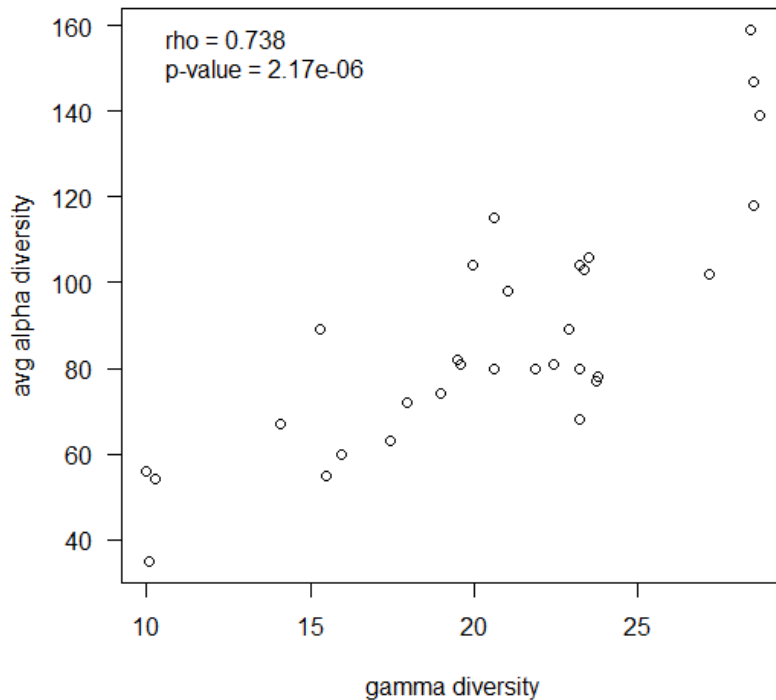
Figure 19: Positive correlation between average alpha diversity and gamma diversity across 31 site units (Spearman's rho = 0.738, p-value < 0.001).

2.4.2 Explaining beta diversity patterns

Beta diversity (as measured by Jaccard dissimilarity) was persistently high in all site units

examined, as expected in communities where alpha diversity is a low proportion of gamma

diversity (Jost et al. 2011) or in communities with many infrequent species (McGlinn and

Hurlbert 2012). This finding is interesting because if environmental filtering were strong, one

would expect low beta diversity (Stegen et al. 2012). In keeping with my assumption of

environmental homogeneity within site units, the finding of high beta diversity supports my

assertion that vegetation is not the only factor considered in the classification process – I would

have expected much lower beta diversity if site units were described primarily based on

similarity in plant community composition. High beta diversity among environmentally similar

plots can be the result of multiple ecological processes including dispersal, drift and speciation,

as discussed in Chapter 1. The results of the null model analyses are consistent with a primary

role for stochastic assembly (as discussed by Chase and Myers 2011) within plant communities defined by BEC site unit (when the regional species pool was restricted to the species observed within a given site unit).

Typically, the relative influence of dispersal and selection cannot be easily disentangled because both are related to distance between sites (Bell et al. 2006); however, by using plot data that controls for environmental variation (environmental selection), I was able to isolate the influence of dispersal following the approach recommended by Gilbert and Lechowicz (2004). I found the evidence for dispersal limitation to be inconsistent, with significant Mantel test results in only 15 of 31 site units (Table 3). It is possible that environmental gradients are still influential and in order to be more definitive on the role of dispersal limitation, future analyses should also test for the strength of the relationship between composition similarity and climatic or other environmental variables. Aside from dispersal limitation, priority effects could explain the strength of stochastic processes; given the low occupancy rates, it is also possible that many species are not widespread and therefore not capable of dispersing in the same order to all new sites following natural disturbances. In ecosystems with many ecologically equivalent species, drift (colonization and extinction) can have an important role in community assembly because there are no selective processes influencing some species more than others (Vellend 2010).

I do recognize that subtle environmental gradients within site units could explain at least some of the observed beta diversity. In addition, natural disturbance history was not examined and is an important factor influencing vascular plant community assembly in BC ecosystems (DeLong 2007). These factors should be considered in future research to fully understand the relative importance of different community assembly processes.

2.4.3 The importance of the regional species pool

The null model analyses with alternate species pools were necessary to test the sensitivity of the results to the definition of the regional species pool (Chase et al. 2011). Expanding the species pool to include species outside the site unit resulted in support for deterministic assembly processes (environmental selection) evident by the negative SES values for most site units (Figures 16 and 17). Evidence against the importance of stochastic processes emerges when species are drawn from multiple community types; that is, there is support for classification of site units based on systematic clustering of species composition within site units. A probable explanation of this observation is environmental-mediated selection caused by environmental variation that occurs among BEC site units, subzones and zones, as variation in species diversity is common across environmental gradients (Rey Benayas 1995, Jones et al. 2008, Qian and Ricklefs 2011, Grace et al. 2011). It is also possible that the classification process is responsible for similarity in species composition within site units when compared to a broader species pool. Alternatively, negative SES values could be present if geographic dispersal limitation was significant; close sites would be more similar than distant sites resulting in systematic clustering of species composition similarity over space (Chase and Myers 2011, Kraft et al. 2011).

I found inconsistent results when the species pool was restricted to the species observed in the BEC subzone / variants (Figure 16). The ICHwk1/111 was the only site unit where beta diversity was no different than expected by randomly sampling species from the regional species pool. It is possible that stochastic processes are influential in the ICHwk1/111. It is also possible that species within the ICHwk1/111 were more common in the BEC variant (ICHwk1) than species observed in other site units and therefore more likely to be selected in random sampling procedures. In the ESSFwcw/110 on the other hand, composition was more dissimilar than

expected based on random sampling from the BEC variant species pool. One possible

explanation for the dissimilarity in the ESSFwcw/110 is under-sampling (Figure 11) – the

ESSFwcw/110 contains few species that are shared among other site units in the ESSFwcw.

Other possible explanations include environmental selection and dispersal limitation that causes

plots within the ESSFwcw/110 to be drastically different from one another (Chase and Myers

2011, Stegen et al. 2012).

Chapter 3: Diversity patterns of lifeforms (trees, shrubs, herbs)

3.1 Summary

Understanding patterns of understory vascular plant diversity, which plays a critical role in ecosystem processes, is important for biodiversity conservation objectives of sustainable forest management (Hart and Chen 2008). In my analysis of beta diversity of vascular plants in Chapter 2, patterns were not considered with respect to specific plant lifeforms; however, plant lifeforms differ in terms of species richness, niche breadth and dispersal capacity (Reilly et al. 2006, Wang et al. 2009, Jayakumar and Nair 2012). It is therefore informative to understand whether patterns of alpha, beta and gamma diversity differed among plant lifeforms. In this chapter I present results from alpha, gamma and beta diversity analyses of tree, shrub and herb forest layers using 809 BEC plots provided by the MFLNRO. The objectives of this chapter are to (i) describe alpha, beta and gamma diversity of each forest layer within 31 site units described by BEC and (ii) to test the hypothesis that beta diversity of plant lifeforms (trees, shrubs and herbs) among sites within BEC site units is no different from that expected under stochastic (random) community assembly.

3.2 Methods

3.2.1 Vegetation plot data

I used the same dataset that I used in Chapter 2 for the analyses of alpha, beta, and gamma diversity patterns of different lifeforms. As described in Chapter 2, the 809 plots are from 31 unique site units belonging to 8 different BEC subzones / variants (Figure 6). The procedures outlined in Chapter 2 for filtering and organizing plot data remain the same. To distinguish

different forest layers, the lifeform designations from the 2009 BC Species List (Meidinger et al. 2009) were used (Table 4).

Table 4: Description of growth forms grouped into tree, shrub and herb designations. Lifeform and growthform data were extracted from the 2009 BC Species List.

Layer designation used	Lifeform	Growthform
Tree	1	Coniferous tree
	2	Deciduous tree
Shrub	3	Evergreen shrub
	4	Deciduous shrub
	12	Dwarf woody plant
Herb	5	Fern or fern-ally
	6	Graminoid
	7	Forb
	8	Parasite or sparophyte

3.2.2 Data analysis

3.2.2.1 Alpha, beta and gamma diversity

For each forest layer, I calculated alpha diversity as the number of species within a plot and mean alpha diversity as the average number of species per plot within a given site unit. I calculated gamma as the total number of tree, shrub or herb species within a site unit. To assess the degree of under-sampling in communities, I plotted species accumulation curves for all site units for each forest layer. Accumulation curves were plotted using the "accumcomp" function in the *BiodiversityR* package in R (Kindt and Coe 2005). Chao and Jackknife 1 species richness estimates were calculated as in Chapter 2, but in this case for tree, shrub and herb species separately.

I calculated observed beta diversity using the Jaccard dissimilarity metric ($\beta_j = 1 - a/(a+b+c)$). I tested for the influence of dispersal limitation using the Mantel test on the correlation between geographic distance and composition similarity for each lifeform as described in Chapter 2. I

applied the permatfull null model (Figure 8) to the presence-absence species matrices for each

forest layer in each site unit in order to determine whether or not species composition differed

from what was expected based on random sampling from the species pool. As was done in

Chapter 2, average expected pairwise beta diversity was compared to average observed pairwise

beta diversity in each site unit and for each forest layer to calculate the Standardized Effect Size

($SES = (mean\ \beta_j - mean\ \beta_{exp}) / s.d.\ \beta_{exp}$). I then used the t-test to determine whether the deviation

between observed and expected values (SES) within each site unit was different from zero.

3.2.2.2 Species pool sensitivity analysis

I repeated the null model beta diversity analyses with three different species pools following the

procedures used in Chapter 2, but this time for each lifeform independently, as follows: (1) all

trees, shrubs or herbs observed in the 809 plots (i.e., gamma diversity), (2) all trees, shrubs or

herbs observed in the BEC subzone / variant and (3) all trees, shrubs or herbs observed in the

dataset. As mentioned in the previous chapter, species pool definitions were kept within the

bounds of BEC due to lack of knowledge regarding species' physiological tolerances and

environment-specific fitness characteristics. Again, additional species in species pools 2 and 3

from plots that were removed from analyses due to under-sampling (i.e., site units with 10 or

fewer plots) were included resulting in 938 plots from which to generate permuted communities

with the expanded species pools. When I calculated the SES for the null model analyses using

species pools 2 and 3, the number of plots in the observed and expected site-by-species matrices

were kept equal.

3.3 Results

3.3.1 Alpha and gamma diversity of different lifeforms

Of the 464 species that I observed in the 809 BEC plots, 75% were herbaceous, 18% were shrub

and 7% were tree species (Table 5). Alpha diversity was variable across plots (large spread

within site units) and differed in mean values among site units (Figure 20). For tree species,

average alpha diversity was as low as 1.71 species in the 02 site unit in the very dry cold SBPS

(SBPSxc/02) and as high as 5.86 species in the 101 site unit in the West Kootenay dry-warm

ICH (ICHdw1/101) (standard deviation = 0.90 and 1.78 respectively). For shrub species, alpha

diversity was as low as 2.58 species in the ESSFwcw/110 and as high as 11.35 species in the 104

site unit in the West Kootenay dry-warm ICH (ICHdw1/104) (standard deviation = 2.15 and 2.63

respectively). For herb species, alpha diversity was as low as 3.10 in the ESSFwm2/104 and as

high as 17.54 species in the BWBSmw/111 (standard deviation = 3.57 and 6.19 respectively).

Highly skewed species occupancy distributions for each lifeform were observed, with most

species occurring infrequently (Figure 21). The proportion of gamma diversity represented in a

given plot was highest for tree species (up to 100%) followed by shrub (up to 73%) then

herbaceous (up to 60%) species. Species accumulation curves showed that herbaceous species

were the most under sampled (Figure 22) when compared to shrubs (Figure 23) or trees (Figure

24).

Table 5: Number of species represented in each growthform. Growthform designations taken from the 2009 Provincial Species code list (Meidinger et al. 2009)**.**

Growthform	No. of species	Total no.
broad-leaved tree	14	
coniferous tree	19	33
deciduous shrub	59	
dwarf woody plant	19	
evergreen shrub	7	85
fern or fern-ally	30	
forb	225	
graminoid	83	
parasite or sparophyte	8	346
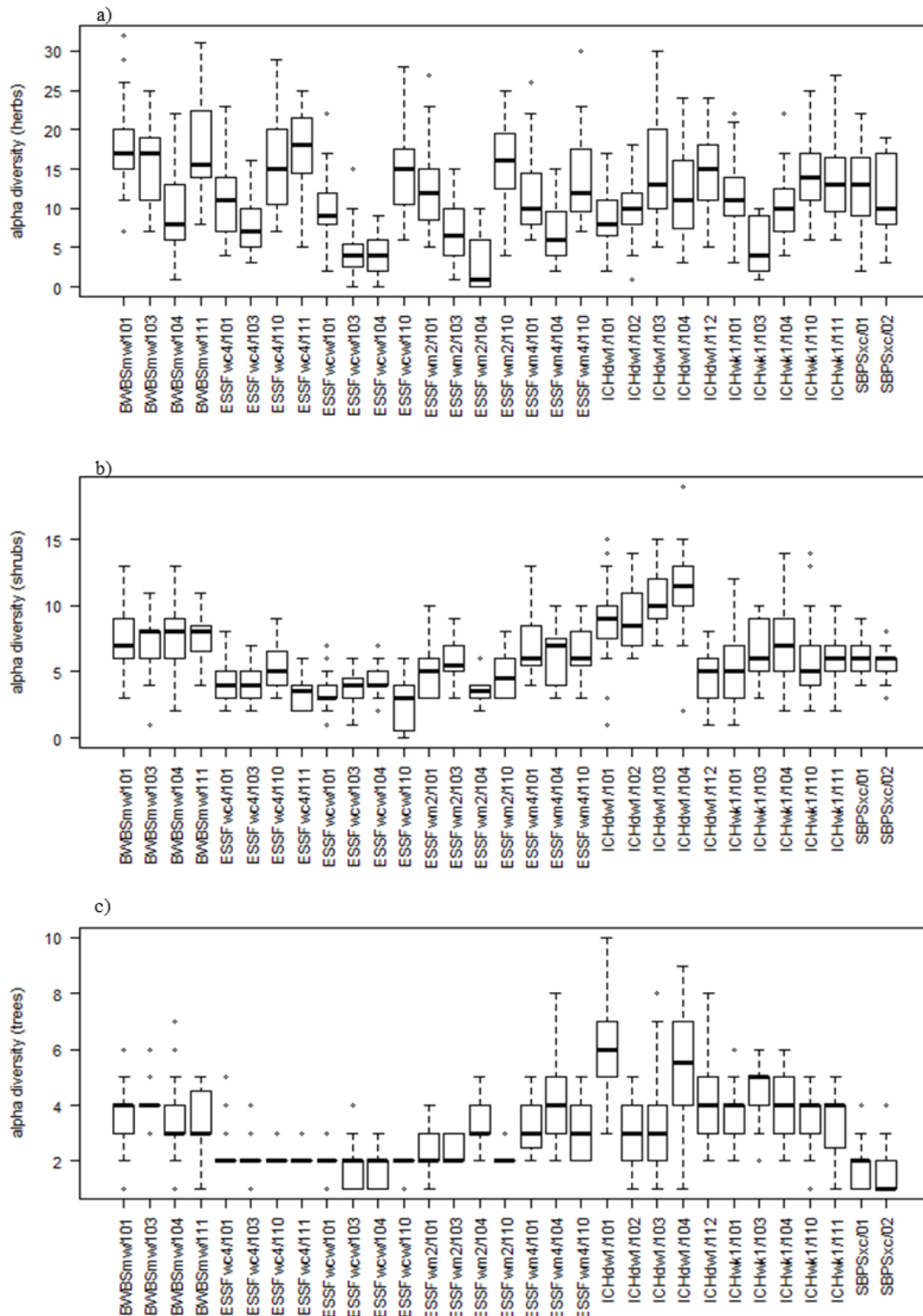
Figure 20: Alpha diversity in 31 site units (809 plots) for a) herb, b) shrub and c) tree species. Each site unit has 10 or more plots.
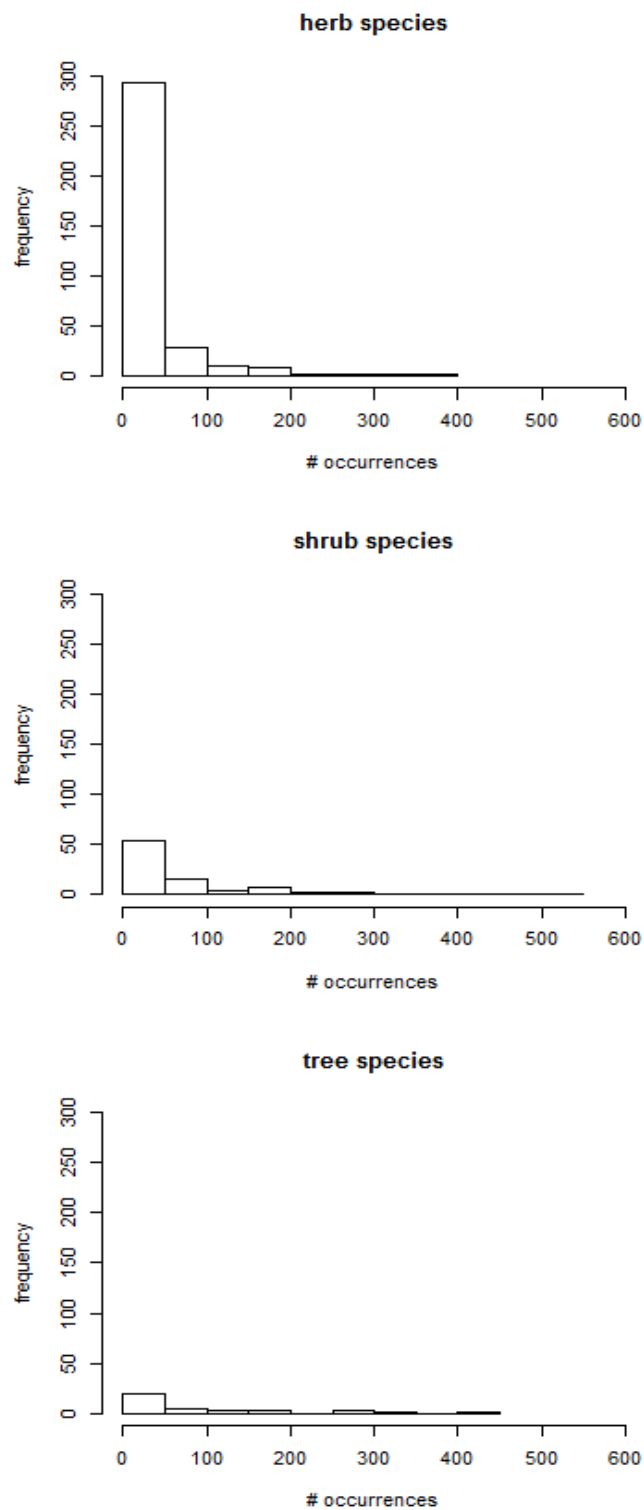
Figure 21: Species occupancy distribution for herb, shrub and tree species across 809 BEC plots. All lifeforms have more infrequent than frequent species.
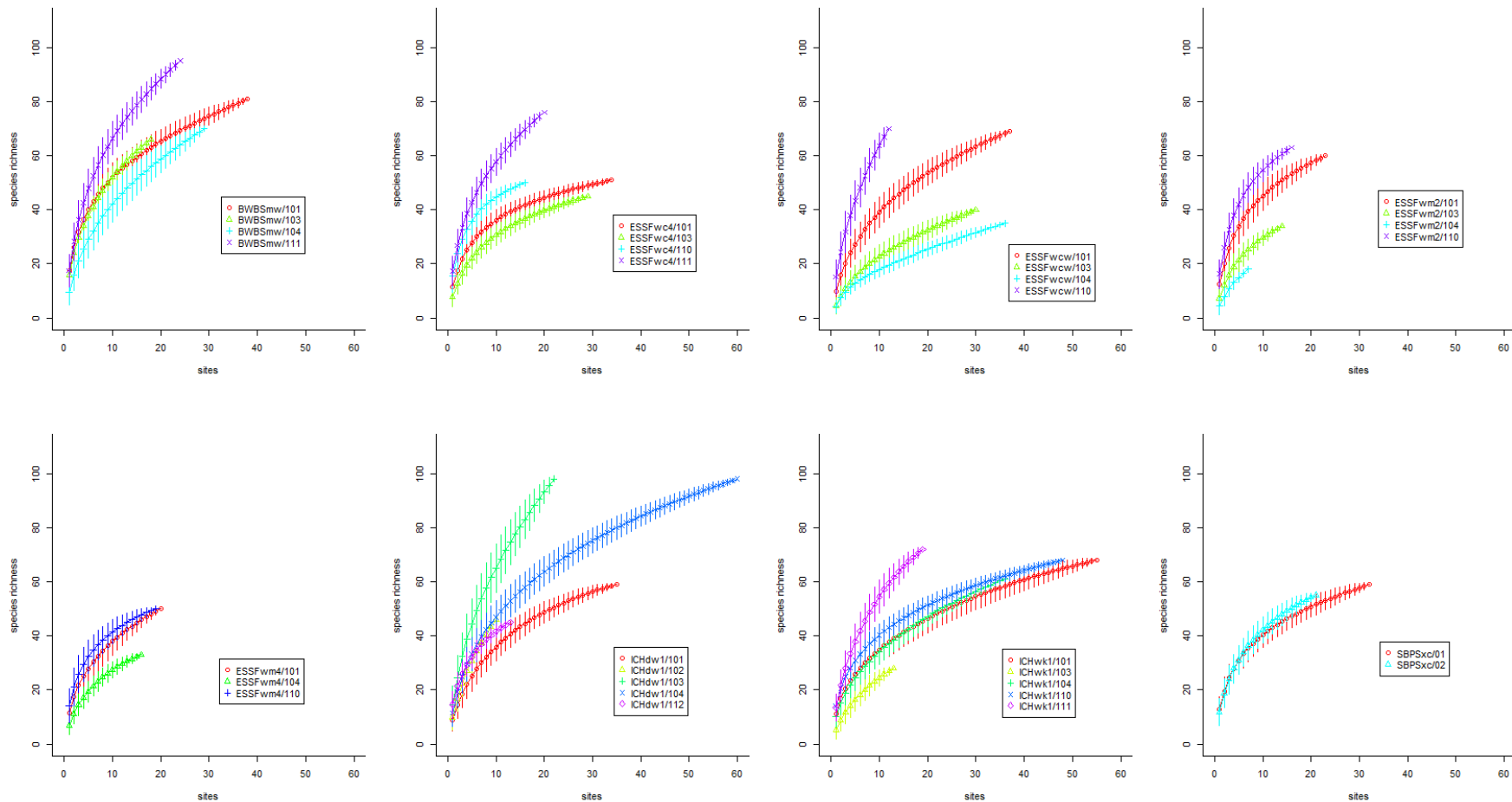
Figure 22: Herb species accumulation curves for 31 site units within 8 BEC subzones / variants. Where accumulation curve slopes do not level off, additional herb species are likely to be encountered should more sampling occur.
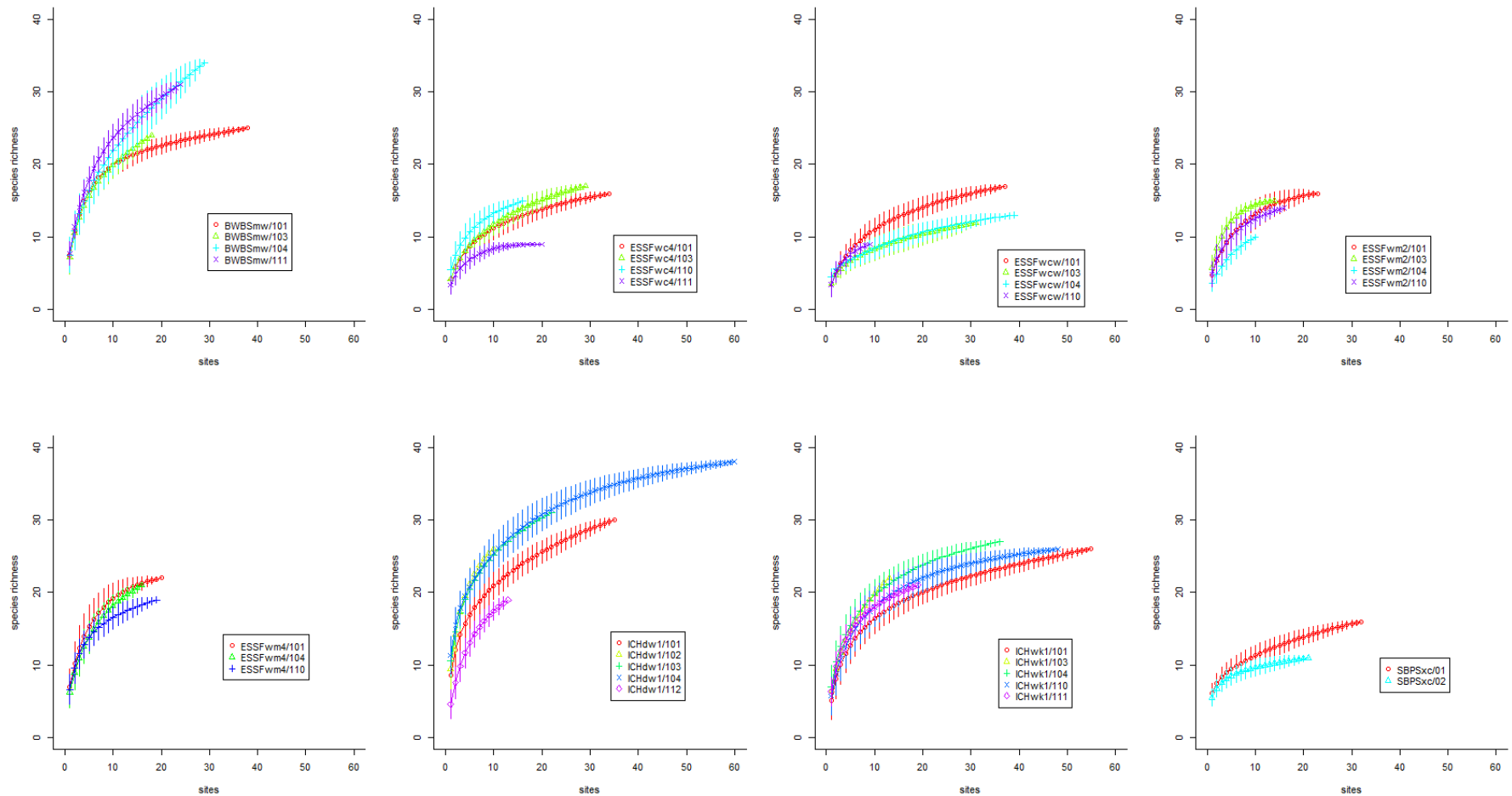
Figure 23: Shrub species accumulation for 31 site units within 8 BEC subzones / variants. Where accumulation curve slopes do not level off, additional shrub species are likely to be encountered should more sampling occur.

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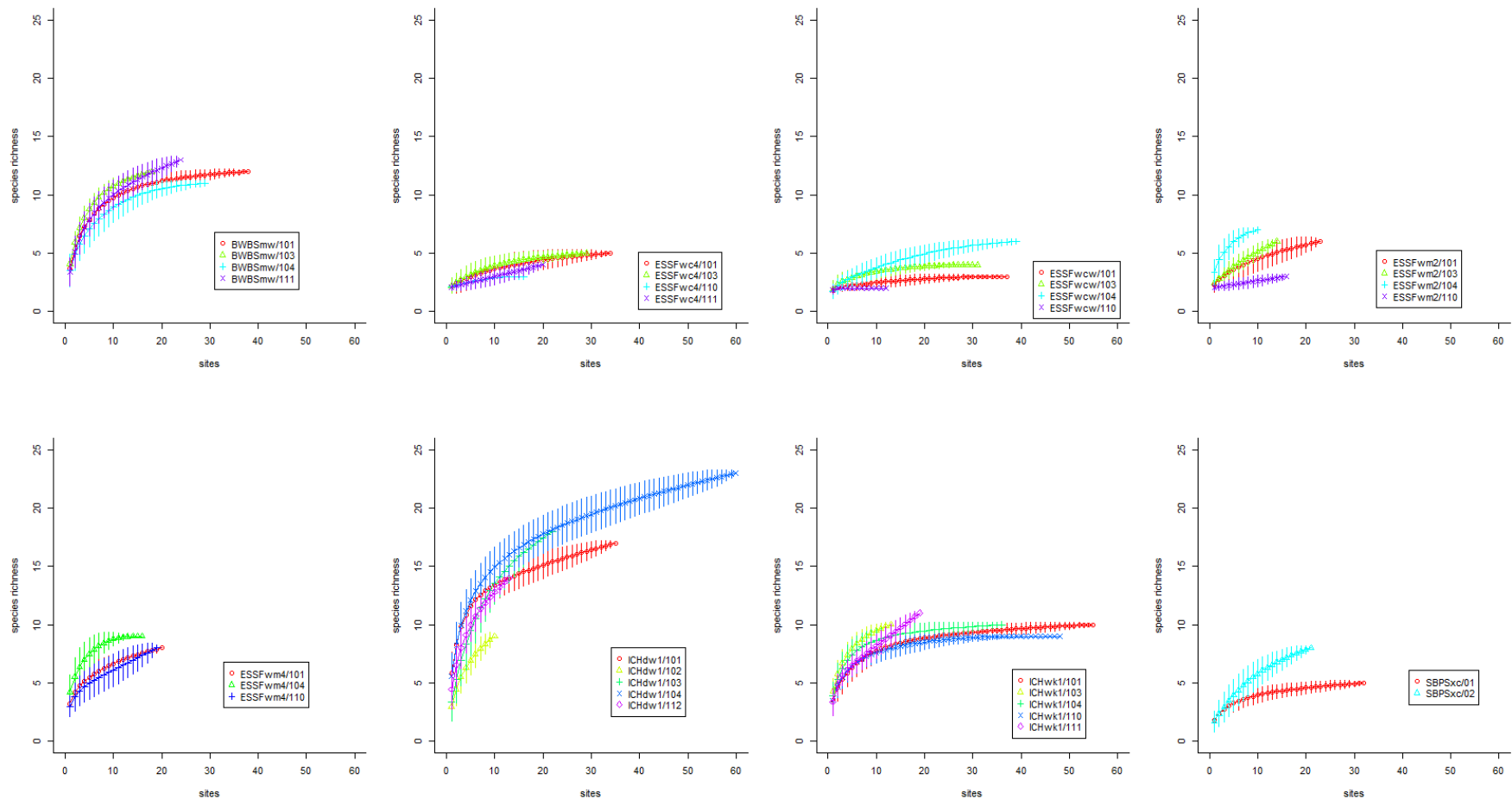
Figure 24: Tree species accumulation for 31 site units within 8 BEC subzones / variants. Where accumulation curve slopes do not level off, additional tree species are likely to be encountered should more sampling occur

3.3.2 Beta diversity of lifeforms

Jaccard dissimilarity was highest for herbs, followed by shrubs then trees (Figure 25): on average, between 63 and 91% of herb species were unshared, between 36 and 78% of shrub species were unshared and between 4 and 70% of tree species were unshared. Consistent with my predictions, significant negative correlations between geographic distance and compositional similarity were most prevalent for herbs (15 site units) followed by shrubs (10 site units) then trees (3 site units) (Table 6). Evidence consistent with a role for dispersal limitation (i.e., significant negative Mantel correlation results at $\alpha = 0.05$) was inconsistent among site units, occurring in at most 15 of 31 site units (herb species). The results of the null model analysis where the species pool was restricted to species observed in a given site unit, showed that dissimilarity between pairs of plots within each of the 31 site units was no different than expected based on random sampling of species from the regional species pool for herb (Figure A7 in the Appendix), shrub (Figure A8 in the Appendix) and tree (Figure A9 in the Appendix) species.
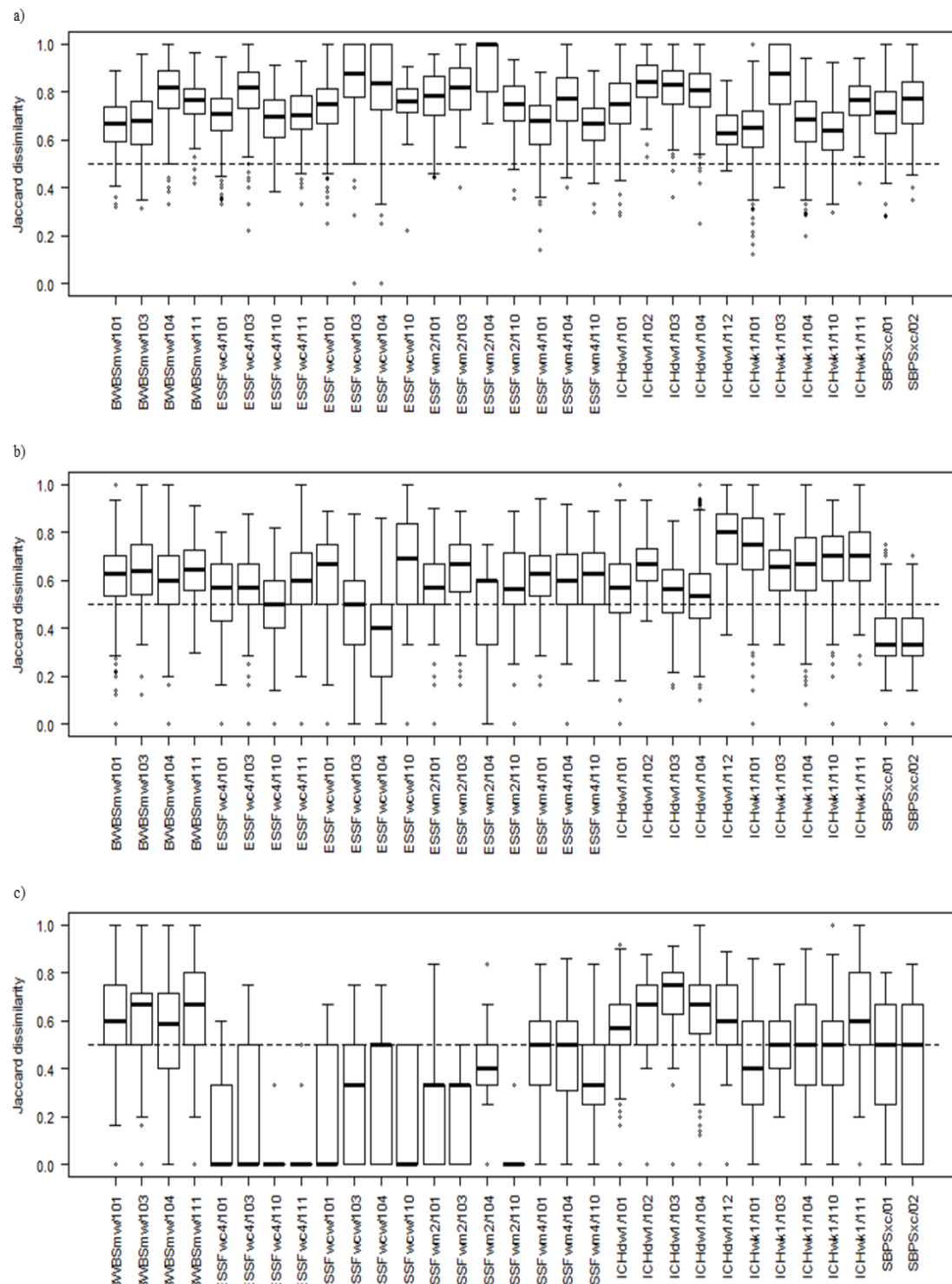
Figure 25: Observed Jaccard dissimilarity in 31 site units for a) herb, b) shrub and c) tree species. Dashed line drawn at Jaccard dissimilarity of 0.5 to ease in visual comparison among lifeforms.

Table 6: Significant negative Mantel correlation results for the relationship between geographic distance and species composition similarity (α = 0.05) for a) herb species, b) shrub species and c) tree species. Mantel tests performed on 31 site units for each lifeform. 9999 permutations used in each analysis.

a)

Site Unit	herb species statistic	significance
BWBSmw/103	-0.3052599	0.0293
BWBSmw/104	-0.1355443	0.0243
BWBSmw/111	-0.1664927	0.0458
ESSFwc4/101	-0.1305655	0.0294
ESSFwc4/110	-0.2696788	0.0049
ESSFwcw/101	-0.1100824	0.0473
ESSFwcw/104	-0.1713967	0.0074
ESSFwcw/110	-0.2818802	0.0228
ESSFwm2/101	-0.2498937	0.0035
ESSFwm2/104	-0.6056407	0.0328
ESSFwm2/110	-0.2431862	0.0158
ICHdw1/103	-0.2167101	0.0053
ICHwk1/101	-0.1277878	0.0036
ICHwk1/110	-0.1134196	0.0177
SBPSxc/01	-0.1550737	0.0211

b)

Site Unit	shrub species statistic	significance
BWBSmw/101	-0.1964083	0.0004
BWBSmw/103	-0.2504798	0.0391
BWBSmw/104	-0.2620714	0.0002
ESSFwc4/111	-0.2357869	0.0262
ESSFwcw/101	-0.1567393	0.0045
ESSFwcw/103	-0.2644282	0.0061
ESSFwcw/104	-0.2134547	0.0083
ESSFwm2/103	-0.2431613	0.0441
ESSFwm4/110	-0.2010355	0.0210
ICHwk1/101	-0.1239581	0.0032

c)

Site Unit	tree species statistic	significance
BWBSmw/101	-0.2122672	0.0005
ESSFwcw/104	-0.1184055	0.0388
ICHwk1/111	-0.3575388	0.0007

For the null model analysis where the regional species pool was expanded to include all species observed in the BEC variant / subzone, I found that 5 site units were no different than expected based on random sampling from the regional species pool (Figure 26) for herb species, while 3 site units for shrub species (Figure 27) and 4 site units for tree species (Figure 28) were no different than expected. Interestingly, the ICHwk1/111 was significantly different from zero with a positive SES value in both the herb and tree analysis. When the regional species pool was expanded further to include all species observed in the dataset, I found that mean pairwise SES values were all negative and significantly different from zero (t test p-values < 0.05) for herb (Figures A10 in the Appendix), shrub (Figure A11 in the Appendix) and tree (Figure A12 in the Appendix) species.
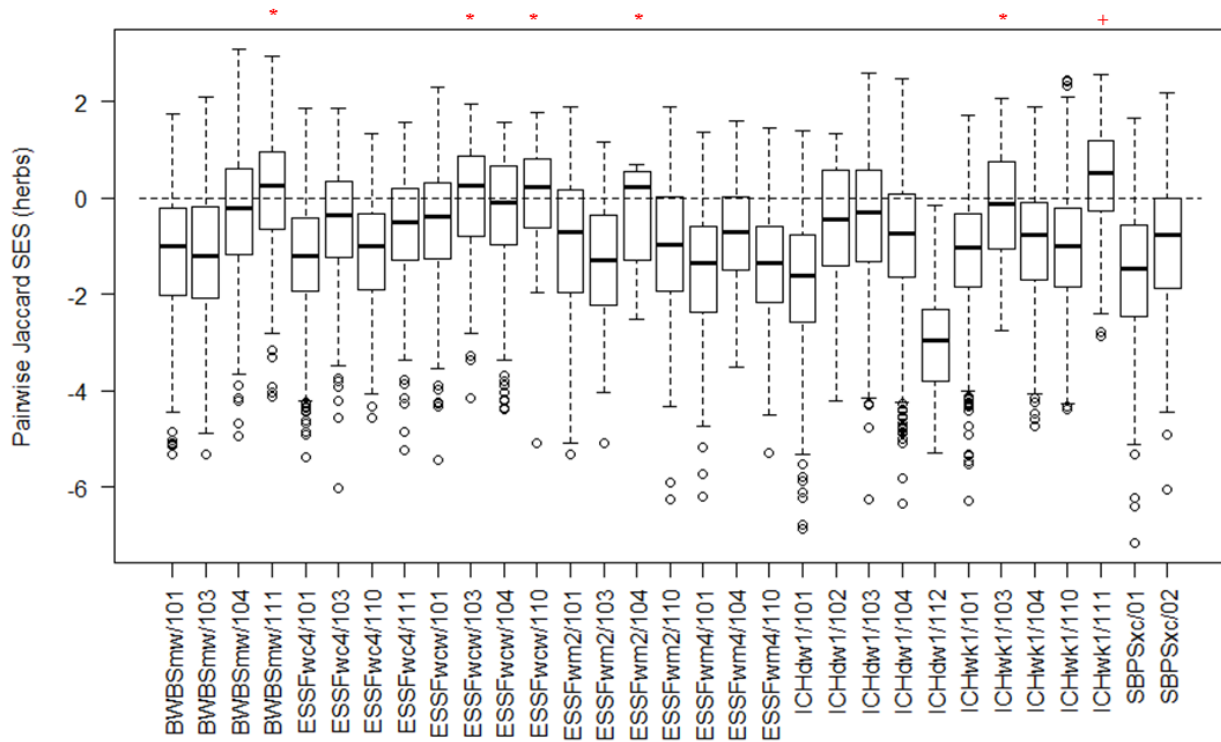
Figure 26: Pairwise Standard Effect Size (SES) values for herb species in 31 site units using Jaccard dissimilarity values. Within each site unit, mean expected SES values are less than zero (negative t-test statistic, p-value < 0.05) for all site units except BWBSmw/111, ESSFwcw/103, ESSFwcw/110, ESSFwm2/104 and ICHwk1/103 (t-test, p-value > 0.05) – noted with * in figure. In addition, ICHwk1/111 was greater than zero (positive t-test statistic, p-value < 0.05) – noted with + in figure. Regional species pool is restricted to those herb species observed in the BEC subzone/variant.
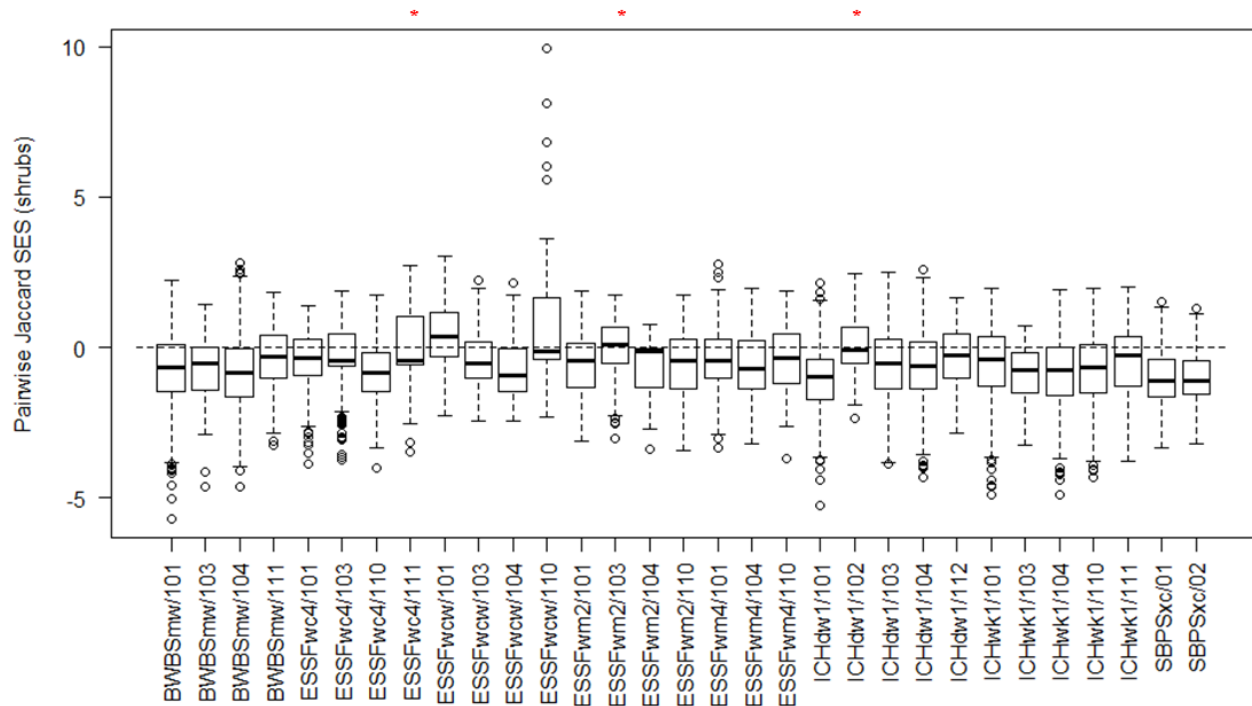
Figure 27: Pairwise Standard Effect Sizes (SES) for shrub species in 31 site units using Jaccard dissimilarity values. Within each site unit, mean expected SES values are less than zero (negative t-test statistic, p-value < 0.05) for all site units except ESSFwc4/111, ESSFwm2/103 and ICHdw1/102 (t-test, p-value > 0.05) – noted with * in figure. Regional species pool is restricted to those shrub species observed in the BEC subzone/variant.
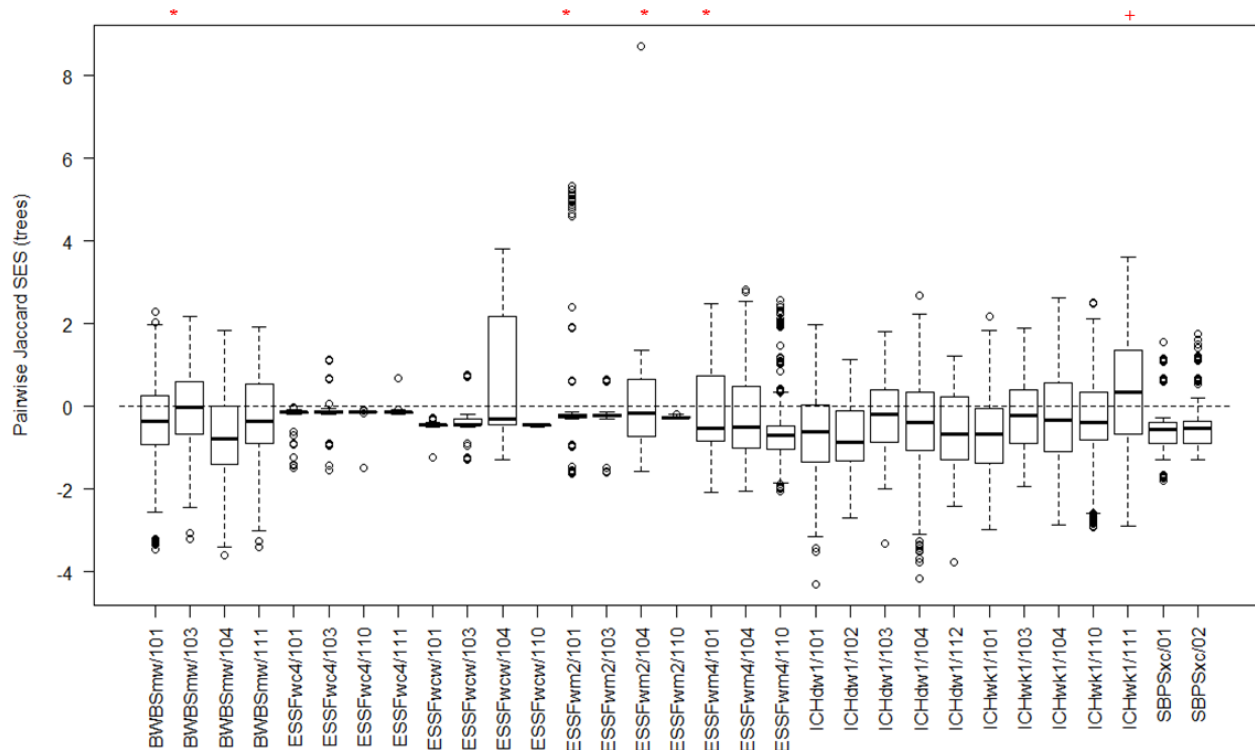
Figure 28: Pairwise Standard Effect Sizes (SES) for tree species in 31 site units using Jaccard dissimilarity values. Within each site unit, mean expected SES values are less than zero (negative t-test statistic, p-value < 0.05) for all site units except BWBSmw/103, ESSFwm2/101, ESSFwm2/104 and ESSFwm4/101 (t-test, p-value > 0.05) – noted with * in figure. In addition, ICHwk1/111 was significantly greater than zero (positive t-test statistic, p-value < 0.05) – noted with + in figure. Regional species pool is restricted to those tree species observed in the BEC subzone/variant.

For herb species, occupancy distributions were skewed regardless of how species pools were defined (Figure 21; Figures A13 and A14 in the Appendix). On the other hand, shrub and tree species occupancy distributions were sometimes even or bimodal within site unit or BEC subzones / variants (Figures A15, A16, A17 and A18 in the Appendix).

3.4 Discussion

Of the lifeforms, tree species were the best represented (slopes of tree species accumulation curves leveled off (Figure 24) when compared to shrubs (Figure 23) or herbs (Figure 22), which is not surprising given the comparably low species richness and wide geographic distributions of tree species (Austin et al. 2008). Highly skewed species occupancy distributions of herb and

70

some shrub and tree species in site units highlight the prevalence of uncommon species in BC. Not surprisingly, I observed highest Jaccard dissimilarity in herb assemblages (Figure 25), in part due to higher gamma diversity and a lower proportion of gamma diversity represented in alpha diversity as compared to shrub and tree species. This finding is consistent with other analyses of beta diversity of different plant lifeforms communities (Rey Benayas 1995).

On average, not more than 37% of herb species and 64% of shrub species were shared among pairs of plots within a given site unit, which, similar to the results in Chapter 2, is somewhat surprising given that BEC relies in part on vegetation to group plots in classifications based on similarities in plant species composition. Supporting my assertion that tree species would have lower Jaccard dissimilarity due to greater dispersal capabilities and wider ecological niches, tree Jaccard dissimilarity was lower than for herb and shrub species. The BEC plots used in this study all originate in mature conifer-dominated forests and therefore one might expect some site units to be completely similar in terms of tree species composition, especially in high elevation communities (ESSF site units) where tree gamma diversity is low (Table 1). On average, there was always some degree of dissimilarity in tree species among pairs of plots in the 31 site units examined in my research.

The null model analysis results when the species pool is restricted to those species observed in a given site unit support the notion that site units have similar vegetation potential because observed Jaccard dissimilarity is no different than expected if one were to randomly sample species from the regional species pool regardless of plant lifeform. I cannot confirm that Jaccard dissimilarity is the result of stochastic community assembly processes; however the processes that are responsible for generating composition dissimilarity appear to be random, which is typical of stochastic processes including drift (Vellend 2010). Importantly, Jaccard dissimilarity

of tree species is already low in many site units suggesting that filtering of species has already occurred, yielding similar composition among most plots (Figure A17).

The sensitivity analysis of expanded species pools yielded similar results to when all species were considered together in Chapter 2: deterministic processes (environmental selection that occurs across environmental gradients) appear to be important for filtering species within a given site unit when the potential species pool spans the geographic extent of the data set because Jaccard dissimilarity is different from that expected by randomly sampling species from the regional species pool (Figures A10, A11 and A12 in the Appendix). The support for deterministic processes is based on findings of Chase and Myers (2011), Myers et al. (2012) and others that negative SES values are indicative of species filtering brought on by dispersal or niche constraints that occur over large geographic and environmental gradients (e.g., Harrison et al. 1992, Pulliam 2000, Cumming 2007, Aitken et al. 2008). Even when the species pool was expanded to species in the BEC subzone / variant (species pool 2), most site units were more different than expected based on random sampling of species from the regional species pool. Jaccard dissimilarity in a handful of site units (Figures 26, 27 and 28) for each lifeform remained no different than expected based on random sampling from the species pool. As discussed in Chapter 2, it is possible that these site units (Table 7) contain a higher proportion of common species with the regional species pool than other site units. It is also possible that stochastic processes such as colonization and extinction dynamics are important. In addition, the ICHwk1/111 was more dissimilar than expected for herb and tree species, but not shrub species suggesting that the herb and tree composition within the ICHwk1/111 is significantly different from the composition of a majority of other site units, especially with respect to the more common species. My research does not focus on the particular processes that could explain why

composition in the ICHwk1/111 is significantly more dissimilar than expected in the tree and herb analysis, but Chase and Myers (2011) and Kraft et al. (2011) explain that positive deviations (i.e., higher dissimilarity than expected) could be due to environmental selection or dispersal limitation.

Table 7: Site units that are no different from expected based on random sampling from the regional species pool when the regional species pool is restricted to herb, shrub or tree species observed in the BEC subzone / variant.

Herbs	Shrubs	Trees
BWBSmw/111	ESSFwc4/111	BWBSmw/103
ESSFwcw/103	ESSFwm2/103	ESSFwm2/101
ESSFwcw/110	ICHdw1/102	ESSFwm2/104
ESSFwm2/104		ESSFwm4/101
ICHwk1/103		

Given the long-distance dispersal capabilities of tree species, it is not surprising that dispersal limitation appears to be least important for tree species as compared to shrub or herb species (Table 6). It is evident that dispersal limitation is sometimes important, especially for shrub and herb species. Given the assumed environmental homogeneity within BEC site units, correlation between geographic distance and composition similarity is likely not the result of co-variation that is often observed between environmental 'distance' and geographic distance (Bell et al. 1993); however this assumption should be explored in future research.

Chapter 4: Stochastic assembly of tree species within BEC subzones / variants

4.1 Summary

In BC, tree species distribution maps generated by Hamann and Wang (2006) explicitly assume that BEC subzones/variants are internally homogenous with respect to tree species (McLane and Aitken 2012). As described by Hamann et al. (2005) tree species % frequency was calculated for each BEC subzone/variant based on occurrence records from BEC plots. In essence, species census data (i.e., BEC plot data) were used to calculate the frequency or probability of occurrence within a defined ecosystem unit (i.e., BEC subzone or variant). The species frequency then replaces the ecosystem unit to generate species distribution maps. While some adjustments were made to remove extremely low frequencies ($< 0.001\%$) and isolated incidences, it was generally assumed that a given tree species could persist to some degree anywhere within a BEC subzone/variant in which it was recorded. This assumption is common to species distribution models (Sinclair et al. 2010, Mbogga et al. 2010) and is not unique to BC (Iverson et al. 2007, Gray and Hamann 2011).

One approach to testing the validity of this assumption is to determine whether current tree species composition within an ecosystem unit is different from what would be expected based on random sampling from the regional species pool. If species composition is no different from that expected based on random sampling from the regional species pool then the assumption that tree species can exist anywhere in the BEC subzone/variant is supported. Evidence inconsistent with the working assumption would come in the form of species composition being more similar than expected based on random sampling from the regional species pool. In this chapter I present results from a null model analysis of beta diversity of tree species within 8 BEC subzones or

variants depending on the classification. It is hoped that the findings will contribute to the understanding of current patterns of tree species diversity in BC.

4.2 Methods

4.2.1 Vegetation plot data

I used a sample of 938 standardized BEC plots to test the aforementioned assumption. The 8 subzones/variants analyzed vary in general climate conditions (Figure 6) and span more than 800 km (Figure 3). All available plots for each BEC subzone or variant were used for the analyses in this chapter. Plot data were filtered following the methods I described in Chapter 2 with the exception of removing plots from site units with fewer than 10 plots. Therefore, there are an additional 129 plots in this analysis (938 total). Tree species include both conifer and deciduous species as per the 2009 BC species list life form designations (Meidinger et al. 2009). Similar to the previous two chapters, a presence-absence site by species table was created for all plots. The corresponding site by environment table was used to subset the site by species table by BEC subzone / variant.

4.2.2 Data analysis

For each BEC subzone / variant, I calculated beta diversity using the Jaccard dissimilarity metric for presence-absence data ($\beta_j = 1 - a/(a+b+c)$). I then used the permatfull null model (Figure 8) (Azeria et al. 2011) to calculate expected Jaccard dissimilarity based on 999 randomizations. Observed alpha diversity, the number of tree species within a given plot, was maintained for each plot and the regional species pool (gamma diversity) was the sum of all species observed in the given BEC subzone or variant. In addition, the randomization procedure maintained the species frequency of the observation data. Observed beta diversity was compared to expected

beta diversity and the standard effect size (SES) was calculated to measure the degree of deviation from expected values in the same methodology as outlined in Chapter 2. I then used the t-test to determine whether pairwise SES values were significantly different from zero. For this analysis, the species pool was restricted to the species observed within the BEC subzone / variant.

4.3 Results

Across 938 plots, there were 34 tree species observed, including 19 coniferous and 15 broad-leaved trees. Species occupancy distributions were variable (Figure 29), but consistent with previous chapters, more uncommon than common species. Interestingly, multiple species occur in many sites, creating bimodal species occupancy distributions in some BEC variants (Selkirk wet-cold ESSF (ESSFwc4), central Purcell low elevation wet-mild low ESSF (ESSFwm4), and central Purcel wet-mild ESSF (ESSFwm2)). Despite variable sampling intensity across BEC subzones / variants, the species accumulation curve levels off in all classifications, suggesting that sampling is sufficient for capturing tree species within BEC subzones / variants (Figure 30).
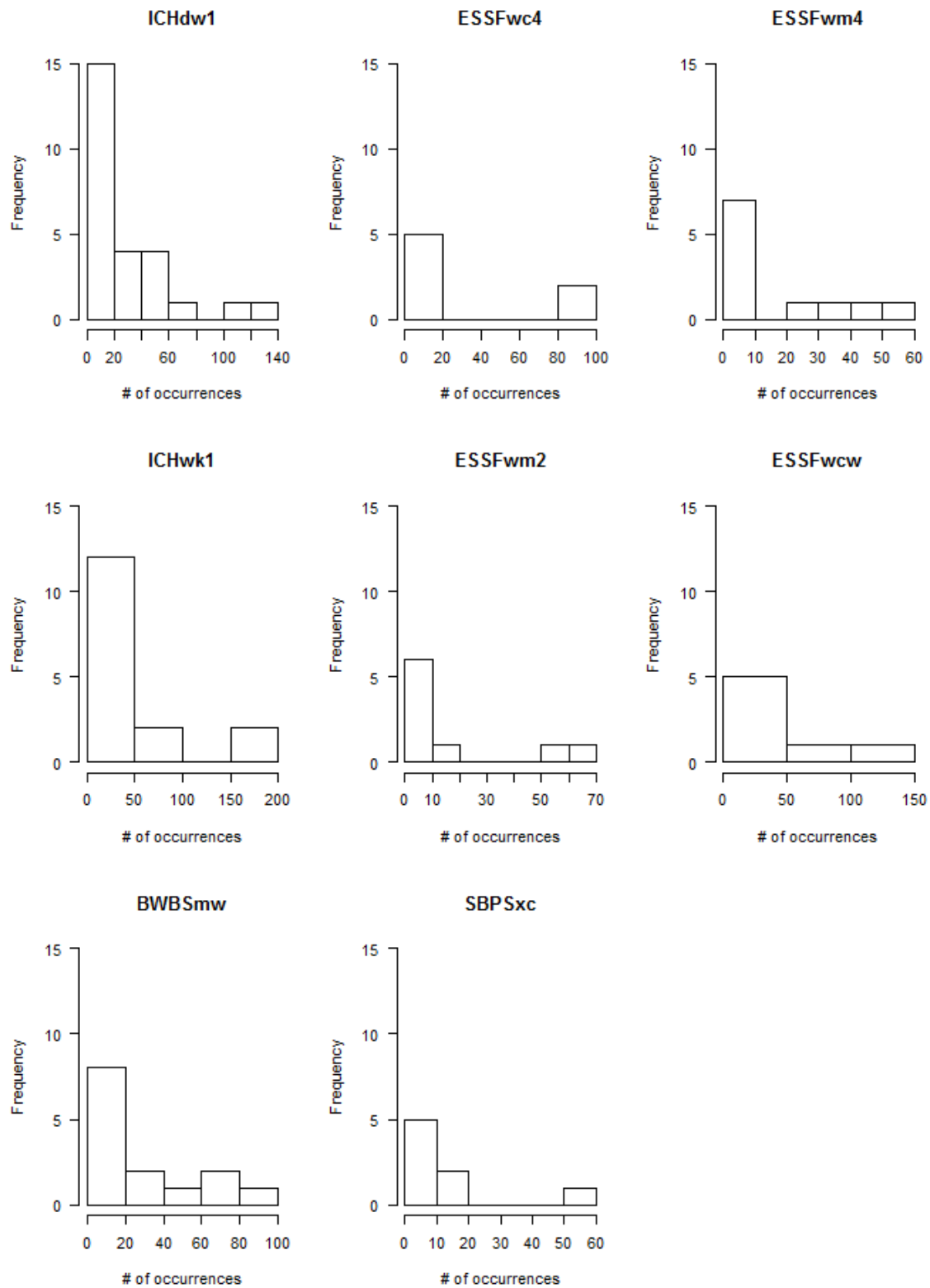
Figure 29: Tree species occupancy distributions in 8 BEC subzones / variants.
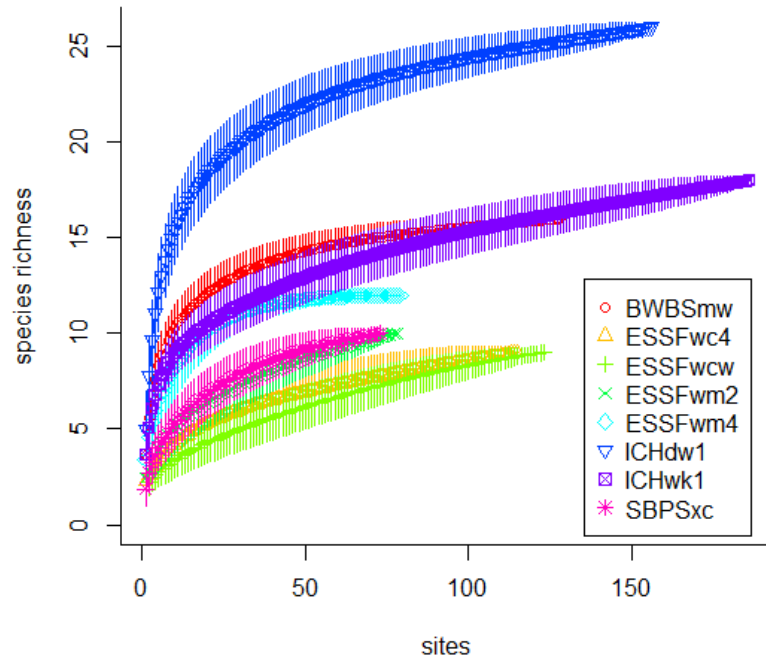
Figure 30: Tree species accumulation curves within 8 BEC subzones / variants. Slopes levelling off in all BEC subzones / variants indicates that sampling of tree species within the BEC subzones / variants analyzed in this research is sufficient.

Jaccard dissimilarity of trees within BEC subzones or variants was highly variable; some BEC

subzones / variants exhibited low beta diversity while others exhibited high beta diversity

(Figure 31). The null model results show that Jaccard dissimilarity in tree species was no

different than expected based on random sampling from the regional species pool (t-test p-values

> 0.05; Figure 32).
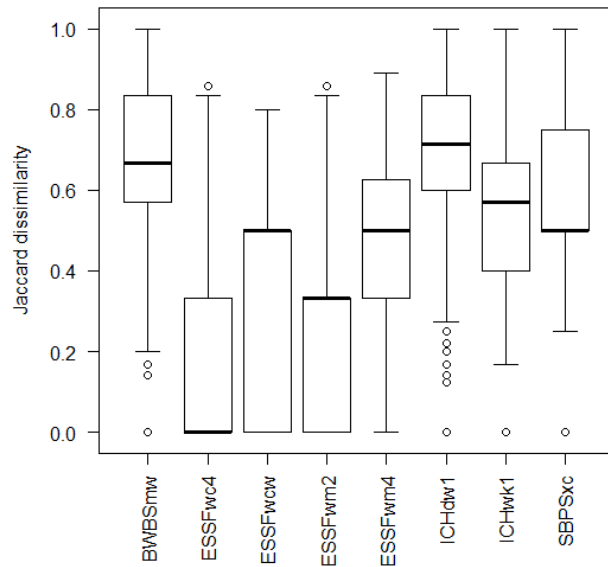
Figure 31: Observed Jaccard dissimilarity for tree species within 8 BEC subzones / variants.
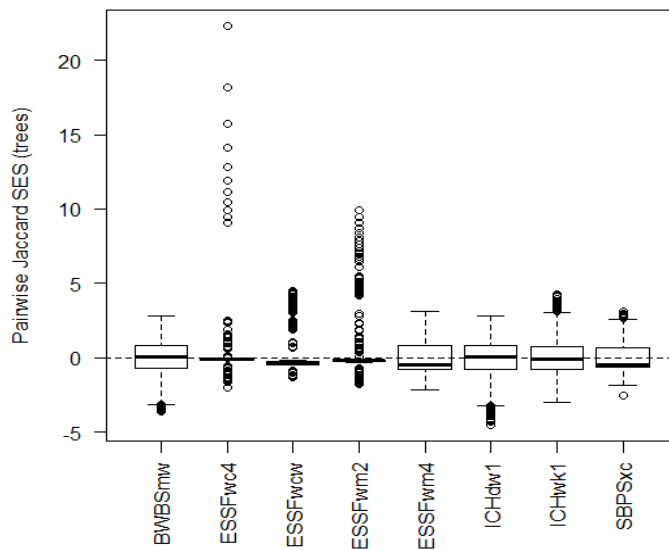
Figure 32: Pairwise Standard Effect Size values for tree species within 8 BEC subzones / variants. Species pool is restricted to all species observed in the BEC subzone / variant. On average, no BEC subzones / variants were different from zero (t-test p-value > 0.05).

4.4 Discussion

Through the use of a null model analysis I determined that Jaccard dissimilarity of tree species

among plots within eight BEC subzones / variants analyzed in this research were in fact no

different than expected based on random sampling species from the regional species pool. This

finding supports the underlying assumption of bioclimate envelope modeling used in BC to

predict tree species range distributions under multiple climate change scenarios. Similar to the

tree species beta diversity analysis within BEC site units, it is important to consider that beta

diversity is already low within the wet-cold woodland ESSF (ESSFwcw), ESSFwc4 and

ESSFwm2 (more than 50% of species are shared among plots). With few tree species in the

ESSF site units (Table 8) examined in my research, it is not surprising that beta diversity is lower

for these BEC subzones / variants. It is also not surprising that null model results reveal that

Jaccard dissimilarity is no different than expected by randomly sampling species from the

regional species pool; there are comparatively few species in the species pool and most species

are common throughout the BEC subzone / variant.

Table 8: Number of tree species within 8 BEC subzones / variants. The number of plots per BEC subzone / variant is also shown.

BEC subzone / variant	No. of species	No. of plots
BWBSmw	16	128
ESSFwc4	9	115
ESSFwcw	9	123
ESSFwm2	10	78
ESSFwm4	12	79
ICHdw1	26	156
ICHwk1	18	186
SBPSxc	10	73

Bioclimate envelope modeling is important for predicting how the climatic niche spaces of

species may shift under rapidly changing climatic conditions (Pearson and Dawson 2003). Due

to the complexity of natural systems, assumptions are ultimately necessary in predictive

modeling. While important, it is essential to consider underlying assumptions of such models and

how different methods exist for testing the underlying assumptions. Patterns of tree species are

more easily quantified than the processes that drive these patterns. Using a null model approach, I found that Jaccard dissimilarity was no different than expected based on random sampling, suggesting that stochastic processes could be influential (Chase and Myers 2011, Chase et al. 2011, Kraft et al. 2012).

Chapter 5: General discussion

To my knowledge, my research is the first research to explore baseline patterns of vascular plant diversity in BC with a focus on the relative importance of different ecological assembly processes (speciation, drift, dispersal and selection). My findings of high beta diversity within site units is important because it highlights the fact that there is significant natural variation in vascular plant species composition within ecosystems, even at fine scales with relatively homogenous environmental conditions. Importantly, my findings were consistent across a broad geographic extent (> 800 km) and multiple ecosystems types (Figure 3). With increased attention on biodiversity management, understanding natural variation in species composition is an important first step in understanding the different ecological processes that drive patterns of diversity. Further, quantifying beta diversity has been shown to be an effective way of deciphering the relative importance of stochastic versus deterministic community assembly processes (Condit et al. 2002, Tuomisto et al. 2003, Chase 2003, 2007, 2010, Gilbert and Lechowicz 2004), especially with the more recent use of null models (Azeria et al. 2011, Chase and Myers 2011, Chase et al. 2011).

Using standardized BEC plots I was able to show whether beta diversity within site units was different than expected by randomly sampling species from the regional species pool. As described by Chase et al. (2011) and Chase and Myers (2011), when beta diversity is no different than expected by random sampling from the regional species pool, it is likely that stochastic processes are important. Within 31 BEC site units, I found that dissimilarity in composition among plots was no different than expected by randomly sampling species from the species pool (potential signal of stochastic processes) as evident by non-significant SES values calculated in the null model analyses. This finding was based on the scenario where the species pool was

restricted to the species observed within a given site unit and was consistent across lifeforms. As described by Hubbell (2001), purely stochastic assembly is expected to reveal a negative association between community composition similarity and geographic distance. My research showed that dispersal limitation was only evident in some site units, and increased in importance from tree to shrub to herb species, leaving other stochastic processes (i.e., colonization and extinction) to play a potentially influential role in community assembly.

Null model results with expanded species pools revealed the importance of deterministic processes for sorting species composition across environmentally heterogeneous areas regardless of plant lifeform; most site units were more similar than expected by randomly sampling species from the BEC subzone / variant species pool and all site units were more similar than expected in the analyses with species pools inclusive of all species in the dataset. However, there were a few site units that were unusual: 1) composition in the ICHwk1/111 was more *dissimilar* than expected by chance when the species pool included all species observed in the ICHwk1 for tree and herb species. This finding suggests the possible aggregation of composition among groups of plots within this site unit as observed in other systems (Azeria et al. 2011, Chase and Myers 2011, Stegen et al. 2012). While I did not formally analyze the source of dissimilarity within the ICHwk1/111, it is suggested in the literature that such aggregation could be the result of environmental filtering, dispersal limitation or priority effects (Chase and Myers 2011, Kraft et al. 2011, Stegen et al. 2012). In the analysis of all species, the ICHwk1/111 was the only site unit in which Jaccard dissimilarity was no different than expected by randomly sampling species from the BEC subzone / variant regional species pool, signaling the potential importance of stochastic processes (Chase and Myers 2011). 2) The ESSFwcw/110 was also more *dissimilar* than expected in the analysis of all species when the species pool was restricted to BEC subzone

/ variant species. 3) While not the case when all species were considered together, 5 site units in the herb analysis (Figure 26), 3 site units in the shrub analysis (Figure 27) and 4 site units in the tree analysis (Figure 28) were no different than expected by randomly sampling species from the regional species pool again suggesting that stochastic processes could be influential and that some site units are more compositionally similar to composition of the surrounding area (i.e., BEC subzone / variant) than other site units.

In support of the underlying assumption of bioclimate envelope modeling that species are equally suited within a defined ecosystem unit (e.g., Hamann and Wang 2006), I found that within BEC subzones / variants, tree species composition was no different than expected by randomly sampling tree species from the regional species pool (Chapter 4). The analysis I completed was the first formal test of the assumption of equivalent potential for tree species within BEC subzones / variants and was completed using a relatively simple approach that could be applied over a larger geographic extent or in other systems where bioclimate envelope modelling is used.

5.1 Broader context of my research

One purpose of BEC is to describe ecosystems and inform forest management decisions in BC (MFLNRO 2012a). At the site unit level of classification, site quality (i.e., equivalent vegetation potential) is deemed to be equivalent among plots (Pojar et al. 1987, MFLNRO 2012a) such that any variation in species composition or environmental characteristics within site units are not anticipated to impact ecosystem-based management decisions. As is the nature of classification systems, some level of natural variability is grouped to create a framework for understanding. In descriptions of BEC (Pojar et al. 1987, Meidinger et al. 1991, MFLNRO 2012a), it is recognized that factors including chance, disturbance, and time influence species diversity and may result in

variation in composition in any level of classification. My research finding of high beta diversity highlights the fact that significant variation exists, especially among herb species, and supports the idea that multiple processes are likely responsible for generating current patterns of vascular plant diversity. Determining the relative importance of different processes is an important step in better understanding of diversity patterns.

Beta diversity within site units does not appear to differ from what would be expected under random community assembly when the species pool is restricted to a given site unit; however, when the species pool expands to include species from a broader environmental gradient (i.e., subzone / variant or plot dataset), beta diversity is most often more similar than expected. This finding supports the classification process: despite high beta diversity, site units are in fact compositionally more similar than if one were to randomly assemble communities from the broader species pool. The finding of high beta diversity also highlights the importance of considering site quality over plant species composition when interpreting site units in the field – vegetation is likely to be variable due to multiple ecological processes that influence species composition in otherwise environmentally homogenous areas.

5.2 Importance of different ecological processes in BC plant communities

While deemed to be insignificant within the geographic extent of my study, it is possible that speciation influences vascular plant diversity in BC, especially near refugia that existed during the last ice age (Gavin 2009, Shafer et al. 2010). It is difficult to quantify the importance of speciation (Pärtel et al. 2007), but a common way to infer the role of speciation is to examine the relationship between gamma diversity and beta diversity (Kraft et al. 2011, DeCaceres et al. 2012) – where regional species pools are large, it is hypothesized high speciation rates have created more ecologically equivalent species that in turn increase beta diversity among sites. My

research shows a weak relationship between observed Jaccard dissimilarity and gamma diversity (Figure 33a). However, the degree to which composition dissimilarity within site units deviates from expected Jaccard dissimilarity does not correlate with gamma diversity (Figure 33b) suggesting that correlation between observed Jaccard diversity and gamma diversity was the result of differences in alpha diversity rather than gamma diversity (i.e., speciation). The geographic extent of the study system only includes temperate and boreal ecosystems that shared the same glacial history (Hebda 2007) whereas most studies examining speciation span continental gradients (e.g., Qian and Ricklefs 2000, Pärtel et al. 2007). In addition, sampling intensity was shown to be correlated to gamma diversity (Figure 9b) implying that sampling rather than speciation could explain species richness patterns. Further investigation of speciation in BC ecosystems would be necessary to better understand the role, if any, of speciation in driving vascular plant diversity patterns in BC.
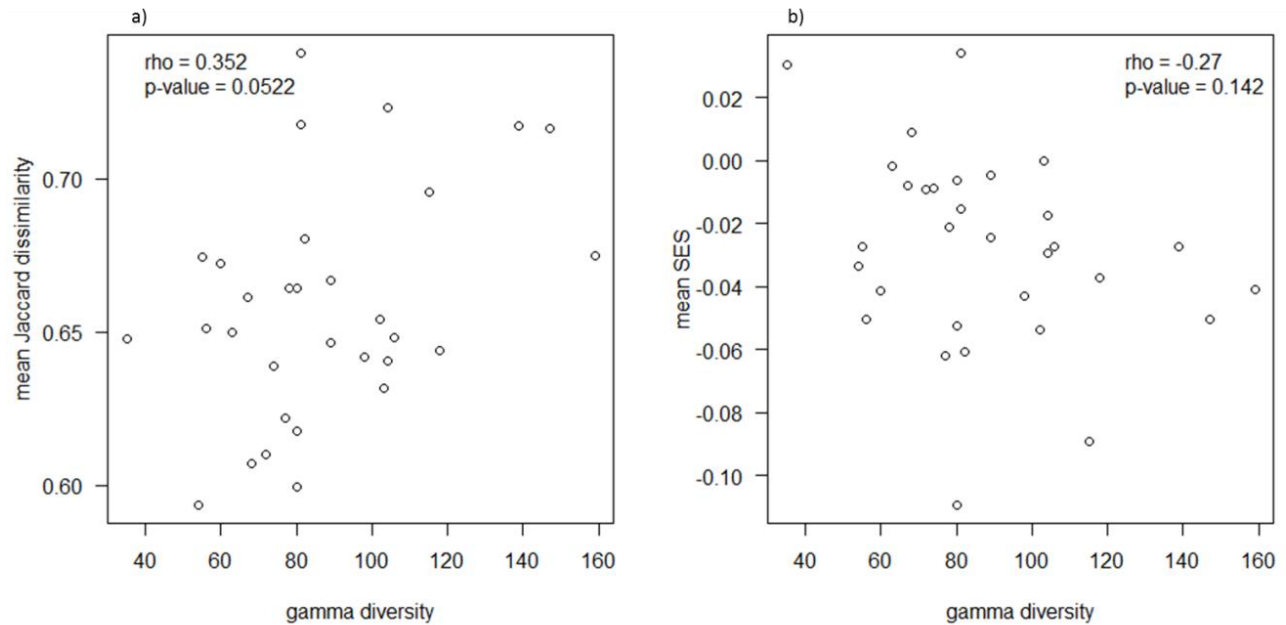
Figure 33: Spearman rank correlation between a) mean Jaccard dissimilarity and b) mean SES and gamma diversity across 31 site units. All lifeforms are included and the species pool was limited to those species observed within the site unit in the null model analsyis. A weak correlation exists between mean observed Jaccard dissimilarity and gamma diversity (Spearman p-value = 0.0522); however when alpha diversity and species occupancy were controlled for in the null model analysis, no correlation was found between SES and gamma diversity.

As described by Chase and Myers (2011), deterministic processes such as environmental selection, are thought to drive community assembly when beta diversity is more similar than expected based on random sampling from the regional species pool. In the site units that I examined, evidence for deterministic processes was most prevalent at large scales; species within a given site unit were more similar than expected when species composition in site units was randomly assembled using all species in the dataset as the species pool (species pool 3). Similarly, many site units were more similar than expected by randomly sampling species from the regional species pool when the species pool was inclusive of species observed within a given BEC subzone / variant. This finding was also common for the independent analyses of tree, shrub and herb species. In addition, the finding of higher dissimilarity than expected (positive SES values) in the ICHwk1/111 (analyses of herb and tree species) and ESSFwcw/110 (analysis

of all species) are most likely due to factors that cause systematic aggregation (Chase and Myers 2011) of composition within the site unit. Deterministic processes such as environmental filtering (Chase and Myers 2011, Chase et al. 2011) or competition (Stegen et al. 2012) could cause beta diversity to be more dissimilar than expected by chance. It is also possible that selective processes are still important, but simply do not result in systematic organization of species composition (i.e., clustering of plots with similar composition within a site unit). Such selective processes could include competition or mutualism (Chapin III et al. 2000, Scheiner and Willig 2007, McGill 2010).

Within site units, it appears as though environmental selection has been controlled for and it is assumed that speciation has negligible influences leaving dispersal and drift to explain Jaccard dissimilarity among plots of a given site unit. Dispersal limitation was also found to be influential in some site units (Table 6); however, it did not consistently correspond to evidence of systematic aggregation of species (higher dissimilarity than expected) in the null model analyses except for tree species in the ICHwk1/111. I do not conclude that dispersal limitation is the cause of higher dissimilarity than expected in the tree analysis in the ICHwk1/11 because, as discussed by Chase and Myers (2011) and Chase et al. (2011), aggregation of sites with composition caused by dispersal limitation can give similar results to aggregation caused by environmental selection. However, it is important to consider that dispersal limitation reduces the ability of predicting composition based on environmental features (Ozinga et al. 2005). Aside from dispersal limitation, it is important to consider other processes within the umbrella of dispersal: for example, priority effects and mass effects could explain systematic clustering of species due to timing of colonization (e.g., Roberts and Gilliam 1995, Moora et al. 2007, Svensson et al. 2009) or due to the spatial organization of community types across the landscape (e.g.,

Simmering et al. 2006, Zeleny et al. 2010, Poggio et al. 2010, Sattler et al. 2010, Steinmann et al. 2011).

Because speciation, selection and dispersal fail to consistently explain beta diversity within BEC site units, it is likely that stochastic processes (i.e., drift) including colonization and extinction dynamics are influential to patterns of beta diversity. The null model results where species pools are limited to those species observed within a site unit support a strong role for stochastic processes because Jaccard dissimilarity was no different than expected by randomly sampling species from the regional species pool. As discussed by Vellend (2010), when many species are ecologically equivalent, drift can have a strong influence on species composition through extinction and colonization dynamics. While drift is seemingly important at fine scales of species composition, it is clear that at larger scales, environmental selection is more influential thus highlighting the importance of spatial scale.

5.3 Research limitations

The natural world is complex, so humans organize it into regions (i.e., ecosystems) through classification, which serve as a framework for ecosystem understanding and management. Within classified regions, it is assumed that conditions of interest are relatively homogenous compared to other regions (i.e., within-region variability is less than among region variability) (Andrew et al. 2013). BEC site units are described as having similar site quality and the same vegetation potentiall (Pojar et al. 1987), but there will be some level of variability in both vegetation and environmental conditions because classification systems generalize otherwise complex natural systems. BEC site units serve to support management decisions such as tree species selection for reforestation or soil sensitivity to compaction (MFLNRO 2012a), and therefore may overlook finer-scale environmental conditions that might explain some variation

in species composition among plots. Even within site units, variation in site factors including aspect, soil moisture and nutrients, etc. exist; however, it is assumed that this variation is not significant enough to influence vegetation potential or site quality. I make the assumption of limited deterministic processes within site units based on relative environmental homogeneity, but I recognize that this assumption should be tested further to strengthen the interpretation of the relative importance of deterministic versus stochastic community assembly processes.

As Chase and Myers (2011) discuss, the null models enable detection of the signal of stochastic assembly processes, but further analyses are required to investigate the relative importance of processes that drive deviation from expected composition dissimilarity. For example, Myers et al. (2012) illustrated using a similar null model approach that underlying mechanisms can still differ significantly despite consistency in null model results; they found that despite similarities in species occupancy distributions and observed beta diversity, environmental variables explained deviation from expected beta diversity in temperate forests whereas spatial factors explained deviation from expected beta diversity in tropical forests. While my research indicates a signal of stochastic processes within site units, there is opportunity to further analyze specific processes that may explain the magnitude of deviation from expected dissimilarity.

Throughout my research, it was evident that the shape of species occupancy distributions was important to consider when interpreting the results. With many uncommon species, it was not surprising that observed dissimilarity was high, similar to observations in other systems (Chase 2007, McGlinn and Hurlbert 2012). Of the lifeforms, tree and shrub species occasionally showed more common species, which was likely a cause of lower observed Jaccard dissimilarity. With many uncommon species and high dissimilarity in vascular plant composition within site units it becomes important to consider the spatial requirements for management and conservation of

ecological processes. In the null model used in my research, processes that influence species occupancy were not considered, but are potentially important for inferences made about the relative importance of different processes (Qian et al. 2013). For example, if deterministic processes cause the skewed occupancy distributions observed in this dataset then it is possible that determinism plays a stronger role than detected.

Null models are only recently gaining use in ecological research, specifically in the analysis of beta diversity. As such, there are limitations in the interpretation of results because all scenarios have not been discussed in the research. For example, Chase (2007) described how sites can be more similar than expected based on random sampling due to environmental filtering of species in the regional species pool, but if the species pool is limited to species observed in the species recorded in the specific dataset being analyzed (i.e., BEC site unit), there are no examples of achieving results that are more similar than expected under random sampling. This highlights the importance of regional species pool definition. If all species are present in at least one plot and many rare species exists, it seems difficult to ever have a scenario where pairs of plots are on average more similar than expected by chance. Simulation experiments testing null model results against species pool definitions and species occupancy distributions would improve predictions about possible outcomes of null model analyses given certain species pools and occupancy distributions.

5.4 Suggestions for future research

Assumptions of the current research could be better evaluated in future research. It would be meaningful to isolate environmentally similar plots (i.e., within the same BEC site unit) and perform more detailed local measures of site factors including actual soil moisture, soil biota, crown closure, etc. to evaluate whether variation is due to finer-scale factors not measured in

BEC data. Further, larger-scale factors including disturbance (natural and anthropogenic) and landscape complexity (i.e., habitat isolation) are known to influence diversity patterns (Simmering et al. 2006, Moora et al. 2007, Svensson et al. 2009, Matthews et al. 2009, Zeleny et al. 2010), but were not considered in my research. Future research on beta diversity should include disturbance and landscape factors in the definition of 'similar' local sites. With respect to plant diversity, it is commonly understood that using % cover rather than presence / absence data are more realistic (Jost et al. 2011). Therefore, future analysis should consider using % cover. However, null model analyses that control for abundance distributions should be interpreted with caution due to the potentially deterministic processes that drive species abundance distributions (Qian et al. 2013).

It is difficult to quantify ecological processes (Lessard et al. 2012), but null models allow one to establish whether current patterns differ from what would be expected based on random sampling from the species pool (Azeria et al. 2011, Chase and Myers 2011). The null model that I used in this research represents a simple null model that only considers species occupancy rates and species richness – it is assumed that species niches and dispersal are equivalent. As Lessard et al. (2012) and Armitage et al. (2012) discuss, including biological constraints such as dispersal probabilities and demographic information will improve inferences made with respect to the importance of different ecological processes. In light of the shortcomings of current null models, analyses should be repeated using multiple null models with different constraints (Azeria et al. 2011, Armitage et al. 2012).

5.5 Conclusion

Across a broad geographic extent and within multiple ecosystem types, beta diversity of vascular plant species was found to be high within 31 BEC site units examined in my research. This

finding is important for the general understanding of natural levels of variation that exist in forested communities. Further, the finding that beta diversity was no different than expected under random community assembly within site units validates the classification system using a null model approach. Using similar analyses, such baseline understanding can be expanded to include other BEC site units across the province. From this baseline understanding, monitoring of beta diversity under managed ecosystems or in changing climate conditions could help inform whether diversity patterns are changing and whether the processes that drive diversity patterns are changing as well. Importantly, my research is a first step in improving the understanding of different ecological processes that all play crucial roles in driving observed patterns of diversity.

In general, plants are used as indicators for whole ecosystem diversity because they contribute to animal habitat and are the base of many food webs (Cingolani et al 2010). Should anthropogenic or other factors contribute to the loss of infrequently occurring species, it is likely that beta diversity among environmentally homogenous areas would decrease. With a potentially important role for stochastic processes at fine scales of community organization, colonization and extinction dynamics as well as priority effects and disturbance regimes need to be considered to fully understand the processes that drive patterns of vascular plant diversity in BC ecosystems, especially at fine scales.

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Appendix A: Supplementary figures
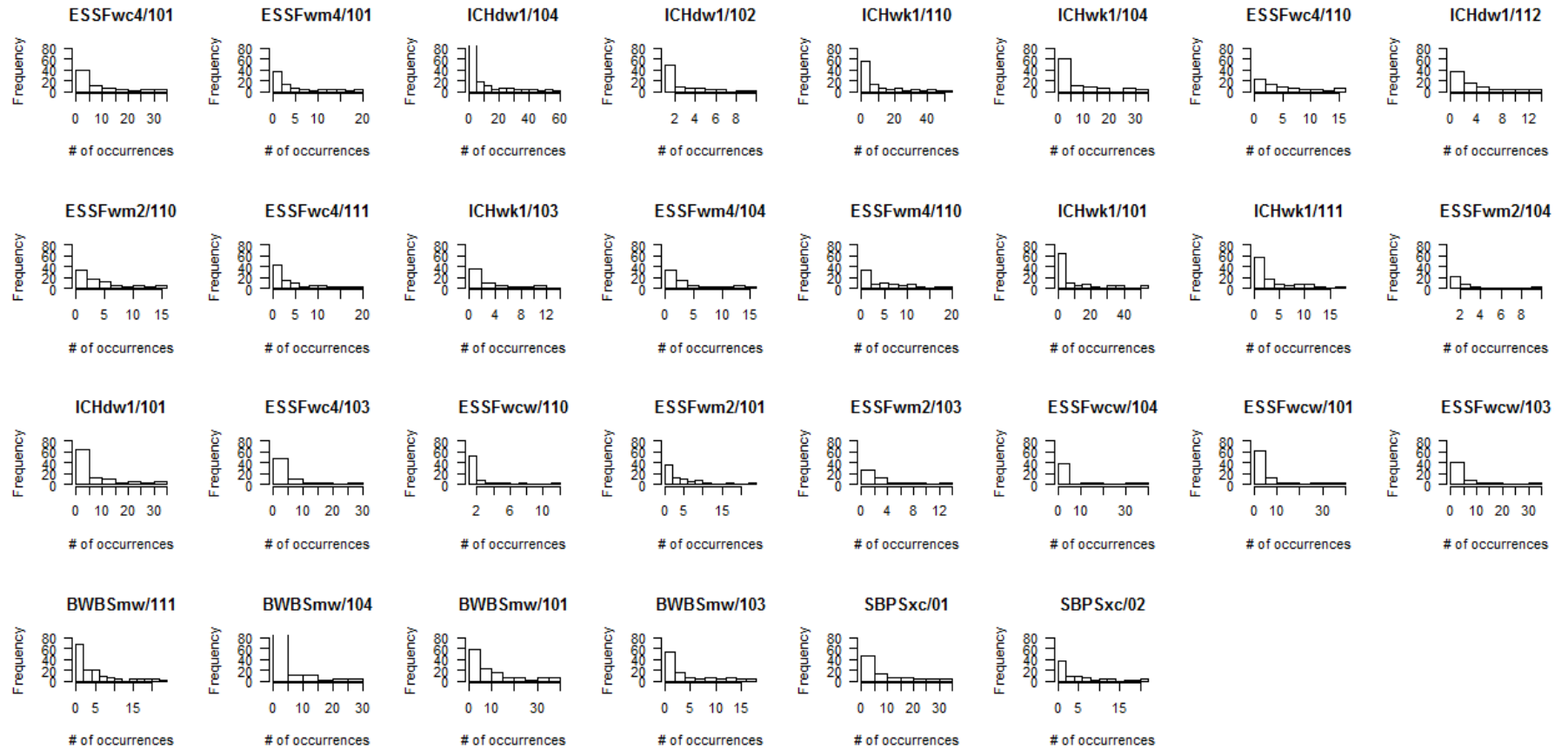
Figure A1: Species occupancy distributions for 31 site units. Each site unit has 10 or plots. All site units have skewed distributions indicating prevalence of uncommon species. The y-axes range from 0 to 80 facilitating comparison across site units.
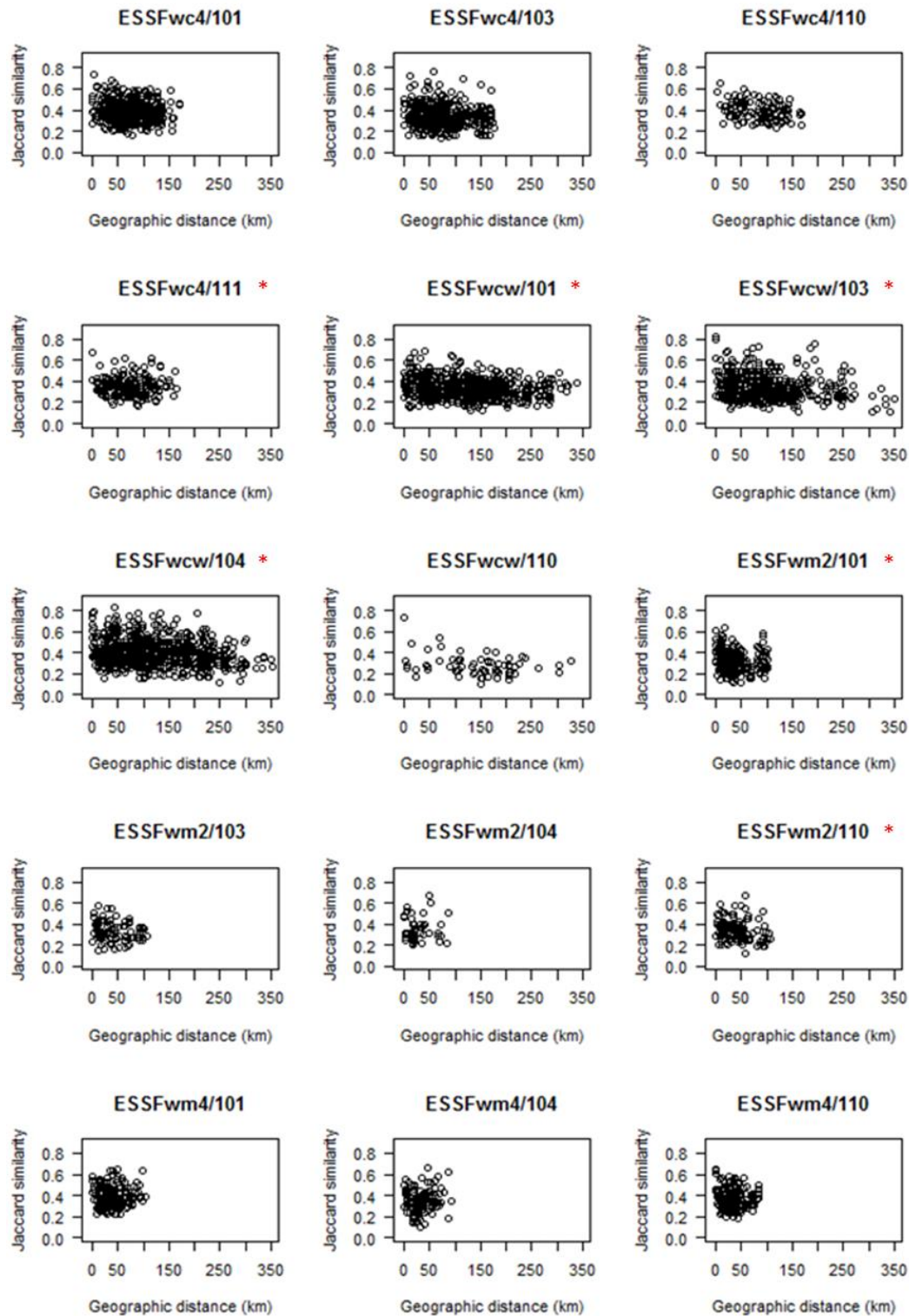
Figure A2: Distance-decay in 15 site units from the Engelmann Spruce Subalpine Fir BEC zone. Signficant negative correlations exist in 6 ESSF site units (indicated by *) of 31 site units total (Mantel r < 0; Mantel p-value < 0.05) .
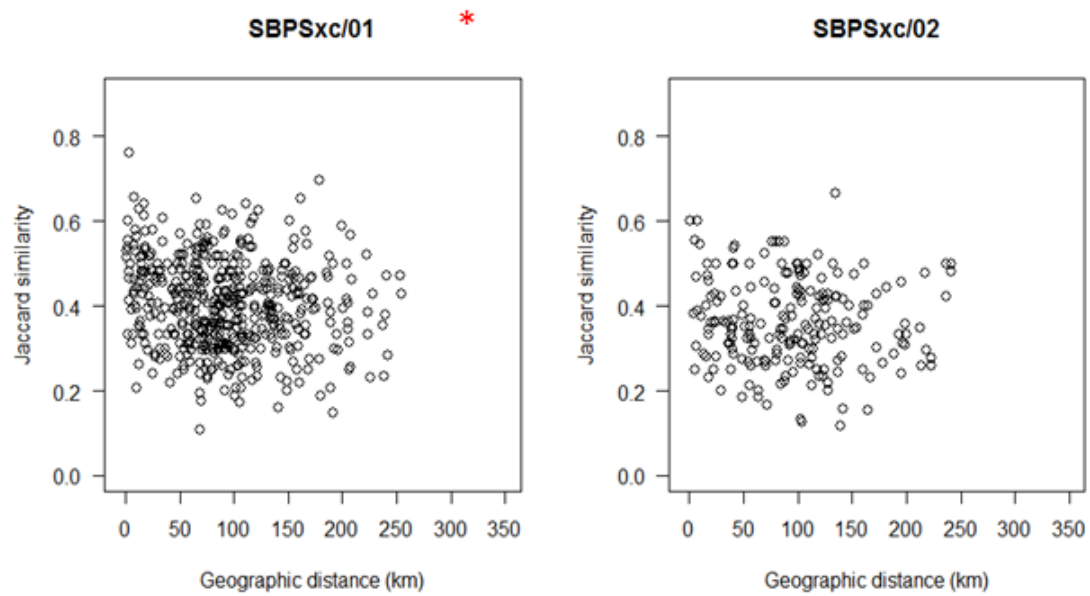
Figure A3: Distance-decay in 2 site units within the Sub Boreal Pine Spruce BEC zone. Significant negative Mantel correlation exists in the SBPSxc/01 (Mantel r < 0; Mantel p-value < 0.05) (indicated by *).
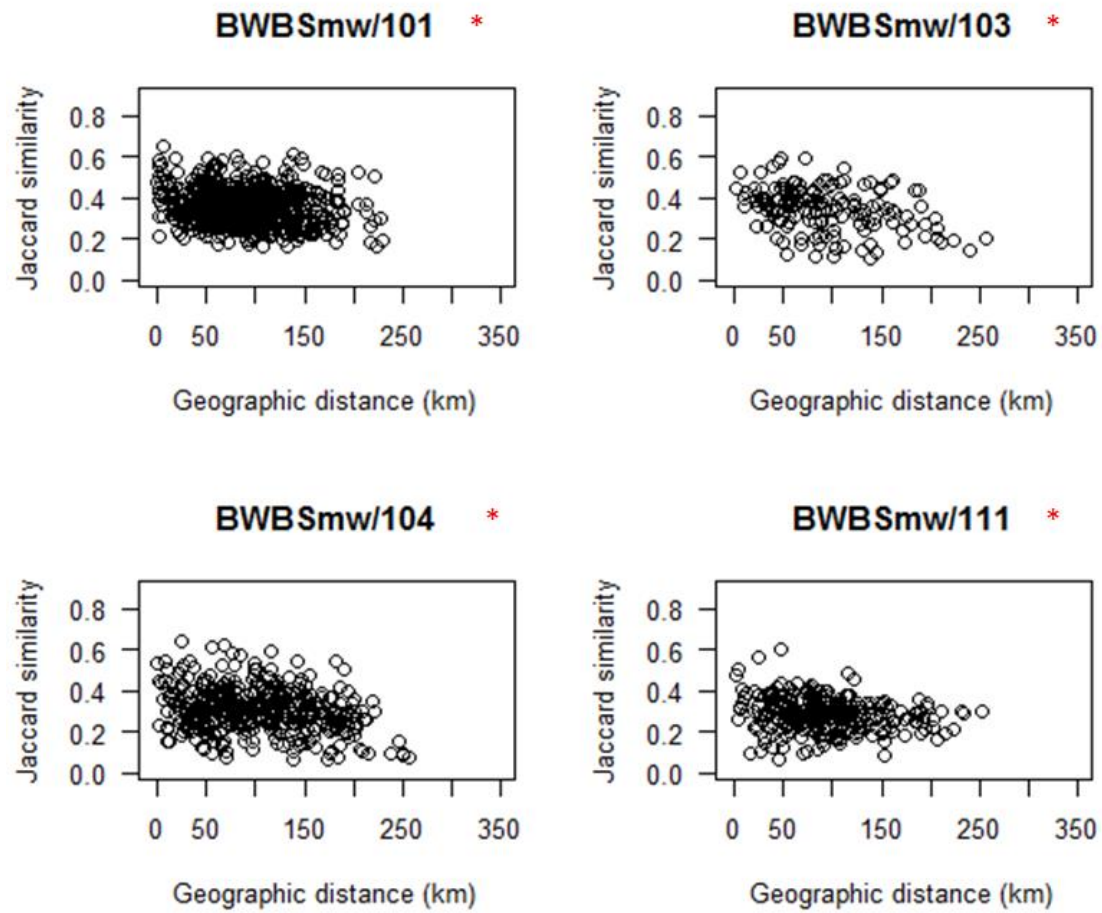
Figure A4: Distance-decay in 4 site units within the Boreal White and Black Spruce BEC zone. All 4 site units show significant negative Mantel correlation (indicated by *) between Jaccard similarity and geographic distance (Mantel r < 0; Mantel p-value < 0.05).
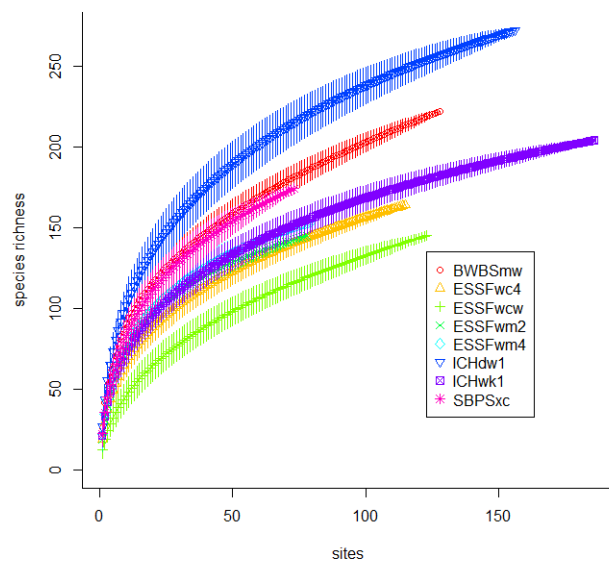
Figure A5: Species accumulation within 8 BEC subzones / variants. Steep slopes indicate that additional species would be encountered with more sampling.
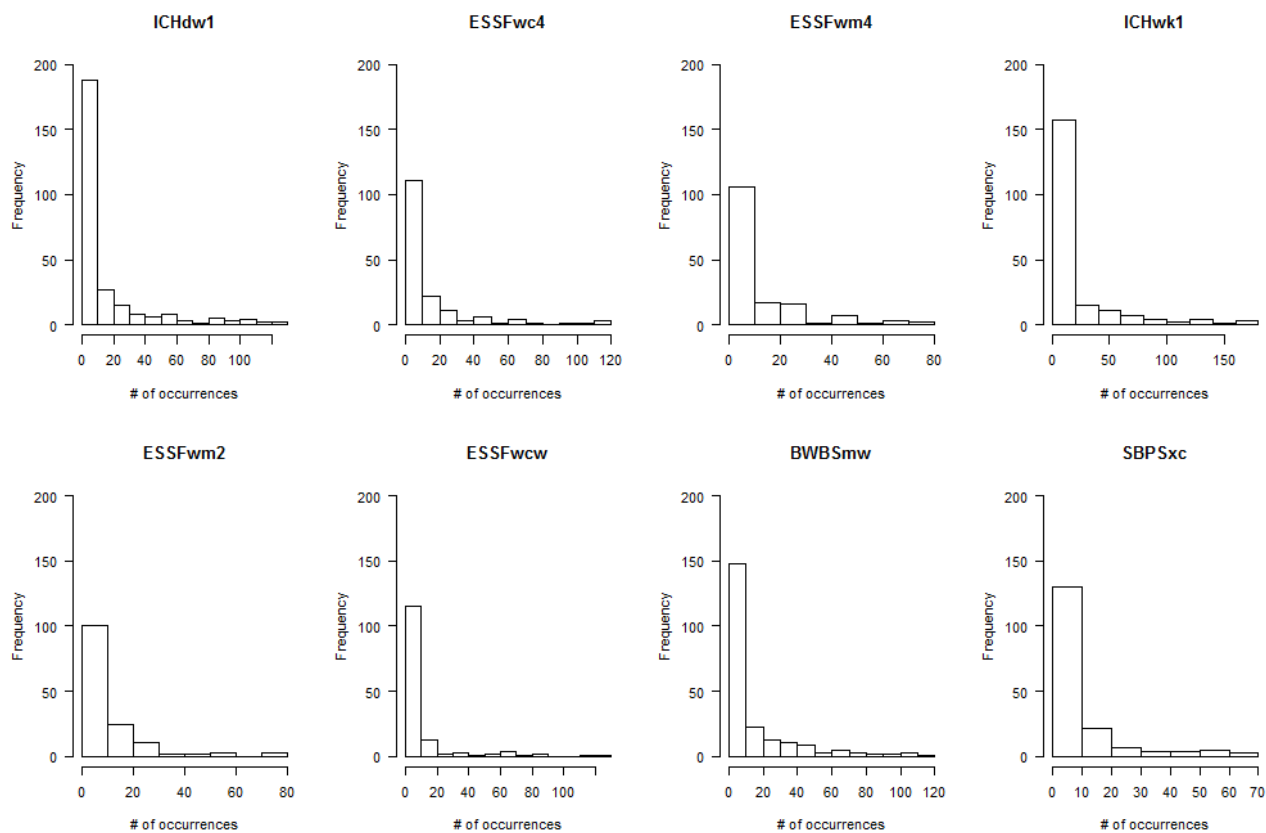
Figure A6: Skewed species occupancy distributions within 8 BEC subzones / variants (all lifeforms combined).
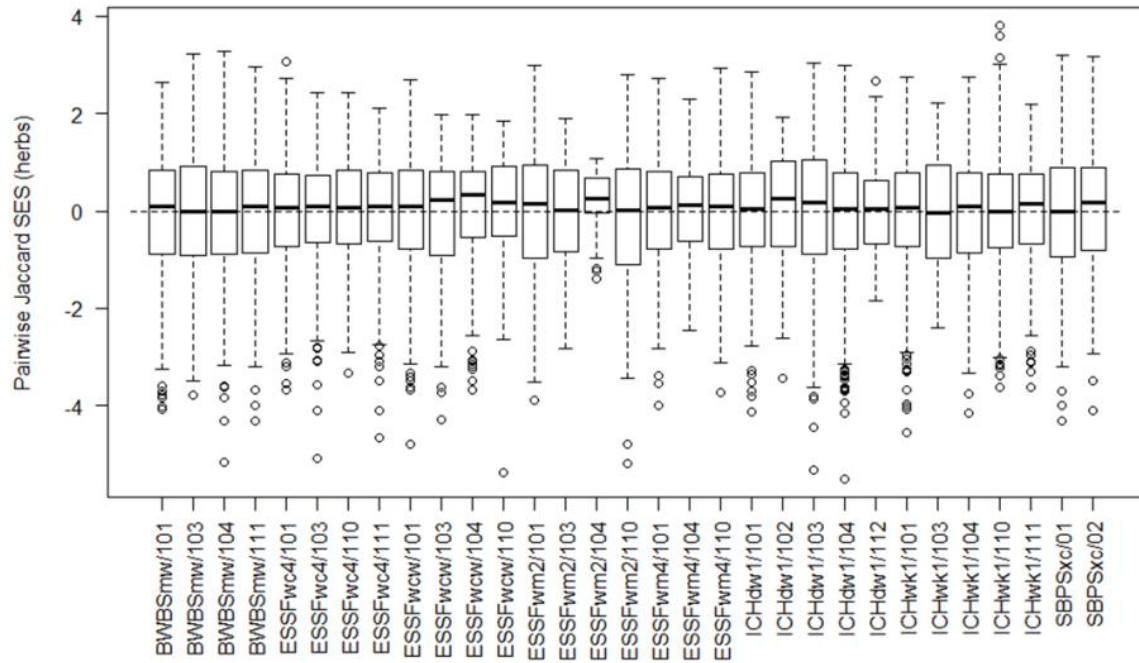
Figure A7: Pairwise Standard Effect Sizes (SES) of herb species for 31 site units using Jaccard dissimilarity values. Species pool restricted to herb species observed within the site unit. Within each site unit, mean expected SES values are no different from zero (t-test, p-values > 0.05).
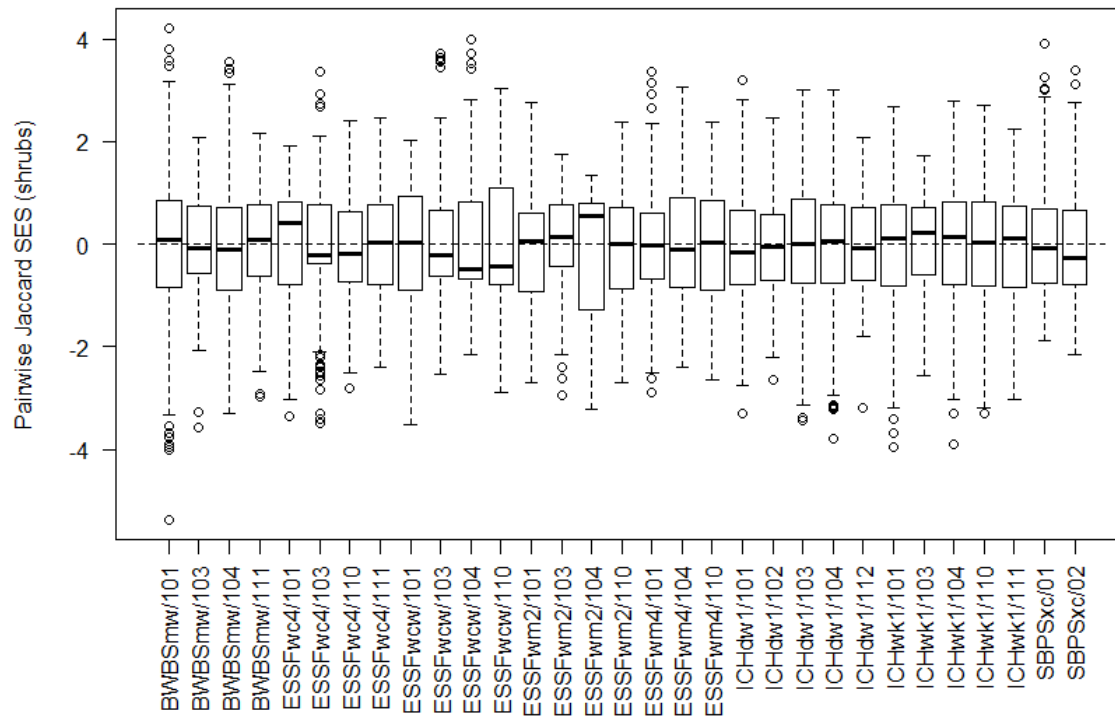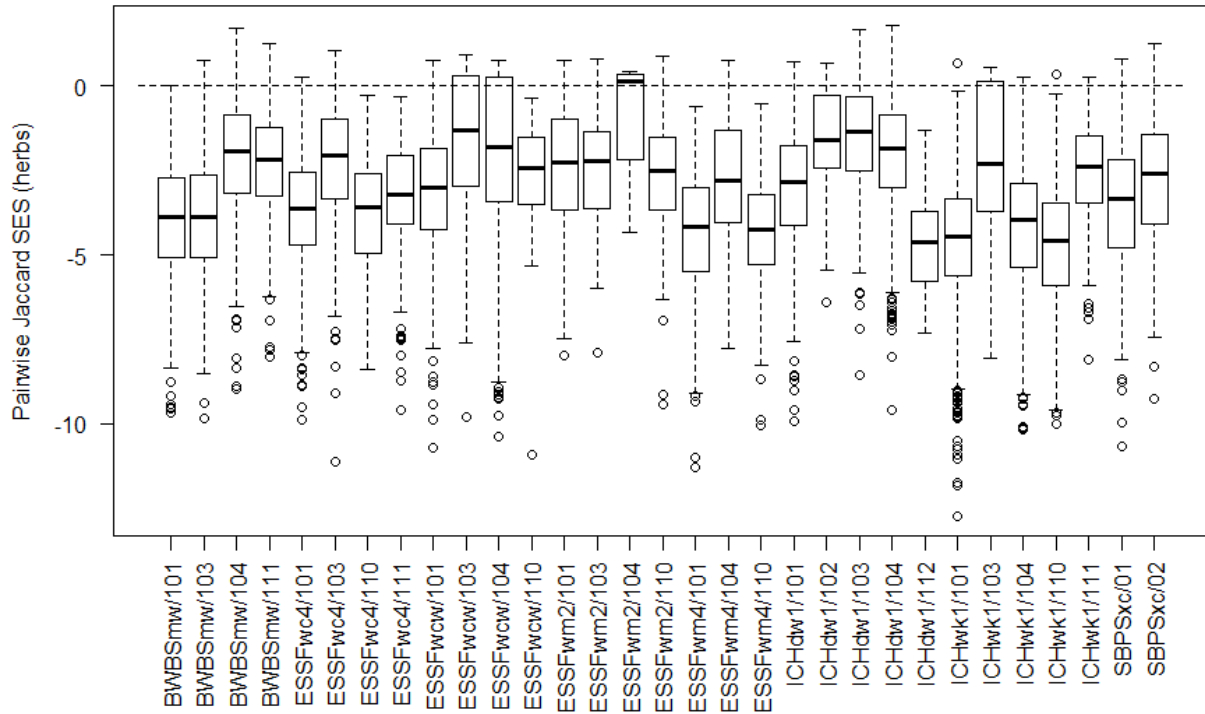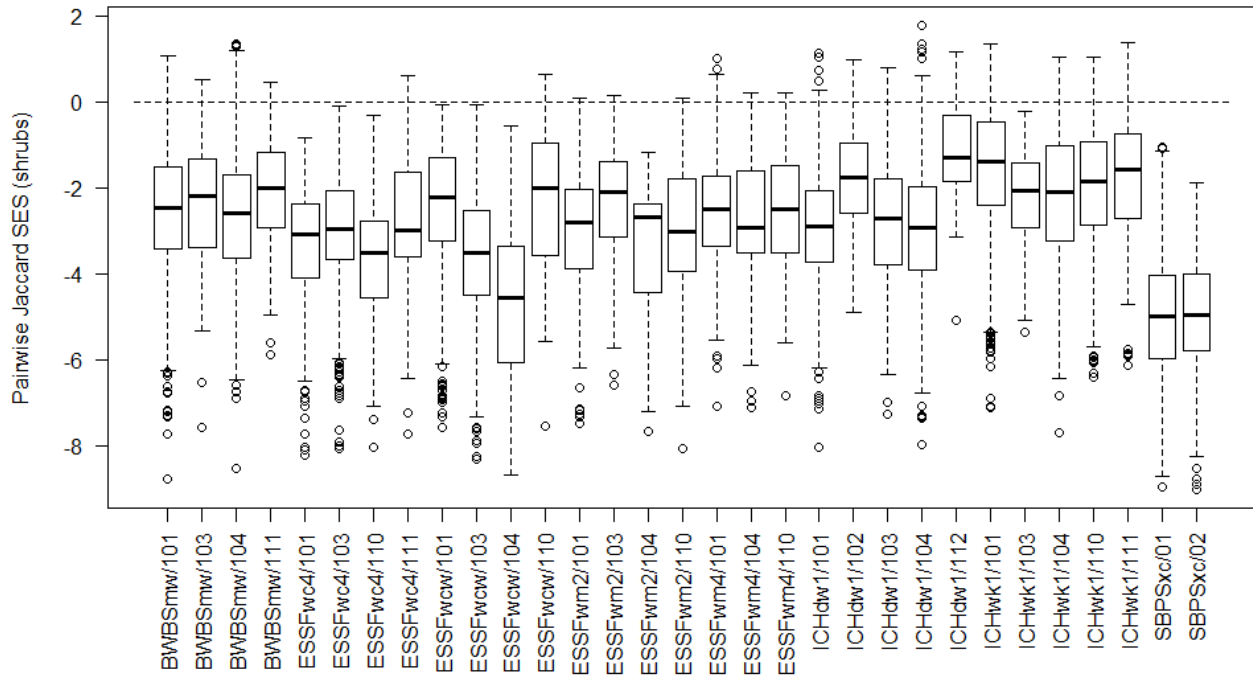
Figure A8: Pairwise Standard Effect Sizes (SES) of shrub species for 31 site units using Jaccard dissimilarity values. Species pool restricted to shrub species observed within the site unit. Within each site unit, mean expected SES values are no different from zero (t-test, p-values > 0.05).
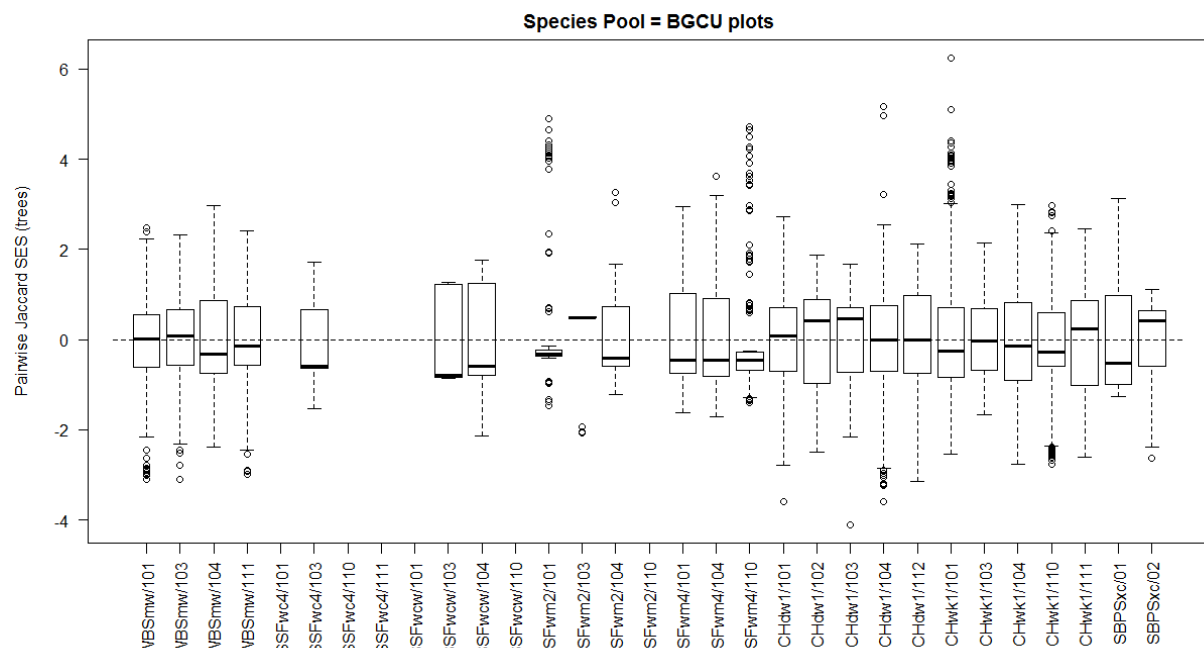
Figure A9: Pairwise Standard Effect Sizes (SES) of tree species for 31 site units using Jaccard dissimilarity values. Species pool restricted to tree species observed within the site unit. Within each site unit, mean expected SES values are no different from zero (t-test, p-values > 0.05).

Figure A10: Pairwise Standard Effect Sizes (SES) of herb species for 31 site units using Jaccard dissimilarity values. Species pool is all herb species observed in the dataset (938 plots). Within each site unit, mean expected SES values are less than zero (negative t-test statistic, p-values < 0.05).
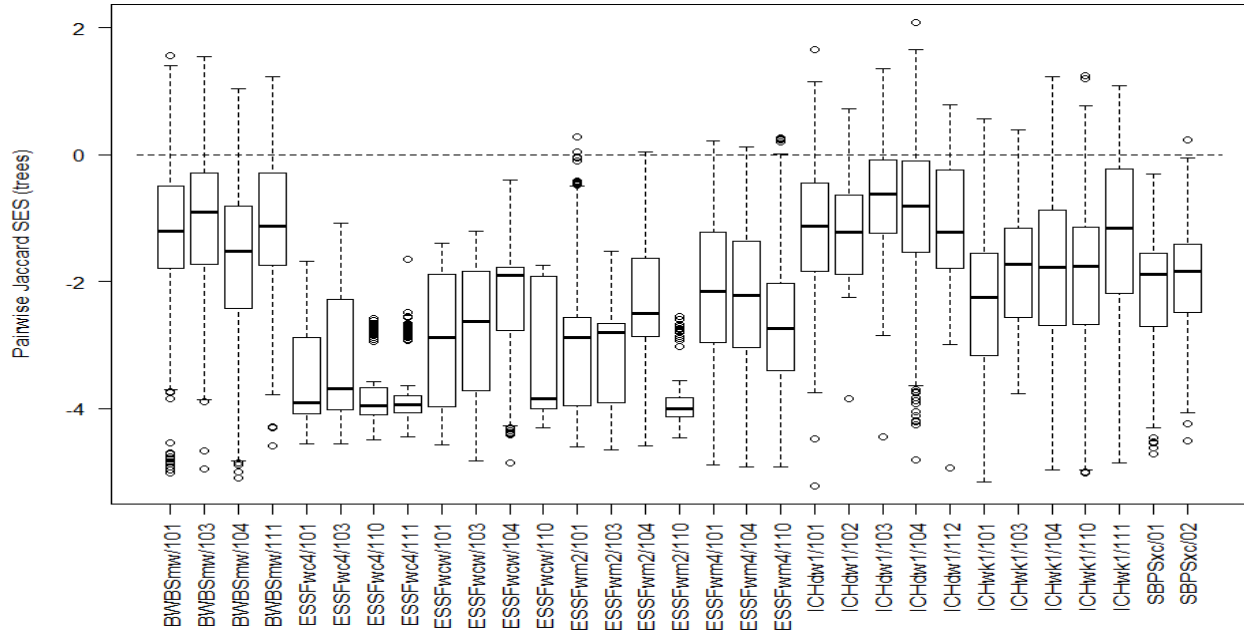
Figure A11: Pairwise Standard Effect Sizes (SES) of shrub species for 31 site units using Jaccard dissimilarity values. Species pool is all shrub species observed in the dataset (938 plots). Within each site unit, mean expected SES values are less than zero (negative t-test statistic, p-values < 0.05).

Figure A12: Pairwise Standard Effect Sizes (SES) of tree species for 31 site units using Jaccard dissimilarity values. Species pool is all tree species observed in the dataset (938 plots). Within each site unit, mean expected SES values are less than zero (negative t-test statistic, p-values < 0.05).
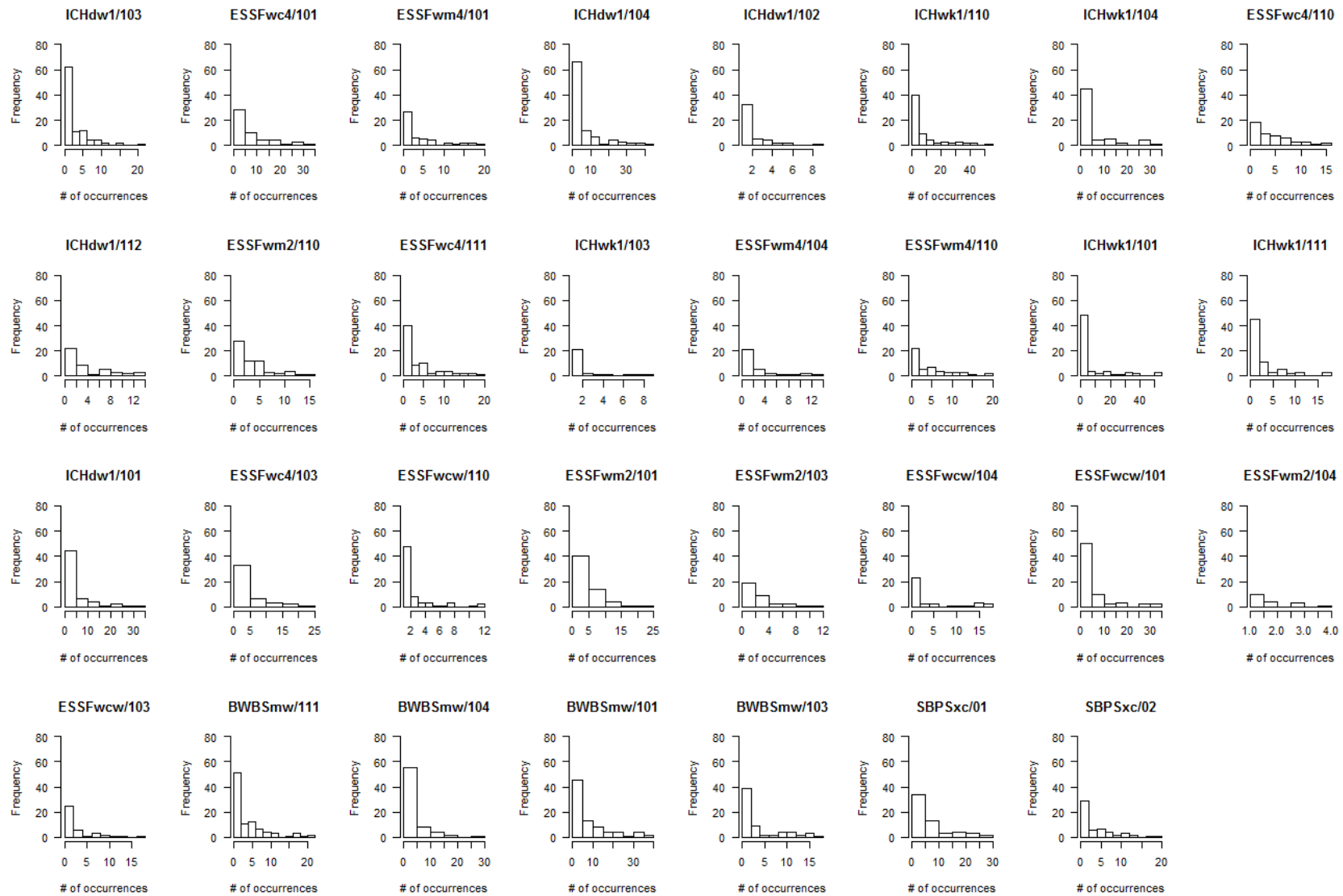
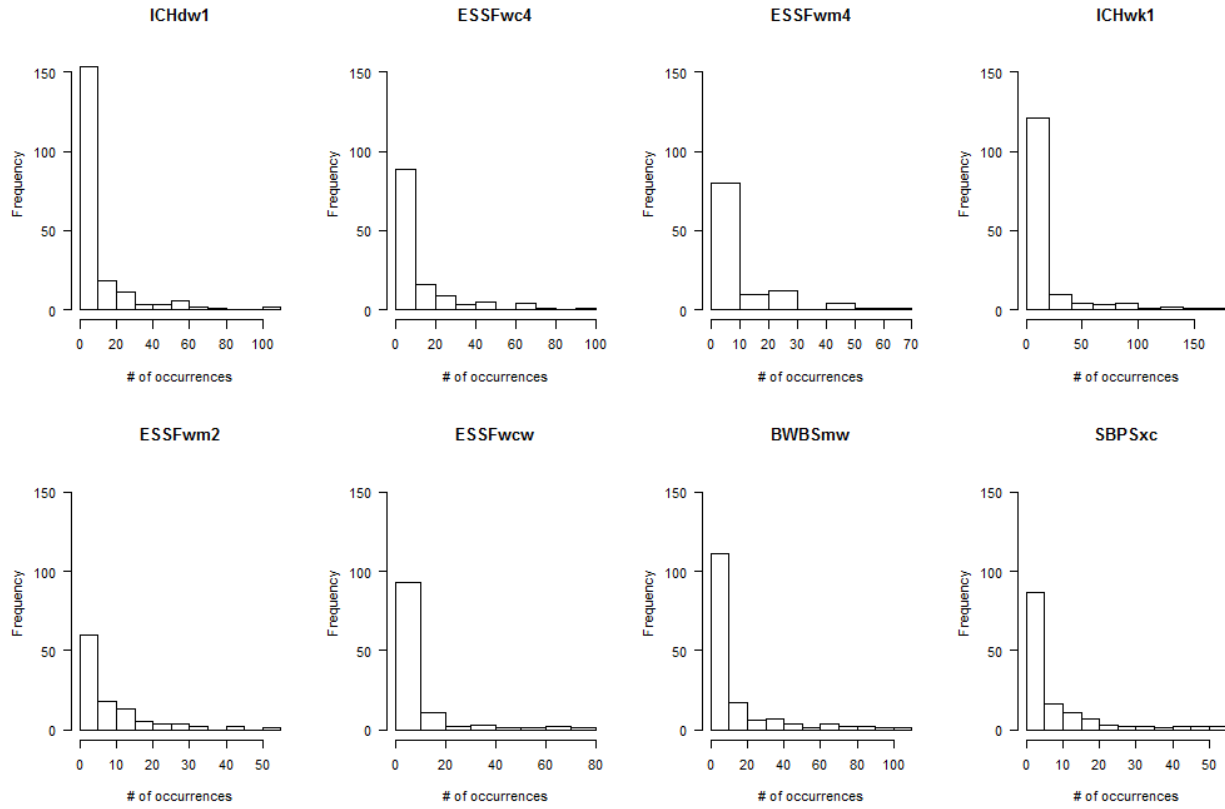**Figure A13: Skewed herb species occupancy distributions for 31 site units.**

Figure A14: Skewed herb species occupancy distributions for herb species within 8 BEC subzones / variants.
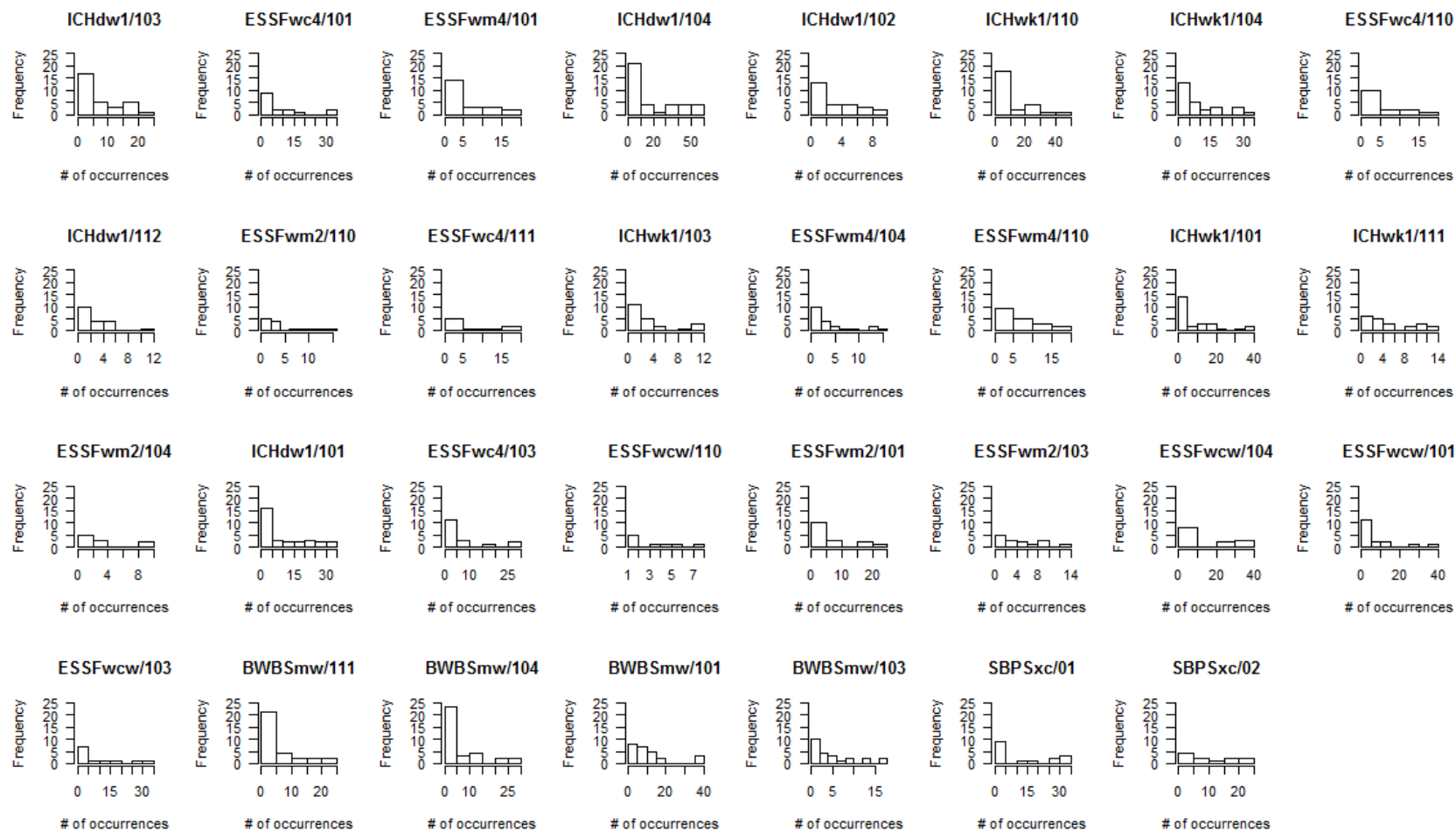
Figure A 15: Shrub species occupancy distributions within 31 BEC site units. Not all site units have skewed distributions.
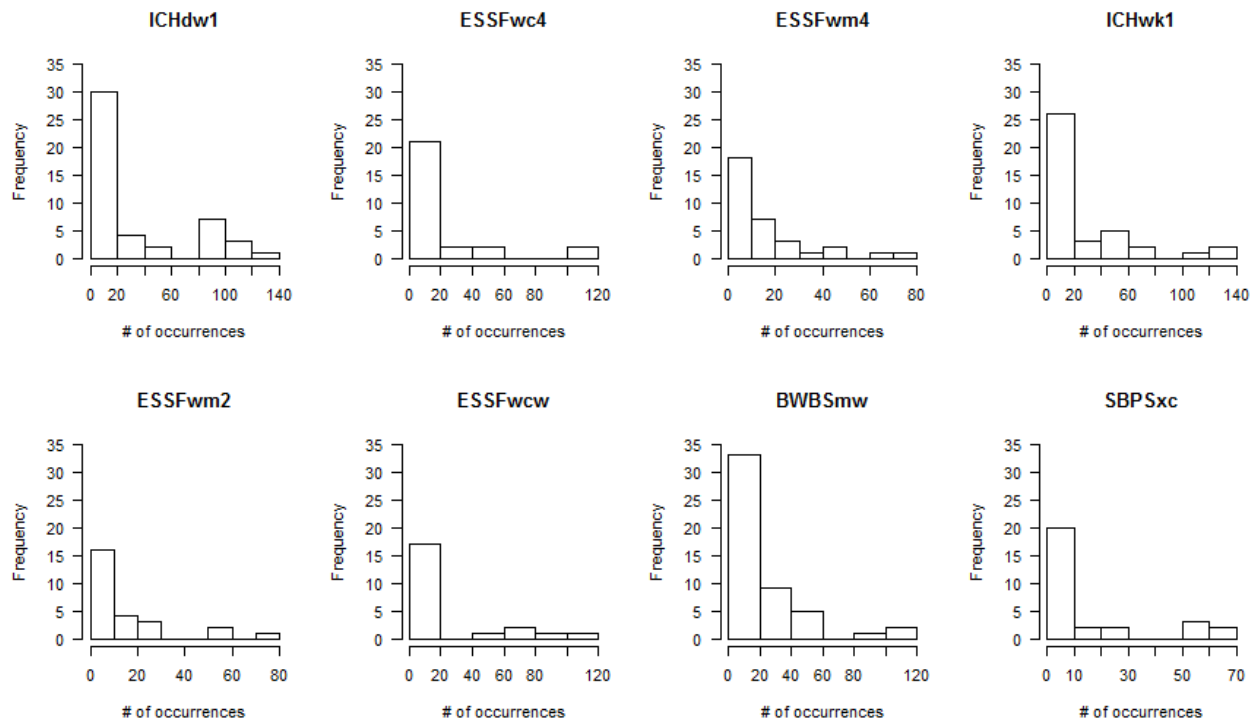
Figure A16: Shrub species occupancy distributions for 8 BEC subzones / variants. Not all site units have skewed distributions.
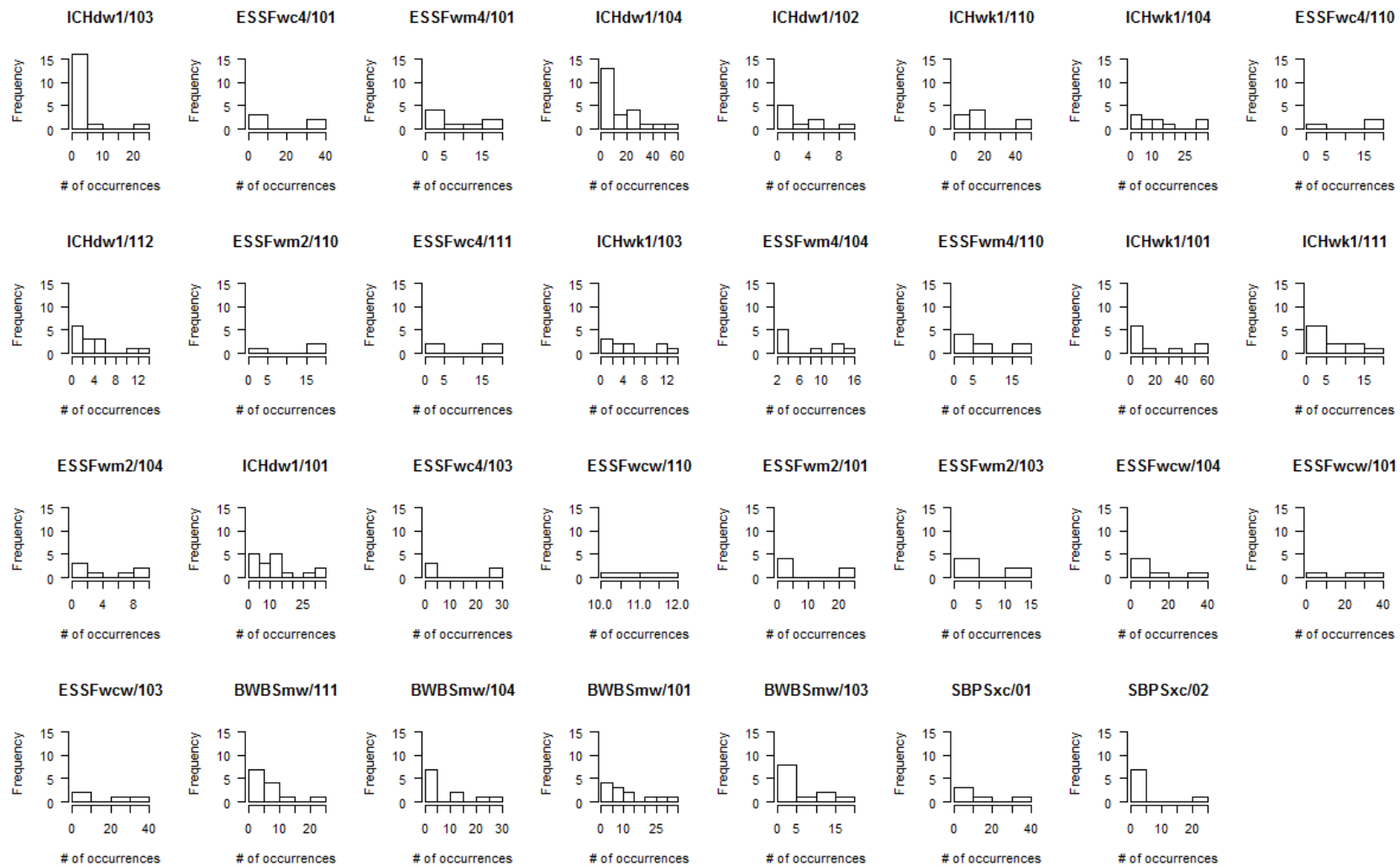
Figure A17: Tree species occupancy distributions within 31 BEC site units. Not all site units have skewed distributions.
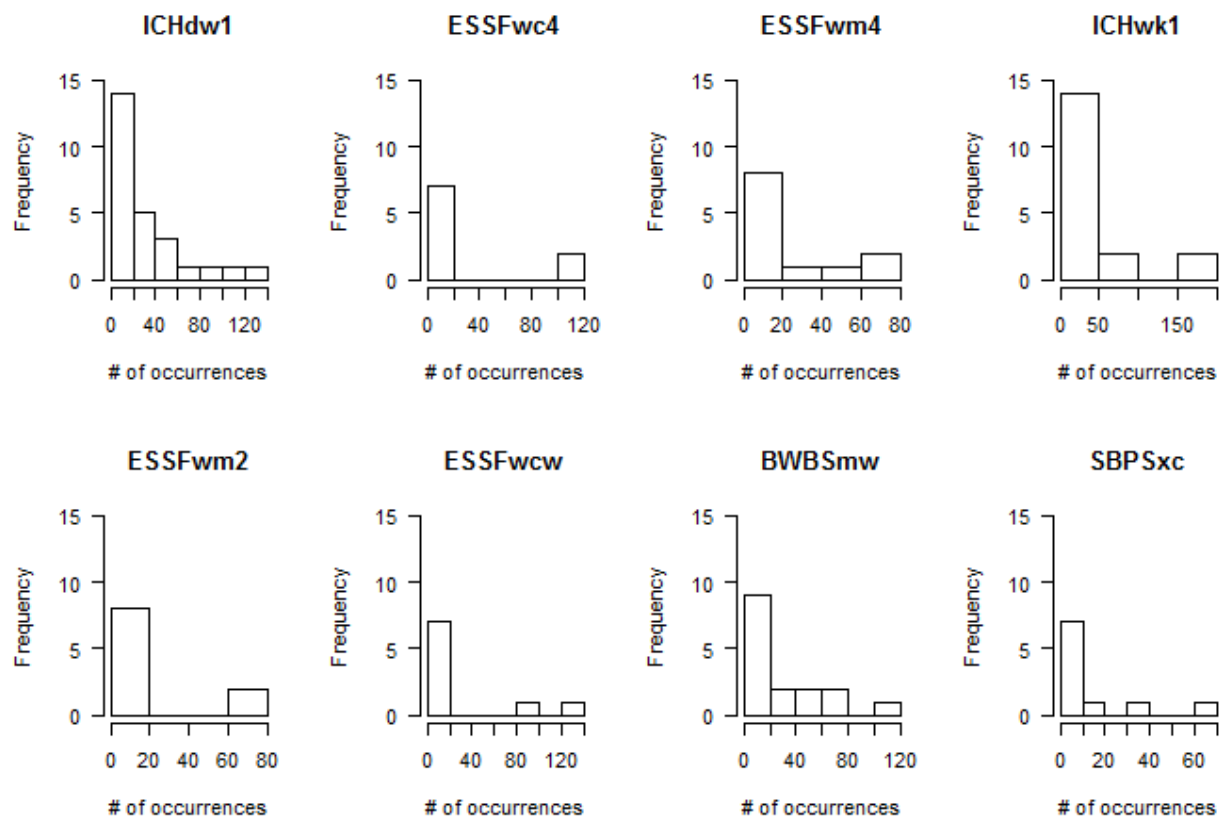
Figure A18: Shrub species occupancy distributions for 8 BEC subzones / variants. Not all site units have skewed distributions.