Title

The Causes and Consequences of Biodiversity Change in the Alpine Tundra of Western North America

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Publication Date

2023

UNIVERSITY OF CALIFORNIA
RIVERSIDE

The Causes and Consequences of Biodiversity Change in the Alpine Tundra of Western North America

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

Doctor of Philosophy

in

Evolution, Ecology, and Organismal Biology

by

Jared D. Anderson-Huxley

September 2023

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Acknowledgements

Completing this dissertation has been a long and difficult process which I would not have completed without the unflagging support of my family, friends, and mentors. First, I would like to acknowledge my advisor Dr. Marko Spasojevic. Marko taught me how to be a scientist, a mentor, a teacher, and a father. I would not have made it through my degree without his advice, humor, and compassion.

Second, I would like to acknowledge my family. Thank you to my wife, Ashley, my daughters, Juniper and Isla, and my dog, Ursula, for comforting me after hard days and reminding me that there are things more important than a career in science. Thank you also, to the other members of my family (Jenna Huxley, Pat Anderson, Fred Huxley, Linda Swatman, Jeff Swatman, Nese Frazier, Kyle Swatman, Alicia Swatman, and Haylee Swatman) for helping me de-stress during holidays and vacations and for helping with emergency childcare situations.

Third, I would like to acknowledge my friends and colleagues at UCR and Niwot Ridge LTER from whom I have learned so much. Thank you to my committee (Dr. Loralee Larios, Dr. Kurt Anderson, and Dr. Kate Ostevik) for their guidance and patience while crafting my dissertation. Thank you to my lab mates (Soren Webber, Tesa Madsen-Hepp, Erin McCann, Ariana Firebaugh-Ornelas, Joey Lodge, Magda Argueta, Jon Henn, Sisimac Duchicela, Caryn Iwanaga, and Advyth Ramachandran) for their expertise, manuscript edits, and stimulating conversations. Thank you to the graduate students of the EEOB department (especially Andrea Keeler, Stuart Schwab, Clarissa Rodriguez, Elisa Henderson, Annika Rose-Person, Chris Cosma, Elijah Hall, and Daniel Pierce) for

creating a friendly working environment and staying strike ready. Thank you to the staff and graduate students of Niwot Ridge LTER (especially Sam Sartwell, Chiara Forrester, Laurel Brigham, and Cliff Bueno de Mesquita) for their help with field work and long hours of conversation while hiking. Thank you to the tireless organizers of UAW 2865, who helped me navigate workplace emergencies and illuminated the bigger picture of academia. Lastly, thank you to the undergraduate students of UCR, who (almost) always came to class excited to learn about ecology and global change.

The text of Chapter 1 of this dissertation is a re-print of the material as it appears in “Area Not Geographic Isolation Mediates Biodiversity Responses of Alpine Refugia to Climate Change”, Frontiers in Ecology and Evolution 2021. The co-author listed in this publication, Marko J. Spasojevic, directed and supervised the research presented in this dissertation.

Dedication

This dissertation is dedicated to my loving wife, Ashley; and my beautiful daughters, Juniper and Isla.

ABSTRACT OF THE DISSERTATION

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by

Jared D. Anderson-Huxley

Doctor of Philosophy, Graduate Program in Evolution, Ecology, and Organismal Biology,
University of California, Riverside, September 2023
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Mountain ecosystems in western North America are highly sensitive to climate change and are warming faster than the global average. Found at the tops of these mountains, the alpine tundra ecosystem is especially threatened due to its fragmented distribution (so called “sky islands”), limited area, and the impossibility of alpine species moving to higher elevations. As a result, alpine sky islands are considered a “sentinel system” for detecting the biological impacts of climate change, and rapid changes in alpine biodiversity are expected in the coming decades. In this dissertation, I explore how climate change is driving shifts in alpine plant biodiversity patterns (chapter 1), how species interactions structure current patterns of alpine biodiversity (chapter 2), and how variation in climatic conditions may affect the relationship between biodiversity and ecosystem function (chapter 3). To investigate these questions, I employ an observational study of regional plant biodiversity across a 12-year period, a neighbor removal experiment paired with spatial point pattern analysis, and structural equation modeling using data from the Niwot Ridge Long Term Ecological Research Program, respectively.

I find evidence that: 1) alpine biodiversity patterns are shifting, notably towards species possessing traits which enable drought tolerance; 2) species interactions and species spatial patterns are largely governed by traits related to plant size like leaf area and height, though the manner in which these traits relate to species coexistence mechanisms changes across alpine community types; and 3) the alpine biodiversity-ecosystem function relationship is also best predicted by size-related traits; however, the ability of these traits to predict ecosystem function varies strongly depending on the amount of winter precipitation. Overall, my dissertation highlights that alpine biodiversity change is detectable over relatively short time periods, and that these changes are likely to have important implications for species interactions and the biodiversity-ecosystem function relationship.

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Introduction

Anthropogenic climate change is altering patterns of temperature and precipitation around the world, threatening biodiversity (Sala et al., 2000; Engler et al., 2011; Garcia et al., 2014). The impacts of climate change on biodiversity are vast and rapidly accelerating, ranging from shifts in the abundance and distribution of local populations to the extinction of entire species (Cardinale et al., 2012; Urban, 2015 De Laender et al., 2016). While some species are directly impacted by shifting abiotic conditions, many more are affected by changes to the intricate web of species interactions which structure ecological communities, with new winners and losers emerging from a rearranged biotic environment (Tylianakis et al., 2008; Liancourt et al., 2013; Alexander et al., 2015). Biodiversity change can have further cascading impacts on the fluxes and pools of energy and materials within ecosystems (i.e., ecosystem function), potentially threatening the vital ecosystem services upon which human society relies (Mooney et al., 2009, 2009; Lee et al., 2015; García-Palacios et al., 2018; Maurer et al., 2020). To preserve the integrity and utility of biodiversity in the face of climate change, it is more important than ever that we work to understand the scale and pace of biodiversity change, the species interaction mechanisms which structure current ecological communities, and the relationship between biodiversity and ecosystem function.

Mountain ecosystems in western North America are particularly sensitive to climate change and are warming faster than the global average (McGuire et al., 2012; Rangwala and Miller, 2012; Pepin et al., 2015). Importantly, these ecosystems provide the majority of the water supply for human consumption in the region and many other key ecosystem services such as snow-based recreation, timber, and critical habitat for rare and endangered species (Baron, 2002). Found at the tops of isolated mountain peaks (so called “sky islands”), alpine tundra is an ecosystem characterized by meadows of wildflowers and grasses (alpine by definition is above tree-line) and harsh environmental conditions (Bowman and Seastedt, 2001; Williams et al., 2015; Korner and Spehn, 2019). Alpine sky islands formed as continuous, low elevation tundra communities began to fragment and retreat upslope following the end of the last glacial maximum (Pewe, 1983). Because of this unusual biogeographic history, alpine plant species face unique challenges in responding to anthropogenic climate change. For example, while lowland species may be able to track rising temperatures by moving to higher elevations, alpine tundra species are already located at the tops of mountains leaving little room for upward movement (Walther et al., 2002). Additionally, the disjointed distribution and limited area of alpine sky islands reduces rates of gene flow and dispersal and magnifies the effects of genetic and ecological drift, resulting in populations and communities which face a higher probability of stochastic change (McGraw, 1995; Newman and Pilson, 1997; Holyoak et al., 2005; Jay et al., 2012; Leibold and Chase, 2017). Due to these factors, alpine sky islands are considered a “sentinel system” for detecting the biological effects of climate change (Engler et al., 2011; (Grabherr et al., 2000; Stanisci et al., 2005; Smith et al., 2009); but see Malanson et al., 2019) and thus an ideal setting to explore the scale and pace of biodiversity change, and cascading impacts on species interactions and ecosystem function.

Climate change is already altering patterns of tundra biodiversity world-wide, with global syntheses demonstrating expanding vegetation cover, encroachment of sub-alpine or low latitude species, and increasing community height over the last several decades (Elmendorf et al., 2012a; Bjorkman et al., 2018; Steinbauer et al., 2018). Despite solid evidence for these global trends, we still lack critical information about how alpine biodiversity change is proceeding at local and regional scales. At a local scale, it is unclear whether rates of biodiversity change differ between individual sky islands and how landscape context may mediate these changes (Spasojevic et al., 2014; Malanson et al., 2015). Island biogeography theory predicts that decreasing island area will increase rates of local species extirpation, while increasing island isolation will decrease rates of new species colonization, potentially leaving smaller and more isolated alpine sky islands primed for greater biodiversity change (MacArthur and Wilson, 2001; Losos and Ricklefs, 2009; Santos et al., 2016). At a regional scale, most current research on biodiversity change in tundra ecosystems is conducted in the Alps, the Tibetan Plateau, or the Arctic, and the lack of data from North American alpine tundra regions may be biasing the results of global syntheses (Wang et al., 2011; Elmendorf et al., 2012b; Wipf et al., 2013; Bjorkman et al., 2018; Steinbauer et al., 2018). Alpine tundra in Western North America is more arid than Europe and less productive than the Tibetan Plateau. Furthermore, the region is experiencing long-term declines in winter precipitation, and thus, biodiversity responses should not be expected to parallel trends observed in other alpine regions (Fyfe et al., 2017; Lesica and Crone, 2017; Mote et al., 2018; Testolin et al., 2020). To capture a holistic picture of global alpine biodiversity change, we must quantify the sensitivity of individual sky islands and additionally prioritize long-term monitoring of North American alpine tundra.

While biodiversity change is, in part, a direct result of shifting abiotic conditions exceeding species physiological limits, it can also result indirectly from changes in the ways species interact with one another (e.g., competition vs facilitation) (Chesson, 2000; Tylianakis et al., 2008; González-Megías and Menéndez, 2012; Liancourt et al., 2013). As climatic conditions shift, some species will gain advantages from their new abiotic context, subsequently allowing them to outcompete and exclude their neighbors (Liancourt et al., 2013; Alexander et al., 2015; Wainwright et al., 2019). For example, Alexander et al (2015) found that transplanting alpine species into sub-alpine communities to simulate the novel communities expected under warming temperatures, resulted in reduced probability of survival, growth rates, and probability of flowering as result of competition with novel competitors. To determine which alpine species may be favored or disadvantaged under new climatic conditions, it is first necessary to develop a mechanistic understanding of how species interactions structure current alpine biodiversity patterns. Functional traits (i.e., morphological, physiological, phenological, or chemical species traits linked to species fitness) provide a window into these interaction mechanisms, as they are linked to fitness and mediate how species respond to, and effect, their abiotic and biotic environment (Mcgill et al., 2006; Kraft et al., 2015; Garnier et al., 2016). By identifying important functional traits, linking these traits to interaction mechanisms, and finally showing how these interactions result in biodiversity patterns, we can take a vital first step in predicting potential changes in balance of alpine species interactions.

Functional traits not only underpin species interactions, but also many of the processes responsible for moving energy and materials through ecosystems (e.g., net primary production, decomposition, nutrient cycling), collectively referred to as ecosystem function (Díaz and Cabido, 2001; Garnier et al., 2016; Cadotte, 2017). Maintaining the integrity of ecosystem function is critical, not just for preserving natural systems, but also for stabilizing key ecosystem services on which human society relies like carbon sequestration, water filtration, and erosion control (de Bello et al., 2010; Grêt-Regamey et al., 2012; Lee et al., 2015). However, climate induced changes in biodiversity, particularly functional diversity, are rapidly altering ecosystem functions and services around the world (de Bello et al., 2010; Funk et al., 2017). For example, warming temperatures at high latitudes have been linked to increases in the average height of Arctic tundra communities, with cascading effects on critical ecosystem functions including primary productivity, decomposition, and carbon cycling (Cornelissen et al., 2007; Cahoon et al., 2012; Elmendorf et al., 2012b; Bjorkman et al., 2018). While decades of research have highlighted the relationship between functional trait diversity and ecosystem function, questions remain regarding how climate change will mediate this relationship in alpine tundra. Specifically, we must advance our understanding of which specific traits and mechanism underlie the biodiversity-ecosystem function relationship in alpine tundra and how these factors may shift with varying climatic conditions.

In this dissertation, I examine patterns of taxonomic, phylogenetic, and functional diversity from the scale of paired species to sky islands across the state of Colorado to better understand the sensitivity of the alpine tundra to climate change. In chapter 1, I use a regional survey of alpine sky islands in the Colorado Rocky Mountains to investigate changes in taxonomic, functional, and phylogenetic diversity patterns over a 12-year period and how these changes are mediated by sky island landscape context. In chapter 2, I couple a neighbor removal experiment with an observational study of local biodiversity patterns to investigate the nature of alpine species interaction mechanisms and how those mechanisms manifest as biodiversity patterns. In chapter 3, I synthesize multiple long-term datasets on climatic conditions, local abiotic variables, species composition, and ecosystem function to explore how climatic variation affects the relationship between biodiversity and ecosystem function. By synthesizing these chapters, I hope to advance our understanding of the causes and consequences of alpine biodiversity change in Western North America.

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Chapter 1

Area, not geographic isolation, mediates biodiversity responses of alpine refugia to climate change

Abstract

Climate refugia, where local populations of species can persist through periods of unfavorable regional climate, play a key role in the maintenance of regional biodiversity during times of environmental change. However, the ability of refugia to buffer biodiversity change may be mediated by the landscape context of refugial habitats. Here, we examined how plant communities restricted to refugial sky-islands of alpine tundra in the Colorado Rockies are changing in response to rapid climate change in the region (increased temperature, declining snowpack, and earlier snow melt-out), and if these biodiversity changes are mediated by the area or geographic isolation of the sky-island. We resampled plant communities in 153 plots at 7 sky islands distributed across the Colorado Rockies at two time points separated by 12 years 2007/2008 to 2019/2020) and found changes in taxonomic, phylogenetic, and functional diversity over time. Specifically, we found an increase in species richness, a trend toward increased phylogenetic diversity, a shift toward leaf traits associated with the stress tolerant end of leaf economics spectrum (e.g., lower specific leaf area, higher leaf dry matter content), and a decrease in the functional dispersion of specific leaf area. Importantly, these changes were partially mediated by refugial area but not by geographic isolation suggesting that dispersal from nearby areas of tundra does not play a strong role

mediating these changes, while site characteristics associated with larger area (e.g., environmental heterogeneity, larger community size) may be relatively more important. Taken together these results suggest that considering the landscape context (area and geographic isolation) of refugia may be critical for prioritizing the conservation of specific refugia sites that provide the most conservation value.

Introduction

Rapid, anthropogenic climate change is altering temperature and precipitation patterns around the world, threatening biodiversity (IPCC, 2014; Díaz et al., 2019). While some changes in biodiversity patterns are inevitable, the impacts of climate change on biodiversity may be mitigated in part via the conservation of refugia: geographic locations or habitat types which are buffered from the most intense and immediate effects of environmental change (Tzedakis et al., 2002; Keppel et al., 2012). Refugia have played a key role in maintaining biodiversity during past (quaternary) climatic changes (Taberlet and Cheddadi, 2002; Byrne, 2008; Carnaval et al., 2009). For example, the climatic stability, rugged terrain, and complexity of soils and microclimates of the Klamath-Siskiyou region of southwest Oregon allowed the region to serve as a refugia for ecological communities that required cool and moist conditions in the past (Whittaker, 1960; Olson et al., 2012, Copeland and Harrison, 2015). Currently, refugia have the potential to maintain biodiversity in the face of anthropogenic climate change (Ashcroft, 2010; Dobrowski, 2011; Ashcroft et al., 2012; Keppel et al., 2012; Keppel et al., 2018). While maintenance of taxonomic diversity has been the traditional focus of refugia conservation efforts, the role of refugia in preserving functional and phylogenetic diversity may be more important as functional traits and phylogenetic identity are thought to more directly control ecosystem function and stability (Díaz and Cabido, 2001; Cavender-Bares et al., 2009, Funk et al., 2017). Despite the recognized importance of climate change refugia in general, there is still a need to better identify specific sites that may serve as high quality refugia given the economic and political constraints on conserving refugial habitats (Keppel et al., 2012; Keppel et al., 2015, Mokany et al., 2017).

Importantly, refugia may differ in their capacity to buffer against environmental changes and therefore promote the persistence of threatened species (Keppel et al., 2015). Within geographic locations or habitat types that are broadly considered refugia, individual sites may vary in their ability to withstand the impacts of climate change based on their landscape context (Gaston and Blackburn, 1996; Ashcroft et al., 2009; Keppel et al., 2015). Specifically, island biogeography theory demonstrates that site area and geographic isolation mediate rates of dispersal and ecological drift (MacArthur and Wilson, 1967), with subsequent impacts on taxonomic, functional, and phylogenetic diversity (Graham and Fine, 2008; Spasojevic et al., 2014; Fernández-Palacios et al., 2015; Carmona et al., 2016). Differences in area and isolation among refugia sites may also alter how those sites respond to shifts in the niche selection regime imposed by climate change (Keppel et al., 2015). For example, larger refugial sites are more likely to contain higher levels of environmental heterogeneity and thus may be able to provide optimal environmental conditions for a greater diversity of species (Currie et al., 2004), functional strategies (Spasojevic et al., 2014), and/or phylogenetic lineages (Leibold et al., 2010) even with changes in regional climate (Keppel et al., 2015). Similarly, larger sites may also be able to support larger populations or communities that are less susceptible to demographic stochasticity (Loreau and de Mazancourt, 2008). On the other hand less isolated refugia sites may be more likely to be connected to other refugia via dispersal and thus may be able to retain species (Leibold et al., 2004), functional strategies (Schleuter et al., 2012), or phylogenetic lineages (Thorpe et al., 2008; Eldridge et al., 2018) negatively affected by changes in regional climate through source-sink dynamics. Understanding how the area and isolation of refugia mediate changes in taxonomic, functional, and phylogenetic diversity caused by climate change is therefore a key next step in prioritizing the conservation of specific refugia sites that provide the most conservation value.

Alpine tundra is an excellent system for understanding how site area and isolation may affect biodiversity change in climatic refugia. Found at the tops of mountains, alpine tundra is characterized by meadows of wildflowers and grasses (alpine by definition has no trees) and harsh environmental conditions (Bowman and Seastedt, 2001; Korner, 2003; 2004). Alpine tundra in Western North America currently displays an archipelago-like distribution, with “sky islands” of suitable, high-elevation habitat surrounded by a matrix of unsuitable, low-elevation habitat (Pewe, 1983). These disjunct sky islands formed when the large, continuous alpine communities present during the last glacial maximum began to fragment and retreat upslope in response to natural climatic warming (Pewe, 1983). Thus, alpine sky islands serve as an *ex-situ* refugia for a formerly widely distributed palaeo-habitat type, as evidenced from molecular data on a wide range of organisms (e.g., Skrede et al., 2006; Shafer et al., 2011). The upslope movement and subsequent fragmentation of tundra habitat produced individual sky islands which vary in their size and geographic isolation (McCormack et al., 2009). This variation in landscape context may serve as a critical mediator of shifts in alpine taxonomic, functional, and phylogenetic diversity in response to climate change as mountain ecosystems in western North America are currently warming faster than the global average, a trend that is expected to accelerate (Rangwala and Miller, 2012; Pepin et al., 2015). Understanding how sky island area and isolation affect biodiversity change will not only help to identify the best refugia sites for this threatened ecosystem, but also potentially generalize to other systems with island-like distributions (e.g., serpentine soils).

Here, we explore if the landscape context (site area and geographic isolation) mediates changes in the biodiversity of refugial alpine sky-islands in the Colorado Rocky Mountains over a twelve-year period. Specifically, we explored how site area and isolation mediate changes in species richness, Shannon's diversity index, community level phylogenetic diversity, community weighted mean trait values, and community dissimilarity in functional traits between our two sampling periods. Based on the tenants of island biogeography (MacArthur and Wilson, 1967; Brown and Kodric-Brown, 1977; Connor and McCoy, 1979, Ottoviani et al., 2020a), we predict: 1) that site area will mediate biodiversity change as larger sites have the potential to support a wider range of habitat types and species and/ or larger populations; and 2) that geographic isolation will mediate biodiversity change as potential local extinction or declining populations may be offset by dispersal from nearby areas of tundra.

Methods

Field sampling

During the summers of 2007 and 2008 we sampled community composition at 7 alpine sites in the Colorado Rocky Mountains (see Spasojevic et al., 2014 for additional details). Using topographic maps, we selected sites to capture variation in size and geographic isolation, while also considering accessibility. All sites sampled were sky islands: alpine tundra habitat completely surrounded by less-suitable habitat for alpine populations such as rock outcrops, subalpine meadows, or coniferous forests. We sampled species composition and abundance in a series of 1-m^2 plots within each site, where the number of plots was proportional to total site area and the arrangement of plots were standardized across major topographic gradients. In alpine tundra, topography plays a key role in shaping biodiversity patterns via snow deposition, and thus this sampling design enabled us to capture the full range of alpine vegetation types including snow-bed (high snow accumulation), moist meadow (intermediate snow accumulation), and fellfield (very low snow accumulation) communities. Within each plot, plant composition was estimated using visual estimations of percent cover of all species with the assistance of a 1m x 1m frame containing a 10cm by 10cm string grid. Across all sites we sampled species composition in 153 plots, with the number per site ranging from 8 at Greenhorn Mountain to 40 at Niwot Ridge (Fig. 1.1) with an average of 23 plots per site. Plot locations were predetermined and spaced evenly along topographic gradients at each site at ~200m intervals. Since community composition in the alpine tundra is strongly determined by the redistribution of snow by wind along topographic gradients (Walker et al., 2001), sampling along topographic gradients allowed us to capture most of the diversity of each site. In 2019 and 2020 we revisited these sites keeping plot number and sampling locations as consistent as possible based on GPS coordinates recorded in 2007/8. Given the relatively low accuracy of GPS units (± 3m) we examine site level patterns of biodiversity changes instead of plot level changes as we are more confident that we accurately resampled each site, if not individual plots (N = 14 in subsequent analyses, 7 sky islands in each sampling period).

Spatial variables

During site visits the approximate alpine area was delineated on a topographic map, and area was later calculated using Image-J (Rasband, 2007). Geographic isolation was calculated as the area (km^2) of non-alpine tundra habitat within a 10km radius of the center of each site (not including the site area) using ArcGIS 9.0. MacArthur and Wilson's (1967) classic theory of island biogeography suggests that area more strongly influences extinction rates and geographic isolation more strongly affects colonization rates. However, advances to this theory acknowledge that geographic isolation can influence extinction rates (the rescue effect: Brown and Kodric-Brown, 1977) and area can influence colonization rates (the passive sampling effect: Connor and McCoy, 1979). Importantly, area in the alpine tundra is often correlated with topographic heterogeneity, where larger sites have a higher probability of capturing a greater variation in topographic variation that will influence biodiversity patterns (Walker et al., 2001).

Trait measurements

To quantify changes in community weighted mean trait values (CWM) and functional diversity metrics among sampling periods we used a combination of trait data that has been collected from previous studies in this system (Spasojevic and Suding, 2012; Spasojevic et al., 2014), from additional measurements conducted at the Niwot Ridge LTER (one of our sites), and from measurements of any new species that were not encountered in our first sampling period. All trait measurements followed established protocols (Perez-Harguindeguy et al., 2013), and were collected on a minimum of 10 individuals for each species. Importantly, in our fist sampling period we compared trait values among the most abundant species present in both northern and southern sites (approximately 25% of our total species pool) and found that there was little variation in mean trait values along this broad north to south geographic gradient (Spasojevic et al., 2014) suggesting that using trait mean values from this database will allows us to examine broad scale patterns of functional diversity.

We focused on four putatively important traits: overall height, specific leaf area (SLA), leaf area, and leaf dry matter content (LDMC). Plant vegetative height, a trait often allometrically related to overall plant size (biomass, rooting depth, lateral spread) as well as to competitive interactions for light (Aan et al., 2006), was measured as length from ground level to the highest photosynthetically-active tissue. We also collected a fully formed adult leaf, with no signs of damage or senescence at peak biomass. Collected leaves were hydrated overnight prior to weighting fresh mass. Leaves were then dried at 55ºC for 4 days and weighed to determine leaf dry mass. Individual leaf area was calculated from the leaf scans using Image-J (Rasband, 2007); leaf area is associated with leaf energy and water balance, with various stressors (heat, drought, cold and high-radiation) tending to select for small leaf area (Cornelissen et al., 2003). Specific leaf area, was calculated as leaf area (cm^2) per unit of dry leaf mass (g) and is associated with the leaf economics spectrum, which characterizes a species capacity for stress tolerance vs resource acquisition (Westoby et al., 2002). Leaf dry matter content was calculated as the ratio of dry mass to fresh mass and is also associated with the leaf economics spectrum(Garnier et al., 2001).

Diversity metrics

To describe differences in biodiversity among sampling periods we first calculated species richness, Pielou's evenness, and Shannon's diversity index using the vegan package (Oksanen et al., 2019) in R version 4.0.2 (R Core Team, 2019). We then calculated two metrics of phylogenetic relatedness: mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) using the PICANTE package (Kembel et al., 2010) in R. Mean pairwise distance is a metric of relatedness which measures the mean branch distance among all species pairs in a community (Webb et al., 2002) and is more sensitive to tree wide patterns of phylogenetic clustering and evenness (Kraft et al., 2007). Mean nearest taxon distance is the mean distance separating each species in the community from its closest relative in the community (Webb et al., 2002) and is more sensitive to patterns of clustering and evenness closer to the tips of the phylogeny (Kembel, 2009). We compared these metrics to null communities by randomizing species co-occurrences 9999 times while maintaining sample richness and species occurrence frequencies. For both of these metrics we calculated a standard effect size (SES, as per Gurevitch et al., 1992) based on a comparison of observed values and null values where

$$SES = \frac{Metric_{Observed} - Mean(Metric_{Null})}{SD(Metric_{Null})}$$

a SES of zero indicates no difference, values greater than zero indicates phylogenetic overdispersion and values less than zero indicates phylogenetic underdispersion. The net relatedness index (NRI) is calculated as the SES of MPD. The nearest taxon index (NTI) is calculated as the SES of MNTD.

For each site in each sampling period we calculated two complementary functional diversity metrics: community-weighted mean (CWM) trait values (Garnier et al., 2004) and functional dispersion (FDis; Laliberte and Legendre, 2010) for each trait. CWM trait values were calculated as the sum across all species of species' trait values weighted by their relative abundance (Garnier et al., 2004). Following Laliberte & Legendre (2010), we calculated FDis as the mean distance of each species, weighted by relative abundances, to the centroid of all species in a site. Although there are many metrics of functional diversity (reviewed in Mouchet et al., 2010; Schleuter et al., 2010), we focused here on FDis because it is independent of species richness, takes into account species abundances, and can be used for single traits or multiple traits (Laliberte and Legendre, 2010). Moreover, Ricotta and Moretti (2011) proposed a unified analytical framework that combines CWM and a close analogue of FDis (Rao's Q). Functional diversity calculations were conducted using the FD package (Laliberte and Legendre, 2010) in R.

Statistical analysis.

To test whether our diversity metrics (i.e., richness, evenness, Shannon's diversity, NRI, NTD, CWMs, FDis) differed among years and if those differences were mediated by refugial area or isolation, we constructed separate generalized linear mixed models (GLMM) with each diversity metric as the response variable and response variable with year, area, isolation, and all possible interactions of those as predictor variables, and site as a random factor – analyses were conducted in JMP version 13.0 (SAS Institute, 2016).

Results

We found that species richness significantly increased between sampling periods (2007/8: 43.3±2.9; 2019/20: 50.9±5.2; $F_{1,3}$=20.67, P=0.02) and that there was a significant interaction with area ($F_{1,3}$=15.29, P=0.03, Fig. 1.2A) where larger sites had a larger increase in richness than smaller sites. We found no difference among years in evenness ($F_{1,3}$=1.16, P=0.36) or Shannon's diversity ($F_{1,3}$=0.04, P=0.84, Fig. 1.2B & 1.2F), and a trend toward increased phylogenetic diversity (NRI: $F_{1,3}$=9.4, P=0.05, Fig. 1.2C & 1.2G; NTD: $F_{1,3}$=5.51, P=0.10, Fig. 1.1D & 1.1H) among years. All non-significant P values are reported in Supplement 1.1.

In the CWM analysis, we found a shift toward a more stress tolerant functional strategy between sampling periods with a significant decrease in leaf area ($F_{1,3}$=43.36,

$P<0.01$; Fig. 1.3B & 1.3F), and a trend toward decreasing SLA ($F_{1,3}=6.56$, $P=0.08$, Fig. 1.3C & 1.3G) and increasing LDMC ($F_{1,3}=8.44$, $P=0.06$, Fig. 1.2D & 1.2H). However, none of these responses were mediated by area or geographic isolation. Height had a significant year by area interaction ($F_{1,3}=27.99$, $P=0.01$, Fig. 1.3A) where height decreased in smaller sites and increased in larger sites between sampling periods and a significant year by area by isolation interaction ($F_{1,3}=24.45$, $P=0.02$).

Lastly, we found FDis of SLA decreased between sampling periods ($F_{1,3}=41.67$, $P=0.007$, Fig. 1.4C & 1.4G) and that there was a significant year by area interaction ($F_{1,3}=24.41$, $P=0.02$) where FDis of SLA decreased more in smaller sites (Fig. 1.4C). Moreover, height had a significant year by area interaction ($F_{1,3}=26.30$, $P=0.01$, Fig. 1.4A) where FDis decreased in smaller sites and increased in larger sites between 2009 and 2019 and a significant year by area by isolation interaction ($F_{1,3}=35.51$, $P=0.01$). Lastly we found no difference among years in the FDis of leaf area ($F_{1,3}=5.24$, $P=0.11$, Fig. 1.4B & 1.4F) or FDis of LDMC ($F_{1,3}=2.41$, $P=0.22$, Fig. 1.4D & 1.4H) and no significant interactions with area or isolation.

Discussion

Overall, we found that taxonomic, phylogenetic, and functional diversity of communities in sky-islands of alpine tundra in the Colorado Rocky Mountains are changing and our initial observations suggest that landscape context may mediate the ability of refugia to withstand the impacts of climate change (Gaston and Blackburn, 1996; Ashcroft et al., 2009; Keppel et al., 2015). Specifically, we found an increase in species richness, a trend toward increased phylogenetic diversity, a shift toward a more stress tolerant functional strategy, and a decrease in the functional dispersion (FDis) of SLA over time. Importantly, we found that refugial area mediated some of these responses, where larger sites had a larger increase in richness than smaller sites, CWM height decreased in smaller sites and increased in larger sites, and FDis of SLA decreased more in smaller sites. On the other hand, none of our responses were mediated by geographic isolation, which may be due to the rarity of long-distance dispersal events (Tackenberg and Stocklin, 2008) for the long-lived, clonally reproducing species which compose alpine communities (Forbis, 2003, Rossetto and Kooyman, 2005, Herben et al., 2015). Collectively, these results suggest that considering the landscape context (area and geographic isolation) of refugia may be important for conserving the refugial sites that provide the most conservation value.

Changes in Taxonomic Diversity

Our observation of increased species richness between sampling periods finds mixed support in the literature. Tundra wide syntheses of observational studies and global change experiments have generally observed decreases in taxonomic diversity as a result of shrub expansion due to increasing temperatures and decreasing snow cover duration period (Elmendorf et al., 2012; Pearson et al., 2013), and models of climate change forecast further losses of species richness as climate change continues to accelerate (Nabe-Nielsen et al., 2017; Niittynen et al., 2020). However, research in alpine tundra specifically has found contrasting results. In non-Mediterranean European alpine systems, Steinbauer et al. (2018) found species richness has significantly increased on 87% of 302 mountain summits since 1871 and that these increases were accelerating through time in conjunction with accelerating increases in temperature and precipitation. Steinbauer et al. (2018) attributed the increase in species richness to the movement of subalpine species into the alpine zone due to the amelioration of harsh abiotic conditions. Numerous other studies from the alpine tundra of boreal and temperate Europe corroborate these results and interpretation (Stanisci et al., 2005; Gottfried et al., 2012; Wipf et al., 2013). Studies in Mediterranean alpine tundra have found more mixed responses, with some reporting decreases in species richness (Pauli et al., 2012), and other studies showing increases largely driven by the upward movement of thermophilic, generalist species (Evangelista et al., 2016; Jiménez-Alfaro et al., 2014). Fewer studies have been conducted in the alpine tundra of western North America and those studies also demonstrate mixed support for species richness increases. In support of our results, at the Niwot Ridge LTER in the Colorado Rocky Mountains (one of our study sites, though we did not use long-term monitoring plots in this study), Spasojevic et al. (2013) found a significant increase in species richness over a 21 year period (sampled at irregular intervals from 1989 to 2010: 1989, 1990, 1995, 1997, 2006, 2008, and 2010) and attributed this trend to the increased establishment of subordinate alpine species as a result of increasing temperature, snow deposition, and nitrogen deposition. However, Scharnagl et al. (2019) found significant decreases in species richness using a different dataset at Niwot Ridge sampled over a 40 year period (sampled every ten years) and attributed the change in richness to an increase in shrub cover and a decrease in average snow depth. The contrasting results may be a result of the differing sampling periods which exemplifies the need for more research in North American alpine ecosystems as these are two of the only published long term monitoring studies focused explicitly on community composition within the Rocky Mountains (Elmendorf et al., 2012; Bjorkman et al., 2018).

Changes in Phylogenetic Diversity

In conjunction with the observed increase in species richness between our two sampling periods, we also found a marginally significant (P=0.05) increase in phylogenetic diversity (using metrics independent of species richness). These patterns suggest that the species present within these alpine refugia are shifting toward being more widely distributed across the phylogeny, capturing greater variation in evolutionary histories, potentially as a result of continued climatic warming relaxing environmental filtering in the alpine. Despite the increased interest in linking evolutionary history with climate change (e.g., Botero et al., 2015; Harrison et al., 2020) few studies have considered changes in phylogenetic diversity in response to climate change within alpine tundra ecosystems. In one of the few studies to indirectly address phylogenetic diversity changes, Lesica and colleagues found that species with artic or boreal evolutionary histories have declined in Glacier National Park (Montana, USA) since 1988, and that this decline is worse for dicots than for monocots (Lesica and McCune, 2004; Lesica, 2014; Lesica and Crone, 2017). While Lesica et al.'s (2004; 2014; 2017) studies point to interesting trends in how coarse phylogenetic groupings may mediate responses to climate change, we were unable to find research that analyzed how community level phylogenetic diversity in the alpine shifted in response to climate change using common metrics of phylogenetic diversity (e.g. Faith's PD, MNTD, etc.). This is an under-appreciated aspect of biodiversity change which requires more attention moving forward (Gerhold et al., 2015), especially in refugia.

Changes in Functional Diversity

The shift towards stress tolerant functional traits we observed contrasts with tundra-wide syntheses (Gottfried et al., 2012; Pearson et al., 2013; Bjorkman et al., 2018; Steinbauer et al., 2018) which have generally found that increased temperatures drive shifts towards communities with greater average heights and trait values related to the resource acquisitive side of the leaf economics spectrum (high SLA and Leaf N content, low LDMC). However, in those syntheses, soil moisture plays a strong role in mediating the effects of regional temperature on functional composition and diversity. For example, Bjorkman et al.'s (2018) analysis of 117 tundra sites throughout the northern hemisphere found that higher temperatures were only correlated with increases in resource acquisitive traits in wetter tundra sites. In sites, where soil moisture was limiting, temperature was correlated less positively with increasing heights and stress tolerant functional traits were favored (Low SLA and Leaf N, high LDMC). In the mountain ranges of the North American West, increased average temperature has been coupled with an overall decline in snowpack and earlier melt-out dates (Fyfe et al., 2017; Mote et al., 2018; Rhoades et al., 2018). Taken together, these regional climatic changes may reduce available soil moisture during the summer growing season, thus selecting for alpine species possessing more stress tolerant functional traits. This is further reinforced by Lesica and McCune's (2004) long term monitoring work in Glacier National Park where shifts towards community types associated with lower soil moisture and more stress tolerant functional strategies have been observed.

Landscape Context

In addition to these changes through time, our results suggest a deeper consideration of landscape context is important in assessing and conserving refugia. We found that some of the variation in taxonomic richness, phylogenetic diversity, functional composition, and functional diversity among sampling periods was mediated by site area but not by geographic isolation. Site area can mediate changes in biodiversity within refugia through several mechanisms. First, larger sites are more likely to contain a greater variety of environmental conditions (Bell et al., 1993; Hulshof and Spasojevic, 2020), which may buffer environmental change. This may be the case in alpine systems where stark topography leads to differential distribution of snow on the landscape, creating strong gradients in stress exposure and resource availability and generating a complex mosaic of distinct vegetation types which differ greatly in species composition and productivity (Bowman and Fisk, 2001; Walker et al., 2001; Bowman et al., 2003; Seastedt et al., 2004; Litaor et al., 2008). Second, larger sites may be able to support populations and communities of larger size and as community size decreases in smaller refugia, the probability of local extinctions is predicted to increase due to demographic stochasticity

(Loreau and de Mazancourt, 2008). Third, larger sites may be easier to colonize than smaller sites potentially counteracting local extinction (Brown and Kodric-Brown, 1977).

Due to the remote locations of our sampling site, we were unable to collect data on environmental heterogeneity or community size at the scale necessary to test these alternative mechanisms. However, we found that increases in taxonomic richness and phylogenetic diversity were greater in larger sky islands and that these sky islands seemed to display increased stability in terms of functional composition and diversity. For example, CWM values for leaf traits shifted more strongly towards stress tolerant functional strategies in smaller sky islands than they did in larger sky islands suggesting that increased temperatures and decreased snowpack may have more intense effects on smaller sky islands. Furthermore, FDis values for SLA declined substantially for smaller sky islands while large sky islands remained relatively constant, indicating a reduction in the breadth of functional strategies that small sky islands can support.

Geographic isolation, on the other hand, did not play a strong role in mediating biodiversity change, likely due the importance of clonal reproduction for many alpine plants and physical constraints on seed dispersal. In other systems, research has demonstrated that a functional tradeoff exists between a species' ability to locally persist through clonal reproduction and its capacity for sexual reproduction and seed dispersal (Rossetto and Kooyman, 2005, Herben et al., 2015). For the long-lived perennial plant species which compose the majority of alpine flora of the Rocky Mountains, clonal reproduction can be just as important as sexual reproduction for recruitment (Angevine, 1983; Eriksson, 1989), potentially obscuring the influence of seed dispersal, and thus geographic isolation, on biodiversity changes (Forbis, 2003. Furthermore, seed dispersal among sky islands is difficult due to the vast distances between areas of suitable habitat (Tackenberg and Stocklin, 2008) and the lack long-distance dispersal mechanisms in alpine species necessary to traverse these distances (Morgan & Venn, 2017).

Limitations and Future Directions

While the trends we found are generally supported by the literature, it is important to note two potential sources of bias within our data. First, the differences in exact plot locations due to inherent inaccuracy of GPS likely led to slightly different sampling locations. In this system, where there is high beta-diversity over short distances (Bowman and Fisk, 2001; Walker et al., 2001; Bowman et al., 2003; Seastedt et al., 2004; Litaor et al., 2008), some of the variation we find could be due to altered sampling locations. Because of this issue, we examined site level patterns of biodiversity changes instead of plot level changes as we are more confident that we accurately resampled each site, if not individual plots. Furthermore, a comparison of dominant species (those composing a cumulative sum of ~70% of site relative abundance) for each site between sampling periods shows that the identity of dominant species is relatively stable and suggests that we sampled similar vegetation types in each time period (Supplement 1.2). Interestingly, this table qualitatively reinforces the results of our landscape context analysis, with larger sites (Niwot, Cornwall, Colorado Mines, Mummy) showing less turnover in dominant species identity than smaller sites (Boreas, Buffalo, and Greenhorn). Second, our sampling intentionally avoided areas with shrubs to instead focus on biodiversity changes in the herbaceous community. Changes in shrub abundance are a major driver of change in the alpine (Elmendorf et al., 2012; Bjorkman et al., 2018) and may explain some of the contrasting results found with other studies that include shrubs. Specifically, our data does not capture potential shrub encroachment into the alpine and associated changes in functional diversity and composition, particularly increases in height, which might accompany this. Despite these limitations, our research suggests that the landscape context of refugia may be an important factor mediating climate change induced shifts in biodiversity patterns.

We further highlight two important future directions for biodiversity research in climate change refugia. First, examining biodiversity patterns across scales (alpha, beta, and gamma) and linking these patterns to explicit mechanisms (environmental heterogeneity, community size) will provide a clearer picture of how landscape context mediates biodiversity change in refugia and how best to conserve refugia. Second, shifts in functional diversity patterns caused by changing climate may be highly influenced by belowground traits (Ottaviani et al., 2020). This aspect of functional diversity deserves more attention, especially in abiotically stressful systems like alpine tundra where plants can allocate up to 80% of biomass to belowground organs (Klimešová et al., 2019).

Conclusion

Despite the recognized importance of refugia for conserving biodiversity in the face of climate change, there is still a need better identify quality refugia (Keppel et al., 2012; Keppel et al., 2015, Keppel et al., 2018). Our results suggest that landscape context has the potential to mediate the ability of refugia to withstand the impacts of climate change (Gaston and Blackburn, 1996; Ashcroft et al., 2009; Keppel et al., 2015). Moreover, our results also highlight that the life history of species in a refugial landscape is important to consider. In alpine tundra, where species have long lifespans (Steinger et al., 1996; Morris and Doak, 1998), clonal reproduction is common (Angevine, 1983; Eriksson, 1989), and many species lack the dispersal mechanisms necessary for long distance movement (Tackenberg and Stocklin, 2008), we found that area played a stronger role in mediating biodiversity change than geographic isolation. In systems with short lived annual species, geographic isolation and its influence on dispersal may be relatively more important. Future research examining the landscape context of refugia across a broader range of ecosystems and species will be critical for generalizing which sites will be most buffered from the impacts of climate change and offer the greatest value for conserving biodiversity.

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Figures

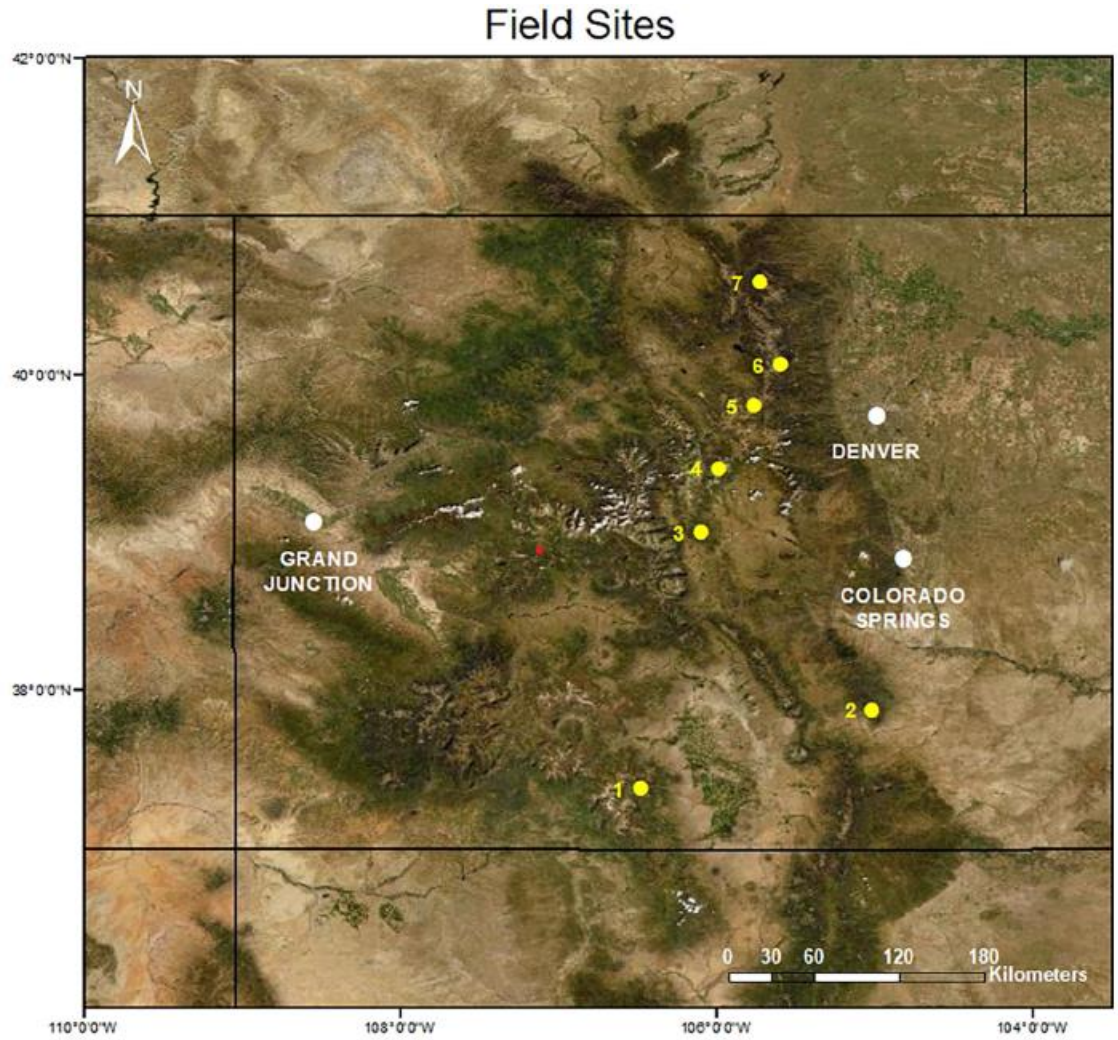

Figure 1.1 Map of sky island sampling locations in the Colorado Rocky Mountains (USA): 1. Cornwall Mountain (Latitude = 37.38046ºN, Longitude = 106.4802ºW), 2. Greenhorn Mountain (37.87668 ºN, 105.0121ºW), 3. East Buffalo Peak (38.99821ºN, 106.0922ºW), 4. Boreas Peak (39.40397ºN, 105.9821ºW), 5. Colorado Mines Peak (39.79991ºN, 105.7594ºW), 6. Niwot Ridge (40.05745ºN, 105.5916ºW), 7. Mummy Range (40.5792ºN, 105.7246ºW).

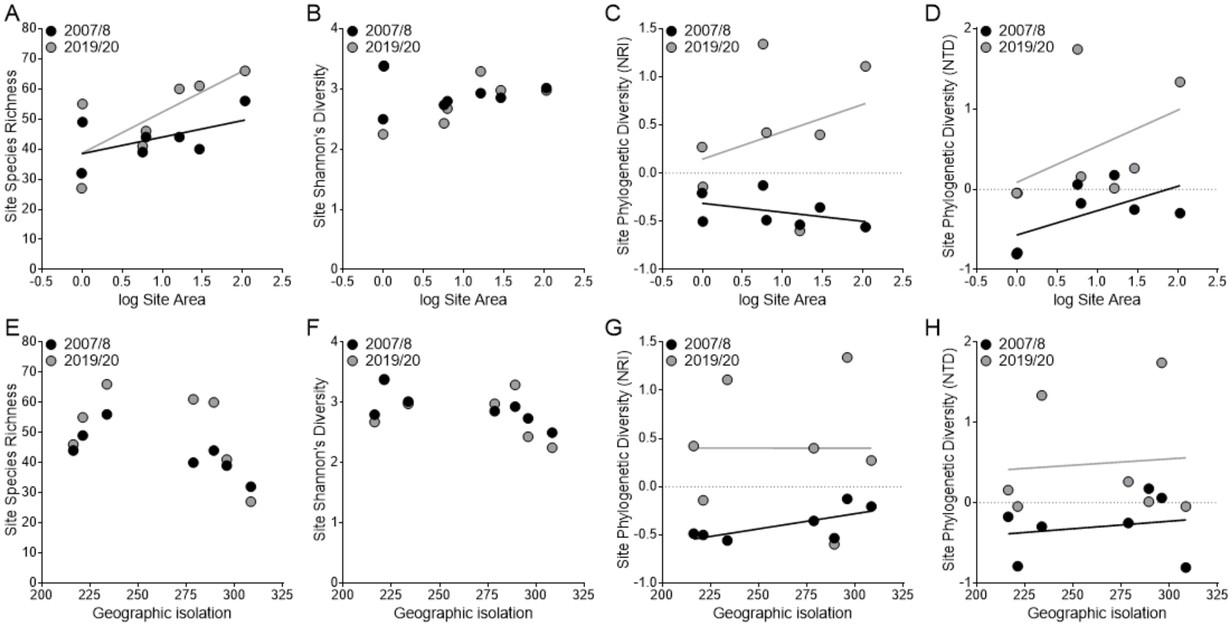

Figure 1.2 Variation in taxonomic and phylogenetic diversity patterns among sampling periods in relation to site area (A-D) and geographic isolation (E-H). Black points and line represent the first sampling period (2007/2008) and the grey points and line represent the second sampling period (2019/2020).

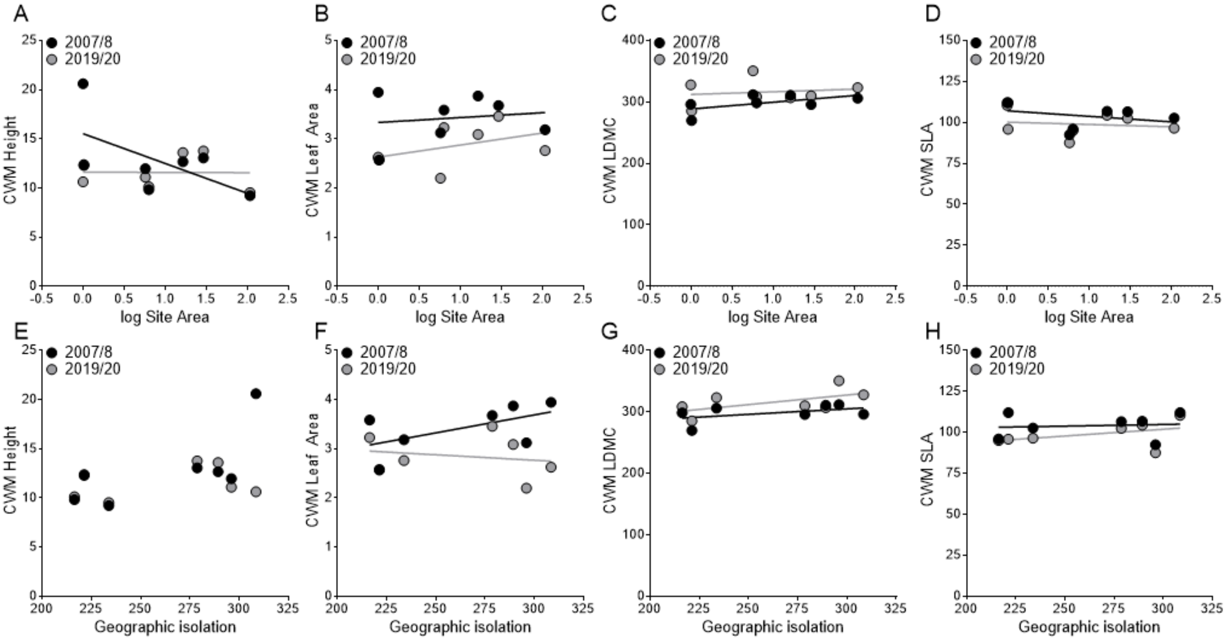

Figure 1.3 Variation in CWM trait values between sampling periods in relation to site area (A-D) and geographic isolation (E-H). Black points and lines represent the first sampling period (2007/2008), and the grey points and lines represent the second sampling period (2019/2020).

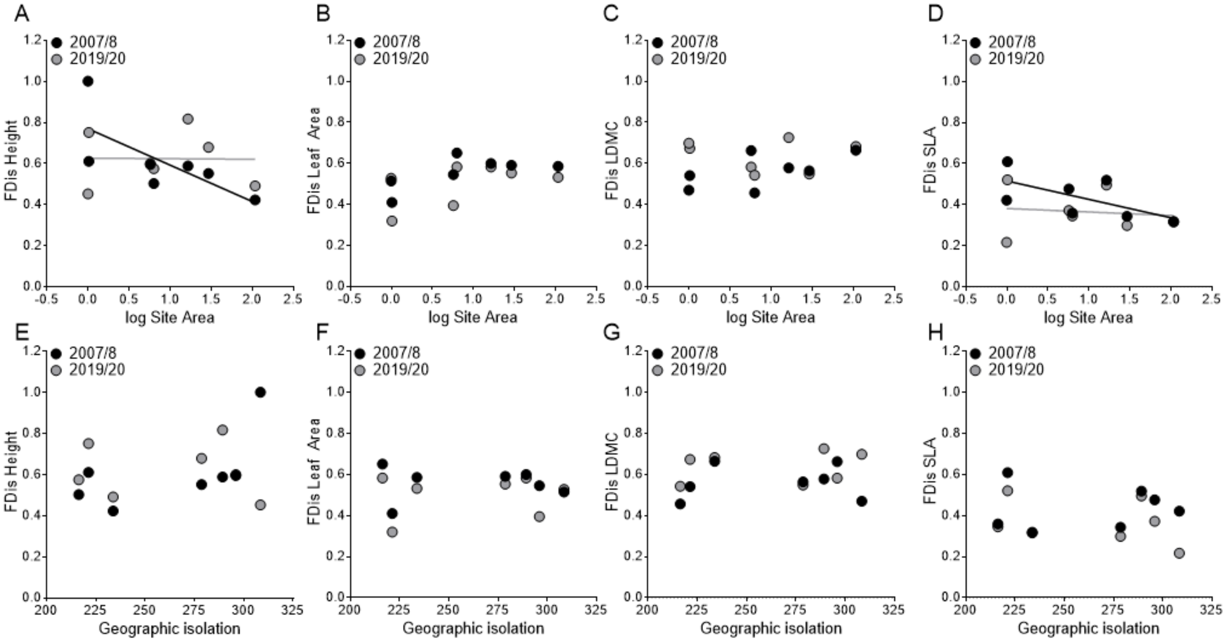

Figure 1.4 Variation in functional dispersion (FDis) patterns among sampling periods in relation to site area (A-D) and geographic isolation (E-H). Black points and line represent the first sampling period (2007/2008) and the grey points and line represent the second sampling period (2019/2020).

Chapter 2

Integrating Experimental and Observational Approaches Facilitates Scaling Species Interactions to Biodiversity Patterns

Abstract

Modern coexistence theory posits that horizontal species interactions are governed by a balance between niche and fitness differences. To investigate how these mechanisms determine the outcome of species interactions and shape local scale biodiversity patterns, research has typically focused on either: 1) simplified experimental systems that test specific mechanisms; or 2) observational studies where these processes are inferred from functional trait or phylogenetic patterns. While each approach has yielded valuable insights, both have drawbacks and few studies have integrated these approaches to explicitly connect mechanistic processes with observed biodiversity patterns. To this end, we paired a three-year neighbor removal experiment involving 22 species pairs in an abiotically mild community, with spatial point pattern analyses conducted in 8 spatially explicit 2m x 2m plots arrayed across a stress-resource gradient in the alpine tundra of Colorado. In the neighbor removal experiment, we found that species interactions were largely determined by hierarchical differences in plant height/leaf area and dissimilarity in leaf area. These same traits were also most important for predicting patterns of pairwise spatial associations across community types in the observational study, suggesting some degree of congruence between experimental and observational approaches. However, the spatial point pattern analysis also identified community

specific context dependence missing from the experimental approach. Specifically, in the abiotically mild moist meadow community, hierarchical differences in plant height and dissimilarity in leaf area had the largest effects on pairwise spatial association patterns, while in the abiotically harsh dry meadow and fellfield communities we found the reverse, with dissimilarity in height and hierarchical differences in leaf area having the largest effects. By coupling process-based experiments and pattern-based observational approaches, we were able to experimentally test coexistence mechanisms, demonstrate how these mechanisms manifest as functional trait patterns in the surrounding natural community, and highlight context dependent responses based on local abiotic conditions. Taken together our results suggest that future research should prioritize process-to-pattern mapping by coupling experiments which test mechanisms with observational studies that quantify real-world biodiversity patterns.

Introduction

A fundamental goal of ecology is understanding how species interactions shape local patterns of biodiversity (Gause, 1934; Macarthur and Levins, 1967; Chesson, 2000; Sutherland et al., 2013; Mittelbach and McGill, 2019). In recent decades, modern coexistence theory has helped resolve how relationships among species determine the outcome of interactions through a balance of niche and fitness differences (Chesson, 2000; HilleRisLambers et al., 2012). Niche differences reflect discrepancies in the strength of interspecific vs intraspecific competition such that when intraspecific competition is stronger than interspecific competition, species at low abundance gain a demographic advantage, which promotes stable multi-species coexistence (Chesson, 2000). Fitness differences, on the other hand, capture differences in absolute competitive ability, where one species maintains an advantage over its competitors regardless of its relative abundance, leading to competitive exclusion when fitness differences are large and coexistence when fitness differences are small (Chesson, 2000). Decades of experiments examining paired species interactions have refined our understanding of niche and fitness differences and the best methods for quantifying these mechanisms (Kraft et al., 2015; Hallett et al., 2019; Pérez-Ramos et al., 2019; Wainwright et al., 2019; Spaak and De Laender, 2020; Spaak et al., 2023). However, challenges remain for scaling up these experiments to observed patterns of biodiversity in nature. While experiments are an invaluable tool for isolating and testing mechanisms, they necessarily use highly simplified designs (e.g., often only two species interacting at a time) and involve a limited number of species from the species pool (Adler et al., 2013; Kraft et al., 2015; Pérez-Ramos et al., 2019; Chang et al., 2023). These limitations make it difficult to translate the results of experiments on to highly complex natural communities which may be composed of hundreds of species and have even led some to argue that experimental approaches are so contingent and localized as to be useless for forming broader generalizations about species coexistence (Lawton, 1999; Simberloff, 2004).

A contrasting approach for investigating coexistence mechanisms is the use of observational studies, where the outcome of coexistence mechanisms in natural communities is inferred through the interpretation of functional trait patterns (Spasojevic and Suding, 2012; Yin et al., 2021; Perea et al., 2022). Traits are thought to provide effective proxies for coexistence mechanisms because they are linked to fitness and mediate how species interact with each other and their abiotic environment (Adler et al., 2013; Garnier et al., 2016; Mcgill et al., 2006; Spaak et al., 2023). For example, niche differences may be represented via trait dissimilarity, where species with more similar traits are expected compete more strongly due to greater niche overlap (Diamond, 1975; MacArthur, 1958; Macarthur & Levins, 1967; Mason et al., 2011; Stubbs & Bastow Wilson, 2004). Subsequently, if niche differences are the primary mechanism determining the outcome of species interactions in an ecological community, patterns of trait overdispersion may be observed as species with similar traits segregate to avoid strong competition (Weiher and Keddy, 1995; Velázquez et al., 2015; He and Biswas, 2019). In contrast, fitness differences are often represented via a trait hierarchy where species possessing dominant trait values maintain a competitive advantage over species with subordinate trait values (Kraft et al., 2014, 2015; Funk and Wolf, 2016; Kunstler et al., 2016; Carmona et al., 2019). This results in the intensity of competition increasing as trait similarity decreases and may result in patterns of trait clustering (underdispersion) at the community level as species possessing similar traits coexist due to neither one being able to establish a competitive advantage (Scheffer and van Nes, 2006; Mayfield and Levine, 2010; Kunstler et al., 2012; Yin et al., 2021). While numerous studies have leveraged trait patterns to explore the supposed action of coexistence mechanisms in nature (Kunstler et al., 2012, 2016; Spasojevic and Suding, 2012; He and Biswas, 2019; Yin et al., 2021), these studies have been widely criticized for their ensconced assumptions, some of which have limited support (Ben-Said, 2021; Gerhold et al., 2015;

Münkemüller et al., 2020). One notable problem is that identical trait patterns can result from multiple distinct processes. For example, environmental filtering, where harsh abiotic conditions limit community membership to a subset of the regional species pool, can also produce patterns of trait clustering indistinguishable from those generated via trait hierarchies (Mayfield and Levine, 2010; Spasojevic and Suding, 2012; Cadotte and Tucker, 2017). Thus, while observational approaches examine natural communities in their full complexity, they cannot definitively attribute patterns to specific coexistence mechanisms (but see: Suding et al., 2003 Gross et al., 2009).

Increasingly, integration of process-focused experiments and pattern-focused observational studies has been advanced as a way to mitigate the weaknesses and highlight the strengths of each of these approaches (Gerhold et al., 2015; Münkemüller et al., 2020). Critically, functional traits provide an avenue for linking experimental and observational approaches since trait dissimilarities and trait hierarchies (acting as proxies for niche and fitness differences respectively) can be used to simultaneously evaluate changes in species demography/performance and species co-occurrence patterns and can be applied across species (McGill et al. 2010). Thus, explicit process-to-pattern mapping in a specific community can achieved via a two-step process where: 1) researchers select a subset of species from the community of interest and conduct an experiment which assesses species demography/performance as a function of relevant trait similarity and trait hierarchy metrics; and then 2) researchers conduct an observational study of trait patterns to determine whether those same trait metrics are correlated with species co-occurrence patterns in natural communities. Employing both experiments and observational studies within a single system ensures that specific mechanisms are rigorously tested and that these mechanisms provide relevant insights into the assembly of natural communities. Despite recognition of the need for this type of integrative approach (Gerhold et al., 2015; Münkemüller et al., 2020), studies which use both experiments and observational studies to explore coexistence mechanisms are rarely conducted.

Here we examine how trait dissimilarity, trait hierarchies, and abiotic gradients shape biodiversity patterns in alpine tundra plant communities by coupling an *in-situ* neighbor removal experiment with spatial point pattern analyses of eight 4m^2 plots arrayed along a stress-resource gradient. By employing the dual approach of experiment and observational study, we can first test the role of trait dissimilarity and trait hierarchies as mechanisms shaping plant performance and then map these mechanisms directly onto species co-occurrence patterns in the surrounding community. Specifically, we ask three questions: 1) How do trait similarities or hierarchies impact species performance in our experiment, and which traits best capture these mechanisms? 2) Do these same trait mechanisms predict pairwise spatial association patterns in natural communities? 3) Do the trait mechanisms which predict pairwise spatial association patterns differ across alpine community types?

Methods

Study Site

This study was conducted in alpine tundra at the Niwot Ridge Long Term Ecological Research site (40.03’ N, 105.35’ W) in the Front Range of the Colorado Rocky Mountains, approximately 40 km West of Boulder, CO USA. Niwot Ridge has a very short growing season (8-10 weeks, June-August) and a long winter, leading to an average annual temperature of -2.2 C and an average annual precipitation of 930 mm that predominantly falls as snow (~75%) (Williams et al., 2011; McGuire et al., 2012; Kittel et al., 2015; Knowles et al., 2015; Bueno de Mesquita et al., 2018). Annual wind speeds on Niwot Ridge average 8.1 m s^{-1} and winds typically blow from west to east (Litaor et al., 2008). Due to the stark topography and high wind speeds on Niwot Ridge, snow redistribution via wind is an important process for determining where snow accumulates on the landscape with cascading impacts on relative levels of soil nutrients, soil moisture, and growing season length (Greenland et al., 1984; Bowman and Seastedt, 2001; Williams et al., 2009). This high environmental heterogeneity in turn generates high plant beta-diversity, with near complete species turnover and differences of up to two orders of magnitude in productivity across gradients as short as 10 m (Spasojevic and Suding, 2012). Some areas have low snow accumulation (dry meadow communities) or close to no snow accumulation (fellfield communities) and contain stress-tolerant species with low levels of productivity due to moisture limitation, nutrient limitation, and high wind speeds (Walker et al., 1993; Bowman and Seastedt, 2001). Areas with intermediate levels of snow (moist meadow communities) are more abiotically mild and contain more resource acquisitive species with higher levels of primary productivity (Walker et al., 1993; Bowman and Seastedt, 2001).

Trait Dissimilarity, Trait Hierarchies, and Phylogenetic Relatedness

For both our experiment and observational study (described below), we first quantified trait hierarchies and trait similarities between all possible species pairs in each study using published trait data on four traits for which there is complete information in our trait database: plant height, leaf area, specific leaf area (SLA), and chlorophyll content (Spasojevic et al. 2022). Height is indicative of a species' competitive ability for light (Westoby, 1998). SLA and chlorophyll content are related to the leaf economics spectrum, which characterizes a species' capacity for stress tolerance vs resource acquisition (Wright et al., 2004; Osnas et al., 2013). Leaf area is indicative of a species' water/energy balance, linked with both rates of transpiration and photosynthesis (Ackerly et al., 2002; Pérez-Harguindeguy et al., 2016). Trait values for each species were calculated as the mean of all individual trait measurements for that species across any community type in the Niwot Ridge trait database as we did not have community specific measurements for all species. Trait hierarchies were quantified as directional trait differences by subtracting the trait value of one species from its companion's trait value, producing a metric which contains information on both the direction and magnitude of trait difference between both species. Trait dissimilarities were quantified by calculating the absolute value of directional trait values (i.e., Euclidean distance), and thus only reflect the magnitude, not the direction, of trait difference.

In addition to calculating individual trait hierarchies and dissimilarities, we also calculated phylogenetic relatedness among all species pairs. Phylogenetic relatedness is often used as a substitute for trait similarity, as closely related species are thought to possess similar traits due to phylogenetic niche conservatism (Webb et al., 2002; Losos, 2008; Cavender-Bares et al., 2009). To calculate phylogenetic relatedness, we first built a phylogeny for all 143 species contained in the Niwot Ridge trait database (Spasojevic et al. 2022) using the mega-phylogeny developed by Jin and Qian (2019) as a backbone. We subset this mega-phylogeny using the "phylo.maker" function from the "V.PhyloMaker" package (Jin and Qian, 2019) and resolved any remaining genus level polytomies using the "multi2di" package in the "ape" package (Paradis et al., 2004). Importantly, resolving polytomies in this way does not affect branch lengths (Paradis et al., 2004). Finally, we estimated phylogenetic relatedness among all species pairs as cophenetic distance using "cophenetic.phylo" function in the "ape" R package (Paradis et al., 2004).

To determine whether phylogenetic relatedness was correlated with functional similarity for any of our 4 traits, we examined patterns of phylogenetic signal for each trait by calculating Pagel's lambda (Pagel, 1999) using the "phyloSignal" in the function "phylosignal" package in R (Keck et al., 2016). Pagel's lambda ranges from 0 to 1, with 0 indicating no phylogenetic signal and values close to 1 indicating traits evolution under Brownian motion model (Pagel, 1999). For studies of ecological communities, this metric has been found to accurately reflect patterns of phylogenetic signal (Molina-Venegas & Rodríguez, 2017) and robustly handle the inclusion of polytomies (Münkemüller et al., 2012). Additionally, Pagel's lambda has been previously used to quantify phylogenetic signal in alpine plants on Niwot Ridge (Spasojevic and Weber, 2021). We calculated Pagel's lambda at four levels: 1) across the entire Niwot trait database; 2) for species used in our neighbor removal experiment; 3) across all communities in our point pattern analysis; 4) within each community type (fellfield, dry meadow, moist meadow) in our point pattern analysis (Supplement 2.1).

Experimental Study – Neighbor Removal

To examine how trait dissimilarities and trait hierarchies affect plant performance**,** we established a neighbor removal experiment involving a series of "interaction arenas" located at the interface between dry- and moist-meadow tundra on Niwot Ridge and monitored changes in the biomass of focal individuals across three years (2018-2020). Interaction arenas were installed in 2018 and constructed using ~10cm (4 inch) diameter PVC collars hammered approximately 10cm into the ground to isolate two naturally growing individuals of different species from their surrounding biotic environment, placing them into direct interaction. The 10cm diameter arena was large enough to contain two interacting alpine plants, which are relatively small, and deep enough to isolate the root interaction zone from the surrounding belowground community (Ashton et al., 2008). If individuals other than the two focal individuals were present within the interaction arenas, we removed their aboveground biomass using scissors upon installation and then maintained this removal for the duration of experiment. Many, but not all, alpine species are clonal and reproduce vegetatively through the growth of rhizomes (Bowman and Seastedt, 2001), so to maintain consistency across species, only single clonal ramets were considered as focal individuals. All species pairs included in the experiment were composed of one individual of *Artemisia scopulorum* (ARTSCO hereafter; Asteraceae) and another individual from one of 22 species (See Supplement 2.1). Each of the 22 species pairings had 15 co-located interaction arenas (330 total arenas): 5 replicates containing an ARTSCO individual and an individual from one of paired species, 5 replicates containing ARTSCO growing alone, and 5 replicates containing the paired species growing alone for a total of 440 individuals across all interaction arenas. ARTSCO was included in all species pairs to act as a control for the strength of competition (Funk & Wolf; 2016), as it is one of the few species which grows abundantly across the tundra (Walker et al., 1993).

For all individuals, we tracked changes in biomass over the 3-year duration of the experiment. In these long-lived, perennial alpine plant species which rarely sexually reproduce, changes in biomass can serve as an effective proxy for performance and ultimately fitness (Sultan, 2001). However, because measuring aboveground biomass requires the destructive harvest of individuals, for the first two years (2018-2019) of the study we collected allometric measurements on all focal individuals which are putatively correlated with biomass including: overall height, vegetative height, longest leaf, and number of leaves. Overall height was recorded as the distance from the ground to the highest tissue, while vegetative height was recorded as the distance from the ground to highest photosynthetically active tissue. The longest leaf measurement was recorded as the distance from the tip of the leaf to the petiole-stem connection, while the number of leaves was determined by simple count. To determine which allometric measurement was most predictive of biomass in each species, we further collected the above mentioned allometric measurements on between 15-40 individuals of each species collected from areas adjacent to each species interaction arenas. We then harvested the aboveground biomass of these individuals, placed the samples in a 60°C drying oven for 24 hours, and weighed their dried biomass. For each species, we performed linear regressions to assess correlations between each of the four allometry measurements and dried biomass, using the line of best fit for the allometric measurement which was most predictive of biomass (i.e., highest adjusted-R^2 value) to retroactively estimate the biomass of focal individuals in the interaction arenas during previous years of the experiment (i.e., 2018-2019) (Supplement 2.1). At the end of the experiment (2020), we harvested the aboveground biomass of all focal individuals in the interaction arenas, placed the samples in a 60°C drying oven for 24 hours, and weighed their dried biomass.

Next, we quantified how interactions between focal individuals affected changes in biomass by calculating relative interaction index scores (RII), which capture how individuals of each species performed when grown in paired vs isolated arenas. For individuals which survived the full 3 years of the experiment's duration (Total = 276/440, 62.7%; ARTSCO = 130/220, 59.1%; non-ARTSCO = 146/220, 66.4%) we calculated biomass change by subtracting biomass at the end of experiment (year 3, 2020) from biomass at the beginning of the experiment (year 1, 2018). Measured biomass was used for 2020 values, while allometric estimates of biomass were used for 2018 values. Because many individuals lost biomass over the course of the experiment, we added a constant of 1 to all values to ensure all biomass change values were positive while retaining their position relative to each other. We then calculated RII scores using the following equation $RII = \frac{(P - A_{mean})}{(P + A_{mean})}$ where (P) stands for the biomass change value of an individual grown in a paired arena (i.e., interacting with an individual of another species) and (A_{mean}) stands for the mean biomass change of all individuals of that same species grown isolated arenas (i.e., not interacting with an individual of another species) (Armas et al., 2004; Carmona et al., 2019). RII is centered at 0 and symmetrically bounded with a minimum of -1 and maximum of 1, with negative RII values indicating that biomass mass changes were more negative in paired arenas than in isolated arenas (i.e., competition), and positive values indicating that biomass changes were more positive in paired arenas than in isolated arenas (i.e., facilitation) (Armas et al., 2004; Carmona et al., 2019).

Finally, we examined how trait hierarchies and trait similarity between species pairs affected RII using multi-model inference methods following the approach outlined in Carmona et al. (2019). To do this, we first filtered out RII values for all ARTSCO individuals, retaining only RII values for species paired with ARTSCO (N = 67) to investigate interaction responses (Funk & Wolf, 2016). We then built a global linear mixed effects model using the “lme4” R package with RII as the response variable, while phylogenetic relatedness, trait similarities, and trait hierarchies for all 4 traits (height, leaf area, SLA, Chlorophyll Content) served as fixed effects (Bates et al., 2014). We also included focal species identity as a random effect. We then used the “dredge” function in the R package “MuMIn” to generate all possible subsets of this global model and rank them according to AICc score (Barton 2020). We constrained subset models so that they could only retain either a hierarchy or dissimilarity term for each trait (e.g., if leaf area hierarchy was included, then leaf area dissimilarity was not; Carmona et al., 2019). We selected all models that had AICc scores within 6 points of the model with the lowest AICc score for model averaging. For model averaging, we examined both conditional and full averages of parameter coefficients. Conditional averages are calculated using only using models which include the parameter of focus, while full averages are calculated using the "zero method" which assigns values of 0 to parameter coefficients when they are missing from subset models, and thus, full averages represent more conservative estimates of parameter significance (Grueber et al., 2011). Lastly, we used the "r.squaredGLMM" from MuMIn to obtain marginal and conditional R-squared values for the global model (Barton 2020).

Observational Study - Spatial Point Pattern Analysis

To determine how the effects of species interactions manifest as spatial co-occurrence patterns at the community level, we analyzed how spatial association patterns between pairs of alpine species changed as a function of trait hierarchies and trait dissimilarities. We used spatially explicit species composition data collected by Bowman and Swatling-Holcomb (2018) for eight 2m x 2m plots arrayed across three community types, representing an abiotic stress-resource gradient (2 in moist meadow, 3 in dry meadow, and 3 in fellfield). In each of these plots, the spatial location (x-y coordinates in centimeters) and species identity of all individuals were recorded (more detailed field methods can be found in Bowman & Swatling-Holcomb 2018; a list of species retained for analysis can be found in Supplement 2.3).

We used this spatially explicit species composition data to quantify spatial associations between all pairs of species by calculating the bivariate pair correlation function (pcf) $g_{i,j}(r)$ for a spatial window of 0-5cm around each focal species using the programitta spatial point pattern analysis program (Wiegand and Moloney, 2013; Velázquez et al., 2016; Wiegand et al., 2017). The pcf $g_{i,j}(r)$ measures the density of individuals of species *j* around focal individuals of species *i* at a given distance of *r* (Wiegand and Moloney, 2013; Wiegand et al., 2017). We chose to set r = 0-5cm, as this produces a 10-cm diameter circle around individuals of the focal species, which is analogous to the size of the interaction arenas used in our neighbor removal experiment. Furthermore, we restricted our analysis of species pairs to only include those with at least 50 individuals per species per plot following the methods and rationale of Bowman & Swatling-Holcomb (2018). This resulted in 460 total species pairs, with 184 in fellfield, 216 in dry meadow, and 60 in moist meadow. Reciprocal species pairs were retained for analysis (i.e., species *i* vs species *j* and species *j* vs species *i*) as species interactions may by asymmetric (Yin et al., 2021). We then calculated the standardized effect size for each species pair's pcf by comparing observed pcf values to 199 null model simulations. We generated null models by keeping the locations of species *i* individuals fixed while moving species *j* using the toroidal shift method, which removes the effects of species interactions by randomizing the location of species *j* with respect to species *i* while retaining the structure of species *j* individuals with respect to each other (Lotwick and

Silverman, 1982). Positive pcf SES scores indicate spatial attraction between species pairs, while negative pcf SES scores indicate spatial repulsion between species pairs (Wiegand and Moloney, 2013; Wiegand et al., 2017). SES scores that have an absolute value larger than 1.96 indicate that observed pcf value is outside the 95% confidence intervals generated by the null model simulations. SES scores greater than 1.96 indicate that attraction between species is significantly different from random while SES scores lower than -1.96 indicate that repulsion between species is significantly different from random.

To determine how pairwise spatial associations changed as a function of trait dissimilarities and hierarchies, we paired the conceptual framework developed by Yin et *al*., (2021) with multi-model inference methods. Within Yin et al.'s (2021) conceptual framework, trait dissimilarity metrics alone (i.e., not trait hierarchies) are initially used to identify relationships between traits and pairwise spatial associations. Positive correlations between trait similarity and spatial associations (i.e., spatial aggregation of species with different traits), indicate the action of *limiting similarity,* while negative correlations (i.e., spatial aggregation of species with similar traits) could indicate either the action of *trait hierarchies* or *environmental filtering,* necessitating further testing (described in the next paragraph). We implemented this approach by first constructing a global linear mixed effects model using lme4 where pcf SES values from all community types served as our response variable, while trait dissimilarity for the four traits, phylogenetic relatedness, and community served as fixed effects (Bates et al., 2014). Additionally, interactions between trait dissimilarity/phylogenetic relatedness and community were included as fixed effects. Treatment species nested within focal species identity and plot ID were included as random effects. To determine which traits were best supported, we used the same methods described in the experimental study section to generate all possible model subsets, select the best model subsets (top 6 AICc), and calculate average model parameter coefficients. We also used the “partR2” function from the PartR2 package to evaluate how much variance was uniquely explained by different parameters within the global model (Stoffel et al., 2021). Because interaction effects between trait metrics and community were found to explain large amounts of variation in pairwise spatial associations in the across-community global model, we then created global models for each community type (moist meadow, dry meadow, and fellfield). These within-community models followed the same model structure as the across-community model (except for the exclusion of the community fixed effect and interaction effects between traits and community) and we performed the same model averaging procedure as described above.

If trait parameters within our community specific models had negative coefficients with 95% confidence intervals that did not overlap zero (indicating strong spatial aggregation of species with similar traits), we conducted further testing to determine whether this relationship resulted from *trait hierarchies* or *environmental filtering* following Yin et *al*., (2021). For trait parameters which had negative coefficients (e.g., height in moist meadow plots), we conducted linear regressions which assessed how pcf SES values changed as a function of either trait hierarchies or trait dissimilarity for each species in each community where it occurred. We then assessed differences in the absolute values of trait hierarchy and dissimilarity coefficients across all species-level models for each trait by community combination using paired t-tests (e.g., height hierarchy vs height dissimilarity model for moist meadow species). If the absolute value of trait hierarchy coefficients was significantly higher than trait dissimilarity coefficients for these species-level models, then we interpreted this as evidence that trait hierarchies were driving the negative relationship between trait similarity and pairwise spatial associations in the within-community models. Alternatively, if the difference between the absolute values of trait hierarchy and trait dissimilarity coefficients was insignificant or if trait dissimilarities were significantly larger, then we interpreted this as evidence for environmental filtering.

Results

Phylogenetic Signal

Across all species used in the neighbor removal experiment or the point pattern analysis observational study (both across and within community types), no traits showed significant phylogenetic signal. Across all species in the Niwot trait database, we found evidence of significant phylogenetic signal for leaf area ($P < 0.01$, Table 1) and chlorophyll content ($P = 0.04$, Supplement 2.1). While leaf area showed signal close to what is expected under a Brownian Motion model of trait evolution (Pagel's $\lambda = 0.98$,), phylogenetic signal for chlorophyll content was much weaker (Pagel's $\lambda = 0.28$). No other trait exhibited phylogenetic signal across the database.

Experimental Study - Neighbor Removal

We found that trait dissimilarities, trait hierarchies, and phylogenetic relatedness (fixed effects) explained 32.7% of the variation in relative interaction index based on the global model (RII; $R^2_c = 32.9\%$). Next, using multi-model inference, we found that leaf area dissimilarity (Figure 2.1A), leaf area hierarchy (Figure 2.1B), and height hierarchy (Figure 2.1C) parameters had the highest sums of AICc weights (i.e., importance) across the 56 models in the top 6 AICc subset and had 95% confidence intervals which did not contain zero when examining conditional coefficient averages (i.e., coefficient averages calculated using only subset models which contain these trait parameters; Supplement 2.4). More specifically, individuals belonging to species which had dissimilar leaf area, larger leaf area, and greater height in comparison to ARTSCO tended to gain biomass relative to their controls, while individuals belonging to species with similar leaf area, smaller leaf area, and lesser height tended to lose biomass. It is important to note that the more conservative full coefficient averages (i.e., those calculated using the “zero method”; Grueber et al., 2011) indicated that no model parameters had confidence intervals which did not overlap zero. However, we use conditional coefficient averages here, as the goal of our of the experiment was to identify trait mechanisms which affect plant performance and determine if they match those observed in the observational study, not to determine which of the significant parameters has the largest effect on plant performance (Grueber et al., 2011).

Observational Study - Point Pattern Analysis

Across all alpine community types, we found that neutral pairwise spatial associations ($-1.96 <$ pcf SES <1.96) were the most common, comprising 81.7% of the total, while significant positive (pcf SES> 1.96) and negative associations (pcf SES < -1.96) made up 14.3% and 3.9% respectively (Figure 2.2A). The proportion of significant positive associations increased with environmental stress, reaching the highest level in the abiotically harsh fellfield (20.7%), intermediate in dry meadow (11.6%), and lowest in the abiotically mild moist meadow (5%). Negative associations showed the reverse trend with the highest proportion in the moist meadow (16.7%), intermediate in the dry meadow (3.2%), and lowest in the fellfield (<0.01%).

Next, in the across-community global model, we found that trait dissimilarity, phylogenetic relatedness, and community type (fixed effects) explained 28.2% of the variation in pairwise spatial associations ($R^2_c = 44.3\%$). More specifically, multi-model inference (using full coefficient averages) indicated that leaf area dissimilarity, height dissimilarity, phylogenetic relatedness, and community type parameters were highly important across the 3 models in the top 6 AICc subset and had 95% confidence intervals which did not overlap 0 (Supplement 2.5). Interaction effects between dissimilarity metrics and community type were also highly important for all metrics except chlorophyll content (Supplement 2.5). Furthermore, we found that these interaction effects explained a much larger fraction of variation in pairwise spatial associations (phylogenetic relatedness x community semi-partial $R^2 = 0.032$; leaf area dissimilarity x community semi-partial $R^2 = 0.069$, height dissimilarity x community semi-partial $R^2 = 0.069$, SLA dissimilarity x community semi-partial $R^2 = 0.05$; Figure 2.2B) than first order dissimilarity effects alone (all first order trait metrics had semi-partial $R^2 < 0.01$; Figure 2.2B), indicating that relationships between traits and pairwise spatial associations differed depending on community type.

Multi-model inference for the within-community models (using full coefficient averages) demonstrated how the direction and magnitude of these relationships shifted across communities. In the moist meadow (global model: $R^2_m = 58.2\%$; $R^2_c = 88.6\%$; Figure 2.2C), we found that species pairs with similar heights tended to be spatially clustered (i.e., negative coefficient), while species pairs with similar leaf areas tended to be spatially over-dispersed (i.e., positive coefficient), as indicated by the high importance of both trait parameters across the 8 models in the top 6 AICc subset and 95% confidence intervals which did not overlap zero. Additionally, we found that more closely related species (i.e., phylogenetic relatedness) showed a slight trend towards spatial clustering. In the dry meadow (global model: $R^2_m = 12.8\%$, $R^2_c = 39.1\%$; Figure 2.2D), we observed the reverse pattern for leaf area across 12 models in the top 6 AICc subset, where species pairs with similar leaf area values tended to be spatially clustered. Similarly, in the fellfield (global model: $R^2_m = 21.8\%$, $R^2_c = 26.1\%$; Figure 2.2E), we found spatial clustering of species pairs with respect to leaf area and additionally observed spatial overdispersion for height and SLA across 4 models in the top 6 AICc subset.

Finally, we found that slopes of trait hierarchies had significantly larger absolute values than trait dissimilarities in 2 of 3 cases when comparing species-level hierarchy and dissimilarity models for trait metrics which displayed significant negative coefficients in the within community models described above (i.e., height in moist meadow, leaf area in fellfield and dry meadow). Specifically, in the moist meadow, we found that the magnitude of slopes from height hierarchy models were significantly greater than slopes from height dissimilarity models (t-test: $P = 0.02$; Figure 2.3A). Similarly, in the dry meadow, slopes from leaf area hierarchy models had larger magnitudes than slopes from leaf area dissimilarity models (t-test: $P < 0.01$; Figure 2.3B). This suggests that hierarchical competition involving these traits, not environmental filtering, likely drives spatial clustering of species pairs in each respective community. In contrast, in the fellfield, slopes for leaf area hierarchy models were not significantly different than slopes for leaf dissimilarity models (t-test: $P = 0.47$; Figure 2.3C) suggesting environmental filtering drives spatial clustering of leaf area in this community. Slopes for each species level model can be found in Supplement 2.6.

Discussion

Process-based experiments and pattern-based observational studies have played vital roles in advancing our understanding of species interactions and biodiversity patterns, but each method has flaws, which can only be resolved through the integration of both approaches (Gerhold et al., 2015; Münkemüller et al., 2020). By coupling a neighbor removal experiment with an observational study using point pattern analysis, we were able to identify trait-based mechanisms affecting the performance of interacting species and then show how these mechanisms relate to patterns of species co-occurrence in the surrounding community. Specifically, in the neighbor removal experiment, we found that height hierarchy, leaf area hierarchy, and leaf dissimilarity predicted changes in biomass among interacting species. Furthermore, our observational study confirmed the importance of height and leaf area but also highlighted how relationships between these traits and pairwise spatial associations shifted across community types, where height hierarchy and leaf area dissimilarity best explained associations in moist meadow, leaf area hierarchy best explained associations in dry meadow, and height dissimilarity and leaf area environmental filtering best explained associations in fellfield. These changes suggest that traits may relate to coexistence mechanisms differently depending on abiotic conditions (Pérez-Ramos et al., 2019). Below, we first independently discuss the results of the neighbor removal experiment and observational study, before integrating these two approaches to provide a more holistic understanding of species interactions and biodiversity patterns in the alpine tundra. This integration highlights how experimental and observational approaches can be used in concert to generate insights that neither method alone could provide.

Experimental Study - Neighbor Removal

Our findings that height hierarchy, leaf area hierarchy, and leaf area dissimilarity simultaneously determined patterns of biomass change in our neighbor removal experiment add to a growing body of evidence demonstrating that plant size traits are often related to performance among interacting species (Alexander et al., 2015; Kraft et al., 2015; Carmona et al., 2019; Ferenc and Sheppard, 2020). Evidence for size-based competitive hierarchies is widespread, with larger plant species (e.g., taller, larger leaf size, larger root systems) exhibiting a competitive advantage over smaller plant species across a variety of systems including grasslands (Carmona et al., 2019; Kraft et al., 2015; Pérez-Ramos et al., 2019), vernal pools (Kraft et al., 2014), novel ecosystems composed of invasive species (Ferenc and Sheppard, 2020), and alpine tundra (Alexander et al., 2015). Competitive hierarchies based on height are especially common, as height mediates the ability of plant species to access light, with taller plants often achieving higher levels of photosynthesis, biomass accumulation, and relative fitness in comparison to shorter plants, (Craine & Dybzinski, 2013; Falster & Westoby, 2003; Westoby, 1998). Larger leaf area may offer a similar photosynthetic advantage, establishing a hierarchy where species with larger leaves attain competitive dominance by capturing more light and shading out smaller leafed competitors (Anten, 2005; Craine & Dybzinski, 2013). However, the importance of leaf area dissimilarity in our experiment suggests that limiting similarity also plays a role in determining plant performance in the alpine tundra, with species potentially partitioning available light through differentiation in leaf size (Anten, 2005; Craine & Dybzinski, 2013). Taken together, the results of this experiment suggests that multiple coexistence mechanisms operate simultaneously, and that while tall species have a competitive advantage, species that can partition niche space with tall species on the basis of leaf area can coexist.

Observational Study – Point Pattern Analysis

Our observational study strengthens the conclusions of previous point pattern research in alpine tundra, demonstrating that neutral, positive, and negative pairwise spatial associations compose the largest, intermediate, and smallest proportions of association types respectively (Bowman and Swatling-Holcomb, 2018; Losapio et al., 2018). Our results also support a trend towards increasing positive associations and decreasing negative associations with mounting abiotic stress (moist meadow < dry meadow < fellfield) which has previously been detected in systems with severe abiotic conditions like alpine tundra and deserts (Bowman & Swatling-Holcomb, 2018; López et al., 2016). Overall, this trend agrees with predictions generated under the stress gradient hypothesis and reinforces research demonstrating an important role for positive species interactions in alpine tundra (Maestre et al., 2009; Butterfield et al., 2013; Kikvidze et al., 2015; Blonder et al., 2018; Losapio et al., 2018).

In keeping with the results of our neighbor removal experiment, leaf area and height were highly correlated with pairwise spatial associations. However, the direction and magnitude of these trait-based relationships shifted dramatically across community types, suggesting that these traits act as proxies for different mechanisms depending on abiotic conditions. In the moist meadow, clustering of species pairs with similar heights (coupled with the large slopes of species-level models for height hierarchy) suggests that in more benign abiotic conditions species engage in hierarchical competition for light with taller species exhibiting a competitive advantage over shorter species (Craine & Dybzinski, 2013; Falster & Westoby, 2003; Walker et al., 1993; Westoby, 1998). This height hierarchy subsequently drives limiting similarity for leaf area (over-dispersion), with differentiation enabling species to access light at different levels of the canopy and larger leaves even allowing shorter species to achieve levels of photosynthesis comparable to taller species (Anten, 2005; Craine & Dybzinski, 2013).

In the abiotically intermediate dry meadow, clustering of species pairs with similar leaf area (coupled with the large slopes of species-level models for leaf area hierarchy) indicates the operation of hierarchical competition based on leaf area instead of height. This suggests that as abiotic stress increases (i.e., higher wind speeds, lower soil nutrients, lower snow cover) and plants are no longer able to mechanically support large heights (Bowman and Seastedt, 2001) species instead compete on the basis of leaf area. However, the examination of species level leaf area hierarchy models does not show a clear hierarchy of trait values. While species with similar, average leaf area values are clustered, we also see strong negative associations arising from two species with leaf area values on opposite ends of the dry meadow spectrum: *Kobresia myosuroides* which has smaller leaves, and *Geum rossi* which has larger leaves, and previous research has demonstrated dominant competitive ability in both species (Theodose and Bowman, 1997; Ashton et al., 2010; Bowman and Swatling-Holcomb, 2018). Thus, leaf area clustering may instead be a result of two competitive dominants producing a bi-directional competitive hierarchy, where trait values on either end of the leaf area spectrum confer a competitive advantage in dry meadow. Future research should explore if possessing trait values which differ from the community average in either direction may result in a competitive and/or demographic advantage.

Finally, in the abiotically harsh fellfield, over-dispersion of species pairs with similar height and SLA suggests the importance of facilitation. Alpine cushion plants dominate in the fellfield and are known to act as nurse plants, ameliorating exposure to harsh abiotic conditions and permitting the growth of taller and/or higher SLA species (i.e., resource acquisitive species) which would not normally occur in open fellfield (Bowman & Swatling-Holcomb, 2018; Butterfield et al., 2013; Kikvidze et al., 2015). While, height and SLA over-dispersion could also potentially result from limiting similarity, facilitation is likely the driving mechanism for over-dispersion due to the high proportion of positive pairwise spatial associations and near total absence of negative associations we detected in the fellfield (Figure 2.2A). This suggests that dissimilar species pairs are positively associated with one another, not that similar species are negatively associated (i.e., limiting similarity). Like dry meadow, fellfield also showed the clustering of species pairs with similar leaf area. However, the lack of significant difference between the slopes of leaf area hierarchy vs dissimilarity models suggests environmental filtering is driving the clustering of leaf area, not competitive hierarchy. This may be the result of micro-topographic species sorting, where large and small leafed species cluster around specific abiotic features. For example, Blonder et al. (2018) found that in a barren, fellfield-like alpine community, species were spatially clustered according to micro-topographic variation in soil characteristics, like moisture and organic matter content.

Integration of Experimental and Observational Approaches

Height and leaf area were important traits across both of our studies, correlated with plant performance in the neighbor removal experiment and pairwise spatial associations across community types in the observational study. This result reinforces previous research conducted in the Swiss Alps, which found that height and leaf area differences predicted the outcome of competitive interactions between alpine species in a turf transplant experiment (Alexander et al 2015). Furthermore, an observational study at Niwot Ridge demonstrated that functional dispersion and community weighted means for leaf area and height showed the strongest responses across an alpine stress/resource gradient out of five examined traits (Spasojevic and Suding, 2012). Importantly, our experiment was conducted at the interface between dry and moist meadow, and we identified height hierarchy, leaf area dissimilarity, and leaf area hierarchy as the primary mechanisms shaping plant performance. We inferred the action of those same mechanisms in our observational study, with moist meadow patterns structured via height hierarchy and leaf dissimilarity and dry meadow patterns structured via leaf hierarchy. This parallel between the results of experimental and observational approaches suggests that: 1) trait hierarchies and dissimilarities affect plant performance during species interactions; and 2) over ecological time, the outcomes of those trait-based species interactions manifest as patterns of species co-occurrence at the community scale.

Other parallels between our experiment and observational study include the lack of importance of chlorophyll content and phylogenetic relatedness, neither of which demonstrated strong relationships with plant performance or pairwise spatial associations. This result also finds agreement with Spasojevic and Suding (2012), who found weak patterns for both metrics. While phylogenetic relatedness showed minor clustering in the moist meadow, this is likely not indicative of the widespread positive association of closely related species, but instead results from strong negative associations caused by the single, dominant monocot species (*Deschampsia cespitosa)* present in the moist meadow point pattern analysis (Walker et al., 1993; Bowman and Swatling-Holcomb, 2018). Though some evidence indicates that phylogenetic relatedness may be useful as a proxy for trait similarity in some cases (Webb et al., 2002; Cavender-Bares et al., 2009), we did not detect patterns of phylogenetic signal at the level of the experiment or observational study, and only minor phylogenetic signal when all species in the Niwot trait database were considered. Other studies at Niwot have also shown weak phylogenetic signal in leaf chemistry traits (Spasojevic & Weber, 2021), suggesting that phylogenetic relatedness is a poor proxy for species functional similarity in individual traits in alpine tundra.

Lastly, our results highlight how the relationship between traits and coexistence mechanisms may change depending on abiotic conditions. This is most clearly exemplified by leaf area which was related to multiple mechanisms in both our experiment and observational study. Specifically, in the observational study, leaf area patterns indicated transitions from limiting similarity to hierarchical competition to environmental filtering with increasing environmental stress. Recent research in other systems has also this highlighted potential context dependence, with Pérez-Ramos et al. (2019) finding that, under control conditions in an experimental grassland system, trait dissimilarity in water-use efficiency promoted stabilizing niche differences, while under drought conditions, a trait hierarchy formed favoring species with high water use efficiency. While numerous studies have demonstrated relationships between traits and coexistence mechanisms (Kraft et al., 2015; Gallego et al., 2019; Yin et al., 2021), fewer have explored how those relationships may change with abiotic conditions across space and/or time and our work suggests that this should be an area of increasing focus for future research.

Study Limitations

While we believe that our study provides a mechanistic link between pattern and process by uniting experimental and observational approaches, it is important to note two limitations related to our experiment which may affect our conclusions. First, our experiment used one species (ARTSCO) to standardize the effect of competition. While this experimental design is commonplace in studies of competition (Funk and Wolf, 2016), a more robust design would involve interactions between all possible pairwise combinations of species (Carmona et al., 2019; Ferenc and Sheppard, 2020). We chose to use a standardized competitor because the high relative abundance of ARTSCO made finding naturally occurring species pairs relatively easy at the moist meadow/dry meadow interface. However, because ARTSCO is on the extreme small end of the alpine leaf area spectrum, we inadvertently generated co-linearity between hierarchy and dissimilarity metrics for leaf area, such that species paired with ARTSCO generally have larger leaves which are also more dissimilar (Figure 2.1A and 2.1B). We attempted to correct this problem during model selection by ensuring that models could not simultaneously contain both hierarchy and dissimilarity terms for any one trait (Carmona et al., 2019).

Second, because our experiment did not extend into the fellfield, we are only able to infer a connection between observed patterns (height/SLA over-dispersion and leaf area clustering) and mechanisms (facilitation and environmental filtering) for this community type, not make mechanistic links as we did with moist meadow and dry meadow. However, it is important to note that both of these inferred mechanisms are well-supported in the alpine literature and we are confident with our inference in this case (Bowman & Seastedt, 2001; Butterfield et al., 2013; Kikvidze et al., 2015; Spasojevic & Suding, 2012).

Conclusions

Overall, we found that both trait hierarchies and dissimilarities for size related traits (height and leaf area) are important mechanisms governing species coexistence, reinforcing similar results from other alpine tundra sites (Alexander et al., 2015) and other ecosystems (Kraft et al., 2015; Carmona et al., 2019; Gallego et al., 2019; Yin et al., 2021). Our experiment and observational study strengthened one another, demonstrating how height and leaf area traits shape plant performance during species interactions and how those interactions ultimately manifest as patterns of species co-occurrence in natural alpine communities. Our results also add to recent research suggesting that traits may relate to coexistence mechanisms differently depending on abiotic context (Pérez-Ramos et al., 2019). Finally, this fusion of experimental and observational approaches represents a rigorous, but practical method for investigating trait-based coexistence mechanisms in systems composed of long-lived, clonally reproducing species like alpine tundra

(Bowman and Seastedt, 2001). Researchers working in other systems composed of long-lived and/or difficult to manipulate species (e.g., forests), may also benefit from adopting and modifying this integrated approach. Future research which explicitly connects experiments with observational studies is key to advancing our understanding of species coexistence, trait-based community assembly, and the links between process and pattern in ecology.

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Figures

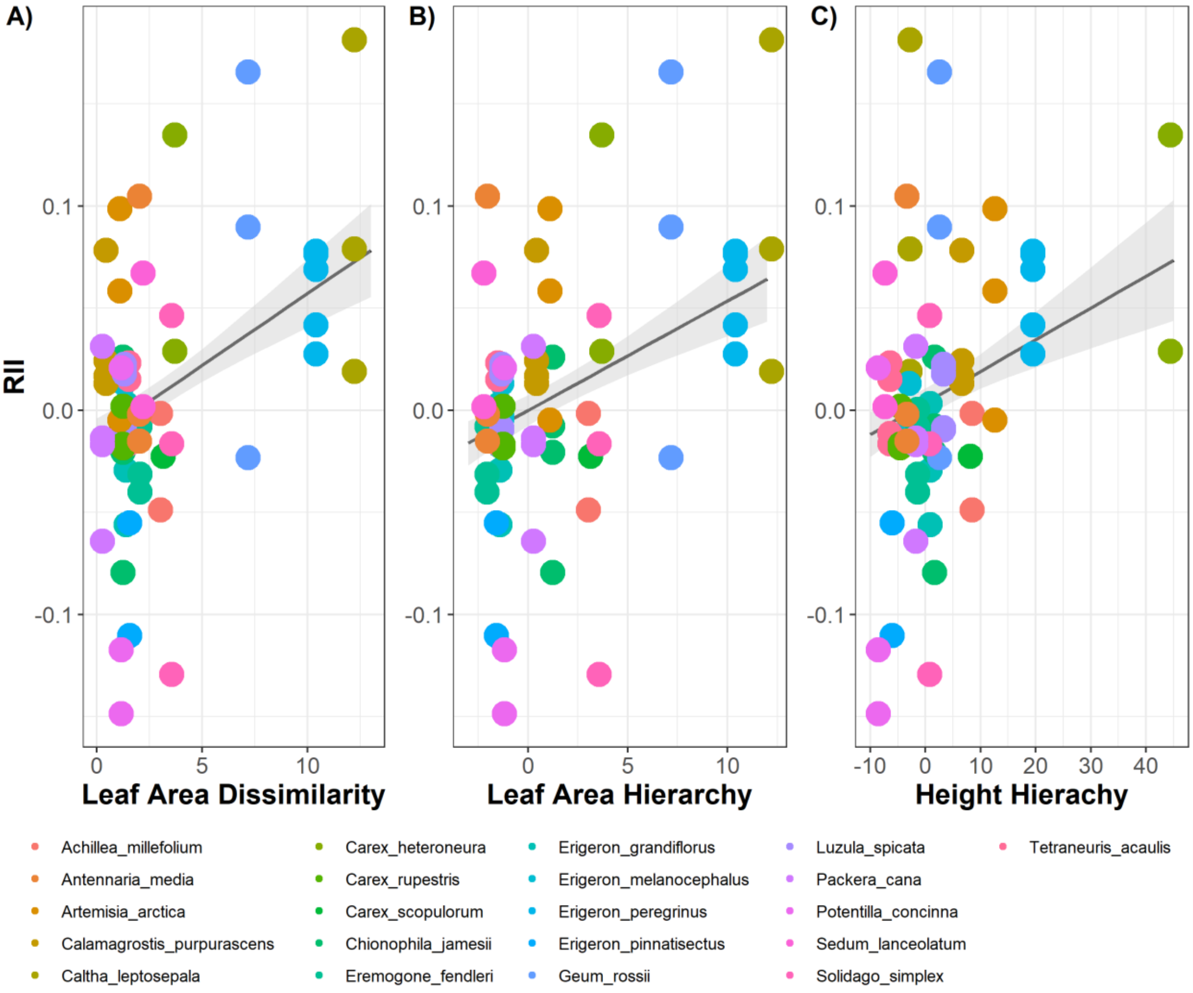

Figure 2.1 Relative interaction index (RII) as a function of leaf area dissimilarity (**A**: Importance = 0.54; simple R^2 = 0.22), leaf area hierarchy (**B**: Importance = 0.28; simple R^2 = 0.22) height hierarchy (**C**: Importance = 0.47; simple R^2 = 0.15). Negative RII values indicate competition, while positive RII values indicate facilitation. Trend lines are from simple linear regressions with 95% confidence intervals. Colors indicate different species.

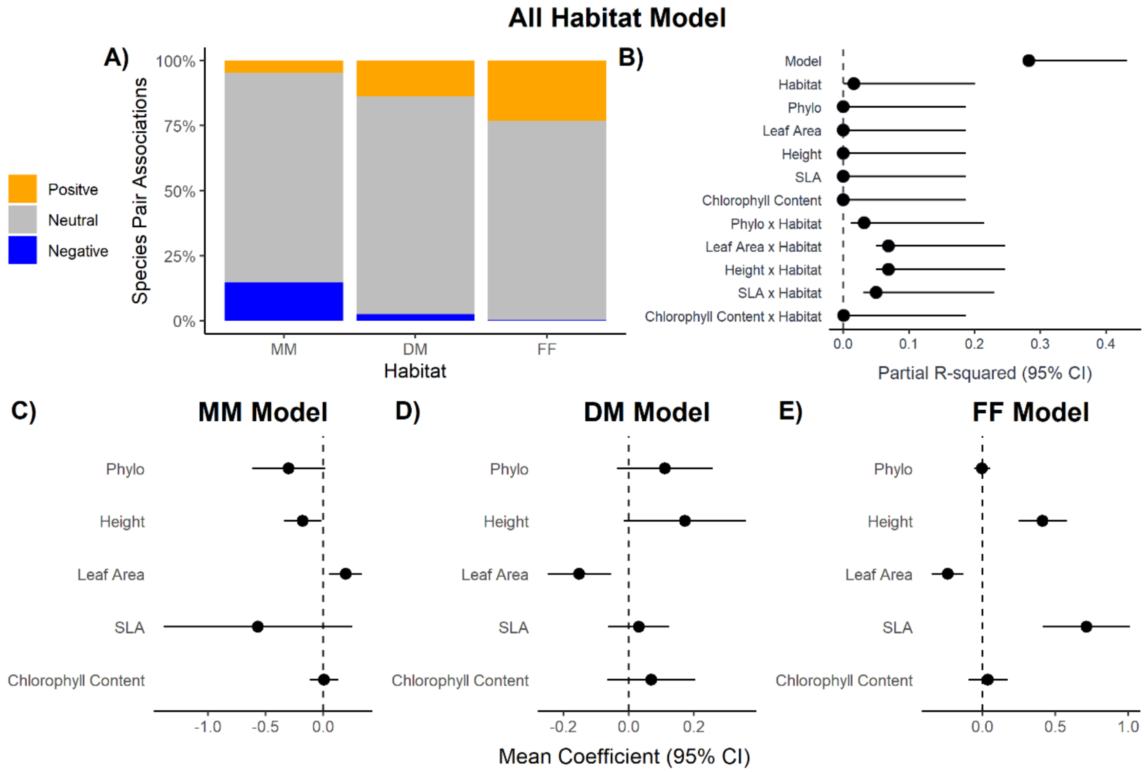

Figure 2.2 (**A**) Percentage of pairwise spatial associations for each community type, colors indicate association type. (**B**) Amount of variation uniquely explained (semi-partial R^2) by model parameters in cross community model; most variation is explained by trait x community interactions. **(C-E)** Full coefficient averages and 95% confidence intervals (CI) for model parameters from community specific models for moist meadow **(C)**, dry meadow **(D)**, and fellfield **(E)**. Negative coefficients indicate negative slopes, positive values indicate positive slopes.

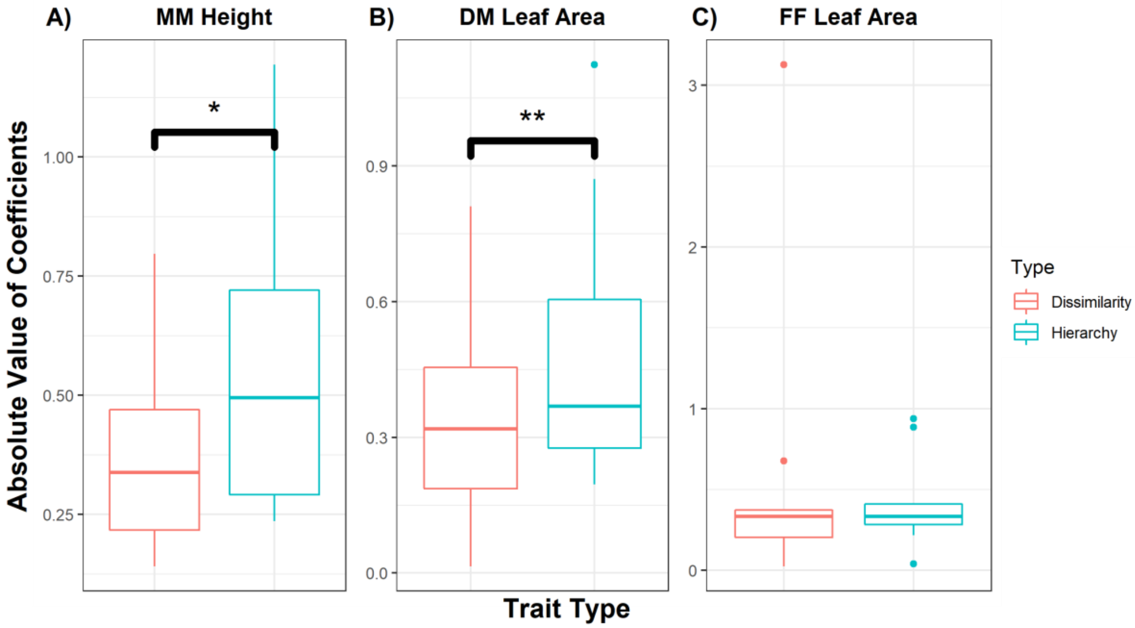

Figure 2.3 Comparisons of the absolute value of slopes for species-level hierarchy models and species level dissimilarity models. Differences in slopes were analyzed using paired t-tests. Only model parameters with negative coefficients and confidence intervals which do not overlap zero in community specific models are analyzed. **(A)** Height comparison for moist meadow species (P = 0.015). **(B)** Leaf area comparison for dry meadow species (P = 0.001); **(C)** Leaf area comparison for fellfield species (P = 0.469).

Chapter 3

Plant functional traits are dynamic predictors of ecosystem functioning in variable environments

Abstract

A central goal at the interface of ecology and conservation is understanding how the relationship between biodiversity and ecosystem function (B-EF) will shift with changing climate. Despite recent theoretical advances, studies which examine temporal variation in the functional traits and mechanisms (mass ratio effects and niche complementarity effects) which underpin the B-EF relationship are lacking. Here, we use 13 years of data on plant species composition, plant traits, local-scale abiotic variables, aboveground net primary productivity (ANPP), and climate from the alpine tundra of Colorado (USA) to investigate temporal dynamics in the B-EF relationship. To assess how changing climatic conditions may alter the B-EF relationship, we built structural equation models (SEMs) for 11 traits across 13 years and evaluated the power of different trait SEMs to predict ANPP, as well as the relative contributions of mass ratio effects (community weighted mean trait values; CWM), niche complementarity effects (functional dispersion; FDis), and local abiotic variables. Additionally, we coupled linear mixed effects models with multi-model inference methods to assess how inclusion of trait-climate interactions might improve our ability to predict ANPP through time. In every year at least one SEM exhibited good fit, explaining between 19.6 – 57.2% of the variation in ANPP. However, the identity of the trait which best explained ANPP changed depending on winter precipitation, with leaf area, plant height, and foliar nitrogen isotope content ($\delta^{15}N$) SEMs performing best in high, middle, and low precipitation years respectively. Regardless of trait identity, CWMs exerted a stronger influence on ANPP than FDis and total biotic effects were always greater than total abiotic effects. Multi-model inference reinforced the results of SEM analysis, with the inclusion of climate-trait interactions marginally improving our ability to predict ANPP through time. Our results suggest that temporal variation in climatic conditions influences which traits, mechanisms, and abiotic variables were most responsible for driving the B-EF relationship. Importantly, our findings suggest that future research should consider temporal variability in the B-EF relationship, particularly how the predictive power of individual functional traits and abiotic variables may fluctuate as conditions shift due to climate change.

Introduction

Global change has drastically altered ecosystem functioning by shifting patterns of biodiversity through species extinctions, range shifts, and changes in abundance (Cardinale et al., 2012; De Laender et al., 2016). While early research on the biodiversity-ecosystem function (B-EF) relationship examined how changing levels of species richness might impact ecosystem function (Tilman et al., 2001; Hooper et al., 2005), recent advances show that functional trait distributions more strongly predict many ecosystem functions than species richness alone (de Bello et al., 2010; Cadotte et al., 2011; Gagic et al., 2015; Cadotte, 2017). Despite this theoretical advance in our understanding of the B-EF relationship, a recent large-scale experiment in European grasslands revealed that joint consideration of 41 functional traits was still only able to explain 12.7% of the variation in 42 ecosystem properties over a 10-year period (van der Plas et al., 2020). However, the same study showed that within individual years, functional traits were able to explain up to 32.6% of the variation in those ecosystem functions. While this discrepancy may be partially attributed to statistical issues with analysis (Hagan et al 2023), the stark contrast in explanatory power between within-year and across-year models also suggests a biological explanation, specifically, that the strength of the B-EF relationship varies dynamically through time. Critically, we lack an understanding of what drives temporal variation in the B-EF relationship as most studies assume that the traits and/or mechanisms underlying the B-EF relationship are static (but see Cardinale et al. 2007, Armitage 2016, 2017, Mori et al. 2017, Qiu and Cardinale 2020) or fail to consider how the multiple functional mechanisms underlying the B-EF relationship operate simultaneously (Mokany et al., 2008; Chiang et al., 2016).

One source of temporal variation in the B-EF relationship may be a shift in which traits best predict ecosystem functions, leading certain traits to be more important during some years and unimportant in others depending on environmental conditions. While environmental context dependence in the B-EF relationship has been demonstrated in numerous systems including benthic macro-invertebrates (Geert Hiddink et al., 2009), mycorrhizal fungi (Jonsson et al., 2001), and temperate forests (Ratcliffe et al., 2017), these studies have generally quantified biodiversity in terms of taxonomic richness and have examined context dependence across spatial, not temporal, variation in environmental conditions. In one of the few studies to explore temporal dynamics in the ability of traits to predict ecosystem functions, Bongers et al. (2021) found that, in an experimental forest system, functional diversity metrics for multiple traits became more reliable predictors of accumulated stand volume as stand age increased. This temporal shift in the relationship between functional diversity and ecosystem function suggests that the predictive power of individual functional traits could trade-off in concert with changing environmental conditions. For example, a single trait may on average only explain a modest amount of variation in ecosystem function over long time periods because that trait is only predictive in “good” years (high resource availability) while not being predictive in “bad” years (low resource availability) when a different trait associated with environmental stress serves as the best predictor. Considering how temporal fluctuations in environmental conditions modify the importance of specific traits could help resolve the seemingly low predictive power of functional traits for ecosystem functions through time.

A second source of temporal variation may arise from shifts in the functional mechanisms underlying the B-EF relationship. Two non-mutually exclusive mechanisms are typically invoked to explain the B-EF relationship: 1) niche complementarity and 2) mass ratio effects. Niche complementarity effects posit that ecosystem functioning should be maximized when species in a community use resources in complementary ways, leading to more complete and efficient consumption of the total resource pool. Because functional traits mediate how species interact with each other and their environment, communities containing a greater diversity of functional traits (often quantified as functional dispersion (FDis); see Cadotte 2017 and methods below) should be better able to engage in complementary resource use, thus enhancing their level of functioning (Tilman et al., 2001; Petchey and Gaston, 2006). In contrast, mass ratio effects focus on how the presence of high performing, dominant species control ecosystem function. Dominant species possess specific traits which confer high fitness and determine their large contributions to functioning, however, these traits should contribute to functioning regardless of individual species identity. Thus community average trait values (often quantified as community weighted means (CWM); see Cadotte 2017 and methods below), can be used to capture relative differences in ecosystem functions (Grime, 1998).

While a large body of research has focused on determining whether niche complementarity or mass ratio effects play a greater overall role in shaping ecosystem functions (Loreau and Hector, 2001; Cardinale et al., 2007b; Wang et al., 2021), these mechanisms are not mutually exclusive (Mokany et al. 2008, Chiang et al. 2016) and their relative importance can shift with changing environment conditions (Armitage, 2017). Studies have shown that, in natural systems, mass ratio effects are generally better predictors of individual ecosystem functions than niche complementarity effects (Mokany et al., 2008; Tobner et al., 2016; Fotis et al., 2018; van der Plas, 2019; Needham et al., 2022), however, research focused on the stress gradient hypothesis suggests that the relative importance of these mechanisms may trade off as species interactions shift along stress/resource gradients (Bertness and Callaway, 1994; Fugère et al., 2012; Wang et al., 2013; Baert et al., 2018). For example, Wang et al. (2013) found that in an experimental grassland system, mass ratio effects tended to better explain net primary production in high-resource/low-stress environments where competition is thought to be the dominant interaction among species (Bertness and Callaway, 1994), while niche complementarity effects became more important in low-resource/high-stress environments where resource partitioning and facilitation are thought to be more prevalent (Bertness and Callaway, 1994; Wang et al., 2013; Wright et al., 2017). Most studies demonstrating this trade-off between B-EF mechanisms have evaluated changes along spatial environmental gradients, however, similar results should be expected within a site as environmental conditions change temporally, with mass ratio effects generally acting as better predictors of ecosystem function, but niche complementarity effects becoming more important during periods of high environmental stress.

Finally, while B-EF research often emphasizes the centrality of biotic mechanisms in shaping ecosystem functions, temporal variation in ecosystem functions can also be directly controlled by fluctuating abiotic conditions. For example, studies have found that in tundra ecosystems, temperature directly influences rates of plant litter decomposition, with higher temperatures leading to faster rates of decomposition independent of litter composition (Hobbie, 1996; Aerts, 2006). Similarly, short-term drought in tropical forest systems has been shown to shift biomass allocation patterns in tree communities from investment in aboveground to belowground tissues without inducing shifts in species or functional diversity patterns (Doughty et al., 2014). Ultimately, abiotic conditions determine both the productive capacity and biotic composition of ecosystems, and thus their direct and indirect influence (i.e., via changes in composition) should be considered concurrently in any complete assessment of the B-EF relationship (Brun et al., 2019).

Here we couple long-term observational data from a natural system with structural equation models (SEMs) and linear mixed effects models to disentangle the complex temporal links between site-level climatic changes, local abiotic conditions, biodiversity patterns, and ecosystem function (Pugesek et al., 2003; Grace, 2008). To explore these dynamics, we used 13 years of data (2008, 2010-2021) on local abiotic conditions, plant species composition, plant functional traits, and aboveground net primary productivity (ANPP) collected in the alpine tundra of Colorado, USA at the Niwot Ridge Long Term Ecological Research (LTER) site. During the last four decades, Niwot Ridge has experienced increasing winter precipitation (e.g., precipitation falling between October-May) and increasing summer temperatures (McGuire et al., 2012; Kittel et al., 2015; Bjarke et al., 2021). Climatic changes at Niwot Ridge (and in the Southern Rocky Mountain region generally), are correlated with shifts in the taxonomic and functional composition of alpine plant communities (Niwot Ridge LTER unpublished data, Huxley and Spasojevic 2021), making this an ideal system to disentangle the complex temporal nature of the B-EF relationship. We predict that: 1) Functional traits associated with plant size (e.g., plant height, leaf area) should generally best predict ANPP, but the identity of the trait which best predicts ANPP will change during climatically stressful years with unusually high winter precipitation or summer temperatures; 2) Mass ratio effects (measured as CWM traits values) will be the primary driver of ANPP, but during climatically stressful years niche complementarity effects (measured as FDis trait values) will become relatively more important than mass ratio effects; 3) Biotic mechanisms (inferred from trait patterns) will generally play a stronger role in shaping ANPP than local abiotic conditions, but the influence of abiotic conditions will become more important during climatically stressful years; and 4) Considering interactions between annual climatic conditions climate and biotic/abiotic variables will improve our ability to predict ANPP through time.

Methods

Study Site

This study uses data collected from alpine tundra on Niwot Ridge (40.03’ N, 105.35’ W) in the Front Range of the Rocky Mountains, approximately 40 km West of Boulder, CO USA, a research site which is managed by the Niwot Ridge Long Term Ecological Research Program (NWT). All data used in this study were collected and curated by NWT staff or researchers affiliated with NWT and are available for public use via the NWT Electronic Data Initiative portal (see “data availability” section and associated data package citations). Niwot Ridge has a very short growing season (8-10 weeks, June-August) and a long winter, leading to an average annual temperature of -2.2 C and an average annual precipitation of 930 mm that predominantly falls as snow (~75%) (Williams et al., 2011; McGuire et al., 2012; Kittel et al., 2015; Knowles et al., 2015; Bueno de Mesquita et al., 2018). Annual wind speeds on Niwot Ridge average 8.1 m s^{-1} and winds typically blow from west to east (Litaor et al., 2008). Due to the stark topography and high wind speeds on Niwot Ridge, snow redistribution via wind is an important process for determining where snow accumulates on the landscape (Greenland et al., 1984; Bowman and Seastedt, 2001; Williams et al., 2009). Predictable patterns of snow accumulation generate high plant beta-diversity, with near complete species turnover and differences of up to two orders of magnitude in productivity across gradients as short as 10 m (Spasojevic and Suding, 2012).

Saddle Climate Data

NWT has maintained continuous, site-level measurements of temperature, precipitation, and other climate variables in the "Saddle" area of Niwot Ridge since 1982 (Bjarke et al., 2021). For the period of our study (2007-2021), daily mean and instantaneous minimum and maximum temperatures were recorded using a Campbell Instruments CR23X data logger (2007-2014) and a CR1000 data logger (2014-2021) (Morse et al. 2022a). Temperature data quality assurance was performed by previous NWT climatologists up through 2014 and has been automated using the GCE Data Toolbox since September 2014. Daily precipitation was measured using Belfort weighing-bucket gauge with Alter shield and recorded by mechanical chart (Morse et al. 2022b). The bucket contains antifreeze to melt snow and prevent collected precipitation from freezing. For the period of our study (September 2007-August 2021), about 3.7% of raw temperature data and 13.7% of raw precipitation data were missing.

Prior to infilling missing data, we performed additional data quality control of temperature and precipitation data as recommended in Brunet et al. (2006) and Kittel (2009) to screen gross errors, tolerance tests, temporal coherence, and spatial coherence. We used 24 stations at NWT LTER or in the region for spatial coherence checks and infilling. Geographic range of stations from Saddle are approximately 28 km south to 35 km north, 22 km east to 18 km west, and 1248 m below to 206 m above. Because of documented blowing snow issues for precipitation at Saddle (Williams et al., 1998), precipitation events were reviewed when 1) Saddle was the only station in the region to record precipitation, 2) the only station of six at NWT to record precipitation and only 1-3 stations in the region recorded precipitation, and 3) Saddle was the only station at NWT to not record precipitation. Additional QC removed 0.3% of temperature values and 1.1% of precipitation values for infilling.

We then followed regression infilling methods for NWT long-term records established by Kittel et al. (2015). Stations were prioritized in infilling based on geographic and elevational proximity to Saddle. We applied an overcatch correction factor of daily precipitation*0.39 recommended by Williams et al. (1998) for October - May and 4 large snow events in the shoulder seasons (e.g., June, September). The most frequent source stations for infilling Saddle daily values were the NWT LTER D1 alpine station for precipitation (informed 36.4% of infill values) and replicate [HMP] instruments at Saddle (77.8%) for temperature.

After QC and gap-filling, daily temperature data were homogenized to account for instrument changes over the electronic record by adjusting temperature data to the most recent instrument at Saddle. We used a 1-year overlap period between the outgoing and incumbent Saddle temperature electronic instruments, as well as an independent, quality-controlled, gap-filled record spanning the entire period of instrument changes (AmeriFlux US-NR1) to apply conservative mean difference adjustments ranging from -0.96 to -1.5C. We performed additional inhomogeneity tests for Saddle temperature and precipitation using R packages RHtestsV4 and RHtests_dlyPrcp (Wang 2008a, Wang 2008b, Wang and Fang, 2013), and Climatol (Guijarro 2022). No breaks were detected for the study period that warranted further homogenization based on the station history (for full Saddle temperature and precipitation datasets see: White et al. 2023a and White et al. 2023b).

Two primary long-term trends have been detected in Niwot Ridge's climate record: 1) an increase in annual winter precipitation (Figure 1A) and 2) an increase in the annual number of growing degree days (Figure 1B, McGuire et al. 2012, Kittel et al. 2015, Bjarke et al. 2021). We calculated winter precipitation as the sum of all daily precipitation measurements recorded between October and May of the following calendar year. Annual growing degree days, on the other hand, were calculated as the sum of mean temperatures for all days where the mean temperature was greater than 0ºC for each "ecological year" (the period starting September 1st and finishing August 31st of the following year, hereafter referred to simply as year), as this timeframe is more biologically relevant than the calendar year for alpine plant communities which experience their growing season between June and August.

Saddle Plot Data

NWT has conducted long-term monitoring of alpine vegetation using 88 1 m^2 plots located in the Saddle. For each of these plots, comprehensive data exist on abiotic variables (topographic variables, snow-depth), biodiversity (species composition, functional traits), and ecosystem function (ANPP) over a 13-year period: 2008 and 2010-2021. Topography was quantified for each plot using three measures: elevation, aspect, and slope. Elevation was estimated using a Trimble GPS with accuracy of +/- 3m. Aspect was measured as the direction of a plot's downhill slope using a compass with a SIN transformation applied for analysis. Slope was quantified using the slope tool in ArcGIS 10.1. Snow-depth data were collected during irregularly timed snow surveys throughout fall, winter, and spring months (September-June) by NWT technicians using snow poles which estimate depth at 10cm intervals (Walker, S. et al., 2022). Due to the irregular timing of snow-depth measurements throughout the year, we used mean snow-depth values for the month of May in our analysis as this month consistently contained at least one snow-depth survey (ranging between 1-3) and because May is typically when Niwot Ridge reaches peak snowpack (Litaor et al., 2008). Only one year (2008) lacked May snow-depth data, and for this year we used snow-depth data collected on April 29th, 2008.

Plant species composition data for each Saddle plot was collected using point intercept methods (Walker, M. et al., 2022a). NWT staff mounted a 1 m^2 quadrat containing a 10 cm x 10 cm string grid on permanent plot corners and then vertically placed a pin flag at each of the 100 grid points, recording the identity of all species contacting the pin flag and their relative vertical position within the canopy. For our analyses, we only used species composition data from the top-most 'hit' to calculate the relative abundance of each species in a plot to remain consistent with previous analyses of NWT's Saddle plot species composition (Spasojevic et al., 2013).

Aboveground net primary productivity (ANPP) data were collected by harvesting all non-woody vascular biomass within 0.2 m x 0.5 m quadrats located near each Saddle plot (Figure 2C). Harvest locations were selected to replicate species composition and biomass distributions in each plot and were rotated annually to prevent over-harvesting from any one area (Walker, M. et al. 2022b). From 2008 to 2018, two biomass quadrats were harvested per Saddle plot; the mean of these harvests was calculated to produce a single measurement per plot. From 2019 to 2021, a single biomass quadrat was harvested per plot.

Functional Traits

NWT maintains a functional trait database (Spasojevic et al. 2022) that has trait data for 84.4% of species that have been found in the Saddle plots and identified to species level, with 55% of those species possessing habitat specific trait measurements (e.g., functional traits for *Geum rossii* measured independently in moist meadow, dry meadow and fell field habitats). In total, we have coverage of at least one trait for 98.3% of the total cover across the 13 years of our study. Eleven traits were included in this study: height, specific leaf area (SLA), leaf area, chlorophyll content, leaf dry matter content (LDMC), foliar percent carbon content, foliar percent nitrogen content, foliar carbon to nitrogen ratio, foliar carbon isotope values ($\delta^{13}C$), foliar nitrogen isotope values ($\delta^{15}N$), and stomatal conductance. Height is indicative of a species' competitive ability for light (Westoby, 1998). SLA, LDMC, chlorophyll content, and leaf chemistry traits are related to the leaf economics spectrum, which characterizes a species' capacity for stress tolerance vs resource acquisition (Wright et al., 2004; Osnas et al., 2013). Leaf area and stomatal conductance are related to a species' water/energy balance (Ackerly et al., 2002; Pérez-Harguindeguy et al., 2016). Finally, $\delta^{15}N$ is related to nitrogen uptake rates and N source

(Craine et al 2015). Trait measurements for each species or species × habitat combination were collected from at least 10 individuals in accordance with the protocols outlined in Pérez-Harguindeguy et al. (2016).

Using the trait values from the NWT functional trait database and the species composition data described in the previous section, we then used the “dbfd” function from the “FD” package in R version 4.1.1 to calculate single trait FDis, and community weighted mean (CWM) trait values for each Saddle plot in every year (Laliberté and Legendre 2010, Laliberté et al. 2014, R core team 2021). Critically, we calculated CWM and FDis values using trait data weighted by species abundances not biomass to reduce circularity in the prediction of ANPP. In alpine systems, species abundance and biomass are not likely to be tightly correlated since many highly abundant species are quite small. Ten plots were discarded from these calculations in each year because they had either greater than 50% shrub or rock cover or were subject to long-term experimental snow depth manipulation. Additional plots were discarded if we did not possess trait data for at least 80% of the vascular plant cover (plot number varied by specific trait and year; the number of plots retained for each SEM can be found in Supplement 3.1).

Structural Equation Modeling

To explore links between the abiotic environment, biotic functional composition, and ecosystem function, we built structural equation models (SEMs) for each trait × year combination (e.g., leaf area SEMs for 2008, 2010, 2011, etc.). SEMs are useful for modeling complex ecological phenomena because they allow for the evaluation of both direct and indirect causal relationships among variables by estimating a global variance-covariance matrix (Grace, 2008). All SEMs in this study used the same meta-model design (Figure 2), based on a robust body of research on alpine ecosystem dynamics at Niwot Ridge (Walker et al., 1993; Bowman and Seastedt, 2001; Suding et al., 2015; Williams et al., 2015).

First, a latent variable representing "topography" was constructed using direct measurements of elevation, aspect, and slope. Our inclusion of "topography" as a latent variable was meant to capture uncertainty around this concept, as all aspects of topography (i.e., microtopographic variation) could not be directly measured. Topography is a major factor determining where snow deposition occurs on the alpine landscape, so we included a direct path from topography to snow depth. Additionally, topography may influence biodiversity patterns and ANPP directly via factors independent of snow deposition (e.g., exposure to wind, solar radiation, etc.), so we included direct paths from topography to CWM and FDis trait values as well as ANPP. Next, we connected snow depth directly to both trait metrics and ANPP, as snow deposition has been shown to influence levels of soil moisture, nutrient availability, and growing season length, which fundamentally control biodiversity and productivity patterns (Bowman and Fisk 2001, Walker et al. 2001, (Bowman et al., 2003; Seastedt et al., 2004), Litaor et al. 2008). We also added a snow depth^2 term, with an identical model position to snow depth, to account for snow depth's quadratic relationship with ANPP where both low and high snow depths can produce low levels of ANPP due to moisture limitation and energy limitation respectively (Walker et al. 1993, Walker et al. 2001).

We then linked our functional trait indices (CWM and FDis) for each individual trait to ANPP, based on fundamental B-EF theory showing that ecosystem functions are simultaneously shaped by the average and variation of community trait values (Chiang et al., 2016; Cadotte, 2017). While some studies have shown that species niche differences are best summarized by multi-trait models and/or metrics (Kraft et al., 2015; Huang et al., 2020), we chose to build separate SEMs for each trait (i.e., each SEM contains the CWM and FDis values for only one trait), for both biological and statistical reasons. Biologically, individual traits have been shown to strongly respond to environmental gradients in the alpine tundra of Niwot Ridge, while multi-trait metrics (e.g., FDis calculated with multiple traits) often show no pattern due to opposing responses in individual traits (Spasojevic and Suding 2012). Furthermore, building SEMs containing metrics for multiple individual traits is statistically challenging as the inclusion of multiple additional parameters would greatly exceed rule-of-thumb estimates for acceptable sample size when using SEMs (10 data points per observed variable) (Bentler & Chou, 1987; Nunnally, 1967).

Finally, we included 2 covariation terms – one between snow depth and snow depth^2 and another between CWM and FDis. These covariation terms account for the fact that that these variable pairs are driven by the same causal links within the SEM and are likely to be correlated (highly correlated in the case of snow depth and snow depth^2) but are not causally related to one another. Using this meta-model structure, we built SEMs that incorporated the CWM and FDis values of each individual trait for each year. With 11 traits and 13 years of data, we could generate a total of 143 possible SEMs across all traits and years. All SEMs were constructed using the “lavaan” package in R version 4.0.2 (Rosseel, 2012).

Statistical Analyses

To evaluate our first prediction that size related traits would generally best predict ANPP but that that this would change during environmentally stressful years, we assessed the predictive power of our trait SEMs and how that predictive power changed as function of winter precipitation and annual growing degree days. We first filtered out any SEMs which did not possess a minimum sample size of at least 70 plots due to low trait coverage (12 of 13 SEMs featuring stomatal conductance, all 13 removed for consistency). We then eliminated SEMs which did not converge (i.e., no solution for the global variance-covariance matrix, 3 SEMs) or contained variables with negative variances (i.e., Heywood cases, 13 SEMs). Next, we evaluated several fit measures for each SEM including the χ^2 statistic, the comparative fit index (CFI), the root mean squared error of approximation (RMSEA), and the standardized root-mean squared residual (SRMR). SEMs with χ^2 P-values greater than 0.05, CFI scores greater than 0.9, RMSEA less than 0.1, and SRMR value less than 0.08 were interpreted as providing a good fit for the data. Two additional SEMs failed to meet these fit criteria, leaving 112 SEMs with good fit across all traits and years (Supplement 3.1, Supplement 3.2).

We then determined which of the SEMs with good fit best explained ANPP in each year by filtering for the trait SEM with the highest R^2 value for ANPP in each year (Figure 3A). Importantly, when selecting the best fitting SEM in each year, we did not compare all 112 SEMs against one another but instead compared different trait SEMs within individual years (e.g., comparing 2008 height SEM vs 2008 leaf area SEM, not 2010 height SEM vs 2008 leaf area SEM). For most years, this meant comparing ~10 trait SEMs. Furthermore, our SEMs were not assembled using any step-wise process of parameter or path deletion/insertion, which has been shown to be a problematic because it ignores model selection uncertainty (Whittingham et al., 2006; Mundry and Nunn, 2009). Instead, we kept model structure consistent across traits and years and varied only the identity of the traits used for the CWM and FDis parameters (Figure 2). Model selection approaches with SEMs have been found to be robust to model selection uncertainty, but typically involve the comparison of AIC or BIC scores which estimate overall model fit and parsimony (Lin et al., 2017; Garrido et al., 2022). Here we focused our model selection approach on R^2 values for ANPP instead of AIC or BIC scores, as we are interested in the identity of trait SEM which best predicts observed ANPP levels not the trait which provides the best overall model fit across all pathways. Trait SEMs which possessed the highest R^2 value for ANPP in at least one year are hereafter referred to as "best fitting SEMs". To determine how changing climate influences our ability to predict ANPP, we then performed linear regressions examining how ANPP R^2 values in our best fitting SEMs varied with annual winter precipitation (Figure 3B-C) and annual growing degree days (Supplement 3.4).

To evaluate our second prediction focused on mass ratio effects vs niche complementarity effects and how the relative importance of these functional mechanisms might shift with climatic stress, we examined the path coefficients directly linking CWM and FDis to ANPP in our best fitting SEMs (Supplement 3.3). Specifically, we performed linear regressions to assess how the strength and magnitude of these path coefficients changed as function of annual winter precipitation (Figure 4 A-C) and annual growing degree days (Supplement 3.4).

To assess our third prediction focused on how biotic mechanisms vs local abiotic conditions determine ANPP and how the relative importance of these factors might shift with climatic stress, we compared the total effects of biotic mechanisms and local abiotic variables in our best fitting SEMs (Supplement 3.3). While the total impacts of CWM and FDis on ANPP can be inferred by examining only direct path coefficients, both direct and indirect effects must be considered when determining the total impact of local abiotic variables on ANPP. Indirect effects are calculated by multiplying the path coefficients of two or more direct path coefficients. For example, to calculate the indirect effect of snow depth on ANPP via CWM, we multiplied the coefficient of the path linking snow-depth to CWM by the coefficient of the path linking CWM to ANPP (i.e., “snow depth to CWM to ANPP” = “snow depth to CWM” * “CWM to ANPP”). Total effects are then calculated for each abiotic variable by summing all direct and indirect path coefficients that lead from snow depth, snow depth^2, or topography to ANPP. For example, to calculate the total effect of snow depth on ANPP, we summed all direct and indirect effects of snow-depth on ANPP (i.e., total effects of snow-depth = “snow-depth to ANPP” + “snow-depth to CWM to ANPP” + “snow-depth to FDis to ANPP”). Here we use both significant and non-significant path coefficients in the calculation of total effects to holistically examine the impact of total abiotic effects. Importantly, excluding non-significant path coefficients would bias our interpretation by removing years where either direct and/or indirect effects are weak. We then compared the magnitude and sign of each abiotic variable's total effects with the total effects of each biotic mechanism and performed linear regressions to assess how the impact of local abiotic variables changed as a function of annual winter precipitation (Figure 4 D-F) and annual growing degree days (Supplement 3.3).

Finally, to assess our fourth prediction that considering the interaction between annual climatic conditions and biotic/abiotic variables would improve our ability to predict ANPP across time, we analyzed our raw data across all years by coupling multi-model inference using linear mixed effects models with variance partitioning. To do this, we built a global linear mixed effects model using the lme4 package (Bates et al., 2014) which featured ANPP as the response variable and trait metrics from our best fitting SEMs (CWM and FDis), abiotic variables (snow depth, snow depth^2, slope, sin(aspect), elevation, annual winter precipitation), and interaction effects between each predictor and annual winter precipitation as fixed effects. Additionally, we included year and plot as random factors to reflect the fact that each plot was repeatedly sampled across years. Interaction effects with annual growing degree days were not included in the model because neither SEM R^2 values nor individual SEM predictors showed significant relationships with this climate variable during SEM analysis. We then used the "dredge" function in MuMIn package (Barton, 2020) to create all possible subset models of the global model and ranked these according to AICc score (Akaike information criterion value corrected for sample size). Next, we selected all models that were within 6 AICc points of the lowest AICc model (347 models total) and used a model averaging technique known as the “zero method” to calculate average parameter estimates (Grueber et al., 2011). This method calculates averages by assigning a 0 value to parameters when they are missing from subset models. Once we identified significant predictors, we used the “partR2” function in the partR2 package (Stoffel et al., 2021) to assess semi-partial R^2 values, in other words, the amount of variation uniquely explained by significant effects, for the global model. This approach allowed us to identify how consideration of significant interactions effects between climate and biotic/abiotic variables improved our ability to predict ANPP across time.

Results

Best Fit SEMs for ANPP

Of the 112 SEMs which met our filtering criteria, at least one SEM in every year exhibited good fit; SEMs featuring 9 different traits (δ^{15}N, LDMC, leaf area, height, SLA, percent nitrogen, percent carbon, carbon to nitrogen ratio, chlorophyll content) exhibited good fit in at least 10 years (Supplement 3.1). The identity of the trait which best predicted ANPP varied across years, with SEMs featuring leaf area, plant height, and δ^{15}N best explaining ANPP in 6, 5 and 2 out of 13 years, respectively (Figure 3A). Other traits did not meet the criterion for best fit and were thus excluded from all analyses discussed below. Importantly, we found that the identity of the trait SEM which best predicted ANPP varied with the amount of annual winter precipitation (Figure 3A). First, we found that leaf area SEMs exhibited good fit in 12 out of 13 years and explained 18.1

to 57.2% of the variation in ANPP (mean = 37.1%). Moreover, we found that ANPP R^2 values in the leaf area SEMs increased with increasing winter precipitation (Figure 3B, $F_{1,10}$=7.128, P=0.024, Adjusted R^2=0.36) indicating greater explanatory power in years with high winter precipitation. Consequently, leaf area SEMs had the best fit in the two highest winter precipitation years (2011, 2017) and failed to converge in the year with the lowest winter precipitation (2012). Second, plant height SEMs also exhibited good fit in 12 out of 13 years and explained a similar amount of ANPP variation as leaf area SEMs (mean = 35.5%, range = 18.6 to 54.6%). However, the relationship between ANPP R^2 values and winter precipitation in these SEMs was non-linear, with explanatory power reaching its maximum in average winter precipitation years and low explanatory power in both low and high winter precipitation years (Figure 3C, quadratic linear regression; $F_{2,9}$=6.35, P=0.019, Adjusted R^2=0.49). The plant height SEM also failed to converge in the year with the lowest winter precipitation (2012). Finally, $\delta^{15}N$ SEMs exhibited good fit in all 13 years but had the lowest average predictive power for ANPP of the three traits (mean = 30.1%, range = 12.8 to 47.3%). R^2 values for the $\delta^{15}N$ SEMs were not significantly correlated with annual winter precipitation (Figure 3D), however, $\delta^{15}N$ SEMs had the best fit in the two lowest winter precipitation years (2012, 2013). No trait SEMs showed significant relationships between ANPP R^2 values and annual growing degree days (Supplement 3.4).

SEM Biotic (Trait) Effects on ANPP

We found that the sign and magnitude of biotic effects inferred from trait-ANPP path coefficients for both CWMs and FDis were consistent among the best fitting SEMs outlined above (Figure 4 A-C). All SEMs showed CWM trait values exerting large and positive effects on ANPP (leaf area SEM: mean = 0.64, range = 0.35 to 1.17; plant height SEM: mean = 0.51, range = 0.23 to 0.80; $\delta^{15}N$ SEM: mean = 0.47, range = 0.27 to 0.86). In contrast, the influence of FDis values on ANPP was weaker and generally negative (leaf area SEM: mean = 0.10, range = -0.25 to 0.01; plant height SEM: mean = -0.32, range = -0.61 to 0.11; $\delta^{15}N$ SEM: mean = -0.19, range = -0.39 to -0.01). We found that some of this variation in the strength of biotic effects (path coefficients), was explained by climatic variation among years. In leaf area SEMs, the CWM ANPP path coefficients showed a significant, positive relationship with annual winter precipitation (Figure 4A; $F_{1,10}$=10.58, P=0.009, Adjusted R^2=0.47), suggesting a stronger relationship in years with greater winter precipitation. In contrast, leaf area FDis was not significantly related to winter precipitation and neither plant height or $\delta^{15}N$ SEMs showed any significant relationships between biotic effects (either CWM or FDis – ANPP path coefficients) and annual winter precipitation. None of the trait SEMs showed significant relationships between biotic effects and annual growing degree days (Supplement 3.4).

SEM Abiotic Effects on ANPP

We found that the sign and magnitude of the total effects for each abiotic variable on ANPP (the sum of all direct and indirect path coefficients for topography, snow-depth, and snow-depth^2) were relatively consistent across trait SEMs and years (Figure 4D-F). Across all best fitting SEMs, topography (which significantly positively covaried with slope and elevation, while aspect was not important) exerted weak and typically negative influences on ANPP (leaf area SEM: mean = -0.09, range = -0.47 to 0.06; plant height SEM: mean = -0.13, range = -0.49 to 0.11; δ^{15}N SEM: mean = -0.08, range = -0.31 to 0.10). Snow-depth also exerted weak and typically negative effects on ANPP across all trait SEMs (leaf area SEM: mean = -0.09, range = -0.47 to 0.06; plant height SEM: mean = -0.10, range= -0.46 to 0.18; δ^{15}N SEM: mean = -0.07, range = -0.43 to 0.28). However, in the δ^{15}N SEMs we found a significant negative relationship between the total effect of snow-depth on ANPP and annual winter precipitation (Figure 4F; $F_{1,11}$=5.92, P=0.033, Adjusted R^2=0.29). Snow-depth^2 had the largest and most consistently negative effect on ANPP (leaf area SEM: mean = -0.32, range = -0.59 to 0.13; plant height SEM: mean = -0.32, range = -0.60 to 0.13; δ^{15}N SEM: mean = -0.32, range = -0.58 to 0.14). Total effects of snow-depth, snow-depth^{2,} and topography on ANPP were not significantly predicted by annual growing degree days (Supplement 3.4).

Climatic Interaction Effects

In our global linear mixed effects model, total fixed effects (R^2_m) explained 22.8% of the variation in ANPP while inclusion of random effects (R^2_c) boosted the variation explained to 54.7%. Multi-model inference revealed that CWM of leaf area (P<0.001), CWM of plant height (P=0.04), FDis of plant height (P<0.001), and snow depth (P<0.001) were retained as significant fixed effects, with all these factors combining to explain a total of 14.3% of the variation in ANPP and trait metrics alone explaining 13.3%. In addition, interactions between CWM leaf area and annual winter precipitation, as well as snow depth and annual winter precipitation, were retained as significant, explaining an additional 2.5% of the variation in ANPP. These two interaction effects were retained in all models within the top 6 AICc subset, indicating that models which did not include them received little support. Model coefficients, AICc scores, and weights for subset models can be found in Supplement 3.5.

Discussion

Recent studies demonstrating that functional traits have weak predictive power for ecosystem functions through time (van der Plas et al., 2020) may be the result of temporal variability in the B-EF relationship, where the individual traits, functional mechanisms, and abiotic variables which best predict ecosystem functions change with annual variation in climatic conditions. Overall, our results are consistent with the hypothesis that traits are dynamics predictors of ecosystem functioning and our analysis revealed that, in an alpine tundra system, the identity of the trait which best predicted ecosystem function varied dynamically with the amount of annual winter precipitation, while the relative importance of the functional mechanisms (CWM vs FDis) and abiotic variables underlying the B-EF relationship remained largely stable. Moreover, multi-model inference with linear mixed effects models reinforced these results, demonstrating that interactions between climate and biotic/abiotic variables significantly affect ANPP across time. However, including these interactions did not greatly increase our ability to predict ANPP and suggests that, in this system, taking these climatic context dependencies into account only modestly improves our understanding of the B-EF relationship. Taken together, our results suggest that that future B-EF research should consider temporal variability in the B-EF relationship, particularly how the predictive power of individual functional traits and abiotic variables may fluctuate as climatic conditions shift due to climate change or in highly variable ecosystems.

Best Fit SEMs for ANPP

Our finding that trait SEMs related to plant size (leaf area and plant height) best explained ANPP in 11 of 13 years adds to a growing body of research showing that, across a wide variety of experimental and natural systems, traits related to plant size are often the best predictors of ANPP (Lavorel and Grigulis, 2012; Chiang et al., 2016; Cadotte, 2017; Gustafsson and Norkko, 2019). While leaf area SEMs performed well on average, the predictive power of these SEMs showed a strong relationship with annual winter precipitation (Figure 3B). Since leaf area values reflect a species' ability to maintain water/energy balance (Parkhurst and Loucks, 1972; Miller and Stoner, 1979; Ackerly et al., 2002), a sustained summer snowpack resulting from higher levels of winter precipitation could provide a source of consistent growing season soil moisture, allowing larger-leaved species to achieve higher levels of stomatal conductance and/or photosynthesis (Pattison and Welker, 2014). Thus, in high winter precipitation years, communities composed of large-leaved species would be able to fix more carbon and produce more biomass than normal, exaggerating the already strong relationship between CWM leaf area and ANPP (Figure 4A). Low winter precipitation years, on the other hand, may produce the opposite phenomenon, where large leaved species are forced to close their stomata more often due to moisture limitation and thus produce uncharacteristically low levels of ANPP (Bowman et al., 1995; Wentz et al., 2019). This minimizes the normally predictive pathway between CWM leaf area and ANPP, leading to failed model convergence in 2012, the year with the lowest amount of winter precipitation.

In contrast to leaf area SEMs, the predictive power of plant height SEMs was maximized in average winter precipitation years and minimized in both low and high winter precipitation years. In these SEMs, predictive power seemed to change due to small increases in the magnitude of both CWM and FDis effects, where the mean and dispersion of plant height exerted slightly larger magnitude effects on ANPP in average precipitation years (Figure 4B). In low winter precipitation years, marginally lower magnitude CWM and FDis effects may result from moisture limitation reducing ANPP in normally productive plots, a similar mechanism to what we inferred for leaf area SEMs. However, in contrast to leaf area SEMs, high winter precipitation years also dampen plant height CWM and FDis effects on ANPP. This could result from high winter precipitation leading to a larger, later melting snowpack reducing ANPP in normally productive plots via energy limitation. Thus, height SEMs perform best in average winter precipitation years when neither moisture nor energy are limiting plots where communities have high mean heights and low height dispersion.

In the two years with the lowest amount of winter precipitation (2012 and 2013), the SEMs which best explained ANPP switched from size related traits to $\delta^{15}N$. This suggests that while winter precipitation may control the relationship between size related traits and ANPP via moisture and energy limitation, δ^{15}N trait distributions are shaping patterns of ANPP through a different mechanism which is not as strongly affected by interannual variation in climate. While the ecological interpretation of δ^{15}N trait values is complex, they are broadly thought to reflect the availability of total nitrogen and variation in nitrogen source (abiotic vs. biotic sources) and have been found to vary along gradients of N availability on Niwot Ridge (Miller and Bowman, 2002; Craine et al., 2015; Spasojevic and Weber, 2021). Since a large fraction of nitrogen in the alpine zone comes from melting snow, long-term patterns of snow deposition set the template for the location and type of nitrogen found across the landscape (Bowman, 1992). Thus, even in years with abnormally high or low winter precipitation, nitrogen availability and source are likely to remain relatively constant. The longer time scale of response for nitrogen availability may be the reason that δ^{15}N SEMs continue to be reasonably predictive of ANPP regardless of annual winter precipitation levels, while the predictive power of height and leaf area SEMs varies more directly with the moisture and energy limitations imposed by fluctuating levels of winter precipitation.

SEM Biotic (Trait) Effects on ANPP

In all best fitting trait SEMs, CWMs exerted a large, positive influence on ANPP indicating that communities with high average leaf area, plant height, and/or δ^{15}N have the highest levels of ANPP. FDis effects on the other hand, were lower magnitude and usually negative, indicating that communities which contain a greater diversity of trait values for height, leaf area, and δ^{15}N had lower levels of ANPP. Taken together, our results offer partial support for our second prediction and add to a growing body of research demonstrating that mass ratio effects are generally more important than niche complementarity effects in determining individual ecosystem functions (i.e., not multi-functionality), particularly in natural systems (Chiang et al. 2016, Cadotte 2017, Fotis et al. 2018, Needham et al. 2022, Brun et al. 2019, van der Plas 2019).

However, the stability of these two functional mechanisms across trait SEMs and temporally varying climatic conditions, conflicts with our second prediction that niche complementarity effects would become more important during climatically stressful years. Moreover, this finding contradicts research from experimental grassland and forest systems suggesting that niche complementarity effects tend to exert a more positive impact on ecosystem functions when environmental conditions become harsher (Wang et al. 2013, Mori 2018; but see Jucker et al. 2016 who found strong spatial but weak temporal B-EF context dependency). This may indicate that niche partitioning among species (i.e., niche differences) is relatively unimportant in determining ANPP in this alpine ecosystem, and instead, ANPP is primarily shaped by the presence of dominant species possessing traits which provide a competitive advantage (i.e., hierarchical fitness differences) in a specific environmental context (e.g., species with high leaf area trait values, especially in high winter precipitation years) (Cadotte, 2017). Alternatively, because our plots are distributed across a fairly large area with high beta-diversity (Spasojevic and Suding, 2012; Spasojevic et al., 2013), differences in CWM and FDis trait values among habitat types could be so large that they mask the positive effects of niche complementarity, which are acting at finer spatial scales. Our cross-community analysis may show negative effects of FDis on ANPP because plots positioned in energy-limited snowbank communities possess high FDis for size related traits and very low ANPP, while plots in abiotically mild moist meadow communities possess low FDis for size related traits and high ANPP. If instead we were to examine the B-EF relationship at a smaller spatial scale by only using plots within an alpine habitat type, the effects of niche complementarity might appear to be positive and relatively more important. For example, facilitation is known to be an important process in dry, wind-swept fellfield communities where dominant cushion plants ameliorate micro-climatic conditions for subordinate species (Butterfield et al., 2013; Kikvidze et al., 2015), perhaps generating a positive relationship between functional dispersion and ANPP within this community type.

SEM Abiotic Effects on ANPP

The relatively low magnitude of total effects for abiotic variables in our best fitting SEMs likely results from direct and indirect effects often displaying opposing signs. For example, in leaf area SEMs the direct pathway linking snow depth and ANPP was strongly negative, but the indirect pathway through the CWM of leaf area was positive (Supplement 3.1, Supplement 3.2). These contradictory effects confirm previous research showing that snow depth plays an important but complicated role in determining ANPP and species composition (Walker et al., 1993), with high snow depth values lowering ANPP directly, while simultaneously driving an increase in leaf area CWM values which then have strong, positive knock-on effects for ANPP. This example highlights the usefulness of SEMs for B-EF research, as they are able to disentangle complex relationships which might be obscured when using other methods like generalized linear modeling or variance partitioning which do not consider indirect effects (Grace et al., 2014, 2016).

Only in the $\delta^{15}N$ SEMs did the total effect of an abiotic variable vary significantly with winter precipitation, with snow depth exerting a negative effect on ANPP in high winter precipitation years but a positive effect in low winter precipitation years. This result suggests that the impacts of snow depth on ANPP are context dependent. In years when winter precipitation is high, increasing snow depth likely restricts ANPP by limiting the length of the growing season, while in low winter precipitation years increasing snow depth boosts ANPP by alleviating moisture limitation. Importantly, this significant trend may only be visible in $\delta^{15}N$ SEMs because they are the only SEMs which converged in all 13 years and possesses a path coefficient value for the lowest precipitation year (2012) in which snow-depth exerted a strong positive effect on ANPP. Overall, our SEMs indicate that local abiotic conditions, particularly snow depth, play an important and context-dependent role in driving ANPP, but that the combination of strongly opposed direct and indirect effects lead to small total effects.

Climatic Interaction Effects

Multi model inference using data across all years largely reinforced our conclusions from SEM analysis, with ANPP once again significantly correlated with CWM leaf area, CWM height, FDis height, and snow depth. While δ^{15}N trait metrics did not appear as significant, this is expected given that δ^{15}N SEMs did not perform particularly well at predicting ANPP and only became the model of best fit in 2012 and 2013 due to poor performance for leaf area and height SEMs in the two lowest precipitation years. Furthermore, the two variables we found had context dependent effects with winter precipitation during SEM analysis, CWM leaf area and snow depth (in δ^{15}N SEMs), also showed up as significant interaction effects in multi-model inference. However, inclusion of these two interaction effects did not greatly increase our ability to predict ANPP across time, and total fixed effects in the global model still explained much less variation in ANPP than the within-year SEMs (van der Plas, 2020). The inability of interaction effects to substantially improve predictive power may result from the fact that this alpine system is composed of hardy, long-lived species which may not quickly respond to annual variation in climatic conditions. While species composition is changing at Niwot and the Rocky Mountains more broadly (Huxley and Spasojevic, 2021), these changes are occurring at the scale of decades (Spasojevic et al., 2013; Scharnagl et al., 2019) and effects on the B-EF relationship may not be clearly visible over the 13-year period of our study. Temporal shifts in the B-EF relationship may be larger in annual communities where species composition can more quickly change in response to local and/or regional changes in climatic conditions, leading to immediate cascading impacts on ecosystem function (Felton et al., 2021; Shaw et al., 2022).

Study Limitations

Though our results suggest that the explanatory power of the functional traits underpinning ecosystem functions can vary dynamically through time, it is important to acknowledge limitations with our observational approach. First, NWT's Saddle plots do not equally represent the diversity of community types found on Niwot Ridge. Certain community types (e.g., fellfield, N = 8 plots; wet meadow, N = 4 plots) are under-represented, potentially biasing our interpretations of which traits and mechanisms are most important across the alpine tundra as whole. The low number of fellfield plots is especially problematic given that facilitation and resource partitioning are known to play an important role in this high stress/low resource community type (Bertness and Callaway, 1994; Butterfield et al., 2013). More data from under-represented community types should be collected so that analyses of the B-EF relationship can be conducted within community types as well as across them. Second, more detailed trait data could improve our ability to explain ANPP across the alpine landscape. Specifically, incorporating temporal changes in intraspecific trait variation could be a major way to improve the power of trait-based approaches for predicting the B-EF relationship through time. Several studies have found that climatic variation can induce large shifts in intraspecific trait values, with subsequent impacts on community-level trait distributions sometimes exceeding the impact of species composition change (Jung et al., 2014; Henn et al., 2018). In this study, we used habitat-specific trait means to capture a degree of spatial intra-specific variation; however, more detailed trait data collection (e.g., measurements in each year) could reveal how temporal intra-specific variation might generate trait-ecosystem function relationships even stronger than those reported here.

Conclusion

In our alpine tundra system, productivity was generally best explained by traits related to plant size (leaf area and plant height), however, this trend changed during low winter precipitation years when $\delta^{15}N$ instead best predicted productivity. Without exception, productivity was better explained by the community average values of these traits rather than their variation, suggesting that, while both mechanisms operate simultaneously, mass ratio effects are relatively more important than niche complementarity in determining productivity in this system. The total effects of local abiotic variables on ANPP were relatively small, however, this was due to complex and contradictory direct and indirect (via trait composition) effects. Lastly, some biotic and abiotic variables showed context dependent relationships with winter precipitation, and consideration of these climatic context dependencies marginally improved our ability to predict ecosystem function through time. Taken together, our results suggest that consideration of temporal variation in environmental conditions and the dynamic nature of trait-environment relationships can improve our understanding of the traits and functional mechanisms underpinning the biodiversity-ecosystem function relationship.

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Figures

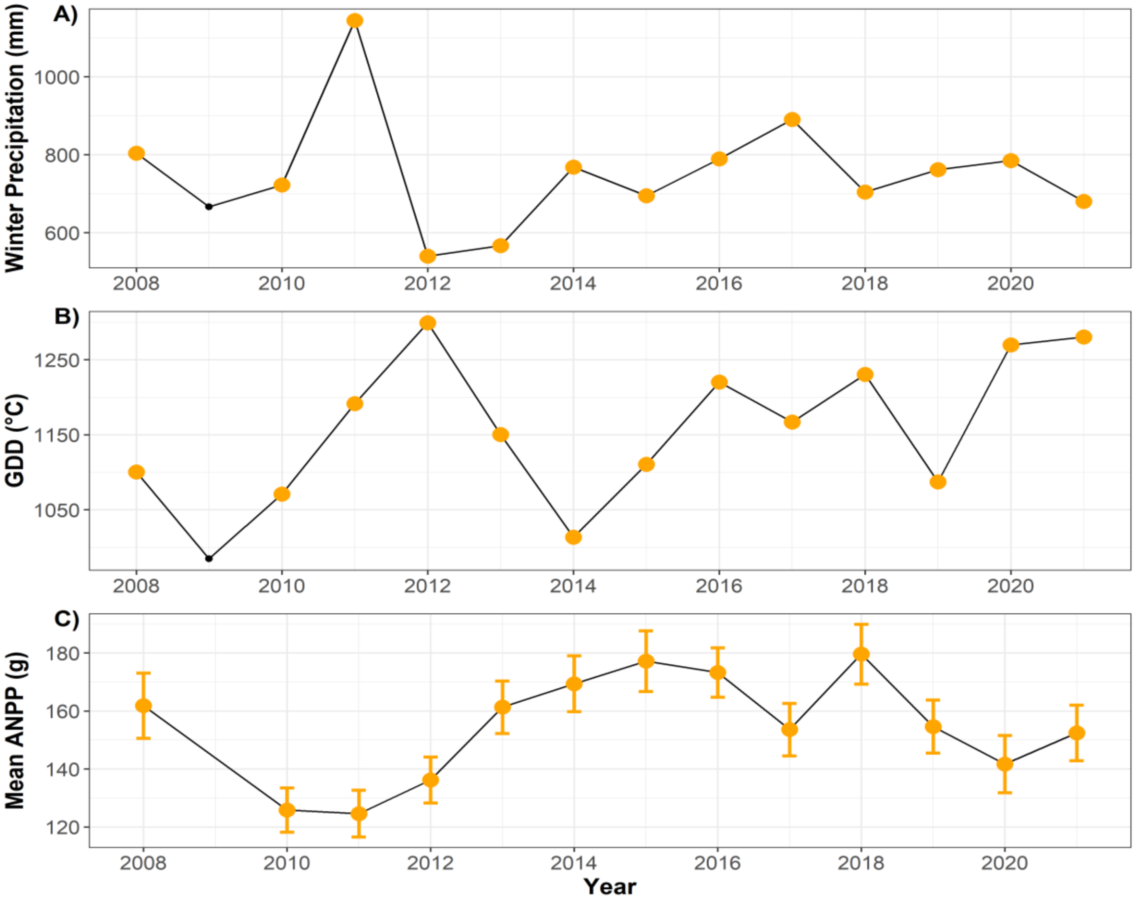

Figure 1: Climatic variables and aboveground net primary productivity measured in the Saddle region of Niwot Ridge from 2008 to 2021. Orange points indicate years included in our study (2008, 2010-2021). A) Annual winter precipitation (between October and May) measured in centimeters; B) Annual growing degree days (GDD; between September – August), measured as the sum of daily temperatures for days where mean daily temperature is greater than zero; C) Mean aboveground net primary productivity (ANPP) measured in grams across all 78 plots; error bars display standard error of ANPP.

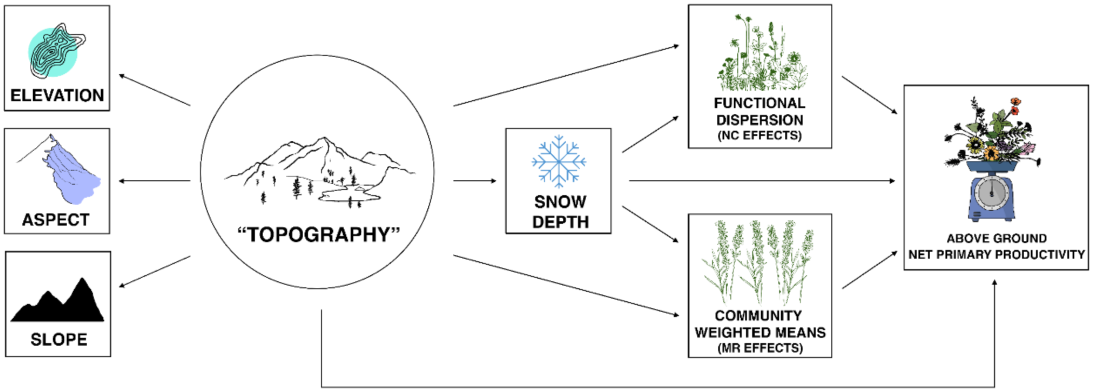

Figure 2: The SEM meta-model used as the basis for SEMs across all traits and years. All pathways are based on research demonstrating causal pathways between topography, snow deposition, functional composition, and aboveground net primary productivity in the alpine zone. "Topography" is a latent variable constructed from elevation, aspect (sine transformed), and slope. Snow depth is measured as average snow depth for the month of May. All SEMs also included a snow-depth^2 term (omitted here for visual clarity) to account for the quadratic relationship between snow-depth and ANPP. Snow-depth^2 occupies the same model position as snow-depth; a covariation pathway was included between the two terms. Community weighted mean trait values were used as a proxy for mass ratio effects (MR effects), while functional dispersion values were used as a proxy for niche complementarity effects (NC effects). A covariation term was included between the community weighted means and functional dispersion parameters. Aboveground net primary productivity was measured as the total annual aboveground vascular biomass harvested in 0.2m x 0.5m quadrats adjacent to each Saddle plot.

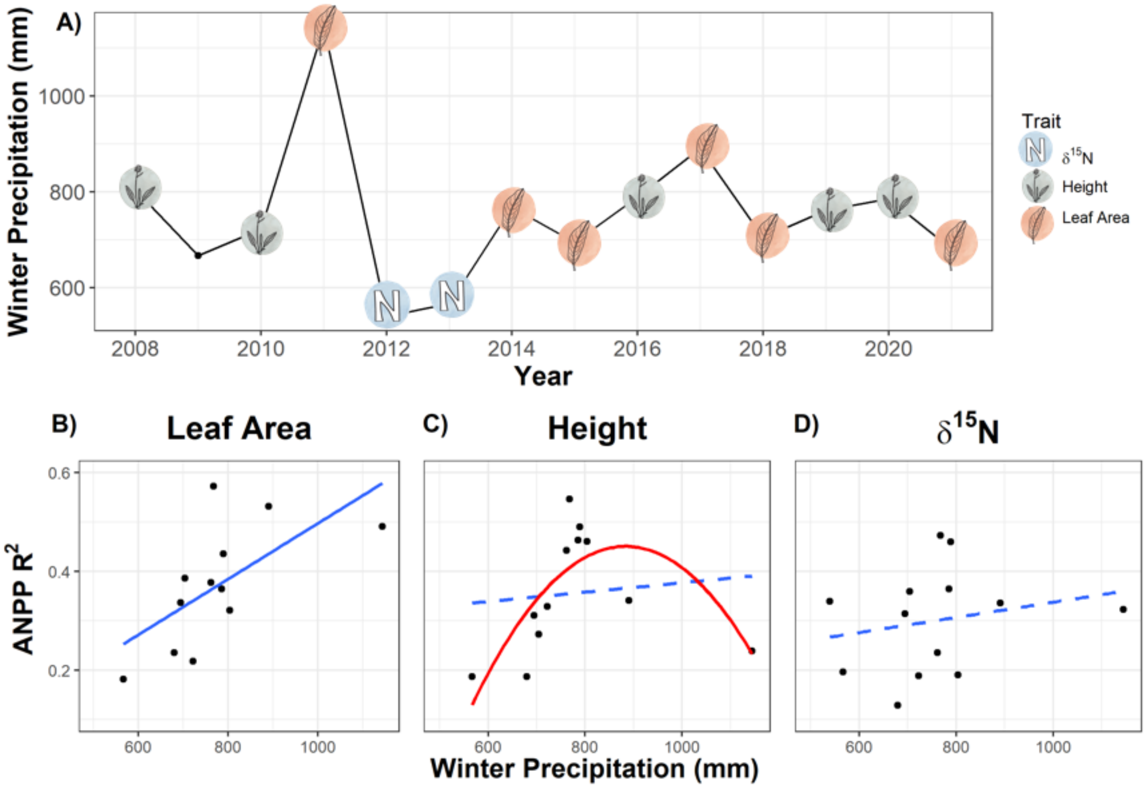

Figure 3: A) Annual winter precipitation (Oct-May) from 2008-2021, shapes show the identity of the trait SEM which best predicted ANPP in each year. Panel two shows the relationship between ANPP R^2 values and annual winter precipitation for trait SEMs incorporating leaf area (B), height (C), and δ^{15}N (D). Lines of best fit from linear regressions between winter precipitation and ANPP are shown for B-D. Solid lines indicate a significant relationship while dashed lines indicate a non-significant relationship. For height, quadratic linear regression (shown in red) is also included, as this model provided a better fit than simple linear regression.

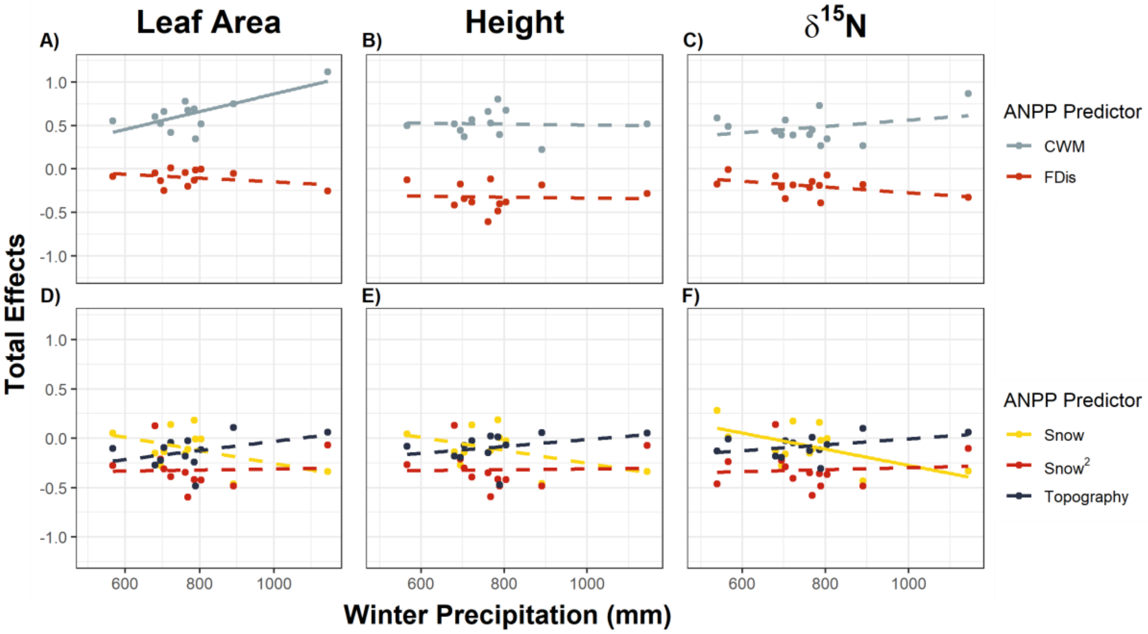

Figure 4: The total effects (sum of all direct and indirect path coefficients) of biotic and abiotic predictors on ANPP regressed against annual winter precipitation (mm) for leaf area (A/D), height (B/E), and δ^{15}N (C/F) SEMs. Different colors indicate the specific predictor variable influencing ANPP; total biotic influences (community weighted means and functional dispersion, A/B/C) and total abiotic influences (snow-depth, snow-depth^2, and topography D/E/F) on top and bottom respectively. Solid lines indicate a significant relationship between winter precipitation and ANPP, while dashed lines indicate a non-significant relationship.

Synthesis

Climate change is reshaping patterns of biodiversity around the world, with mountain ecosystems suffering disproportionate effects. To improve our understanding of climate impacts on mountain ecosystems, we investigated the causes and consequences of biodiversity change in the alpine sky islands of the Colorado Rocky Mountains. We found that alpine biodiversity patterns are rapidly changing, with increases in species richness, phylogenetic diversity, and the abundance of stress tolerant species (e.g., chapter 1). Many of these changes were mitigated in larger sky islands, suggesting that these sites are likely to serve as more effective climatic refugia for alpine species and should be prioritized for conservation action. Additionally, we found that species interactions and co-occurrence patterns in the alpine tundra are mediated by traits related to plant size (height and leaf area), but that these traits acted through different mechanisms depending on abiotic conditions (chapter 2). Changing patterns of height and leaf (chapter 1) are likely to impact these mechanisms, affecting how species compete, facilitate, and partition niche space with one another. Lastly, we found that net primary productivity in alpine tundra was also best predicted by plant size traits (chapter 3). However, in years with low winter precipitation this normally predictive relationship collapsed, demonstrating the strong effect of temporal variation in climate on the biodiversity-ecosystem function relationship. Taken together, the research outlined in this dissertation advances our understanding of shifting biodiversity patterns, the processes which drive those patterns, and the functioning of the ecosystems in a rapidly changing world.