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Fractally Sampling Diversity-Environment Relationships to Understand Plant Assemblage Health Across Spatial Scales

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FRACTALLY SAMPLING DIVERSITY-ENVIRONMENT RELATIONSHIPS TO UNDERSTAND PLANT ASSEMBLAGE HEALTH ACROSS SPATIAL SCALES

by

Elizabeth G. Simpson

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Biology & Ecology

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ABSTRACT

Fractally sampling diversity-environment relationships to understand plant assemblage health across spatial scales

by

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Utah State University, 2023

Major Professor: William D. Pearse, Ph.D.
Department: Biology

Humans affect the health of ecosystems which provide services that support their livelihoods and well-being. Monitoring how abiotic and biotic factors change across environments provides insight into the processes that support ecosystem health. Since these processes occur at and across spatial scales, there is a need for sampling methods and analysis that directly assess how spatial scale affects ecological processes. Throughout this dissertation, I address this need by testing the efficacy of a nested sampling design that fractally spaces sampling locations in equilateral triangles in northeast Utah rangeland that has visually distinct vegetation types across aspect—from sagebrush steppe on south-facing slopes to conifer forest on north-facing slopes. In the first chapter, I look at how evolutionary history and relationships (phylogenetic diversity and structure) change across topography and spatial scale to identify which spatial scales have the most influence on diversity-environment relationships at this fieldsite. In the second chapter, I assess how the mean and variance of functional diversity change in response to soil temperature and texture-defined microenvironments to understand the potential for assemblages to respond to changing conditions in the future. In the third chapter, I leverage the flexibility of the fractal design to assess diversity-environment relationships at a larger spatial extent, with a specific focus on rangeland management concerns. Overall, I found that both phylogenetic and functional diversity shifted most strongly across aspect. Compared to north-facing slopes, soil temperature on south-facing slopes was hotter and more variable and supported more closely related assemblages, with less variance in functional traits, and shorter, more resource-conservative functional strategies. These results indicated a broad-scale environmental filter across aspect and suggested that the function of north- vs. south-facing assemblages might be at risk for contrasting reasons. On south-facing slopes, assemblages potentially do not have the variety of functional strategies needed to respond to more stressful conditions. Conversely, on north-facing slopes, assemblages may not have the resource-conservative strategies needed to persist if temperatures become hotter and more variable. When I applied this monitoring system in a range management context I found that managers' concerns would be best addressed by focusing on reducing bare ground and undesirable species via management actions that maintain vegetation heterogeneity and increase species richness across all vegetation types. A fractal-based sampling design can efficiently and flexibly sample diversity-environment relationships to understand ecological processes broadly and in a management context.

(177 pages)

PUBLIC ABSTRACT

Fractally sampling diversity-environment relationships to understand plant assemblage health across spatial scales

Elizabeth G. Simpson

Humans influence the health of ecosystems and rely on healthy ecosystems to support their livelihoods and well-being. By looking at how the parts of ecosystems interact we can understand and improve ecosystem health. Ecosystem interactions change across spatial scales or different size patches of area. For example, individual organisms interact with each other at small spatial scales, while at large spatial scales, communities of organisms interact with weather conditions. However, many research studies do not look at how ecosystem interactions change across spatial scales. To address this gap in ecological research, I use a fractal sampling design which samples at the vertices of equilateral triangles nested within each other. This design allows me to investigate how spatial scale influences the relationship between plant communities and the environments they live in. I tested this design in northeast Utah rangeland where the vegetation changes depending on whether a hill faces south (more shrubs and grasses) or north (more conifer trees). In the first chapter, I look at how plant biodiversity metrics based on the tree of life (phylogenetic diversity) change across terrain and spatial scale. This analysis identifies which spatial scales influence the relationship between diversity and environment at the fieldsite. In the second chapter, I assess how the characteristics that plants have adapted to survive and thrive (functional diversity) change in response to soil temperature and water dynamics. This chapter describes the potential for plants to respond to changing conditions in the future. In the third chapter, I look at diversity-environment relationships across a larger landscape to address rangeland management concerns about an increase in undesirable species and bare ground. Overall, both phylogenetic and functional diversity changed across south- to north-facing hills. In contrast to north-facing hills, the soil temperature on south-facing hills was hotter and more variable. Plant communities on south-facing hills were more closely related, shorter, and better adapted to survive with fewer resources, like water, and had more similar features than on north-facing hills. These communities might struggle to survive if this area becomes hotter for the following contrasting reasons. On south-facing hills, plant communities may not have enough difference in features to respond to more stressful conditions, but on north-facing hills, communities may not adapt to fewer resources quickly enough. In the context of range management, the amount of undesirable species and bare ground should be prioritized as a concern. Additional monitoring at relatively small spatial scales may help guide management actions. Maintaining different types of healthy vegetation and increasing the number of species in each vegetation type will help achieve the goal of decreasing undesirable species and bare ground. Overall, a fractal sampling design effectively assessed how plant diversity—both phylogenetic and functional—changed in different environmental and management conditions and identified when spatial scale influenced ecological interactions and ecosystem health.

To my family, especially my dad; your kindness, curiosity, and creativity inspire me daily.

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Elizabeth G. Simpson

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ACRONYMS

ANOVA	analysis of variance
C	celsius
cm	centimeter(s)
COMDIST	inter-community mean pairwise distance
CWM	community weighted mean
FDis	functional dispersion
g	gram(s)
GPS	global positioning system
HOBO	Honest Observer by Onset
L	liter(s)
LA	leaf area
m	meter(s)
m.a.s.l.	meters above sea level
mm	millimeter(s)
MST	mountain standard time
PC	principal component
PCA	principal components analysis
PD	phylognenetic diversity
PhyloSor	PhyloSørenson's index
SD	standard deviation
SES_{MNTD}	standard effect size of mean nearest taxon distance
SES_{MPD}	standard effect size of mean pairwise distance
SLA	specific leaf area
SRM	Society of Range Management
U.S.A	United States of America
USDA	United States Department of Agriculture
WCNF	Wasatch-Cache National Forest

CHAPTER 1

INTRODUCTION

Humans have monitored and managed ecological systems for millennia to simultaneously support themselves and ecosystem health (Raygorodetsky, 2017). While careful management does not always result in healthy ecosystems, many landscapes managed by local and indigenous people harbor large amounts of the world's wild and domesticated diversity (Díaz et al., 2019). When ecosystems are managed well, they support peoples' livelihoods and wellbeing via ecosystem services (Costanza et al., 1997; Reid et al., 2005). Additionally, management can result in ecosystems with greater taxonomic and functional diversity than surrounding ecosystems (Armstrong et al., 2021) as well as resources and habitat for other taxa, like wildlife and pollinators (Middleton, 2013). Observing how biodiversity varies across environmental gradients, will typically include some conditions that are more stressful (*e.g.*, that have less water available) and can be used to understand how ecosystem health varies under different conditions (Costanza, 1992). Understanding the ecosystem dynamics that support biodiversity can inform management actions, including restoration, that maintain and allow diverse, adaptive, resilient ecosystems. Multiple knowledge systems, including indigenous and local knowledge and Western science, provide frameworks and evidence for understanding the mechanisms and outcomes of balance in relationships between humans and their environment (Tengö et al., 2014).

In this introductory chapter, I broadly contextualize the work in this dissertation via four, interlinked topics. (1) I discuss why studying the diversity of vascular land plants, the focal taxa of this dissertation, can provide information about an ecosystem's health. This discussion highlights some of the important interactions between plants and the abiotic and biotic components of their ecosystem, with a focus on how these interactions might affect the health of an actively grazed rangeland. Then, (2) I explain how whether different types of biodiversity (*e.g.*, phylogenetic and functional) change across environment can provide insight into the ecological processes that assembled that diversity. I utilized phylogenetic and taxonomic diversity throughout all of the chapters and focus on how functional diversity can provide insight based on the biological insurance hypothesis in chapter three. (3) Since spatial scale affects these processes and the patterns they produce, I give an overview of how I assessed changes in these patterns using a spatially-explicit fractal-based sampling design, which is used for all of the work I describe (Figure 1.1). Finally, (4) I discuss how I translated this abstract set of research concepts and analysis into a set of recommendations that address local range health management concerns in the final chapter.

1.1 Foundational taxa: vascular land-plants

I focus on the taxonomic, phylogenetic, and functional diversity of vascular land plant assemblages because plants provide a foundational source of food, habitat, and materials that most other taxa, including humans, directly or indirectly rely on to survive and thrive. I highlight some of the critical interactions between plant assemblages and biotic and abiotic ecosystem components to demonstrate their connectivity and justify my choice of plant biodiversity as an indicator of ecosystem health (Figure 1.2). In active rangeland, plant assemblages provide forage for livestock (and other herbivores) which provide food security, livelihood, and sociocultural value for ranchers and the communities they live in (Figure 1.2, green arrows). When adaptively managed, grazing supports more diverse and productive plant assemblages (Castillo-Garcia et al., 2022; Veen et al., 2014). More diverse plant assemblages support more diverse soil microbe assemblages, even after short periods of restoration (Figure 1.2, brown arrows; Herzberger et al., 2014). And, in balance, diverse soil microbial assemblages support more diverse plant communities (Schnitzer et al., 2011) which are often more productive (Garcıa-Palacios et al., 2018; Madani et al., 2018; Tilman et al., 2006).

Plants also play a critical role in regulating heat and water transfer in the environment (*i.e.*, climate), slowing down the evapotranspiration-condensation cycle, which cools the overall environment and keeps water in the system (Figure 1.2, arrows in blue; Hesslerová et al., 2019; Zhao et al., 2017). Additionally, variation in plant structure and composition, along with litter from dead plant matter, slows water infiltration into the groundwater supply and regulates soil multifunctionality across different precipitation regimes (Figure 1.2, arrows in turquoise; Ding & Eldridge, 2021). The presence of cattle also influences climate, because cattle contribute methane to the atmosphere, increasing greenhouse gases which leads to higher temperatures globally (Figure 1.2, arrow in red). However, improving grazing management practices and pastures using fertilization, and sowing legumes and perennial grasses, can increase carbon sequestration in rangelands (Figure 1.2, arrow in blue; Booker et al., 2013; Conant et al., 2017; Derner & Schuman, 2007; Schuman et al., 2002).

1.2 Using diversity-environment relationships to understand ecological and evolutionary processes

The biodiversity and structure of a healthy ecosystem depend on many factors, including the underlying ecological and evolutionary mechanisms that operate at and across different spatial and temporal scales. Quantifying changes in observed patterns of diversity across environment can provide inference into the ways that more locally-operating mechanisms, like environmental filtering and competitive exclusion, shape assemblage composition and structure (Graham et al., 2014). To assess environmental filtering in a strict sense, a study must experimentally test whether an abiotic condition prevents a species from establishment or persistence in the absence of biotic interactions (Kraft et al., 2015). However, a definition of environmental filtering that includes how biotic interactions affect species' establishment and persistence, and how these interactions vary across environmental conditions, best captures the complexity of interacting ecological process (Cadotte & Tucker, 2017). In lieu of extremely detailed, time-intensive, manipulative studies, observational, correlative studies can essentially detect environmental filtering as long as three lines of evidence provide strong support in the following manner. (Cadotte & Tucker, 2017). Assemblages must have (1) more clustered phenotypes or evolutionary relationships than expected by chance, that are (2) associated with an environmental gradient that could mechanistically constrain species, and (3) that more closely related species must have more similar traits (*i.e.*, traits must be phylogenetically conserved).

Many metrics can be used to quantify biodiversity, but some provide more nuanced information about how that diversity arose and which ecological processes might be shaping diversity (Purvis & Hector, 2000). For example, phylogenetic structure metrics quantify the evolutionary relationships between species in an assemblage and provide insight into the relative importance of abiotic and biotic mechanisms that shape that assemblage (Cavender-Bares et al., 2009; Mayfield & Levine, 2010; Mouquet et al., 2012; Webb et al., 2002). These interpretations rely on whether or not species' traits are phylogenetically conserved, which highlights the importance of also looking at functional diversity in tandem with phylogenetic diversity. Even without tracking changes in diversity across environment, phylogenetic structure metrics provide valuable insight into how the diversity and traits of local communities have assembled from the regional species pool (Gerhold et al., 2015). Additionally, assemblage-level functional diversity quantifies the overall strategies plants use to acquire resources in a given set of abiotic and biotic conditions and conversely the effect they have on the ecological processes and environmental conditions around them (Lavorel & Garnier, 2002; Mason & De Bello, 2013; Reich, 2014; Suding et al., 2008).

1.3 Assessing spatial scale in ecological studies

Critically, the ecological processes that produce biodiversity patterns occur at and across different spatial and temporal scales (Chave, 2013; Levin, 1992). Community assembly is classically understood via an oversimplified heuristic of abiotic and biotic filters that constrain species at sequentially smaller spatial and temporal scales (Cadotte & Tucker, 2017; Vellend, 2010). At broad scales, speciation, selection, drift, and dispersal shape the species pool (Vellend, 2010). Then, processes occurring at smaller scales—like competition and environmental filtering—assemble communities from that pool of species (Chesson, 2000; Kraft et al., 2015). However, in reality, diversity arises and persists via mechanisms that interactively vary in strength and importance across both space and time (Chesson, 2000).

Community ecologists capture these processes across scales by categorizing diversity based on relative spatial scales and the relationships between scales (Whittaker, 1960). This ranges from the total diversity in a region (γ-diversity) to the diversity within an assemblage (α-diversity), and differences in diversity between assemblages (β-diversity). These categorizations provide a useful framework for understanding diversity varies across space within a study (Crist et al., 2003; Loreau, 2000; Sfenthourakis & Panitsa, 2012; Zhang et al., 2014). However, they do not explicitly address the question of what spatial scale extent or grain diversity varies at.

Sampling designs more specifically address the problem of failing to capture the spatial scale the ecological processes are happening at in a study (Jackson & Fahrig, 2015; Wheatley & Johnson, 2009). Self-similar, spatially-independent, fractal-based sampling designs like the one I use (based on Ewers et al., 2011; Marsh & Ewers, 2013), effectively assess how diversity-environment patterns vary across spatial scales. Their use stems from work that shows that equilateral-triangle-fractal-based sampling designs as efficient, flexible tools for assessing ecological patterns and processes (Albert et al., 2010; Halley et al., 2004; Kallimanis et al., 2002; Luzuriaga et al., 2012).

1.4 Assessing rangeland health management concerns

In working landscapes, like rangelands, collaboration and communication between managers, researchers, and other stakeholders informs and produces more useful science that focuses on improving humans' livelihoods and wellbeing (Enquist et al., 2017). To apply the research system I developed to address rangeland management, I started by having discussions with local land managers about what projects they were focused on and what concerns they had about the health of the range. This helped me understand the intersection between the information that they need and what I could provide based on the research system (Sarewitz & Pielke, 2007). These discussions informed analysis based on their concerns about the prevalence of bare ground and a perceived increase in undesirable forage species. By focusing the analysis on managers' concerns I was able to provide specific recommendations about short- and long-term management changes that could improve range health and sustainability (Maczko et al., 2016).

1.5 Overview of chapters

This dissertation looks at how different attributes of biodiversity provide insight into the ecological dynamics that support ecosystem health at a fieldsite in the Bear River Range in northeastern Utah (Figures 1.1, 1.3). The second chapter investigates how plant phylogenetic and taxonomic diversities vary across topographically-defined environmental gradients, with a specific focus on how a spatially-explicit sampling design can provide insight into the effect of spatial scale on diversity-environment relationships. This chapter highlights the efficiency and efficacy of a fractal-based sampling design to capture different information about the evolutionary history and relationships within assemblages, and the ecological processes phylogenetic diversity can inform, at different spatial scales. The third chapter leverages insight from the biological insurance hypothesis to look at how community-level functional diversity varies in response to variation in microenvironment (near-surface soil temperature and texture). This chapter looks at how assemblages currently respond to environmental stressors and resource availability and compares that to phylogenetic diversity, with the goal of understanding how functionally-equipped assemblages might be to respond to future changes in climate. The fourth chapter applies insights from the previous two to assess and address management concerns related to rangeland-specific conditions. This chapter compares range indicators of soil stability, hydrological function, and biological (vegetation) integrity to a more commonly collected indicator, utilization, in a spatially-explicit context. Taken together, these chapters provide a framework for translating basic science into usable management recommendations to understand the health of an ecosystem that supports human livelihood and wellbeing.

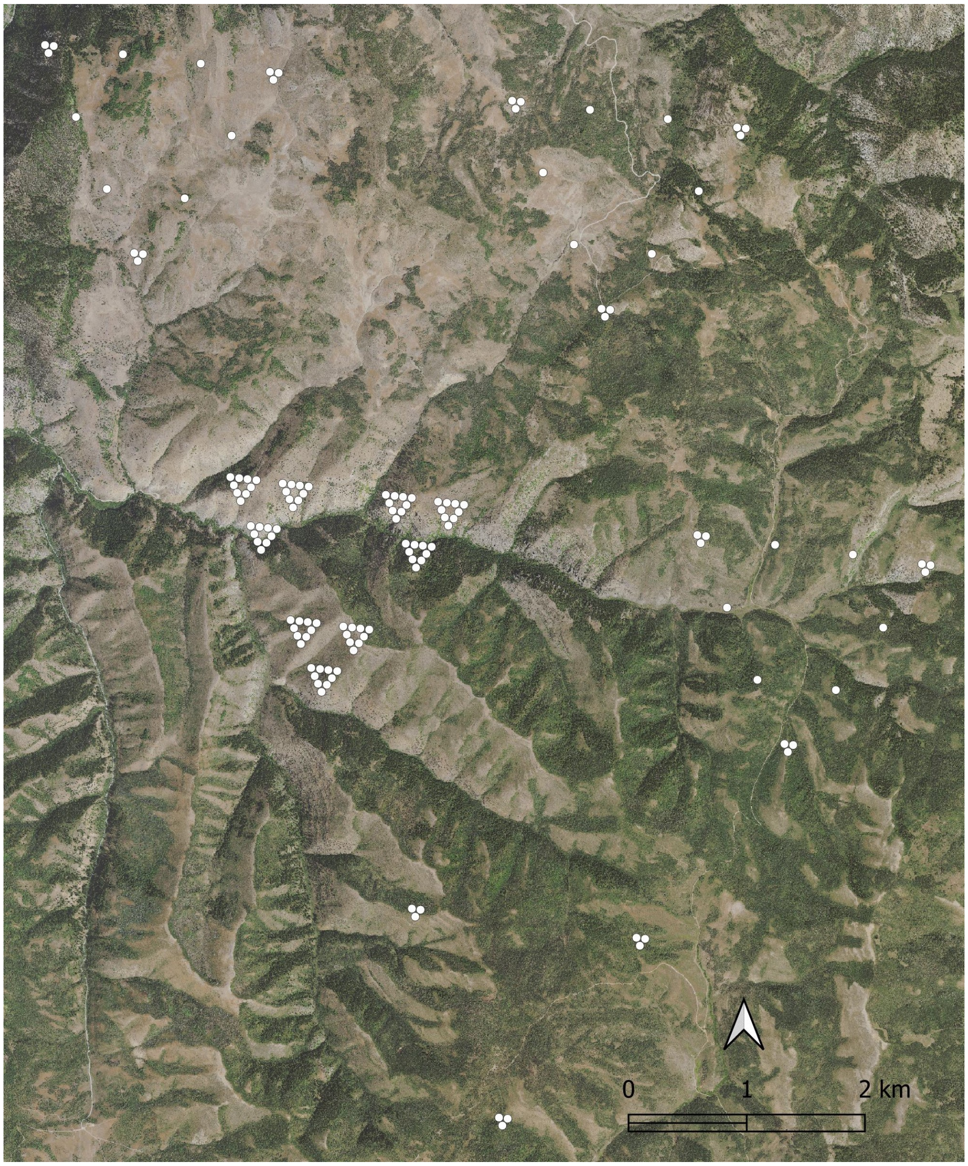

Fig. 1.1: **I used a fractal-based sampling design to assess the effect of spatial scale on diversity-environment relationships.** The core plots assessed in 2017-2021 are shown in the left center of the map. The extended plots, which were added in 2019 to assess range health, are shown in the four surrounding triads. Background vegetation cover imagery (National Agriculture Imagery Program) from August 2021 courtesy of the U.S. Geological Survey.

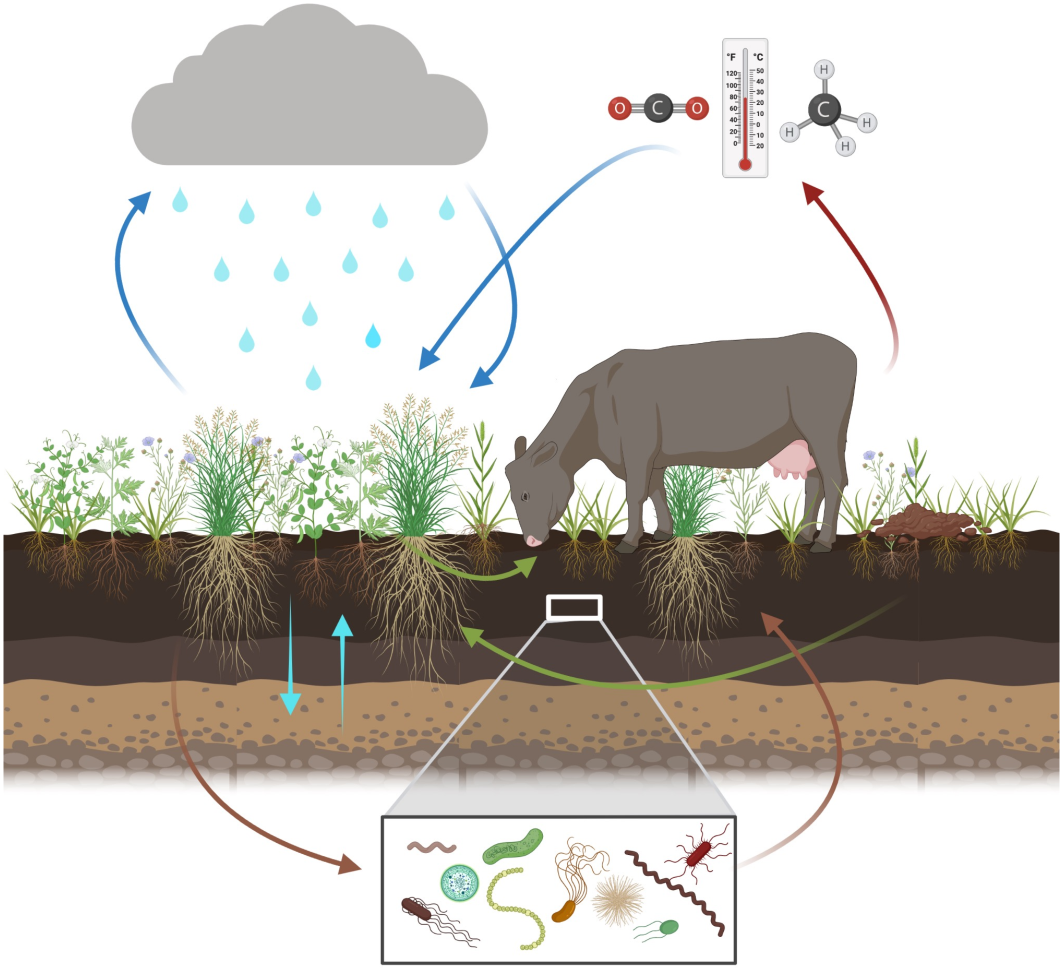

Fig. 1.2: **Ecological health depends on the balance in interactions between organisms and environmental factors.** This diagram centers plants as foundational taxa and shows some of the direct and indirect interactions between plants and abiotic and biotic factors in active rangeland. Green arrows show interactions between plants and grazers, specifically livestock. Brown arrows show interactions between plants and soil microorganisms. Turquoise arrows show interactions between plants and groundwater. Blue and red arrows show interactions between plants and climate, indicating cooling and heating effects, respectively. The main text describes these interactions in detail. *Created with BioRender.com.*

Fig. 1.3: **Visually different communities occur on north- versus south-facing slopes in the Bear River Range in northeast Utah.** Confer forest covers north-facing slopes (on left) while mostly sagebrush steppe and juniper woodland cover south-facing slopes (on right). Riparian vegetation grows along the Right Hand Fork of the Logan River in the center of the photo. Photo taken by the author.

CHAPTER 2

FRACTAL TRIADS EFFICIENTLY SAMPLE ECOLOGICAL DIVERSITY AND PROCESSES ACROSS SPATIAL SCALES

This is the accepted version of the following article: Simpson, E. G., Pearse, W. D. (2021). Fractal triads efficiently sample ecological diversity and processes across spatial scales. *Oikos, 130*(12), 2136-2147., which has been published in final form at https://doi.org/10.1111/oik.08272.

Abstract

The relative influence of ecological assembly processes, such as environmental filtering, competition and dispersal, vary across spatial scales. Changes in phylogenetic and taxonomic diversity across environments provide insight into these processes, however, it is challenging to assess the effect of spatial scale on these metrics. Here, we outline a nested sampling design that fractally spaces sampling locations to concentrate statistical power across spatial scales in a study area. We test this design in northeast Utah, at a study site with distinct vegetation types (including sagebrush steppe and mixed conifer forest), that vary across environmental gradients. We demonstrate the power of this design to detect changes in community phylogenetic diversity across environmental gradients and assess the spatial scale at which the sampling design captures the most variation in empirical data. We find clear evidence of broad-scale changes in multiple features of phylogenetic and taxonomic diversity across aspect. At finer scales, we find additional variation in phylodiversity, highlighting the power of our fractal sampling design to efficiently detect patterns across multiple spatial scales. Thus, our fractal sampling design and analysis effectively identify important environmental gradients and spatial scales that drive community phylogenetic structure. We discuss the insights this gives us into the ecological assembly processes that differentiate plant communities found in northeast Utah.

2.1 Introduction

In ecology, well-designed studies carefully consider how to sample patterns that result from complex, interacting ecological processes. These assembly processes, such as environmental filtering (Kraft et al., 2015), competition (Mayfield & Levine, 2010), dispersal (Vellend, 2010) and facilitation (Valiente-Banuet & Verdú, 2007), shape the diversity and structure of assemblages and operate at and across spatial scales. For example, density-dependent biotic interactions tend to occur at local scales; environmental filtering often constrains species at community scales; and biogeographic processes define the source pool at regional to continental scales (Cavender-Bares et al., 2009; Weiher et al., 1998). Many processes, such as dispersal, explicitly operate across multiple spatial scales (Chave, 2013). When researchers quantify biodiversity patterns to understand these processes, they must choose a sampling design and analyses that account for the effect of spatial scale on these metrics. This study demonstrates how a spatially explicit and flexible sampling design can effectively sample diversity–environment relationships and provide insight into how spatial scale may affect those relationships.

Both the spatial grain, or sampled resolution, and the spatial extent, or total study area, of a sampling design affect observed biodiversity (Levin, 1992; Rahbek, 2005; Wiens, 1989). For richness metrics, a larger spatial grain and extent increases (and eventually saturates) the number of species captured by that study (Adler et al., 2005; Crawley & Harral, 2001; Fridley et al., 2005). For phylogenetic structure metrics, increasing spatial extent results in a larger source pool and more phylogenetically clustered assemblages (where co-occurring species are more related than expected by chance; Cavender-Bares et al., 2006; Swenson et al., 2006). Increasing a study's spatial grain has a similar effect—assemblages shift from being overdispersed (containing species less related to one-another than expected by chance) to being clustered or phylogenetically random (Swenson et al., 2007). While these are general, and not universal, patterns, it is uncontroversial to state that a study's spatial grain and extent affect observed diversity (Cavender-Bares et al., 2009; Pearse et al., 2013; Vamosi et al., 2009). However, it is often challenging to know the spatial scales that influence a system's diversity patterns a priori, and thereby select an appropriate grain and extent to best measure ecological processes of interest (Jackson & Fahrig, 2015; Wheatley & Johnson, 2009).

Fractal sampling designs provide a potential solution to the problem of knowing the appropriate spatial extent at which to measure biodiversity by spacing samples at locations that are self-similar across smaller and larger spatial scales (Ewers et al., 2011; Marsh & Ewers, 2013). For example, in a recent simulation study to test the efficacy of these designs, Marsh and Ewers (2013) arrange sampling points in equilateral triangles. They sample at smaller spatial scales by adding three points in an equilateral triangle with side lengths $1/3$ the length of the current distance between points, centered on each sampling point. These types of designs capture information more efficiently than grid or transect designs (Kallimanis et al., 2002) for a comparatively smaller time, effort and financial input per sampling location than many other sampling strategies (Albert et al., 2010; Halley et al., 2004; Luzuriaga et al., 2012). Additionally, fractal designs do not need to be oriented across a linear environmental gradient already known to affect diversity, making them useful for exploratory work in landscapes, like mountains, with multi-directional environmental gradients (Marsh & Ewers, 2013).

Despite strong potential, we do not know of any studies that empirically test the effectiveness of fractal sampling designs to detect α-diversity and structure across environment and spatial scale. We outline, in Figure 2.1, a equilateral-triangle-based fractal sampling design, whereby we add two new points, not three, to nest triangles within each other (*cf.* Marsh & Ewers, 2013). This allows us to intensify or expand the design as needed, to assess questions at different spatial extents, without the need to abandon plots as sampling is intensified or expanded to build up a long-time series of data. We demonstrate and test the effectiveness of this design via three avenues. First, we show how our fractal design concentrates statistical power across spatial scales, compared to a distribution of random sampling designs with the same number of points. Then, we simulate two sets of periodically-variable diversity-environment landscapes to assess how well four sampling designs—fractal, random, grid and transects—capture these relationships. Finally, we use our fractal sampling design to assess changes in plant assemblage diversity and structure, and inferred ecological processes, across aspect, slope and elevation in northeastern Utah.

For the empirical component, we chose five biodiversity and structure metrics to explore how a variety of commonly used metrics can be sampled, and change across a landscape. How researchers measure and summarize biodiversity affects their conclusions about what diversity is present, how that diversity arose and what processes shaped and are shaping that diversity (Purvis & Hector, 2000). We aim to rapidly quantify assemblage composition and structure, consider the imprint of evolutionary history in local contexts (Tucker et al., 2017), and to use phylodiversity as a proxy for functional traits whose data we lack (but see Swenson, 2013). First, we use species richness as a quick, simple way assess how many species are present in different conditions (Paillet et al., 2010; Sluis, 2002). We chose Faith's phylogenetic diversity (PD) to build on species richness by adding information about the evolutionary history of species (Faith, 1992). We also surveyed species' abundance, to quantify the evenness, or relative abundances of these species, via a metric that accounts for richness and evenness in tandem (*e.g.* Simpson's diversity; Simpson, 1949). We use phylogenetic structure metrics, standard effect sizes of mean nearest taxon distance (SES_{MNTD}) and mean pair- wise distance (SES_{MPD}) to contrast the species within a local assemblage to those in the source pool of species that the local assemblage putatively assembled from (Kembel, 2009; Webb, 2000). This provides insight into the interaction between locally co-occurring species and the source pool that evolved at a larger spatial scale (Gerhold et al., 2015). Additionally, these structure metrics can provide some, albeit imperfect, insight into the processes, like environmental filtering and competition, that assemble communities (Cavender-Bares et al., 2009; Mayfield & Levine, 2010; Mouquet et al., 2012; Webb et al., 2002). We intend to avoid making overextended claims about assembly processes based on the patterns we observe (Mayfield & Levine, 2010).

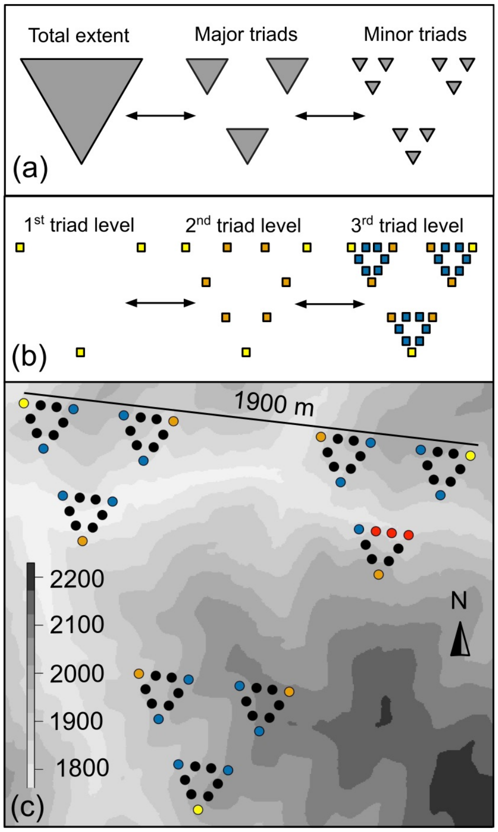

Fig. 2.1: **Our fractal sampling design places vegetation survey plots at the vertices of nested equilateral triangles to assess diversity–environment relationships across spatial scales.** (a) To build this design, we nested equilateral triangles inward from the total extent of the study, at 1/3 the distance of the total extent to make major triad groups. Then, we nested equilateral triangles inward from the major triads, at 1/3 the distance of the major triad group, to make minor triad groups. This process could be repeated to add additional triad groups at smaller spatial scales. (b) We sequentially placed sampling plots at the vertices of the equilateral triangles. First, we placed three initial plots (yellow), at the vertices of the total extent make the 1st triad level. Then, we added two additional plots at the vertices of the major triads, that did not have plots at them already. These new plots (orange) are nested within the 1st triad level, and thus only two additional sites are needed because none of the outer site positions need be moved (*cf.* Marsh & Ewers, 2013). All 9 plots at the vertices of the major triads make up the 2nd triad level. Analogously, we established the 3rd triad level (blue) within the 2nd triad level, and the 4th triad level within the 3rd triad level [black, shown in (c)]. (c) We applied this fractal sampling design at Right Hand Fork. We established and surveyed an initial set of three triad levels of plots in summer 2017 and re-surveyed them in 2018 [colors match the triad levels in (b)]. To assess whether we had sampled at a fine enough spatial scale to capture changes in diversity across environment, we added and surveyed a 4th triad level during summer 2018 (black). The nested nature of our design allowed us to add these plots within the sampling arrangement, allowing us to continue monitoring the 3rd triad level sites. Distance between plots in the 1st, 2nd, 3rd and 4th triad levels are 1990, 663, 221 and 74 m respectively [*i.e.* as in (a), each triad is nested in third]. Due to safety concerns, we did not (re-)survey some plots in 2018 (red). Background grayscale shows elevation based on five-meter digital elevation model (Utah Automated Geographic Reference Center, 2007).

In terms of environmental gradients, we focus on aspect, which can interact with elevation, because it often drives shifts in plant assemblage diversity in mountainous environments in the Northern Hemisphere (Cantlon, 1953; Fridley, 2009; Olivero & Hix, 1998). These shifts often occur in tandem with changes in soil nutrient and microbial properties (Gilliam et al., 2014) and can result in differences in productivity between north and south-facing plant communities (Gong et al., 2008). Additionally, these effects can be mechanistically explained by interactions, such as the amount of winter light and the heat load that understory evergreen shrubs experience in summer (Warren, 2008). When assemblages and their attributes do not change across aspect, despite changes in environmental conditions, this can indicate the dominance of human disturbance via traditional land use (Måren et al., 2015).

We hypothesize that our design's multi-directionality will efficiently detect changes in plant community diversity and structure across these environmental gradients. We leverage the spatially explicit layout of our fractal design to couple this diversity–environment assessment with a variance components analysis that pinpoints the spatial scale(s), or extent(s) at which each assemblage metric varies most. Via theoretical and empirical methods we demonstrate and test the efficacy of a fractally-nested design to efficiently detect changes in diversity and structure across environmental gradients, especially in periodic environments with self-similarity across spatial scales.

2.2 Material and Methods

We aimed to theoretically demonstrate and empirically test the ability of nested fractal sampling to quantify how diversity and phylogenetic structure vary across environment and at what spatial scale that variation drives differences between assemblages. Below, we outline our approach to address each of these aims in turn. First, we demonstrated how a fractal sampling design provides more statistical power across spatial scales than random sampling. Additionally, we simulated two sets of periodically-variable diversity–environment landscapes to assess how well fractal designs capture the true relationships between diversity and environment compared to other classic sampling designs. Then, we assessed whether diversity metrics vary across elevation and aspect by surveying vascular plant assemblages using this sampling design in the field. We model these relationships at the 4th, 3rd and 2nd triad level within our sampling design (Figure 2.1b–c) to determine the spatial scale or sampling intensity needed to detect these relationships. Finally, we assessed whether spatial scale influences these metrics, by partitioning the variance associated with calculating that metric across the spatial scales in our fractal design. All software packages referenced below are for R (<www.r-project.org>), and all data collected and code to reproduce analyses are openly released (Simpson & Pearse, 2021a, 2021b).

2.2.1 Study site, description and survey methods

Our field site, located along the Right Hand Fork of the Logan River in Cache National Forest, UT (41°46'12"N, 111°35'30"W), contains a variety of potentially interacting environmental gradients (Figure 2.1). The elevation spans 1719—2106 m.a.s.l. from riparian to ridge-line habitat. Numerous cliffs, rocks and up to 54°slopes add fine-scale variation across the site. Overall vegetation types visually reflect aspect direction; sagebrush steppe on south-facing slopes and conifer forest on north-facing slopes (Lowry et al., 2007). Local land-use includes recreation along two trails that cross the site and permitted livestock grazing in about half of the plots (USDA Forest Service, 2018). We determined sampling location coordinates a priori at our site using a fractal sampling design (Figure 2.1) and navigated to these locations using a GPS, accurate to within 10 m.

At each 1-m^2 plot we comprehensively surveyed each vascular plant species' percent canopy cover by dividing each plot into four quadrants and using a 0.25-m^2 10 x 10 grid with 0.025-m^2 grid cells to standardize cover estimates. Plants were identified using local herbarium resources, identification experts, and field guides. During June–August 2017, we established and surveyed 27 plots in three triad levels at 1990, 663 and 221 m apart. During June–October 2018, we added an additional 54 plots in a 4th triad level at 74 m apart (81 plots total). Due to safety concerns (the sites were on or close to cliffs) we only surveyed 78 of these plots in 2018. At each plot we measured topographic variables that are known to indirectly affect numerous ecological processes. Aspect affects the amount of sunlight plants receive as well as winter snow-cover, soil water retention and soil temperature. This impacts the water and light resources available to plants, key factors in determining ecological processes like environmental filtering and competition. We measured aspect in degrees using a compass and converted it to a north–south gradient using a cosine function. Slope can also impact insolation via shading and steeper slopes are more likely to erode and cause disturbance. We measured slope in degrees uphill and downhill from each plot using a clinometer and averaged these values. Finally, we also measured elevation, in meters, using the altimeter in a GPS, because temperature and moisture gradients across elevation can and often do affect plant communities. At our fieldsite, we expect plant community and structure to vary primarily across aspect and secondarily across elevation and slope. We report here results from the 2018 survey, but release the surveys, sampling locations and meta-data for both the 2017 and 2018 surveys along with replicated analysis for the 2017 data (Simpson & Pearse, 2021a, 2021b). All trends are qualitatively identical between the two surveys (Appendix A).

2.2.2 Overview of our nested fractal sampling design

We outline our sampling design here, and in Figure 2.1. First, we placed three sampling locations at the vertices of an equilateral triangle whose side length spanned the total spatial extent of the study area (Figure 2.1a, c, 1990 m) to make the 1st triad level (Figure 2.1b). From each of the points, we added two additional sampling locations inward at the vertices of three new equilateral triangles whose sides were 1/3 the length of the total extent, to make the 2nd triad level. We continued to nest sampling locations inward to add a 3rd and (in 2018) a 4th triad level. We show the full sampling design, with four triad levels in Figure 2.1c. By only adding two sites as each triad level (spatial scale), instead of three (*cf.* Marsh & Ewers, 2013), where each successive triad is centered at what would be the higher level's site), we saved 31 plots for the 2nd triad level, 32 plots for the 3rd triad level, and thus when we added a 4th triad level (in 2018) to our existing field system we saved 27 plots. The improved the efficiency of our fractal sampling design gave us temporal continuity in sampling locations as we investigated a finer spatial extents in our study area.

The spatial arrangement of a sampling design affects its statistical power at different spatial scales and ability to accurately detect information. Marsh and Ewers (2013) formally demonstrated the statistical power of fractal, and other sampling designs, to capture environmental gradients of an unknown direction. To do this, they compared the bearing between each pair of sampling points in a design to the distance between those points. They showed that a full fractal design, similar to the one we present, as well as regular grid and random designs all have consistent ability to capture multi-directional environmental gradients across spatial scales, while transects do poorly unless oriented directly across a known gradient. We distilled their analysis to focus on how our fractal design concentrates statistical power across spatial scales compared to a random sampling design, specifically, the number of pairwise comparisons at each distance between sampling points. In Figure 2.2, we compare the pairwise distances among plots for fractal designs (in red and blue) with a distribution of randomly-placed designs (n = 1000, in gray). Fractal designs concentrate pairwise distances (or comparisons) of plots at specific spatial scales (in red, Figure 2.2), sacrificing comparability (and so statistical power) at some distances (in blue, Figure 2.2). This maximizes information content across all the spatial scales within the study's spatial extent. Conversely, random sampling designs diffusely compare sites across spatial scales, concentrating information at the median spatial distance within the study's spatial extent.

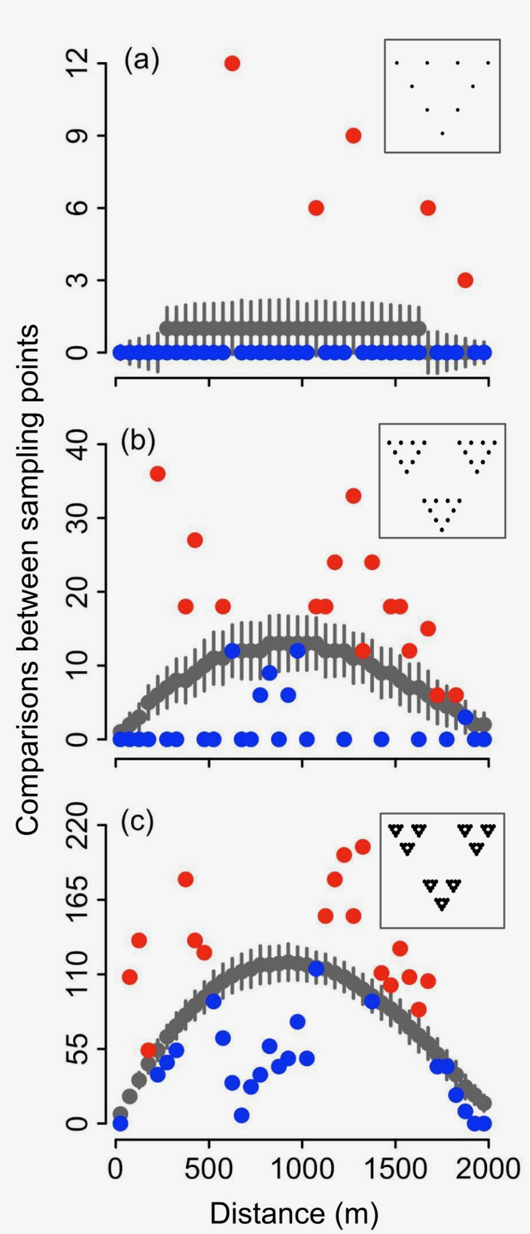

Fig. 2.2: **Our fractal sampling design concentrates statistical power across spatial scales (red dots) compared to random sampling designs with the same number of sampling locations (gray dots).** (a) 2nd triad, 9 plot, (b) 3rd triad, 27 plot and (c) 4th triad, 81 plot fractal sampling designs, built as described in Figure 2.1, all show the number of comparisons possible across a maximum sampling distance of 1900 m for a fractal sampling design (red and blue dots) compared to the distribution of comparisons possible for 1000 randomly chosen sampling locations (gray dots, 95% confidence intervals shown as bars). Points in red demonstrate where there are more comparisons for a given distance class than the random sampling design distribution; (a) 5/9 plots, (b) 13/27 plots and (c) 20/81 plots. Conversely, points in blue demonstrate fewer comparisons for a given distance class than the distribution of random sampling locations. The layout of the fractal sampling points is embedded in the upper right corner of each plot.

We also simulated how well our fractal design captured changes in α-diversity across environment in two sets of landscapes: a mountainous landscape, with multidirectional periodic variation similar to that found at Right Hand Fork, and a linear, periodic landscape, with a uni-directional gradient containing periodic variation (Appendix B). We compared our fractal design with random, grid and transect designs with the same number of points. In all of these simulations, which we present in Appendix B, our fractal-based design better captures the true relationship between diversity and environment. We emphasize that we do not claim that fractals are always the correct choice for any given ecological question or landscape, but we suggest that they are appropriate when attempting to capture unknown variation across variable landscapes. Our simulations did not assess how fractal schemes partition diversity across multiple spatial scales, since they have already been shown to do this effectively by Marsh and Ewers (2013).

2.2.3 Diversity and structure across environment and spatial scale

We represent the α-level diversity and structure of the plant assemblage at each plot using five classic and commonly used diversity metrics that quantify different facets of biodiversity—species richness, Simpson's diversity, Faith's PD, SES_{MPD} and SES_{MNTD}. Each of these five metrics provide different insights about biodiversity and the potential drivers of community assembly (Tucker et al., 2017). Two of our diversity metrics, species richness and Faith's PD (Faith, 1992), both capture the richness of diversity at each plot. We calculated a non-abundance weighted Faith's PD by adding the phylogenetic branch lengths of all species present in a community, including the root of the phylogeny, using pez::.pd (Kembel et al., 2010; Pearse et al., 2015). We expected this metric to correlate with species richness but also to show stronger trends across environmental gradients when the community composition across a gradient differs, because it accounts for relatedness among species and provides more information about a community composition. We also assessed a diversity metric that accounts for richness and evenness, Simpson's index of diversity (Simpson, 1949), to see if changes in abundance of the species affect diversity. We calculated Simpson's index of diversity using vegan::diversity, which subtracts the sum of the squared proportional abundance of each species in the community from one (Oksanen et al., 2019). This results in values from 0, which represents no diversity in terms of richness and evenness, to 1 which represents infinite diversity.

The two phylogenetic structure metrics we chose—SES_{MPD} and SES_{MNTD}—place the relative phylogenetic dispersion of each assemblage in the context of a wider source pool (Kembel, 2009; Webb, 2000). This provides context for how each sampled community may have assembled from the possible source pool, as opposed to drawing from a larger phylogeny which may include taxa that are not relevant to the sampled community. We determined the non-abundance weighted SES_{MPD} using pez::.ses.mpd which directly draws from picante::ses.mpd, to calculate the standard effect size of the mean pairwise distances of the observed community compared the mean pairwise distances in a randomized, null, community (n = 999; Kembel et al., 2010; Pearse et al., 2015). We repeated this process for SES_{MNTD} to assess the mean nearest taxon distance for each sampled community. Our focus on species' presence/absence (*i.e.* ignoring abundance information) makes our SES_{MPD} and SES_{MNTD} metrics more comparable with Faith's PD and species richness. For all phylogenetic metrics we used the phylogenetic tree generated from Zanne et al. (2014) using pez::congeneric.merge (Pearse et al., 2015).

We assessed whether each diversity metric changed across environment using an additive linear model of each metric across aspect, slope and elevation for all 78 plots. If a metric varied significantly across one of these environmental gradients (α-level = 0.05), we modeled and plotted just that metric and gradient (Figure 2.3). To test the ability of our design to detect changes in diversity– or structure–environment relationships at different spatial scales, we re-fit these models using only the 26 plots from the 3rd triad level and only the 9 plots from the 2nd triad level. Our goal was to identify the spatial scale(s), and sampling intensity, where our fractal-based sampling scheme effectively detected diversity responding to environmental gradients. If the 95% confidence intervals for diversity environment-relationships calculated at different triad levels fully overlapped, we considered the environmental response to be consistent at these different levels of sampling. Even if the slopes of these relationships differ, total overlap of the confidence intervals supports reduced sampling as effective for detecting the observed diversity–environment relationships. The flexible nature of our fractal design, allowed us to add points at a 4th triad level in 2018, to assess whether the diversity–environment relationships we observed in 2017 differed at the smaller, more intense sampling extent we added in 2018.

We assumed that there were no limitations on plant seed dispersal within a 1900 m spatial extent; therefore, we initially defined the source pool as the species sampled in all 78 plots. However, to investigate how source-pool definitions may affect the diversity–environment relationships we observe, we also used the triad groupings (Figure 2.1a), as different source-pool definitions, to calculate the phylogenetic dispersion of each assemblage. We compared the source pool defined by the total extent (which was used in the above analysis, shown in Figure 2.3) to source pools defined by the major and minor triad groupings. At a given triad level (each column in Figure 2.4), we compared how each diversity–environment relationship changes as we change the spatial scale of the source pool (each row in Figure 2.4) used to calculate the phylogenetic dispersion of each assemblage. We perform this analysis for both phylogenetic dispersion metrics (SES_{MNTD} and SES_{MPD}) that changed across environment (Figure 2.4, Appendix A). This tests whether responses to the environmental gradient are consistent across hierarchically-defined source pools. Then, to test whether the source-pool definition affects the overall values of the structure metric, we used a paired t-test to compare each metric calculated with the total extent source pool to one derived from the major triads, and from the major triads to the minor triads (Appendix A). This tests whether source-pool definition systematically affects our metrics of phylogenetic structure.

In an independent, but complementary, analysis we assessed whether our design captured different information at different spatial scales, using a variance components analysis to contrast how variance partitions across our nested triads. We calculated the amount of variation in each diversity metric attributable to a given triad grouping in our fractal design using variance components analysis following Crawley (2012). We fit a Bayesian linear hierarchical model with default priors using rstanarm (Goodrich et al., 2020), structured to sequentially partition the variance present in the modeled diversity metric from the largest-scale, major triad grouping (3 groups) through to the smallest-scale (intensified) triad grouping. We fit our model in a Bayesian rather than frequentist framework to avoid singular fits associated with fitting the largest triad grouping, which contains only three groups. To ensure that our Bayesian approach to estimating variance was robust, we compared our observed data to underlying data whose nested structure was randomly broken. Thus, in 999 bootstrap randomizations, we randomly permuted sites' locations and performed the same variance components analysis. We ranked our observed (real, unpermutted) data within these bootstrap randomization, significant at $\alpha = 0.05$, to statistically test whether each biodiversity metric showed an unexpected amount of variance at that spatial scale.

2.3 Results

We used our fractal sampling design to assess changes in biodiversity and phylogenetic structure metrics across environment and spatial scale. We sampled the most species (125) at the 4th triad level (78 plots) and found subsequently smaller numbers of species if we only looked at the points at the larger triad levels where less sampling locations, and therefore less sampled area led to lower total species numbers. We found 97 species at the 3rd triad level (26 plots) and 64 species at the 2nd triad level (9 plots). However, no matter which triad level we looked at, we surveyed a mean of 11 species/plot within a range of 5–21 species/plot. At both the 4th and 3rd triad level we found a mean Simpson's index of diversity of 0.71 with a range of 0.25–0.90 across all 78 plots. This range narrowed slightly at the second triad level, with a Simpson's index of diversity of 0.74 and a range of 0.37–0.89 across all 9 plots. Species richness and Simpson's diversity did not vary across any of the environmental gradients tested at any of the triad levels.

All phylodiversity metrics (PD, SES_{MPD}, and SES_{MNTD}) varied significantly across aspect, when sampled at the 4th four triad level (78 plots). SES_{MPD} also varied slightly across elevation (Figure 2.3, slope = 0.002). For SES_{MNTD}, sampling at the 2nd and 3rd triad levels (*i.e.* with 9 and 26 sites) would have been sufficient to detect these relationships in the 2018 survey (Figure 2.3, slopes equal 1.462 and 1.244 respectively, compared to 4th triad level where slope equals 1.184). Note that we deem the 2nd and 3rd triad levels sufficient because the 95% confidence intervals for these diversity–environment relationships overlap with that of the 4th triad level. Similarly, the 3rd triad level would have been adequate to detect changes in SES_{MPD} (slope equals 0.357, compared to a slope of 0.284 at the 4th triad level) and Faith's PD (slope equals 274.517, compared to a slope of 277.865 at 4th triad level) for the 2018 survey as well.

Different source-pool definitions did not substantially affect these patterns (Figure 2.4). We found similar trends in the 2017 data, detecting changes in SES_{MNTD} and Faith's PD across aspect at the 3rd triad level (Appendix A). Changing the source-pool definitions did affect the overall mean of SES_{MNTD}, but not SES_{MPD}. Overall, SES_{MNTD} was more overdispersed in the context of narrower source pools (total extent versus the major triads: mean difference = 0.215, SE = 0.034, paired t_{77} = 6.258, p-value < 0.001; major triads versus minor triads: mean difference = 0.282, SE = 0.049, paired t_{77} = 5.758, p-value $<$ 0.001). SES_{MPD} showed no such pattern (all $p > 0.05$). More details are given in Appendix A.

For each diversity metric, we used a variance components analysis to assess the variance associated with each spatial scale in our fractal sampling design, independent of how that metric does or does not change across spatial scale (Figure 2.5). Species richness and Faith's PD significantly associated with the largest, major triad grouping, accounting for 75% and 84% of the variance in each of these metrics, respectively. Additionally, Faith's PD significantly associated with variance in both other triad groupings, 2% and 11% of the variance at the minor and intensified levels respectively. In a similar pattern, species richness associated with 6% of the variance at the intensified, or smallest, triad level. Both SES_{MNTD} and SES_{MPD} picked up larger amounts of variance across spatial scales. They accounted for 27% and 34% of variance (SES_{MNTD}) and 16% and 16% of variance (SES_{MPD}) at the minor and intensified triad levels, respectively. Simpson's index of diversity did not

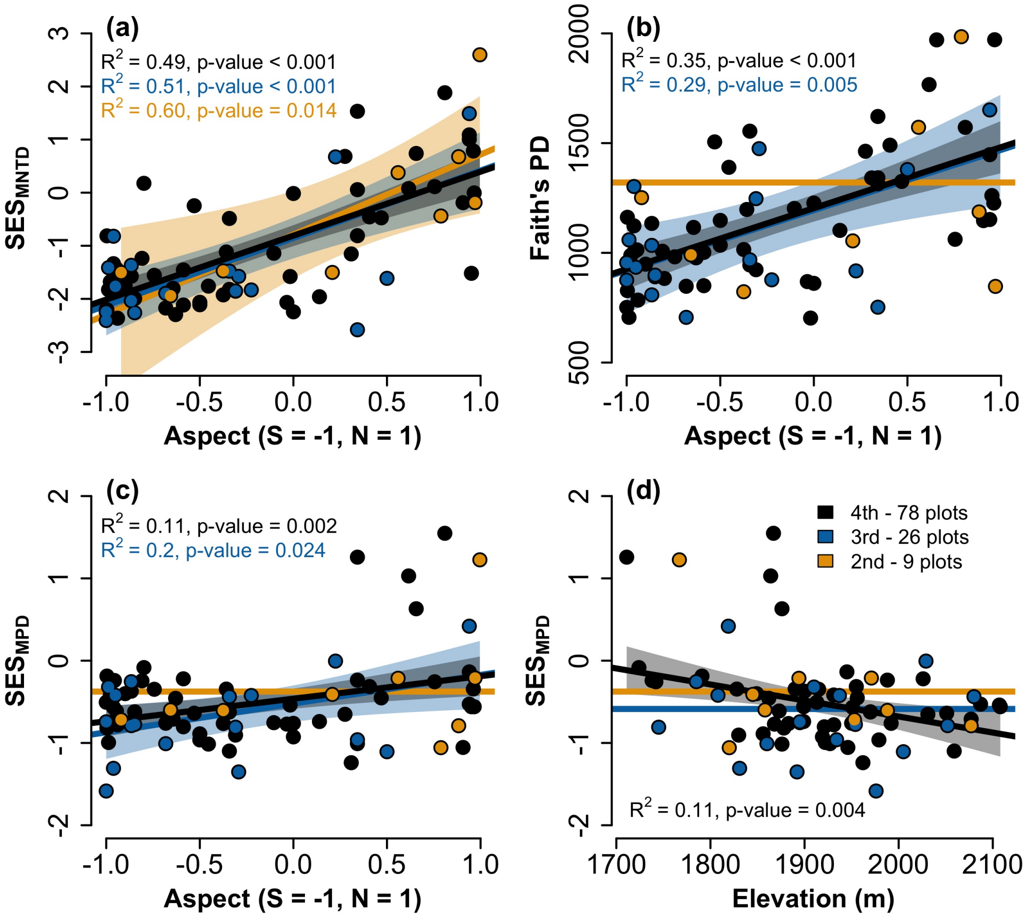

Fig. 2.3: **Phylogenetic diversity changes across environmental gradients at multiple spatial scales within our fractal sampling design.** (a) SES_{MNTD}, (b) Faith's PD and (c) SES_{MPD} were greater on more northern aspects, and (d) SES_{MPD} decreased as elevation increased. While models of diversity across environment were tested for all triad levels (Figure 2.1b) only significant models are plotted (with 95% confidence intervals). We detected a change in SES_{MNTD} across aspect at the 4th, 3rd and 2nd triad levels and a change in SES_{MPD} across aspect at the 4th and 3rd triad levels. While changes in Faith's PD across aspect and SES_{MPD} across elevation were detectable only at the finest sampling of the fourth triad level, SES_{MNTD} was more sensitive and thus able to detect changes with less sampling. Points are color-coded based on their triad level and match colors in Figure 2.1; black is the 4th level with 78 surveyed locations, blue is the 3rd level with 26 surveyed locations and orange is the 2nd level with 9 surveyed locations.

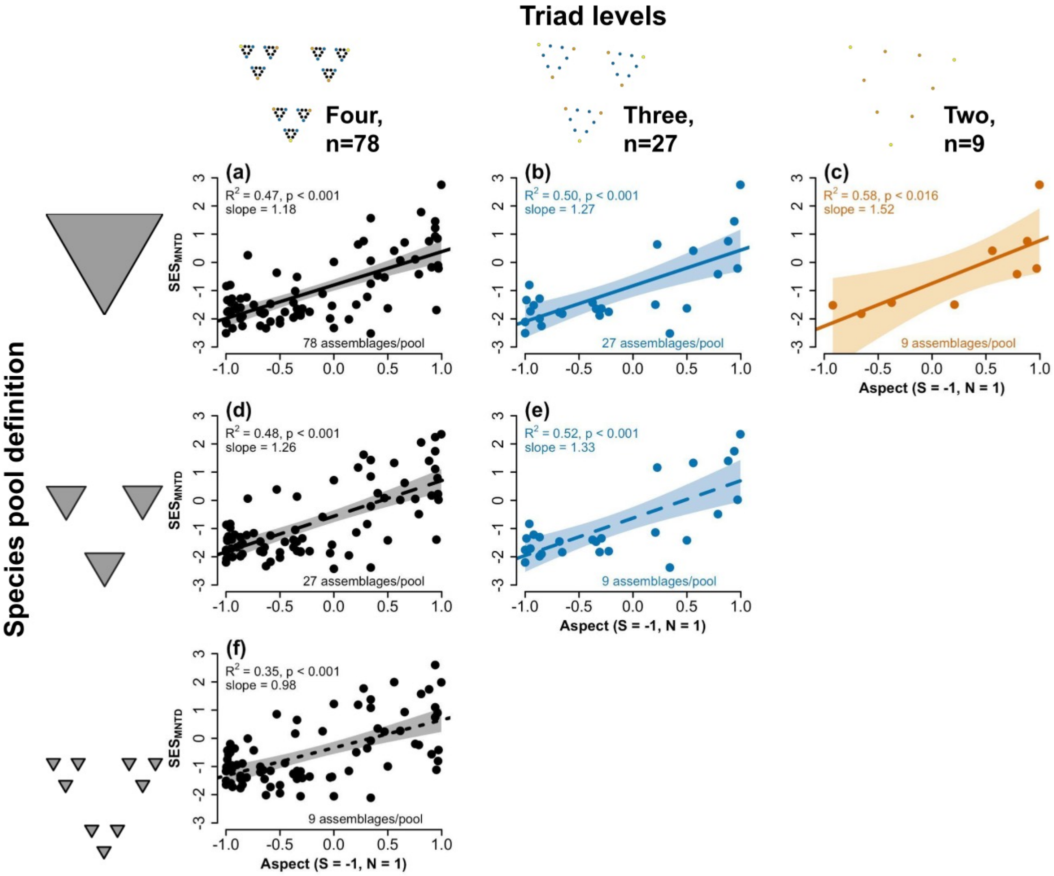

Fig. 2.4: **Changes in the source-pool definition do not affect the overall phylogenetic structure–environment relationships we detected, which indicates that environmental filtering plays a strong role in shaping assemblages at Right Hand Fork.** Our design allowed us to easily test the effect of source-pool size on the diversity–environment relationships we detected. Here we show how SES_{MNTD} changes across aspect, depending on triad level and source-pool definition. Even when the source pool for a given plot is limited to the major (d–e) or minor (f) triad grouping, this does not strongly change the trend we observed when using the total extent of plots as the source pool (a–c). (a–c) show the same analysis as Figure 2.3a, expanded to show how the number of assemblages per source pool decreases from the 4th to 3rd triad level. Colors match Figure 2.1 and 2.3. We include the same analysis for SES_{MPD} across aspect and across elevation in Appendix A.

associate variance with any of the triad levels (Appendix A).

2.4 Discussion

Our fractal sampling design captured empirical changes in multiple plant biodiversity and phylogenetic structure metrics across different environmental gradients and spatial scales. Among the diversity metrics we calculated, Faith's PD, which sums the evolutionary history of species in a community, significantly changed across aspect (Figure 2.3) and accounted for the most information about plant communities, at the largest spatial scale (Figure 2.5). Conversely, SES_{MNTD}, a phylogenetic structure metric that focuses on more recent evolutionary history, and also varied across aspect (Figure 2.3), detected the most information about how assemblages change at smaller spatial scales (Figure 2.5).

A key advantage of our fractal design is that it can be intensified or expanded to investigate additional spatial scales. When we initially sampled each plant community in 2017 (3rd triad level, 27 plots), we also detected trends in Faith's PD and SES_{MNTD} across aspect (Appendix A). However, we did not detect significant differences in the amount of observed variation across spatial scales compared to our null expectations (Appendix A). This motivated us to add a 4th triad level, or spatial scale, when we sampled in 2018 (and whose data we focus on here) to further investigate whether we captured the spatial scales influencing these metrics. Below, we further discuss how this design provides a practical and effective way to assess how diversity, structure and inferred ecological processes change across environment and space.

2.4.1 Abiotic conditions dominate broad-scale assembly

We predominantly detected changes in diversity and structure across aspect. We show shifts from lower PD, phylogenetically clustered assemblages (containing closely related species) on south-facing slopes (negative SES_{MNTD} and SES_{MPD}; Figure 2.3) to higher PD, more distantly related assemblages on north-facing slopes (near-zero to positive SES_{MNTD} and SES_{MPD}; Figure 2.3). Studies of species diversity across aspect find that communities on south-facing slopes tend to contain fewer species than north-facing

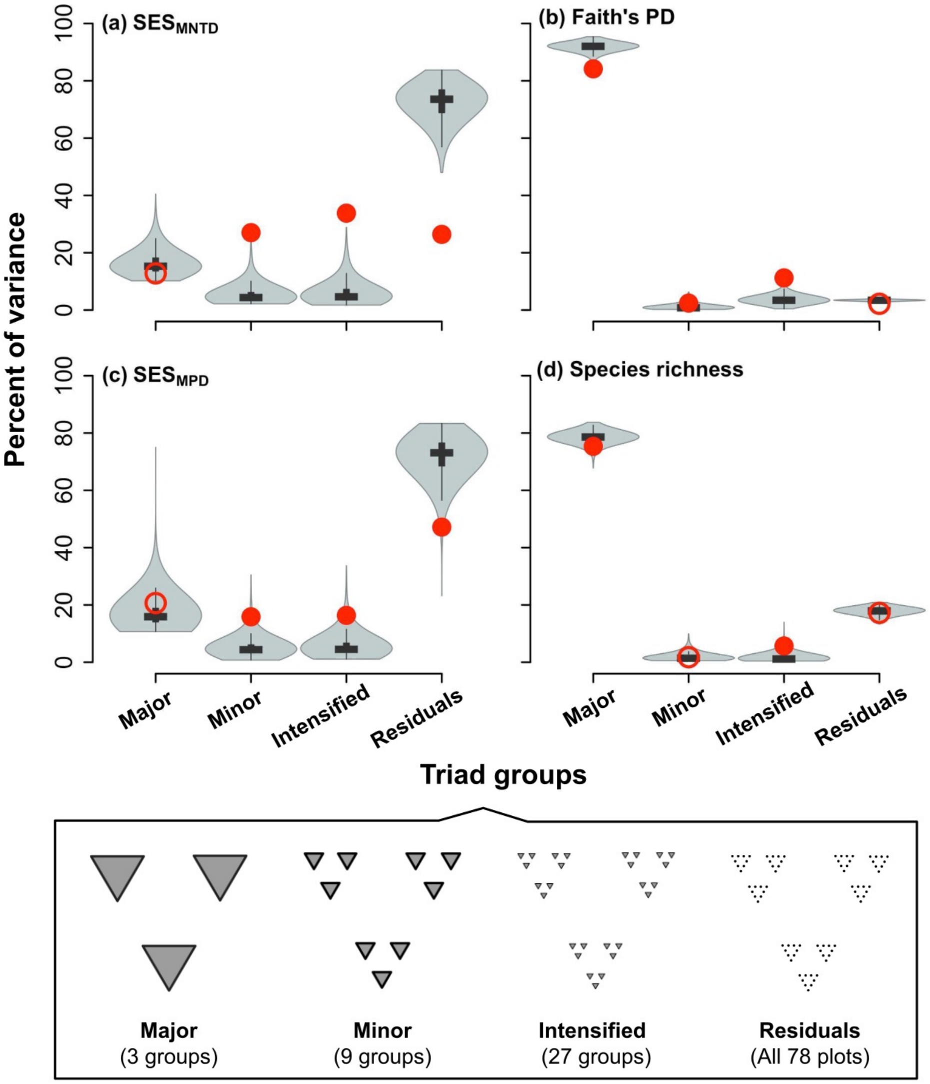

Fig. 2.5: **Decomposing the variance in each diversity metric across the triad groupings (Figure 2.1a) allows us to pinpoint the spatial scales most strongly affecting those metrics.** For each diversity metric, (a) SES_{MNTD}, (b) Faith's PD, (c) SES_{MPD}, (d) species richness, the red dots show the percent of variance captured by each successive spatial scale in our fractal sampling design, calculated using a variance components analysis. Randomized diversity values for each triad level (999 iterations) shown as gray violin plots. Filled red circles indicate percent of variance values that are significantly different from the randomized diversity variance at each triad level (violin plots). These spatial scales directly account for a portion of the variance in each of these diversity metrics. p-values for calculated percentages of variance that are significantly different from the random distribution of potential variation captured by each triad level: SES_{MNTD} (2nd = 0.002, 3rd < 0.001, 4th = 0.001, Faith's PD (1st = 0.001, 2nd = 0.048, 3rd < 0.001), SES_{MPD} (2nd = 0.010, 3rd = 0.021, 4th = 0.004), and species richness (1st = 0.026, 3rd = 0.011).

slopes (Cantlon, 1953; Fridley, 2009; Olivero & Hix, 1998), while we found no difference in the number of species on opposing slopes. However, they also find that south-facing assemblages tend to have more consistently similar species compositions, compared to north-facing assemblages. Many eco-phylogenetic studies use prior knowledge about their system to generate specific hypotheses about why they would observe phylogenetic clustering as a result of environmental filtering; for example, in rainforest trees (Webb, 2000) and freshwater fish (Helmus et al., 2007). However, these studies also recognize the contribution of biotic interactions, like competition and facilitation, to these patterns.

We propose that lack of water likely limits what species can grow and persist at Right Hand Fork, especially on south-facing aspects. Experimental evidence demonstrates that water limitation dominates community assembly processes in semi-arid environments. In contrasting conditions of water availability, Luzuriaga et al. (2012) found a shift in biotic interactions, from competition between all plants present when water was limited to facilitation between perennials and annuals when water was abundant, in a Mediterranean climate in central Spain. In the Northern Hemisphere, greater sun exposure on south-facing slopes intensifies heat, plant tissue damage and reduces soil moisture (Lowry et al., 2007), which likely limits the number and type of species able to grow and persist (Keddy, 1992; Weiher et al., 1998). Conversely, north-facing slopes receive less sun exposure which results in cooler temperatures and better soil moisture retention—a more favorable set of growth conditions in an otherwise resource-limited environment (Moeslund et al., 2013). The trends we find in phylogenetic diversity and structure metrics align with these studies. Specifically, the metrics we calculate that account for species richness (SES_{MNTD} and SES_{MPD}) change across aspect and demonstrate that environment constrains phylogenetic diversity to clades whose members can tolerate these conditions. However, we recognize that it is difficult to differentiate between environmental filtering and competition in an empirical study and that competition can also lead to clustering in phylogenetic metrics which may be contributing to the patterns we observe (Mayfield & Levine, 2010).

Source-pool definitions can also affect observed clustering and overdispersion in phylogenetic structure metrics, like SES_{MNTD} and SES_{MPD}. For example, decreasing the spatial extent of the source pool often results in comparatively more overdispersed assemblages, where species are less related to one another than expected by chance (Cavender-Bares et al., 2006; Pearse et al., 2013; Swenson et al., 2006). Our fractal sampling design allowed us to investigate the potential effect of source-pool definition on both the overall values of phylogenetic dispersion metrics and on the phylodispersion–environment relationships we observed. Decreasing the source-pool size from the total extent, to the major triads, to the minor triads (Figure 2.1b) caused the overall values of SES_{MNTD} to become comparatively more overdispersed (but still clustered, Appendix A). Critically, even when the source pool is defined as the major triad group an assemblage is in, we detect a similar relationship between SES_{MNTD} and aspect (Figure 2.4). Additionally, defining the source pool as the minor triad group an assemblage is in weakens the relationship between SES_{MNTD} and aspect but does not fully dampen it. This is surprising because the source pool 'extent' for these dispersion metrics is $^1/_9$ of the total extent of the study, a much smaller spatial scale. Our ability to detect the same statistical response of diversity to environment strongly suggests that environmental filtering is driving diversity and assemblage structure across aspect and spatial scales.

We recognize that we have not experimentally quantified whether species presence or absence relies solely on abiotic conditions (as is necessary to prove environmental filtering; Kraft et al., 2015), but we do show that changes in environment map onto changes in ecological communities. By combining spatially explicit structure of our sampling design with a variance components analysis, we can precisely pinpoint the spatial scales at which environment is likely to be structuring community assembly. For Faith's PD and species richness, the total extent (1990 m), captured the most variance in these metrics (84% and 75% respectively). Surprisingly, these values account for significantly less variation than our null expectations, and we suggest this surprising result stems from two opposing forces. First, species richness (and so Faith's PD, which is often correlated with it; Tucker et al.,

2017) is likely driven by processes such as lineage diversification that operate across broader spatial scales than we measure here. We are currently extending the sampling of our fractal system further in an attempt to capture additional processes operating across ecological timescales. Second, while these metrics are less sensitive to finer-scale processes than our other metrics, they do still detect some pattern, thus reducing the variance explained at the broadest scale.

The similarity in variance partitioning patterns between Faith's PD and species richness shows that generally speaking, they represent similar information about communities in this system (Tucker & Cadotte, 2013). However, we were able to detect changes across environment with Faith's PD but not species richness. This, coupled with our fractal design's ability to capture slightly more variance in Faith's PD than species richness (9%), supports the use of phylogenetic diversity as a more predictable and informative metric about assemblage composition.

2.4.2 Small-scale biotic assembly

Operating within the context of broad spatial scale phylodiversity differences driven by aspect, we found evidence that local-scale biotic interactions likely also influence assemblages' phylogenetic structure. Both SES_{MPD} and SES_{MNTD} detected the most variation in assemblage structure at finer scales (SES_{MNTD}, 2nd and 3rd triad level, 27% and 34% respectively, SES_{MPD}, 2nd and 3rd triad level, 16% and 16% respectively; Figure 2.5). Since these metrics are calculated using a source pool of potential species, they account for broad-scale structure when assessing local context (Kembel, 2009; Webb et al., 2002), unlike our other metrics. We suggest this makes these metrics more sensitive to differentiation at and across local spatial scales, giving us a more nuanced picture of local assemblage variation. Perhaps most striking, SES_{MNTD} demonstrates strong spatial structure at the middle two scales (2nd and 3rd triad) in our sampling design, accounting for close to $^2/_3$ of the variance in this metric. We might expect SES_{MNTD} to show stronger trends than SES_{MPD} if we assume, as do many ecophylogenetic studies, that traits evolve in a manner consistent with Brownian motion. Under Brownian motion, close relatives' traits are both expected to be more similar, but also more reliably similar (Letten & Cornwell, 2015), perhaps making metrics that focus on those close-relative differences themselves more predictable. This insight, along with assumed phylogenetic conservatism, supports SES_{MNTD} as a strong structure metric to detect assemblage differences at and across the local spatial scales we assessed at Right Hand Fork.

2.4.3 Conclusion

We conclude that changes in phylogenetic diversity, structure and inferred ecological process across environment and spatial scale can be efficiently detected using a fractal design and variance components analysis. Phylogenetic diversity metrics gave us more information about assemblage composition than species richness or Simpson's diversity alone. Faith's PD accounted for broader patterns of species presence in response to overall environment, while and SES_{MNTD} and SES_{MPD} reflected how biotic interactions generate localized environmental heterogeneity. Our spatially explicit design allows systematic comparison of patterns and hypotheses at multiple spatial scales. An advantage of our fractal approach is that it is impartial with regard to any particular environmental gradient, and can be intensified and extended after establishment, which we leveraged to examine variation at a smaller spatial scale than initially sampled. This flexibility allows us to continue to investigate questions about the relationship between diversity and environment and the way spatial scale affects those relationships. For example, this sampling framework could be extended to study other drivers of community assemblage across a landscape such as soil temperature and texture. Systematic exploration of this system via a fractal sampling design will continue to allow us to investigate diversity and structure across scale and environment using this powerful and efficient sampling design.

CHAPTER 3

VARIATION IN NEAR-SURFACE SOIL TEMPERATURE DRIVES PLANT ASSEMBLAGE INSURANCE POTENTIAL

Abstract

Studying how assemblages vary across environmental gradients provides a baseline for how assemblages may respond to climate change. Per the biological insurance hypothesis, assemblages with more variation in functional diversity will maintain ecosystem functions when species are lost. In complement, environmental heterogeneity supports landscape-scale ecosystem functionality (*i.e.* spatial insurance), when that variation includes environments with more abundant resources. I use the relationship between vascular plant functional diversity and microenvironment to identify where assemblages are most likely to maintain functionality in a mountainous fieldsite in northeastern Utah, USA. I assessed how life history strategies and information about phylogenetic differences affect these diversity-environment relationships. I found less functionally dispersed assemblages, that were shorter and more resource-conservative on hotter, more variable, south-facing slopes. In contrast, I found more functionally dispersed assemblages, that were taller and more resource-acquisitive on cooler, less variable, north-facing slopes. Herbaceous and woody perennials drove these trends. Additionally, including information about phylogenetic differences in a dispersion metric indicated that phylogeny accounts for traits I did not measure. At the fieldsite, soil temperature acts as an environmental filter across aspect. If soil temperature increases and becomes more variable, the function of north- vs. south-facing assemblages may be at risk for contrasting reasons. On south-facing slopes, assemblages may not have the variance in functional diversity needed to respond to more intense, stressful conditions. Conversely, assemblages on north-facing slopes may not have the resource-conservative strategies needed to persist if temperatures become hotter and more variable. I

suggest that studying dispersal traits, especially of perennial species, will provide additional insight into whether this landscape will maintain function as climate changes.

3.1 Introduction

As Earth's climate warms and becomes more variable (IPCC, 2018), ecological assemblages face new environmental conditions that cause species loss. Biotic and abiotic factors influence whether species loss affects overall ecosystem functionality. The biological insurance hypothesis (Loreau et al., 2021; Yachi & Loreau, 1999) proposes that an assemblage with more variation in species' functional responses to environmental stressors better maintains ecological function, even if few species perform a given function (Elmqvist et al., 2003; Mori et al., 2013; Suding et al., 2008). In complement, environmental heterogeneity supports landscape-scale ecosystem functionality when patches with less stressful conditions and more abundant resources support species that would otherwise go locally extinct (Greiser et al., 2020; Maclean et al., 2015). Quantifying how functional diversity varies across environmental gradients identifies the environmental conditions where assemblages are best equipped to maintain functionality. These relationships provide a foundation for monitoring and management decisions that protect ecosystem functioning (Cardinale et al., 2012; Díaz et al., 2018).

Species' characteristics, interactions, and dispersal rates respond to resource gradients in a spatial context (Leibold et al., 2004). In line with this framework, functional traits reflect how plants acquire resources and affect the ecosystem around them (Lavorel & Garnier, 2002; Mason & De Bello, 2013; Reich, 2014; Suding et al., 2008). For example, the leaf economic spectrum describes how plants invest resources into their leaves (Díaz et al., 2016; Wright et al., 2004). In resource-poor, variable environments plants tend to invest resources into leaves that last longer and produce more photosynthate over longer timescales, a conservative strategy. In contrast, plants in resource-rich environments tend to invest fewer resources into leaves that will not last as long but produce more photosynthate in a shorter time span, an acquisitive strategy.

The mean and variance in functional diversity metrics calculated from functional traits provide complementary information about the current and future functionality of assemblages. Individual traits, summarized at the assemblage level as the community weighted mean (CWM) of that trait (Lavorel et al., 2008), represent the strategies plants most commonly use in an environment. The CWM of traits often shifts as the environment changes, as a result of phenotypic plasticity and/or species turnover. For example, as summer temperatures warmed in the Arctic, assemblages grew taller as a result of immigration by taller, but still local, species (Bjorkman et al., 2018). However, leaf traits only responded at wetter locations, where species invested fewer resources into leaves, potentially allocating those resources to higher growth rates. The variance in all measured functional traits (*e.g.* functional dispersion; Laliberté & Legendre, 2010) provides insight into the environmental conditions where species are relatively more or less likely to maintain function as conditions change in the future. For example, in high alpine meadows in Colorado, assemblages had more variance in plant functional strategies in response to an increase in spatially variable environmental conditions (Stark et al., 2017).

An assemblage well-equipped to maintain ecological function contains species with more variation in functional response traits (Díaz et al., 2013; Lavorel & Garnier, 2002). However, these traits must not be strongly correlated with the effect traits that provide ecosystem services (Díaz et al., 2013). For example, per this hypothesis, an assemblage with more variation in resource investment strategies (measured as response traits) will maintain more consistent productivity (measured by effect traits) in response to variation in water availability, as long as resource investment and productivity traits are not correlated. However, a global aggregation of local studies found that, broadly, plant assemblages contain less variation in functional traits than expected by chance (Bruelheide et al., 2018). This finding indicates a need to understand the environmental conditions where plant assemblages have more biological insurance potential locally.

While environmental changes (*e.g.*, increased moisture) may result in more resources for species, others (*e.g.*, increased temperature) may cause more stress that plants need to adapt to. I hypothesize that the mean and variance of plant traits summarized at the assemblage level will reflect current differences in resource availability and environmental stress. To test this hypothesis, I look at how the mean and variance in functional traits vary across microenvironment — near-surface soil temperature and soil texture — at a fieldsite in northeastern Utah (Figure 3.1). I identify which strategies plants most commonly use in different environments using the CWM of functional traits that provide insight into the tradeoff between resource abundance and environmental stress. In complement, I identify where assemblages will likely maintain function in the future by assessing the variance in all measured functional traits. Since life history strategies typically encompass similar functional strategies (Díaz et al., 2016), I test whether particular life history groups drive these diversity-environment relationships. If a life history group drives these diversity-environment relationships, this group may be a good candidate for continued monitoring and management. Finally, I assess whether including information about phylogenetic differences between species changes the relationship between function and microenvironment. Taken together, the results of this assessment guide management actions by determining where and how plant assemblages will be able to maintain functions and ecosystem services.

3.2 Materials & Methods

I assessed how the functional strategies and insurance potential of assemblages change across microenvironments at twenty-six 1-m^2 fractally-arranged vegetation plots in a long-term study site along the Right Hand Fork of the Logan River in Cache National Forest, UT (41°46'12"N, 111°35'30"W; Figure 3.1). At this site, the spatial arrangement of these plots and sampling intensity effectively captured environmental variation and responses across the landscape (Simpson & Pearse, 2021c). I assessed the relationship between plant functions and microenvironments in a spatial context, *i.e.* I do not intend to assess the direct temporal response of function to the environment. Additionally, I looked at whether information about life history strategies and phylogenetic differences changed the understanding of ecological differences I assessed from functional diversity. Data processing and analyses were performed in R (v. 4.2.1; R Core Team, 2022) and all software packages *in italics* below are R packages, unless otherwise noted. All data collected and code to reproduce analyses will be openly released.

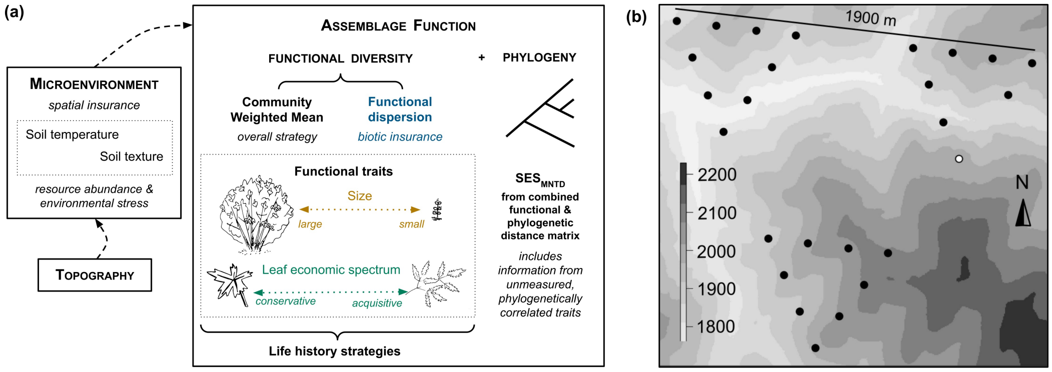

Fig. 3.1: **Assessing changes in functional diversity across microenvironment identifies where assemblages have the highest potential of maintaining function in response to changing conditions.** (a) Environmental heterogeneity, often driven by differences in topography, provides spatial insurance when microenvironments with more resources and/or less stressful conditions support species that would otherwise be lost as climate changes. Per the biological insurance hypothesis, assemblages with more variation in function (*e.g.* functional dispersion, Laliberté & Legendre, 2010) can better respond and maintain function as climate changes. The CWM of individual functional traits (Lavorel et al., 2008) provides insight into the overall functional strategy individuals in an assemblage utilize. Life history strategies potentially affect the relationships between these metrics and microenvironments. Additionally, SES_{MNTD}, calculated from the combined functional and phylogenetic distances between the most closely related pairs of species (Cadotte et al., 2013), shows whether phylogeny represents differences between species that were not accounted for in the traits I measured. Color coding of the functional metric text used throughout the figures. (b) I assessed these relationships at twenty-six 1-m^2 plots along the Right Hand Fork of the Logan River in northeast Utah (Simpson & Pearse, 2021c). One plot was excluded from the final analysis because the temperature sensor was removed by wildlife disturbance (in white). Background grayscale shows elevation based on a five-meter digital elevation model in meters (Utah Automated Geographic Reference Center, 2007).

3.2.1 Vegetation cover assessment & functional trait collection and processing

I measured the total canopy cover of vascular plant species in each 1-m^2 plot during June–July 2018. I included cover from species rooted outside of the plot because this best represents the total functionality of the assemblage for abundance-weighted functional diversity measures. To standardize cover assessment, I used a quadrat divided into four 0.25-m^2 quadrants and assessed percent cover with a 10 x 10 grid of 0.025-m^2 grid cells. I identified plants using local herbarium resources and field guides and standardized taxa names using The World Flora Online (<http://www.worldfloraonline.org/>).

I collected functional traits based on their representation of the two main axes of variation in aboveground plant traits at both the species (Díaz et al., 2016) and assemblage (Bruelheide et al., 2018) levels. Plant size (the mean and maximum height) and leaf traits [specific leaf area (SLA) and leaf area (LA)] quantify contrasting functional strategies a plant uses to access light and integrate resources, via competition or facilitation with neighboring individuals (Reich, 2014). I also chose these traits because they both respond to environmental conditions and affect ecosystem functions (Lavorel & Garnier, 2002). To focus on the functional consequences of potentially losing response diversity, I assumed that current variation in functional trait strategies across environment represents a unified functional strategy of response and effect traits, without directly measuring ecosystem function (Elmqvist et al., 2003; Reich, 2014; Suding et al., 2008). All functional trait data were taken in or near the twenty-six plots during June–July 2018 and June–July 2019 and were collected, processed, and analyzed following Perez-Harguindeguy et al. (2016). I focused on interspecific variation in all traits.

Height traits. Globally, plant height represents the overall strategy of how a species lives (*e.g.*, its lifespan), grows (*e.g.*, time to maturity), and reproduces (*e.g.*, seed mass and the number of seeds it produces; Díaz et al., 2016; Moles et al., 2009). In cold, dry places, like the overall climate at the fieldsite, a wide range of height strategies typically succeed compared to warm, wet environments, where tall species dominate. Because many of the species in the plots are graminoids and forbs, which can be very variable in height, I aimed to measure the height (cm) of up to twenty-five randomly selected individuals of each species within each 1-m^2 plot. If there were less than ten individuals in a plot, I continued measuring individuals from within ten meters of the plot. I measured from the ground to the top of the main photosynthetic tissue, not including inflorescences, seeds, or fruits if those extended beyond the tallest leaves. Drooping foliage was measured as-is to assess the general canopy height of the plant. Across all plots, for each species, I calculated one measure of average plant height and one measure of the maximum plant height achieved by that species. Calculating both height measures allowed us to look at an average measure of how height responds to environmental conditions across the site (mean height) compared to the maximum height that species achieved in all of the plots.

Leaf traits. I calculated the specific leaf area (SLA), the total fresh leaf area (LA; mm^2) divided by its oven-dry mass (g), to quantify the resource acquisition strategy of each species. I aimed to collect at least five leaves from five individuals for each species within twenty meters of each plot. I adjusted the number of leaves based on size; from three leaves for large-leaved species to twenty leaves for small-leaved species. I collected leaves from each individual randomly, and when possible, chose fully-developed sun leaves that were undamaged by herbivory or pathogens. I placed the leaves from each individual in a sealed, plastic bag, to retain their moisture, and kept them flat using cardboard that was tied together for transport back to the lab. The same day, I scanned the leaves with a high-resolution flatbed scanner. Then, I dried them at 70 °C for 72 hours and weighed them to determine their oven-dried leaf mass (g).

I used an automated, threshold-based pipeline (‘stalkless’ Pearse et al., 2018) to calculate the leaves’ surface areas (mm^2). This workflow relied on thresholding the contrast between dark and light pixels in an image to separate the leaves, or darker areas of the image, from the lighter background. As a baseline, I set the threshold to the mean intensity of each scan plus two times the standard deviation of each scan’s intensity. The program identified all regions of the scan greater than the threshold as leaves and calculated LA by counting the pixels in all of the regions larger than the mean region size plus two standard deviations as processed LA. I checked all of the processed images from the scans and adjusted the threshold to capture the correct shape of each leaf. To focus on interspecific variation in the leaf traits and avoid poor scans, I chose the best sample of leaves from a species, if multiple samples were collected. To choose the best sample, I prioritized fully-developed, undamaged leaves, followed by those collected in 2019 when I used a scanner that produced more precise images, and finally, all else equal, focused on samples taken from environments where the species was relatively abundant and the topography was most consistent with ’average’ topography at the site.

3.2.2 Quantifying microenvironment

Near-surface soil temperature. Local seasonal temperature variation directly affects both ecosystem and individual plant functions and relates to other important microclimate conditions, like the consistency of snow cover (Lembrechts et al., 2020). To measure near-surface soil temperature, I buried a HOBO 8K Pendant®Temperature/Alarm Data Logger (UA-001-08) in a ten-centimeter deep hole at each of the plots. I anchored the logger into the sides of the hole with metal landscaping pins attached to the logger with zip ties. Then, I covered the logger with soil and rocks, to match the surrounding landscape and protect the sensor from disturbance by wildlife. Each logger was set to record the temperature every 90 minutes and start logging at midnight the following day using HOBOware software (<https://www.onsetcomp.com/hoboware-free-download/>). I downloaded temperature data during September 2018 and September 2019 to get a full year of temperature data. One sensor was lost in 2018, because of substantial wildlife disturbance (it appeared to be pulled out by a grazer or dug up by a rodent, Figure 3.1, in white), resulting in temperature data at twenty-five plots. To summarize inter-annual temperature variables, I converted the temperature readings to °Celcius using *weathermetrics* (Anderson et al., 2013) and manipulated the date and time to be able to assess the first and last month and day temperature readings recorded at each plot using *lubridate* (Grolemund & Wickham, 2011) and *dplyr* (Wickham et al., 2021). Then, I subset the time frame to a year of temperature data, from September 28, 2017, at 00:00 (Mountain Standard Time, MST) to September 28, 2018, at 00:00 MST, and calculated the annual mean, maximum, minimum, and standard deviation in temperature at each plot.

Soil texture. I used the hydrometer method [following procedure and calculations in Ashworth et al. (2001), based on Bouyoucos (1927)] to assess soil texture from soil samples collected at the twenty-six core plots in mid-summer 2018. At the same position about half a meter from each plot, I removed the organic matter and collected soil from a ten-centimeter deep by eight-centimeter wide hole and transferred it back to the lab to be aired dried for further processing. I physically broke up the soil clumps so that particles would disperse by sieving the soils to two millimeters and further grinding them with a mortar and pestle. I chemically dispersed the soil using a 50 g/L sodium hexametaphosphate solution and finished dispersing the solution by inverting the cylinder several times. I took hydrometer measurements at forty seconds and two hours to determine the amount of sand, silt, and clay in each soil sample. Finally, I used the package *soiltexture* to classify these percentages into soil classes based on the USDA soil texture triangle (Moeys, 2018).

3.2.3 Statistical Analysis

I aimed to quantify how biological variation, as measured by functional diversity and phylogeny, relates to environmental heterogeneity, as measured by microenvironment (see the framework in Figure 3.1). First, I looked at whether differences in topography (aspect, elevation, and slope) predict differences in microenvironment (near-surface soil temperature and soil texture). Then, I assessed whether topography-predicted microenvironmental conditions predicted functional diversity — mean and variation. I analyzed whether these relationships differ depending on plant life history strategy, *i.e.* whether a plant is an annual/biennial, herbaceous perennial, or woody perennial because these groupings tend to have more similar traits, compared to all plant species. Finally, I incorporated information about ecological differences from both phylogenetic and functional differences to determine if phylogeny quantifies differences between species that were not represented by the traits I measured.

Microenvironment-topography relationships. I looked at how microenvironment varies across topography to quantify how near-surface soil temperature and soil texture spatially vary across the fieldsite. Since the analysis is based on twenty-five plots, I aimed to isolate relationships between one microenvironmental variable and one topographic variable to properly estimate coefficients. Soil texture can affect soil temperature (Akter et al., 2015), so I assessed whether each temperature variable correlated with the components of soil texture (percentage of sand, silt, and clay) by calculating the correlation coefficient, Pearson's r. Then, I looked at how each microenvironmental variable — the mean, standard deviation, maximum, and minimum temperature and amount of sand, silt, and clay —

correlated with three topographic variables — aspect, elevation, and slope, because drainage patterns can affect soil particle distribution (Brown et al., 2004).

Functional diversity-microenvironment relationships. I quantified the functional strategies in each assemblage using functional dispersion (FDis; Laliberté & Legendre, 2010) and the community weighted mean (CWM, Lavorel et al., 2008) of each of four traits — specific leaf area (SLA), leaf area (LA), mean height and maximum height. I calculated FDis, the mean distance of all species' traits to the weighted centroid of the assemblage in multivariate trait space, using *FD::dbFD* (Laliberté et al., 2014). I calculated the abundance-weighted version of this metric to assess how the prevalence of species contributes to that assemblage's potential to maintain function in the future. First, I generated a species-by-species distance matrix from (weighted) functional traits using the Gower (dis)similarity coefficient (Gower, 1971). Because of large differences in the units of the different traits I measured, I standardized each trait to have a mean of zero and a unit of variance. Then, I performed a principal coordinate analysis (PCoA) on this uncorrected species-species distance matrix to generate PCoA axes that were used as 'traits'; all four PCoA axes were maintained. To verify that the closely related leaf and height traits were not over-inflating FDis, I also calculated FDis with just two traits — maximum height and SLA. Again, I used *FD::dbFD* to calculate the abundance-weighted CWM of the four traits for each assemblage (Lavorel et al., 2008). This provided more detailed information about the functional composition of each assemblage; in the case of the traits I chose, about overall plant size and leaf economic strategies.

To ensure I did not over-fit the data, I needed to be selective in choosing environmental predictors of functional diversity at the twenty-five plots. So, I assessed which temperature and texture variable each functional diversity metric temperature correlated most strongly with using Pearson's r. This resulted in one temperature and one texture explanatory variable in each additive linear model of functional diversity across microenvironment. I modeled the CWM of leaf traits, LA and SLA, and FDis as a function of mean soil temperature and the amount of clay in the soil. I modeled the CWM of height traits, mean and maximum, as a function of the interannual variation [standard deviation (SD)] in soil temperature and the amount of sand in the soil. FDis calculated with two traits—maximum height and SLA—was modeled as a function of mean soil temperature and the amount of sand in the soil. I logged all functional diversity metrics to improve normality and used ANOVA to test whether both, either, or none of the environmental variables best predicted diversity metrics.

Effect of life history strategies on functional diversity-environment relationships. I determined whether each species assessed was a woody perennial, herbaceous perennial, or annual/biennial using a local flora (Shaw et al., 1989), and subset the species in each assemblage into these groups. Then, I calculated all five functional metrics for each of these subsets, as described above. Across the entire site, I calculated the overall FDis and CWM of LA, SLA, and maximum and mean height for each life-history strategy. Then, at the assemblage level, I used model-averaging (using *MuMIn::dredge*; Bartoń, 2022) to statistically test whether each life-history strategy's diversity and changes across environmental gradients, differed from one another. All predictor variables were z-transformed to make their resulting coefficients a measure of the relative importance of each explanatory variable (Grueber et al., 2011).

Effect of phylogenetic differences on understanding ecological differences. Species' phylogenetic relationships may represent ecological differences not captured by the functional differences I measured. I assessed whether or not phylogeny added information about ecological differences using the mean nearest taxon distance (SES_{MNTD}). This metric averages the distance between nearest neighbors for all species in the assemblage and compares that to a randomized, null assemblage drawn from the wider source pool ($n = 999$, Kembel, 2009; Kembel et al., 2010; Pearse et al., 2015; Webb, 2000). I calculated SES_{MNTD} from the combined functional and phylogenetic distances between the most closely related pairs of species using the phylogenetic weighting parameter a. This 'traitgram' approach (Cadotte et al., 2013) means that, when $a = 0$, SES_{MNTD} reflects only functional differences, while when $a = 1$, SES_{MNTD} is generated from a distance matrix of only phylogenetic differences. Importantly, when a is intermediate between the two, it reflects both phylogeny and traits (when $a = 0.5$ it reflects both equally), and so the relative contributions of both can be assessed.

For phylogenetic distances, I used the phylogenetic tree for vascular land plants from Zanne et al. (2014) and added missing species using *pez::congeneric.merge* (Pearse et al., 2015). I set the phylogenetic weighting parameter to calculate abundance-weighted SES_{MNTD} eleven times ($a = 0, 0.1, 0.2, ...0.9, 1$), using *pez::.ses.mntd*, to see whether phylogenetic and functional information reveal related, or complementary, information about the system. Finally, I looked at both how SES_{MNTD} varied overall, and how the relationship between SES_{MNTD} and microenvironment changed, as the amount of difference from functional and phylogenetic information varied.

3.3 Results

3.3.1 Microenvironment-topography relationships

There were no significant correlations between the two types of microenvironment variables, soil temperature and texture (Appendix C). Near-surface soil temperature and soil texture varied across different elements of topography, soil temperature across aspect, and soil texture across elevation (Figure 3.2). Overall, near-surface soil temperature variables — the mean, maximum, and standard deviation in temperature — were higher on south-facing slopes than north-facing ones. On average, south-facing slopes had a 6.7 °C warmer mean temperature, 21 °C warmer maximum temperature, and 4.6 °C more variation in temperature than north-facing slopes. The average minimum temperature at each plot (-1.7 +/- 0.39 °C) did not vary across aspect.

The soil texture at all plots was loamy, including nine sandy loams, eight silty loams, seven loams, and one loamy sand (Figure 3.2). The texture of these soils are all low in clay (10-30%), with moderate amounts of silt (20-60%) and the highest range in the amount of sand (20-80%). Both the percentage of sand and clay significantly varied across elevation. Elevation predicted lower amounts of sand (about 35%) and higher amounts of clay (about

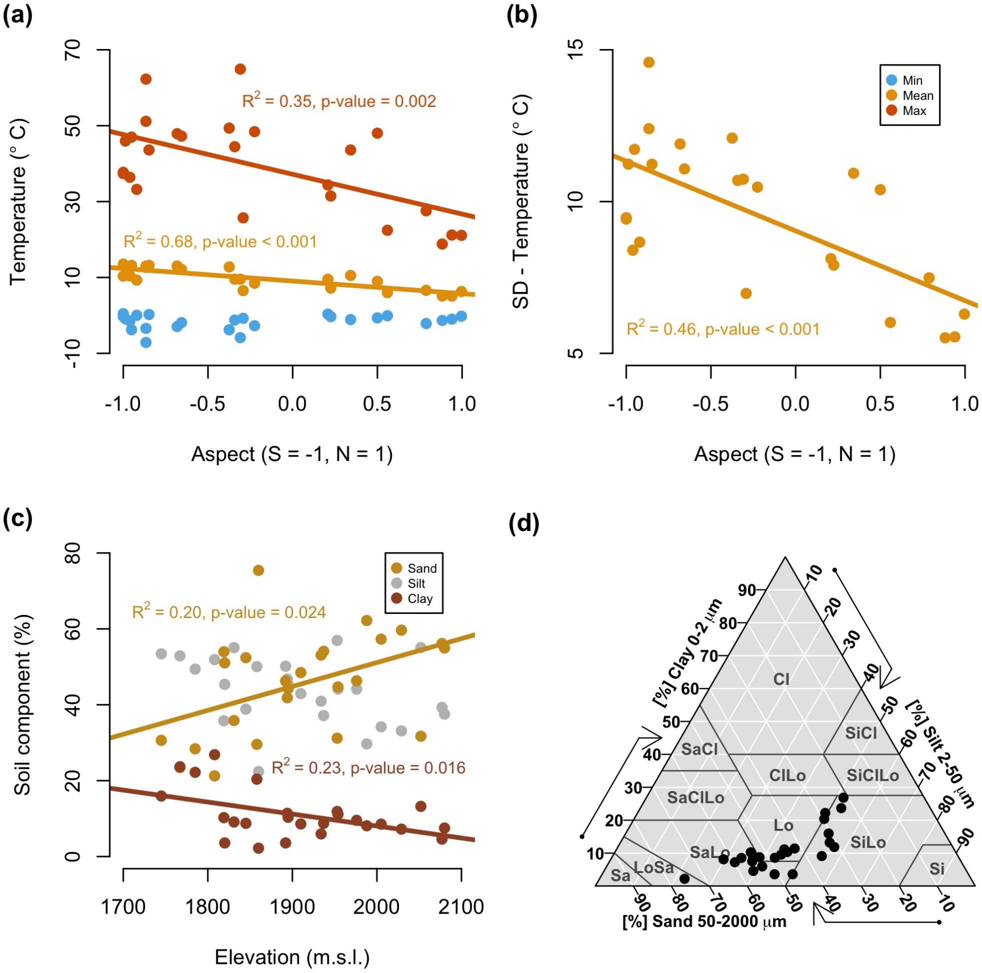

Fig. 3.2: **Near-surface soil temperature and soil texture vary across topography at Right Hand Fork.** (a) The mean (yellow, slope = -3.33, $F_{1,23} = 49.59$) and maximum (red, slope = -10.49, $F_{1,23} = 12.61$) near-surface soil temperatures are significantly higher in more south- than north-facing plots. The minimum temperature does not significantly change across aspect (light blue, average = -1.69 °C). (b) The variance in temperature at each plot also significantly decreased from south- to north-facing plots (slope = -2.30, $F_{1,23} = 19.47$). (c) The percent of sand and clay vary inversely across elevation with lower amounts of sand (yellow, slope = 0.063, $F_{1,23} = 5.85$) and higher amounts of clay (brick red, slope = -0.032, $F_{1,23} = 6.79$) at lower elevations. The amount of silt in the soil did not significantly change across aspect (gray, average = 43.70 %). (d) All of the soils at Right Hand Fork are loams with lower amounts of clay (0 - 30 %), moderate amounts of silt (20 - 60 %), and moderate to high amounts of sand (20 - 80%).

15%) at the lowest elevation plots (1745 m.s.l.) and higher amounts of sand (about 55%) and lower amounts of clay (about 5%) at the highest elevation plots (2080 m.s.l, Figure 3.2). The amount of silt in the soil did not significantly vary across elevation (average = 43.7%).

3.3.2 Functional diversity-microenvironment relationships

I obtained four traits for 84 out of the total 100 species identified. I scanned and weighed a total of 7,213 leaves and obtained LA from the stalkless pipeline for 6,613 of those leaves. Prioritizing the best sample of leaves for each species resulted in 3,454 leaves that were used to generate the leaf traits in the analysis presented here. I measured the height of 1,831 individuals, all of which were used to calculate the mean and maximum height variables. Microenvironments with the lowest mean soil temperatures, which tended to be on north-facing slopes, supported assemblages with larger leaves, more acquisitive strategies, and more functional dispersion (Figure 3.3, Appendix C). Conversely, plots with less inter-annual variation in soil temperature, also found on north-facing slopes, predicted taller assemblages, whether measured as the mean or maximum. When FDis was calculated with two traits, the relationship between functional dispersion and mean temperature was very similar [FDis (4 traits) slope = -0.316, FDis (2 traits) slope = -0.321, Appendix C]. The relationship between height and the inter-annual variation in temperature was also similar whether it was calculated as the maximum height a species achieved or the mean height of the species across the site (maximum height slope = -0.218, mean height slope = -0.233, Appendix C).

3.3.3 Effect of life history strategies on functional diversity-environment relationships

Site-wide, functional diversity varied across the life history strategies — woody or herbaceous perennial, and annual/biennial. Herbaceous perennials made up the largest group of species ($^{54}/_{84}$) and had the most acquisitive leaves and largest leaf area (Appendix C). Annuals and biennials made up the next largest group of species ($^{17}/_{84}$) and had the

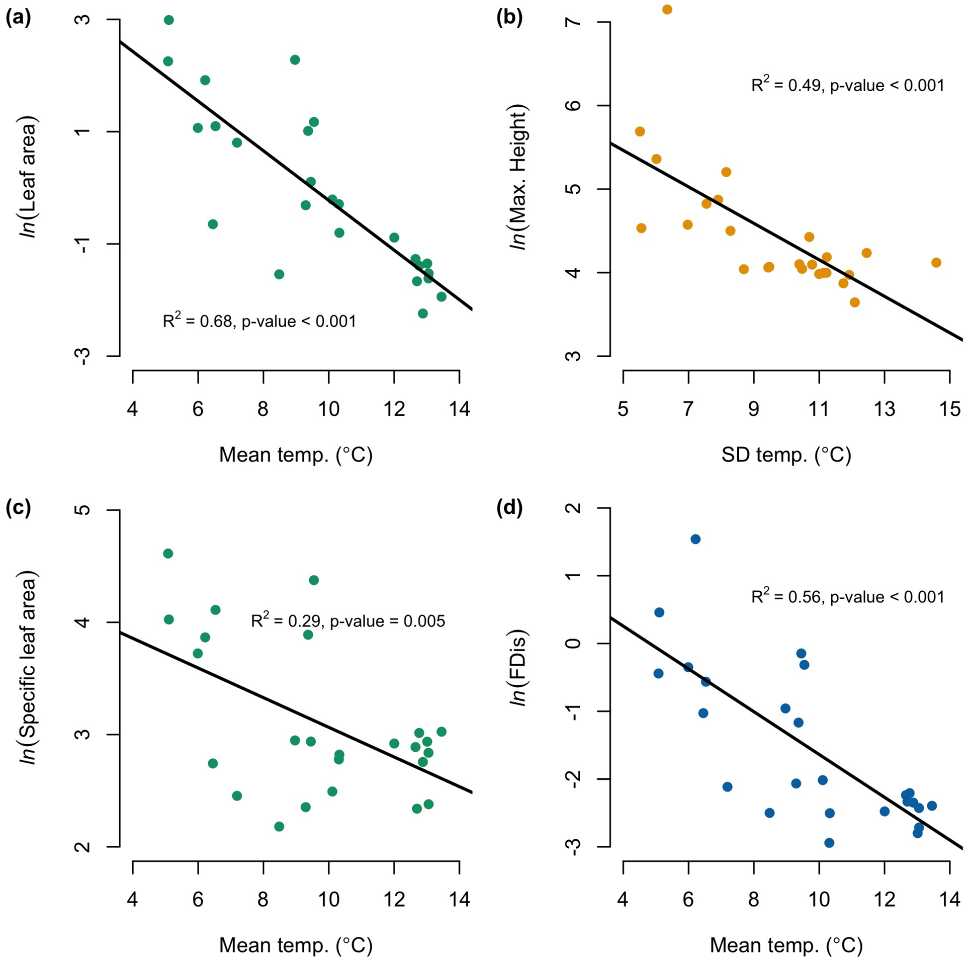

Fig. 3.3: **Increases in mean soil temperature predict a decrease in the CWM of leaf traits and functional dispersion, while an increase soil temperature variation predicts a decrease in the CWM of maximum height.** (a) Plots with cooler mean soil temperatures support larger leaves [higher logged CWM of LA (mm^2), slope = -0.442, $F_{1,23} = 49.97$], (c) leaves with more acquisitive leaf economic strategies [higher logged CWM of SLA (mm^2 g^{-1}), slope = -0.132, $F_{1,23} = 9.426$], and assemblages with more variance in functional strategies [*i.e.* more biological insurance; higher logged FDis, slope = -0.316, $F_{1,23} = 29.54$]. (b) Plots with less variation in soil temperature support taller assemblages [higher logged CWM of maximum height (cm), slope = -0.218, $F_{1,23} = 21.85$]. Color coding described in Figure 3.1.

smallest functional dispersion (therefore, lowest biological insurance), least acquisitive and smallest leaves, and shortest height. Woody perennials had more than four times the functional dispersion of herbaceous perennials (the largest amount of biological insurance) and were the tallest group.

The life history strategy of species affected the relationship between functional diversity and microenvironment. Herbaceous and woody perennials drove the interaction between leaf area and mean temperature and functional dispersion and mean temperature (Figure 3.4). Both groups had larger leaves and higher dispersion when the mean temperature was lower. Woody perennials had a small effect on the relationship between functional dispersion and the amount of clay in the soil; functional dispersion was higher when the amount of clay in the soil was higher within this group. Herbaceous perennials had the biggest effect on the relationship between specific leaf area and mean soil temperature (Appendix C); species in this life history group had more acquisitive leaves when mean temperature was lower. The CWM of mean and maximum height was mostly driven by the presence of woody perennials, *i.e.* assemblages containing woody perennials were taller overall (Figure 3.4, Appendix C). Additionally, when variation in temperature was lower, woody perennials achieved taller maximum heights. Overall, I did not detect a change in the functional diversity of annuals and biennials across microenvironment.

3.3.4 Effect of phylogenetic differences on understanding ecological differences

Broadly, functional and phylogenetic differences between species contributed similar information about the ecological differences between species at Right Hand Fork. Across the whole site, SES_{MNTD} was highest when calculated only from functional differences ($a = 0$), second highest when only calculated from phylogenetic differences ($a = 1$), and lowest when calculated from about half functional and half phylogenetic difference ($a = 0.5$, Figure 3.5). However, none of the values of SES_{MNTD} I calculated across the phylogenetic weighting parameter (a) were significantly different. That said, the relationship between SES_{MNTD} and environment (both soil temperature and texture) significantly changed as the value of a changed. The relationship between SES_{MNTD} and mean temperature was

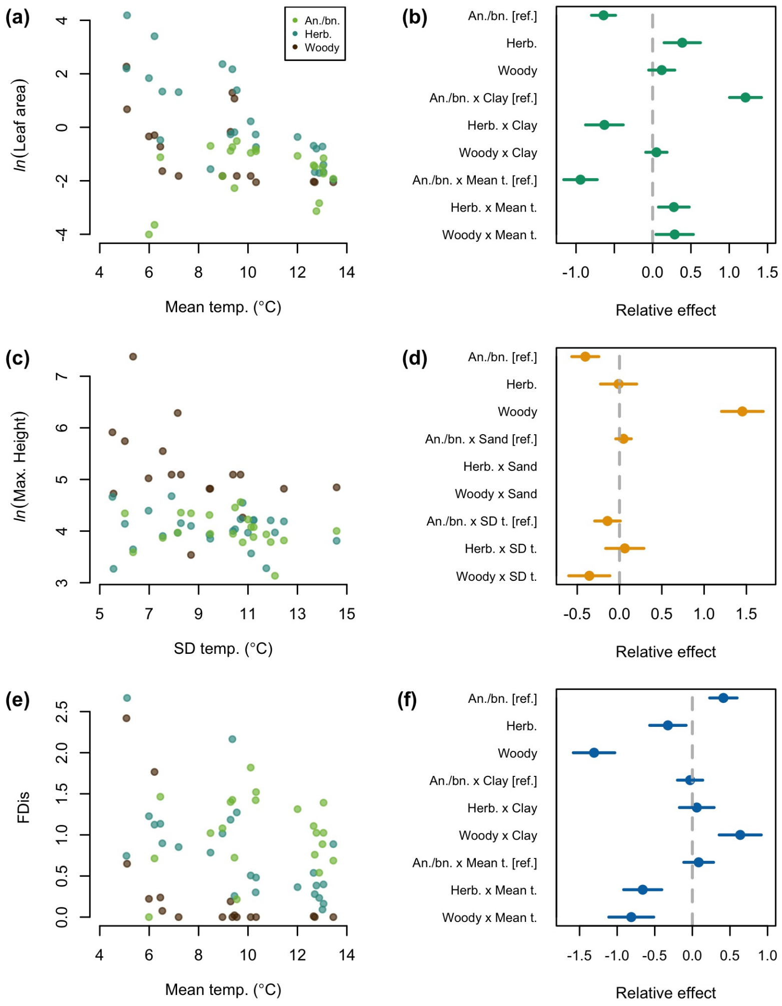

Fig. 3.4: **Life history strategies affect the relationship between functional diversity and microenvironment.** Plots in the left column show how the logged CWM of (a) leaf area, (c) maximum height, and (e) [unlogged] functional dispersion vary across the temperature variable they were most correlated with when subset by life history strategy — annuals/biennials (green), herbaceous perennials (blue), and woody perennials (brown). Plots in the right column show the relative effect of each explanatory variable in models that look at how these life history strategies affect the relationship between each functional metric (in the left column) and both the soil temperature and texture variable most correlated with that functional metric. Coefficient values are reference contrasts from those labeled as such. Values further from zero indicate that a variable or interaction between variables has a greater effect on a functional metric. For example, when a life history strategy interacts with one of the microenvironment variables and has a large relative effect, as woody and herbaceous perennials interact with mean temperature in (b), plants with these life history strategies have a larger impact on the relationship between that functional metric and microenvironmental variable.

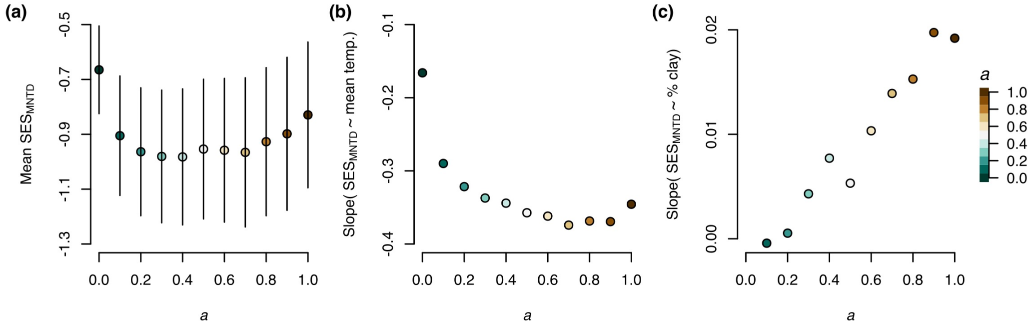

Fig. 3.5: **Adding phylogenetic information about ecological differences strengthens the relationship between SES_{MNTD} and microenvironment.** The phylogenetic weighting parameter a changes the amount of information about ecological differences used to calculate SES_{MNTD} from all functional difference (teal, $a = 0$) to all phylogenetic difference (brown, $a = 1$). (a) Overall, including phylogenetic differences does not provide significantly different information about ecological differences than just using functional differences. (b) The relationship between SES_{MNTD} and mean temperature is stronger when SES_{MNTD} is calculated from about half functional and half phylogenetic differences or more phylogenetic than functional differences. (c) Similarly, the relationship between and the amount of clay in the soil is stronger when just calculated from phylogenetic differences.

least strong when SES_{MNTD} was calculated only from functional metrics (slope = -0.17) and most strong when calculated from about half functional and half phylogenetic difference or a greater amount of phylogenetic difference ($a > 0.5$, slope = -0.36). Similarly, the relationship between SES_{MNTD} and the amount of clay in the soil became more strong, albeit subtly, as phylogenetic differences were included (slope = -0.01 to slope = 0.02).

3.4 Discussion

The relationship between functional diversity and microenvironment quantifies where and how assemblages might maintain function in topographically complex, mountainous terrain in northeastern Utah. Broadly, I found a shift in overall functional strategy and biological insurance potential across soil temperature gradients across aspect. Herbaceous (and to some degree, woody) perennials had the strongest effect on these relationships. Integrating information about the functional and phylogenetic differences in a dispersion metric (SES_{MNTD}) indicated that phylogeny represents ecological differences between species that

I did not measure.

Here, I discuss the implications of changes in near-surface soil temperature for overall plant survival and growth across this landscape. Then, I describe how shifts in functional diversity — driven mainly by the CWM of leaf traits and dispersion of herbaceous perennials — point to an environmental filter across aspect. This trend highlights a contrasting potential for persistence, and management opportunities, on north- vs. south-facing aspects. Finally, I discuss how the addition of phylogenetic differences enhances the understanding of ecological differences in these assemblages. Throughout, I highlight how assessing functional diversity and microenvironment, within the framework I describe, can inform management actions focused on maintaining plant assemblage functions and ecosystem services.

3.4.1 Topography shapes microenvironment

At the local spatial scales I sampled at (1900 m extent and smaller), aspect-driven topographic complexity moderates a site-wide climate regime. Across aspect I measured a 6.4 °C mean temperature change. Mean temperature correlated most strongly with aspect (Figure 3.2, $R^2 = 69\%$). Other mountainous environments throughout the northern hemisphere likely show similar trends, because south-facing aspects receive more solar radiation which increases soil temperature and evapotranspiration (Jackson, 1967). However, I did not find differences in soil texture across aspect, indicating that this topographic gradient does not influence water regimes (Brown et al., 2004). A global study of temperate grass-/shrub-lands with similar mean annual temperatures (MAT = 7.23 °C, compared to a MAT = 8.4 °C at Right Hand Fork) also found that topography better predicted environmental heterogeneity in temperature than precipitation (Jiang et al., 2017). The strong relationship between mean temperature and aspect shows that small changes in near-surface soil temperature likely moderate resource availability, like soil moisture, that drive differences in functional strategies. If mean temperatures increase across this site, the variance and maximum temperatures could become more correlated with topography than the mean temperature (Lewis & King, 2017). This would indicate a shift to a more variable climate regime associated with topographic complexity.

Near-surface soil texture varied across elevation, but not aspect. Soils at higher elevations were coarser with high sand (55%) and low clay content (15%) and overall, soils at Right Hand Fork are characterized by high sand content (>20%, Figure 3.2). Per the inverse-soil texture effect, coarse-textured soils decrease bare soil evaporation by allowing water to infiltrate to deeper soil layers (Noy-Meir, 1973; Walter et al., 1973). This leads to greater (overall) water availability in deeper layers that supports higher plant productivity and more woody plant growth in arid climates (Dodd & Lauenroth, 1997; Pennington et al., 2017; Renne et al., 2019; Sala et al., 1997). However, these soils hold less water and nutrients at the surface (Austin et al., 2004). Per this effect, the coarse composition of the soil at Right Hand Fork may support taller plant assemblages than would be present if the soil was finer. To verify this insight I need to measure soil depth, soil moisture content, and texture at multiple depths in the soil column because this insight only applies to deeper soils. I could also measure the root traits of herbaceous perennials; if they exhibit more conservative strategies and deeper rooting this would provide support for the inverse-soil texture effect.

3.4.2 Microenvironment predicts functionally-distinct assemblages

An increase in the mean and interannual variation of temperature across north- to south-facing aspects supported functionally distinct assemblages (Figure 3.3). Plots with cooler and less variable temperatures contained assemblages that were taller, more functionally dispersed, and had more acquisitive leaf economic strategies. Conversely, plots with hotter and more variable temperatures supported assemblages that were shorter, less functionally dispersed, and had more conservative leaf economic strategies. This trend indicates that environmental filtering dominates on south-facing slopes, especially for herbaceous and woody perennials. Limited resources (*e.g.* less water) and environmental stress (*e.g.* higher temperatures) likely act as this filter, but biotic interactions may also contribute (Cadotte & Tucker, 2017; Cornwell et al., 2006; Kraft et al., 2015; Mayfield & Levine, 2010). Annuals and biennials appear to avoid this filter and use similar functional strategies across this temperature gradient. Soil texture did not predict functional differences in the aboveground traits I measured. This aligns with global studies where temperature predicts plant traits more strongly than precipitation (Moles et al., 2014). However, measuring traits more directly related to water acquisition (*i.e.* root traits) may provide better insight into how microenvironmental variation in water regimes influences assemblage function.

Abiotic and biotic factors operate across spatial scales to shape traits observed at small spatial scales; however, similar conditions can support assemblages with vastly different community-weighted trait values (Bruelheide et al., 2018). For example, in high-elevation Colorado mountains near the UT fieldsite I worked in, shorter plants with smaller leaves and more resource-conservative strategies were also found in locations with higher mean and variance in temperature (Stark et al., 2017). However, higher temperatures likely only constrain plant height and result in leaves with more conservative resource acquisition strategies in places where overall water availability is limited. In a study in the Arctic that compared locations with more and less moisture, warmer summer temperatures resulted in taller, more resource-acquisitive, aboveground plant traits, but only at the wet locations (Bjorkman et al., 2018). Notably, this pattern was mostly driven by species turnover, rather than intraspecific changes in functional traits.

Right Hand Fork spans active grazing allotments (USDA Forest Service, 2022a), where consistent vegetation production, especially by herbaceous perennials, supports people's livelihoods. Additionally, herbaceous perennials drive shifts in the CWM of leaf traits and functional dispersion across mean temperature. As a result, it will be important to continue monitoring to understand how changes in the climate regime, especially soil temperature, might affect forage production. Environmental heterogeneity, especially aspect, has the potential to provide spatial insurance for these assemblages. Often, species are expected to move up in elevation and poleward in latitude in response to warming temperatures (Rubenstein et al., 2020). However, especially in arid, mountainous environments, aspect can buffer the overall effect of warming temperatures, supporting vegetation assemblages in ways that are similar to what I observed (Albrich et al., 2020; Yang et al., 2020). In response to increasing temperatures, species can also move across aspects and up in elevation, as seen with salamanders and lizards (Feldmeier et al., 2020).

Critically, even if cooler, north-facing slopes do not provide a buffer against increasing temperatures, vegetation often responds differently on north- vs. south-facing slopes, which makes this an important topographic element to include in range shift studies and management plans (Ackerly et al., 2020; Elliott & Cowell, 2015). Heterogeneity in soil resources also supports more diversity in functional traits, broadly speaking (Price et al., 2017). Future studies looking at how species adapt and move in response to changing environmental conditions should include responses to microenvironmental conditions, like aspect, not just broad climate regimes. This will facilitate a better understanding of subtle species shifts to, or maintenance within, more favorable environments to the preservation of the overall functionality of ecosystems (Fridley et al., 2011). Measuring dispersal traits, and monitoring how assemblage dispersion and forage production change over time, would further identify the potential for aspect to provide spatial insurance across this landscape.

3.4.3 Phylogenetic difference informs ecological difference

The overall value of SES_{MNTD}, a measure of dispersion, was similar whether I calculated it from solely functional or phylogenetic information (Figure 3.5). However, the relationship between dispersion and environment was strongest when information from both phylogeny and functional traits were included. This example of how phylogenetic differences can support functional differences [see also de Bello et al. (2017)] adds to the ongoing debate about how many axes of functional variation are needed to understand diversity-environment relationships (Laughlin, 2014; Mouillot et al., 2021). While the traits I measured provide information about how assemblages change across environment, the changes I detect are, if anything, conservative. Given the strength of these conservative trends, I suggest that the most effective use of management resources to understand the potential for this landscape to keep producing forage would be to track the productivity (and potentially variance in dispersal and water-acquisition traits) across aspect-driven temperature gradients.

3.4.4 Conclusion

Overall, I found evidence for differences in assemblages' insurance potential and trait strategies driven by a 6.4°C shift in mean near-surface soil temperature across aspect, which likely affects water availability on these slopes. Assemblages on the warmer south-facing slopes showed less insurance potential (lower function dispersion) and had more resource-conservative leaf traits and shorter stature, consistent with adaptation to a harsher environment than north-facing slopes. The assemblage-level traits on north-facing slopes were consistent with cooler, less harsh environmental conditions. While I found taller species with more acquisitive leaf traits in these plots, they also had higher functional dispersion, indicating higher insurance potential on these slopes. Across the same temperature gradient, and differences in soil texture, adding information about phylogenetic difference to a metric of functional difference strengthened the relationship between ecological difference and environment. These results support the use of functional, and phylogenetic, diversity-environment relationships to understand assemblages' current insurance potential and how it might respond to future change. I suggest that monitoring temporal trends in these relationships over time would provide more information about inter-annual variability in these relationships. For example, decreases in the FDis of assemblages over time might signal the increasing impact of an environmental filter, like higher temperatures, less precipitation, or land use intensification (Laliberté et al., 2010). I also advocate for more inclusion of aspect-differentiation in range-shift studies and vegetation management plans, because I found strong variation in assemblages' insurance potential and related evolutionary history in response to this gradient.

CHAPTER 4

QUANTIFYING RANGE INDICATOR HETEROGENEITY SUPPORTS MANAGEMENT OF RANGE CONDITIONS

4.1 Abstract

Maintaining and restoring working landscapes, like rangelands, supports human livelihoods and ecosystem health. Numerous indicators provide insight into range ecosystem conditions, such as soil stability, hydrological function, and the integrity of biological communities. Intentional shifts in range management strategies in the Western U.S.A. over the last century now prioritize the long-term health of rangeland ecosystems. This paradigm aims to understand and manage landscape heterogeneity; however, sampling methods commonly used to monitor range conditions do not typically measure variation across space. I address this gap using a spatially-explicit, nested sampling design to assess how indicators of rangeland health vary across space, environment, and grazing categories in rangeland in northeastern Utah. Based on the results I recommend monitoring and management that addresses undesirable range conditions—bare ground and undesirable species cover—at moderate spatial scales within the study design (one-km^2) in pastures grazed by cattle. In tandem, I recommend monitoring and management that maintains and when possible expands desirable range conditions, like good forage cover and vegetation biodiversity, at smaller spatial scales (0.002-km^2). Applying the insights about range indicator heterogeneity in the context of managing adaptively will help maximize rangeland functionality for humans while also supporting the health of ecosystems both now and in the future.

4.2 Introduction

As members of ecological systems, humans use and manage landscapes for their benefit. Within this context, working lands conservation promotes management that supports livelihoods and maintains ecosystem health (Kremen & Merenlender, 2018). In public rangeland systems, livestock provide food, fiber, and culturally important ecosystem services for people (Sayre et al., 2012). In balance, appropriate livestock management maintains and restores ecosystem functions (Spratt et al., 2021; Teague & Kreuter, 2020). Appropriate management recognizes that ecosystems with a long history of grazing rely on disturbances like large ruminant herbivory and fire which interact with abiotic conditions to produce a patchwork of different habitats (Knapp et al., 1999; Milchunas et al., 1988).

Adaptive, regenerative management strategies (Huntsinger & Sayre, 2007; McGinty et al., 2009) focus on long-term landscape heterogeneity as a desired range-wide condition (Fuhlendorf et al., 2017; Teague & Kreuter, 2020). This focus contrasts with a management paradigm that aims to maximize livestock productivity in the short term. Throughout the western U.S.A. the prevalence of intense grazing associated with European colonization (*i.e.* the latter paradigm) resulted in uniform vegetation across rangelands and decreases in palatable forage species (Herbel, 1979). Fire and drought interacted with this inappropriate grazing strategy and led to increases in invasive, introduced species and bare ground as well as more homogeneous, less productive, and less resilient range ecosystems (Archer et al., 2017; Briggs et al., 2005; Morrow & Stahlman, 1984).

If not already homogenized, restoring rangeland to desirable conditions requires strategies tailored to the different conditions in patches across the range and the resources available for restoration. An adaptive, regenerative management plan addresses patches with undesirable biotic and abiotic conditions and monitors the effectiveness of management actions across all patch types (Huntsinger & Sayre, 2007; McGinty et al., 2009). In a rangeland system, this often includes adjusting the timing, frequency, intensity, and type of grazer (Budd & Thorpe, 2009; Davies & Boyd, 2020). For example, if a manager wants to reduce the cover of an undesirable, invasive species like cheatgrass (*Bromus tectorum*) across a range, their management plan might include carefully timed grazing in patches with diverse perennial vegetation and better forage, avoiding grazing and strategically reseeding non-invasive, good-forage vegetation in patches most likely to support establishment, and accepting and managing some patches as annual grasslands (Davies et al., 2021).

Effective range management relies on monitoring to assess whether management strategies result in desired range conditions (Budd & Thorpe, 2009; Veblen et al., 2014). Managers measure indicators that provide insight into three broad range conditions: soil stability, hydrological function, and the integrity of the biological community (Butler et al., 2003). Often, an indicator provides insight into more than one of these range conditions. For example, the indicator *bare ground*—the amount of bare soil—provides insight into all three categories. More bare ground indicates lower soil stability because higher erosion typically occurs across bare ground. All else equal, water infiltrates bare ground more quickly leading to drier topsoil and lower hydrological function. Indirectly, high cover of bare ground indicates a lack of biological integrity (which is itself another indicator: *vegetation cover*). However, this indicator provides the best insight into soil stability and hydrological function. The integrity of the biological community is better assessed by directly measuring vegetation-related indicators and other biotic factors of interest. Typically, managers choose a set of indicators that provide complementary and contrasting information about whether current management achieves desired range conditions or needs to be changed to avoid degradation (Butler et al., 2003; O'Brien et al., 2003). This allows management to maximize functionality for humans (*e.g.*, produce forage for livestock) while sustaining the ecosystems that support that forage, under current and changing climate conditions (McCollum et al., 2017; Spratt et al., 2021; Teague & Kreuter, 2020).

Increasingly, managers recognize the importance of heterogeneity in rangeland ecosystems. Heterogeneity, especially in vegetation diversity, quantity, and quality allows grazers to respond to variable forage requirements (*e.g.* higher quality forage need during lactation) and environmental conditions (*e.g.* availability of forage during drought, Fuhlendorf & Engle, 2001; Fuhlendorf et al., 2017). However, sampling methods commonly used to monitor rangeland conditions (*e.g.* random and/or transect sampling) do not focus on measuring variation across space (Fuhlendorf et al., 2017). To address this methodological gap, I used a spatially explicit sampling design (Simpson & Pearse, 2021c) to assess how range indicators change across spatial scales and environmental conditions, thereby quantifying range condition heterogeneity. To connect this study to current range management, I had listening-focused conversations with the local range specialist, Anthony VonNiederhausern, and assisted him and Sheryl Goodrich with range monitoring for Wasatch-Cache National Forest (WCNF) in northeastern Utah during the summer of 2020. Through interactions that spanned over two years, we identified a common goal of understanding, maintaining, and improving vegetation cover along with the abiotic factors that influence that cover. The following background information and study aims directly result from our collaboration.

Like many rangelands throughout the western U.S.A., the range within WCNF was negatively impacted by inappropriate grazing practices, including overstocking and intense, unregulated grazing, from the mid-1800s to 1900 (Hansen, 2013; McGinty et al., 2009). Over the last century, strategies to improve the conditions of the sheep and cattle range across this landscape achieved varying outcomes, including the restoration of productive, diverse, multi-use rangeland (Hansen, 2013). In the last two decades, management focus shifted to restoring and maintaining the long-term, regional-scale functionality of these range ecosystems (USDA Forest Service, 2003). Similar to a broad trend throughout the western U.S.A., this focus differs from the past management style that sought to maximize short-term production from small, localized spatial scales. The broad-scale focus of the new WCNF plan aligns with studies that advocate for managing local patches to maintain and improve the regional-scale conditions of the landscape (Davies & Boyd, 2020).

Range monitoring in WCNF focuses on general, long-term trends in indicators that assess how much plant matter livestock eat and the integrity of plant communities and soil stability over time. The indicators most commonly and consistently collected include *vegetation cover* (the identity and percentage of plant species in fixed-sized plots over time), *photo points* (pictures taken at the same locations and from the same perspective to track broad, visual changes in vegetation cover), *stubble height* (the height of herbaceous plants after grazing, often measured at the greenline, or the area where continuous vegetation begins when moving away from a water channel), and *utilization cages* (cages that prevent cattle and other ungulates from grazing and provide a reference height of herbaceous species to compare stubble height too (USDA Forest Service, 2022a)). These indicators focus on the integrity of the biological (vegetation) community and soil stability (*vegetation cover* and *photo points*) and how much plant matter grazers remove (*stubble height* and *utilization cages*). All indicators are collected at predetermined, fixed locations which provide information about current and long-term trends in vegetation in relation to current management strategies. However, this monitoring system cannot answer broad-scale questions about heterogeneity in range conditions across the landscape when concerns arise. For example, permittees are concerned about the visually increasing cover of large, homogenous patches of bulbous bluegrass (*Poa bulbosa*) and mule-ears (*Wyethia amplexicaulis*). Both of these species provide poor forage for cattle and are likely increasing as a combination of grazing pressure and other factors, like climate change.

The design I used to sample the landscape at multiple spatial scales arranges sampling locations at the vertices of nested equilateral triangles (Simpson & Pearse, 2021c). I implemented this design across thirty-six-km^2 of cattle and sheep grazing allotments (Figure 4.1 USDA Forest Service, 2019a, 2020, 2022a). By assessing range conditions across the landscape with a spatially-explicit sampling design, I aimed to identify (1) what spatial scales indicators vary at, (2) how variation in abiotic conditions drives variation in indicators, (3) whether categorical information about current management influences indicator-environment relationships and (4) how all the indicators I measured, including utilization, relate to each other. The first aim quantifies indicator heterogeneity versus homogenization and the results will provide guidance about which spatial scales might be best to conduct future monitoring at. The second aim will determine how much inherent variation in the environment (*e.g.* topography) drives variation in range indicators. This analysis helps separate the causality of inherent variation versus disturbance-driven variation (*i.e.* by

Fig. 4.1: **Plots arranged in nested equilateral triangles span cattle and sheep grazing pastures in the WCNF.** Vegetation cover and soil texture data were collected at eighty one-m^2 plots in 2019 (white and black points). In 2020, a more focused assessment of utilization was conducted at nineteen plots (black points) located in cattle pastures with visually high coverage of undesirable species, bulbous bluegrass and mules ears. Livestock pastures are labeled and outlined in black (USDA Forest Service, 2022b) and the background shows topography from a five-meter digital elevation model (Utah Automated Geographic Reference Center, 2007) and vegetation cover from the National Agriculture Imagery Program (August 2021) courtesy of the U.S. Geological Survey.

grazing), which both potentially influence the range indicators measured (Fuhlendorf et al., 2017). The third aim addresses the potential effect of grazing patterns, using categorical information about the current grazing management strategies. The fourth aim assesses which indicators most relate to the abundance of bulbous bluegrass and mule-ears. The first two aims provide a baseline quantification of the spatial scale of range (indicator) heterogeneity and what inherent factors might drive that variation. The latter two aims identify grazing conditions, locations, and indicators to focus future monitoring and potential management actions on to achieve more desirable conditions across this range.

4.3 Methods

I assessed indicators of range condition within three ecosystem attributes—soil stability, hydrological dynamics, and the integrity of plant communities—at an actively grazed fieldsite in northeastern Utah. First, I looked at what spatial scale the indicators varied at. Then, I determined whether inherent environmental variation drives variation in indicators and whether categorical information about grazing management affects the relationships between indicators and the environment. I used the results from these analyses to make suggestions about the appropriate spatial scale to continue monitoring indicators and to identify what environmental and management conditions predict undesirable indicators. Finally, I looked at the relationship between undesirable species and the other indicators, including an indicator of utilization, which is currently used by managers and range users to understand forage use at this site.

Cover data to calculate the indicators was collected at eighty plots in 2019 and this data was used for all analyses except the final one related to utilization (Figure 4.1). Utilization (and cover) data were collected at a subset of nineteen plots in 2020 to assess the relationship between an indicator more consistently collected by range managers and undesirable species. I also collected cover data at forty-five plots in 2020; code to replicate the 2019 analyses with this year of data will be released when published. All analyses were performed in R (v. 4.0.3; R Core Team, 2022) and all software packages below *in italics* are R packages unless otherwise noted. All data collected and code to reproduce analyses will be openly released when published.

4.3.1 Field system

I studied rangeland conditions at a long-term fieldsite spanning thirty-six-km^2 of rangeland in the Temple and Right Hand Fork areas of WCNF near Logan, UT [(41°47'27"N, 111°35'20"W), Figure 4.1]. Complex, hilly topography supports a variety of vegetation types from sagebrush steppe to mixed conifer and aspen forest (Lowry et al., 2007). This fieldsite provides a good location to study range conditions in the context of (1) highly heterogeneous vegetation which may support overall better forage and diversity and (2) rotational grazing plans, where cattle are moved throughout pastures throughout the grazing season, which have been used for the last quarter century (Von Niederhausern, 2020). At each plot, I measured three topographic variables—aspect (cosine-transformed degrees) with a compass, elevation (m.a.s.l.) with a GPS, and slope (°) with a clinometer. I calculated the slope as the average of the slope uphill and downhill from the plot.

The fieldsite spans seven pastures in three grazing allotments (USDA Forest Service, 2019a, 2020, 2022a). The Annual Operating Instructions for each allotment describe the current grazing plan which has been used for the last quarter century. I used this categorical information about the current grazing management practices to determine how they may be affecting range conditions. The Logan Canyon Cattle Allotment contains pairs of pastures grazed by 1478 cow/calf pairs in an alternating-year rotational schedule (USDA Forest Service, 2022a). In 2019, one herd of cattle grazed the Cottonwood pasture from mid-June to mid-August and then was moved to the Maughn Hollow pasture to graze from mid-August to late September. Following the same timeline, a separate herd of cattle grazed the Mud Flat pasture first, followed by the Cottonwood pasture. The Long Hollow sheep allotment contains five units where 1268 ewe/lamb pairs graze in rotation across four out of five of these each year, allowing one unit to rest every four years (USDA Forest Service, 2020). In 2019, sheep were grazed from early July through late September; Unit 1/Ephraim's Grave was grazed first followed by a pasture that plots were not located in, Unit 2 (Hunsaker Spring), and Unit 5 (Hunsaker Corral). In the Ricks/Steel allotment, 855 ewe/lamb pairs were rotated from the SW end of the allotment through to Hardware Ranch (Figure 4.1, all off the map, USDA Forest Service, 2019a).

4.3.2 Range condition indicators

I measured at least one range indicator in each of the three range condition ecosystem attributes—soil stability, hydrological dynamics, and the integrity of plant communities. Whenever possible, I measured range indicators that align with the indicators monitored by the range specialist for WCNF, Anthony VonNiederhausern. He prioritizes monitoring indicators related to vegetation cover and quality because this provides critical information about the amount and quality of forage available for cattle and sheep. In complement, he monitors bare ground because this indicates potential overgrazing and soil stability (*i.e.* erosion) concerns and utilization, or how much forage livestock eat. In addition to collecting data to quantify indicators similar to these whenever possible, I looked at indicators easily calculated from ground cover data. These indicators potentially provide information about maintaining and improving vegetation cover as well as the abiotic factors that support that vegetation.

To assess soil stability I looked at bare ground and moss and lichen cover. While hydrological function closely relates to soil stability, I also looked at litter cover and soil texture—the amount of sand, silt, and clay in the soil—to focus on this ecosystem attribute. To understand the integrity of the biological community I looked at species richness and two phylogenetic diversity metrics—Faith's phylogenetic diversity (Faith's PD) and mean nearest taxon distance (SES_{MNTD}). Additionally, I calculated undesirable species cover—bulbous bluegrass and mule-ears—and good forage species cover (see Appendix D for a table of the sixteen cool-season perennial grasses included). Finally, I assessed utilization at a subset of plots where undesirable species are a management concern. The details and justification for collecting the underlying data for each of these indicators are described below.

Ground & vegetation cover. Many indicators rely on surveying ground cover because this can vary considerably in response to grazing pressure and management (Butler et al., 2003). I measured ground and vegetation cover, including bare ground, rock, log, moss and lichen, and litter cover, at eighty one-m^2 plots from June - September 2019. Vegetation cover was assessed at peak standing biomass (estimated from field guides and observation, Perez-Harguindeguy et al., 2016) for as many species as possible. I prioritized surveying plots earlier in the season in plots where grazers would be turned out first. For each 0.25-m^2 quadrant within the one-m^2 quadrat, I used a 0.25-m^2 10x10 grid with 0.025-m^2 grid cells to consistently sample all types of ground cover. For vegetation, I assessed total canopy cover, including overlapping and overhanging foliage rooted outside the plot to make sure that all potential forage was surveyed. This means that vegetation cover could be greater than 100% cover. Plant species were identified using local herbarium resources, field guides, and standardized taxa names (<http://www.worldfloraonline.org/>). I calculated the absolute percent cover for each plot by taking the mean of these four quadrants. Each indicator related to ground cover was calculated as follows. First, I subtracted any cover by rocks and logs from one hundred to determine the amount of available cover within the plot. Bare ground, moss and lichen cover, and litter cover were all calculated as the percentage of available cover covered by bare soil, moss and lichen, and litter, respectively. Undesirable species cover and good forage species cover were also calculated as a percentage of available cover.

Soil texture. While litter cover provides insight into how easily water evaporates from and infiltrates, soil texture provides deeper insight into soil water dynamics (Pennington et al., 2017; Renne et al., 2019). Different sizes of particles indicate the balance between how well soil holds versus drains water, support different types of range vegetation, and inform how easily a soil can be compacted (Sanaei et al., 2019). I assessed soil texture using the hydrometer method [following procedure and calculations in Ashworth et al. (2001), based on (Bouyoucos, 1927)], from soil samples collected at eighty plots in the summers of 2018 and 2019. Mineral soil was collected from a ten-centimeter deep by eight-centimeter wide hole at the same position a half-meter from each plot. Then it was transferred back to the lab to be aired dried. Each sample was physically broken up by sieving it to two millimeters and grinding it with a mortar and pestle. Then the soil was chemically dispersed using a 50 g/L sodium hexametaphosphate solution. Hydrometer measurements were taken at forty seconds and two hours to determine the amount of sand, silt, and clay in each soil sample. Finally, I used the package *soiltexture* to classify these percentages into soil classes based on the USDA soil texture triangle (Moeys, 2018).

Biological diversity. In addition to species richness, or the total number of species in a sampled community, I calculated two phylogenetic diversity metrics. Phylogenetic diversity metrics incorporate the evolutionary history and relationships between species in a community to understand community assembly dynamics like environmental filtering and competition (Cavender-Bares et al., 2009; Webb et al., 2002), but see Mayfield and Levine (2010). While the empirical evidence linking evolutionary history to phenotypic diversity to ecosystem functioning is highly context-dependent, measuring phylogenetic diversity provides insight into how management actions influence ecological processes across the rangeland (Tucker et al., 2019). In a range context, phylogenetic diversity metrics may provide more information about the quality and potential stability of vegetation than other biodiversity metrics, like species richness alone. The two phylogenetic metrics I calculated as indicators of the integrity of the biological community— Faith's PD and SES_{MNTD}— provide information about the total evolutionary history and relatedness of plants in a community (more or less related than expected by chance), respectively (Faith, 1992; Kembel, 2009; Webb, 2000). I used the phylogenetic tree from Zanne et al. (2014) to generate the tree specific to species at the fieldsite using *pez::congeneric.merge* (Pearse et al., 2015). This comprehensive phylogenetic tree included all but three of the species I identified in the fieldsite.

Pre- and post- grazing plant height. I assessed pre- and post-cattle plant height in nineteen one-m^2 plots found in the Cottonwood, Chicken Creek, and Mud Flat pastures in 2020 (Figure 4.1). These pastures contain large patches of undesirable species—bulbous bluegrass (*Poa bulbosa*) and mule-ears (*Wyethia amplexicaulis*) that concern managers and permittees. These plots are also located on low-angle slopes where cattle are more likely to graze (*e.g.* compared to the plots in the south end of the Maughn Hollow pasture). I measured cover, as described above, and pre-grazing plant height in early to mid-June 2020, prior to the cattle being let out onto the range. Post-grazing plant height was measured in late September to early October 2020, after the cattle were moved off of the range. In order to make sure all species were represented, I measured the height of up to 10 individuals of each species found in the plot. I measured from the ground to the top of the main photosynthetic tissue, not including inflorescence, fruits, or seeds if those extended beyond the tallest leaf [following Perez-Harguindeguy et al. (2016)].

To quantify the overall vegetation height in each plot, before and after cattle grazing, I calculated the community weighted mean (CWM) of plant height for the plot. The CWM of any (plant) functional trait, like height, weights the trait values measured for each species in a plot by the abundance of each species in the plot (Lavorel et al., 2008). This metric adjusts the contribution of a species to potential forage for cattle by giving more weight to common species and less weight to rare species. Finally, I calculated utilization as the difference between the CWM of pre- and post-cattle plant height as a percentage. If the percentage is lower than 100 I assume that cattle (repeatedly) ate some of the available forage while if it is higher than 100 that means that additional growth outpaced cattle usage. This metric does not exactly duplicate utilization/stubble height measurements used by range managers and users (SRM Rangeland Assessment and Monitoring Committee, 2018). Instead, I used a conceptually similar metric that provides a more generalized measure of how much total vegetation cattle eat at these plots and that is directly comparable with internationally established plant functional trait standards, in an attempt to draw parallels between how academics and managers are working with these data.

4.3.3 Statistical analysis

What spatial scales do range indicators vary at? To determine what spatial scale(s) indicators vary at (*i.e.* the spatial scale of heterogeneity for an indicator), I performed a variance components analysis [VCA, following Crawley (2012)]. A VCA partitions variation in an indicator across spatial scales. If significant variation in an indicator occurs at a particular spatial scale, this scale would be a good candidate to conduct further monitoring, especially if conditions are undesirable. I fit the model in a Bayesian rather than frequentist framework to avoid singular fits associated with fitting the model at the largest spatial scale, which contains only five groups. I fit a Bayesian linear hierarchical model with default priors using *rstanarm* (Goodrich et al., 2020), structured to sequentially partition the variance present in the range condition indicator from the largest spatial scale (1.72-km^2 extent) through to the smallest spatial scale (0.002-km^2 extent) within the sample design. To ensure that the Bayesian approach to estimating variance was robust, I compared the observed data to underlying data whose nested structure was randomly broken. Thus, in 999 bootstrap randomizations, I randomly permuted sites' locations and performed the same variance components analysis. I ranked the observed (real, unpermutted) data within these bootstrap randomization to statistically test whether each range indicator showed a statistically significant amount of variance at that spatial scale ($\alpha_{crit} = 0.05$).

Does inherent variation drive variation in indicators? Understanding whether indicators are more different in more different environmental conditions provides insight into the inherent factors that maintain heterogeneity across a landscape. For all cover and soil texture indicators, I calculated a Euclidean distance matrix which represents the distance between each potential pair of indicator values. To understand the integrity of the biological community, I calculated three β-diversity metrics that quantify compositional and phylogenetic differences in plant communities. The first metric, Sørenson's Index (calculated using *vegan::vegdist*; Oksanen et al., 2019), summarizes how many species two communities have in common and how many are unique to each community (Magurran, 1988). A value of 0 for the pairwise dissimilarity between two sites means that they have all the same species in common, while a value of 1 indicates no species in common. Sørenson's Index does not account for species abundances, and therefore, will likely over and underestimate the importance rare and more abundant species respectively. However, this metric effectively detects turnover in composition across environmental gradients, which makes it well suited for my objectives (Faith et al., 1987). The second metric of vegetation composition I looked at, Phylosørenson's Index (Phylosor; Bryant et al., 2008), is similar to Søreonson's Index, but instead of comparing richness between communities, looks at how much phylogenetic branch length each pair of communities shares (subtracted from 1, calculated using *pez::.phylosor*; Pearse et al., 2015). It ranges from 0, where both communities share all of the same taxa and therefore, evolutionary history, to 1 where both communities share zero branch length. The third metric of vegetation composition, the inter-community mean pairwise distance (COMDIST, was calculated using *pez::.comdist*; Pearse et al., 2015; Webb et al., 2008), compares the broader phylogenetic structure, or relatedness, between communities by contrasting the average branch length between species in each pair of communities, and is analogous to the α-phylodiversity metric SES_{MNTD}. I calculated the non-abundance-weighted version of COMDIST to maximize comparisons with the other two metrics. This metric complements Phylosor by identifying which communities have very different evolutionary relationships from others.

I used linear quantile regression to model the differences in each of these indicators across differences in environment (elevation, slope, and aspect) to understand whether there were differences in these indicators that are bigger (or smaller) than expected given the environmental differences (Koenker, 2022). This type of regression is similar to linear regression, in that it aims to understand the relationship between two variables. However, it differs in that it is performed on a specific quantile of the data, *e.g.*, the mean or median (τ=0.5), and minimizes the sum of weighted absolute deviations at that quantile to find the line that best fits the data, which makes it appropriate for use with distance matrices (Cade & Noon, 2003; Legendre & Legendre, 2012).

Do management strategies used for the past quarter-century influence indicator-environment relationships? The current management plans at this fieldsite include rotational grazing and pasture rest to maintain robust forage and wildlife habitat year-to-year. To identify whether these management strategies may be affecting range indicators, I looked at whether livestock type (cattle, sheep, or none) and pasture affected the relationship between range indicators and environmental conditions. For each indicator, I performed a nested analysis of variance (ANOVA) to test whether different subgroups within the data—the type of livestock grazing or the pasture a plot is located in—affected the relationship(s) between the indicator and environment. I used multiple linear regression to look at how each metric responded to additive environmental factors—elevation, slope, and aspect. In two separate models, I interacted these additive terms by each categorical factor—livestock type and pasture. This analysis identified the broad (categorical) conditions that affect these different indicators and whether they vary across environment. If these categorical conditions and/or environment significantly predict an indicator, these conditions will be good candidates for focusing management action.

Which indicators, including utilization, relate to undesirable species cover? To see how all of these indicators relate, I focused on the nineteen plots in the pastures where undesirable forage species, bulbous bluegrass and mule-ears, are most prevalent—Chicken Creek, Cottonwood, and Mud Flat. In 2020, I collected all of the same indicators collected at the plots in 2019, as well as pre- and post-cattle plant height to assess utilization. I used a scaled principal components analysis (PCA) to identify how all of these indicators are related to each other. PCA sequentially minimizes the variation in all of the data to generate orthogonal (at a right angle) axes, until all the variation in the data is minimized. Each variable, or in this case indicator, will associate most strongly with one of the axes and multiple variables can associate with one axis. Indicators that are highly correlated with each other will load positively or negatively onto the same axis, indicators that are negatively correlated will load onto opposite signs of an axis, and indicators that are not related will load onto different axes. I chose the number of axes to retain and discuss following Jackson (1993). This analysis summarized the relationships between all of the indicators of range conditions in these nineteen plots.

4.4 Results

At the eighty plots surveyed in 2019, I identified a total of 158 vascular plant species; 155 of these were included in calculating the plant biodiversity indicators—species richness, Faith's PD, and SES_{MNTD}. The soil texture in most plots was loamy; specifically silt loam

(28/80), sandy loam (25/80, loam (21/80), clay loam (3/80), and loamy sand (1/80, Appendix D). Two plots had clay soil texture. Ground cover-related indicators in many plots point to desirable range conditions. Over half of the plots (43/80) did not contain the two undesirable species—bulbous bluegrass and mule-ears—that concern managers and permittees and most plots (73/80) have below 40% cover by these two species (the threshold at which this indicator is considered undesirable; USDA Forest Service, 2003, 2019b). Many plots do not have any bare ground (23/80) and over half (58/80) have below the 15% cover threshold that typically concerns managers. Most plots (70/80) include some cover by desirable forage species.

What spatial scales to range indicators vary at? I used a variance components analysis to identify the spatial scales in the sampling design where indicators significantly varied, indicating the spatial scale of heterogeneity in the indicators. Overall, indicators related to undesirable conditions—bare ground and undesirable species cover—varied at moderate spatial scales, while indicators related to desirable conditions—good forage cover and biodiversity indicators—varied at the smallest spatial scale (Figure 4.2, Appendix D). Bare ground varied at both moderate spatial scales; 14% and 19% at 0.91-km^2 and 0.021-km^2, respectively. Undesirable species showed a similar pattern, but with 26% of the variance at both moderate spatial scales. Litter cover significantly varied at the smaller of the moderate spatial scales (25% at 0.021-km^2) and also showed significantly lower variance than expected in the residuals (15%). Good forage cover had 48% variance at the smallest spatial scale (0.002-km^2) and all biodiversity-related indicators also significantly varied at this spatial scale—species richness (10%), Faith's PD (18%), and SES_{MNTD} (33%, Appendix D). Like litter cover, good forage, Faith's PD, and SES_{MNTD} all had significantly lower than expected variance in the residuals—good forage had 16%, Faith's PD had 1%, and SES_{MNTD} had 48%. Faith's PD also had lower than expected variance at the largest spatial scale (80%, Appendix D).

Does inherent variation drive variation in indicators? Assessing whether differences in environment drive differences in indicators quantifies whether inherent variation in the environment (*i.e.* topography) supports variation, or heterogeneity, in the indicators.

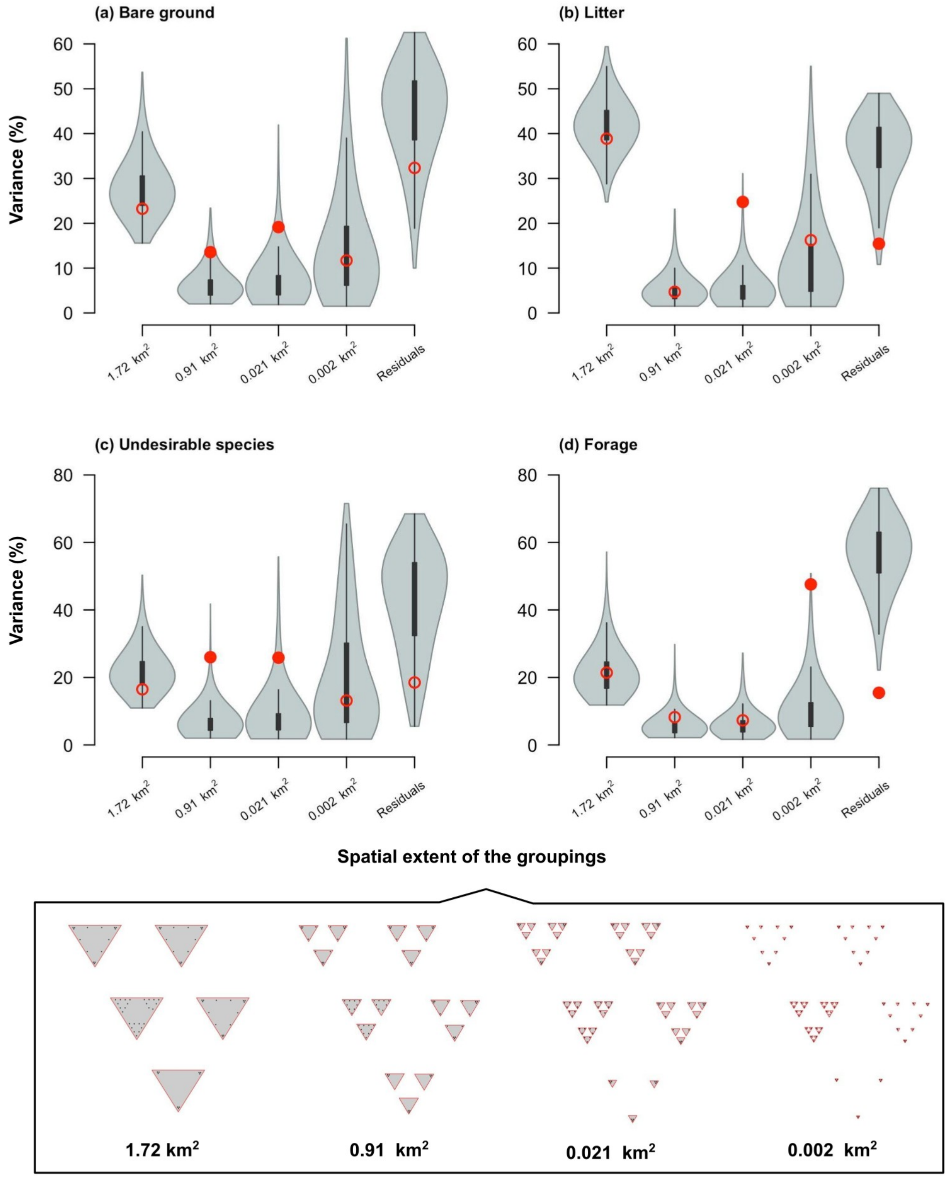

Fig. 4.2: **Bare ground and undesirable species vary at moderate spatial scales, while litter cover and forage vary at smaller spatial scales.** For each indicator—(a) bare ground, (b) litter cover, (c) undesirable species cover, and (d) good forage cover—a red point shows the observed amount of variation at a given spatial scale in contrast to a distribution of randomized diversity values at each spatial scale (999 iterations, gray violin plots). Filled red points indicate observed values that are significantly different from the randomized distribution. P-values of spatial scales with significantly different observed variance than the null distribution: bare ground (0.91-km^2 = 0.047, 0.021-km^2 = 0.034), litter (0.021 km^2 = 0.003, residuals = 0.014), undesirable species (0.91-km^2 = 0.006, 0.021-km^2 = 0.046), [good] forage (0.002-km^2 = 0.002, residuals = 0.001). Figures and statistics for all other indicators are reported in Appendix D.

Across all eight plots, the maximum difference in aspect was two, the maximum difference in elevation was 500 meters, and the maximum difference in slope was forty degrees. The minimum difference in all topographic variables was zero. Across topographic differences, both compositional and phylogenetic differences were strongly and significantly different in more different topographic conditions. On the most different aspects, community composition (Sørenson's Index) was 17% more different, and phylogenetic difference (Phylosor) was 8% more different than communities found on the same aspect (Figure 4.3). Similarly, on the most different slopes community composition and phylogenetic difference were both 11% more different, and at the most different elevations community composition was 9% more different, and phylogenetic difference was 5% more different (Appendix D). Across a range of differences in topography, many different pairs of communities did not share any species (Sørenson's Index = 1). For example, both a plot with moderate richness located next to a cliff in the riparian zone and a north-facing plot with high richness in conifer forest did not share any species with different south-facing plots with lower richness in sagebrush steppe vegetation. However, even the pairs of communities that do not share any species share at least some evolutionary history; all pairs of plots had Phylosor values less than 0.8. All other indicators were more subtly different at the maximum topographic difference (less than 5% different), but all significant changes in indicator difference across environmental differences are plotted in Appendix D.

Do management strategies used for the past quarter-century influence indicator-environment relationships? Categorical information about the grazing management plan used for the last quarter century influenced the relationships between bare ground and slope, SES_{MNTD} and aspect and elevation, and undesirable species and both aspect and elevation (Figure 4.4, Appendix D). Overall, sheep and cattle grazed across similar slope and aspect distributions, but cattle were grazed at lower elevations (1700–2000 m.a.s.l). Sheep were typically grazed at higher elevations (2000–2300 m.a.s.l.), but some plots were located as low as 1750 m.a.s.l. Cattle and sheep had similar numbers of plots with greater than 15% bare ground, eleven and ten plots respectively. However, in plots where sheep grazed,

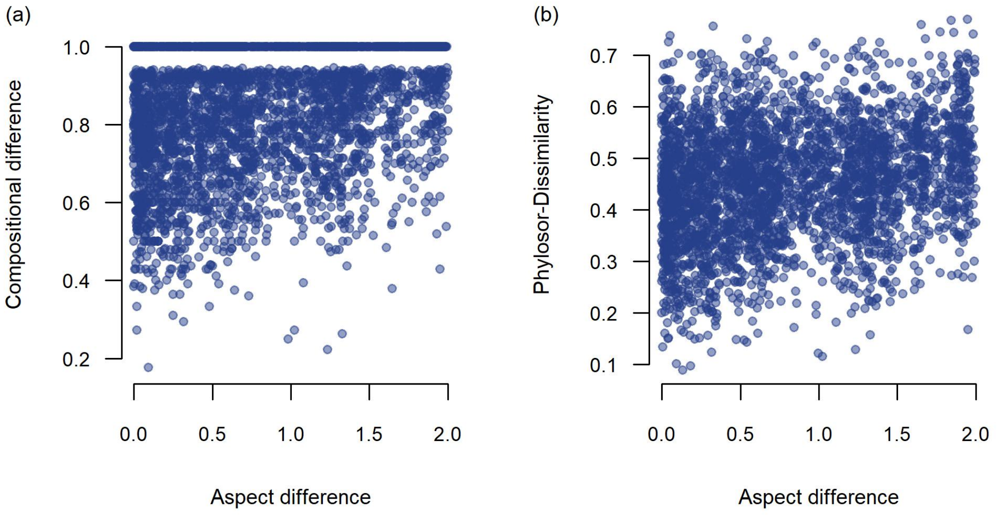

Fig. 4.3: **Differences in topography support compositional differences in plant communities.** On opposing aspects (*e.g.* north vs. south) plant communities have (a) more different species compositions (as measured by Sørenson's Index, slope = 0.084, p-value < 0.001) and (b) more phylogenetic difference (as measured by PhyloSor, slope = 0.041, p-value < 0.001). Differences in elevation and slope support qualitatively similar differences in taxonomic and phylogenetic plant community composition (Appendix D).

bare ground was not related to topography, while in plots where cattle grazed the amount of bare ground increased as the slope increased (Figure 4.4). Six of the plots grazed by cattle that had greater than 15% bare ground were found on twenty-five to thirty-five-degree slopes. Similarly, cover by undesirable species was associated with cattle grazing (6/7 plots greater than 40%) and increased with elevation, while sheep grazing did not influence the relationship between undesirable species and elevation. Specifically, the plots in the Mud Flat pasture had higher cover by undesirable species and this pasture influenced the relationship between that indicator and aspect (Figure 4.4). Otherwise, south-facing aspects typically had higher cover by undesirable species than north-facing aspects. SES_{MNTD} increased across aspect, with more closely related communities than expected by chance on south-facing slopes and less closely related communities than expected by chance on north-facing slopes (Figure 4.4). The three plots that were not in a pasture (black squares)

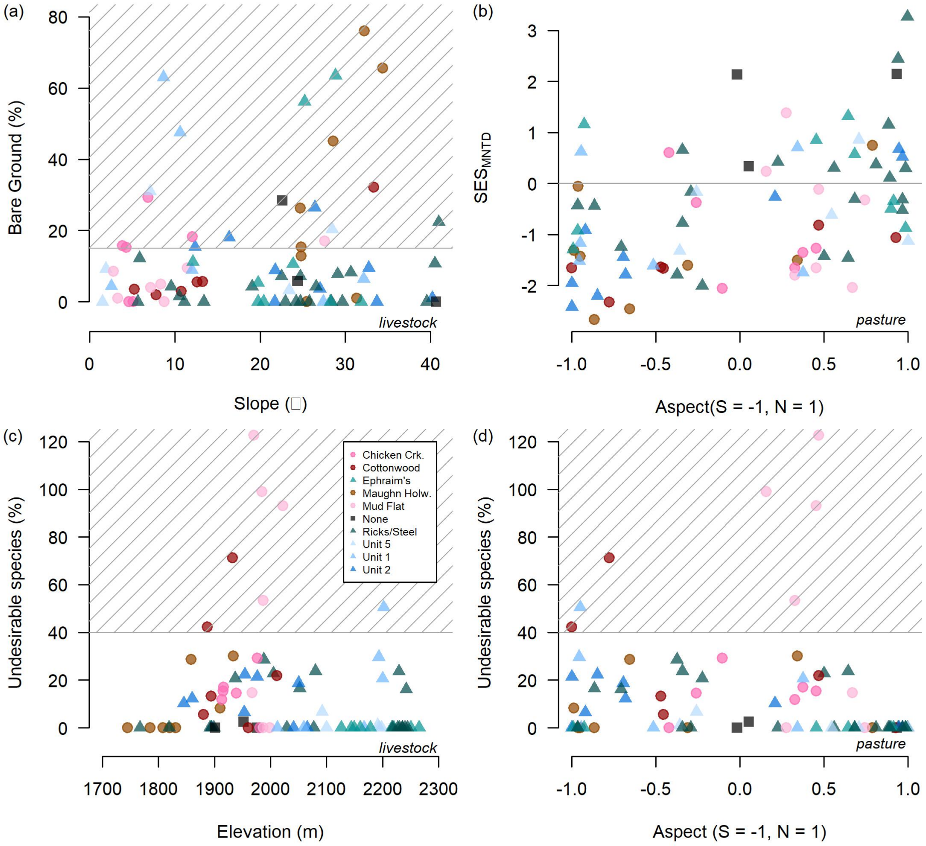

Fig. 4.4: **Both the type of livestock and pasture location affect the relationship between grazing indicators and the environment.** The relationship between (a) bare ground and slope and (c) undesirable species and elevation differ based on what type of livestock graze a plot. While bare ground increases as slope increases in plots where cattle graze, it does not change across slope in plots where sheep graze ($r^2 = 0.30$, $F_{10,69} = 2.911$, $p = 0.004$). Similarly, undesirable species increase as elevation increases in plots where cattle graze, but do not change across elevation in plots where sheep graze ($r^2 = 0.34$, $F_{10,69} = 3.597$, $p < 0.001$). Conversely, the relationship between (b) SES_{MNTD} and aspect and (d) undesirable species are both impacted by a particular pasture. Overall, SES_{MNTD} is higher on north- versus south-facing aspects, and plots that are not in a pasture (black squares) have an overall higher SES_{MNTD} ($r^2 = 0.69$, $F_{38,41} = 2.370$, $p = 0.004$). Undesirable species do not show a particular trend across aspect; however, that may be because of the effect of high cover by undesirable species in the Mudflat pasture (pink circles, $r^2 = 0.71$, $F_{38,41} = 2.642$, $p = 0.001$). The gray shading in (a), (c), and (d) marks the standard above which each indicator points to an ecosystem functioning-at-risk (15% and 40% respectively, USDA Forest Service (2003, 2019b)). The bottom right corner of each plot lists the categorical management grouping that significantly affects the relationship between an indicator and the environment.

influenced this relationship; all three of these communities were less closely related than expected by chance. While other indicators shifted across topography (Appendix D), they were not influenced by the categorical variables of the grazing plan—the type of livestock grazing or the pasture the plot was located in.

Which indicators, including utilization, relate to undesirable species cover? I used a PCA to determine which of seven indicators, including utilization, were most closely associated with high cover by bulbous bluegrass and mule-ears. This analysis focused on cover and utilization data collected in 2020 at nineteen plots in the three pastures with the largest patches of these undesirable species. The three principal component (PC) axes kept explained 75.4% of the total variation in these indicators. Along the first PC axis (39.7% of explained variation) I found negative correlations between coverage by bulbous bluegrass and mule-ears and all three diversity metrics I looked at—species richness, Faith's PD, and SES_{MNTD} (Figure 4.5). This result means that plots with higher diversity, as measured by any of these metrics, have lower coverage by these two unpalatable species. Utilization, bare ground, and the amount of clay in the soil are associated with the second PC axis (18.4% of the explained variation), and utilization shows a negative correlation with the other two metrics along this axis (Figure 4.5). This result means that plots with higher utilization have lower amounts of bare ground and less clay in the soil. Litter was associated most strongly with the third PC axis (17.5% of explained variation) and had a weak, negative relationship with the three diversity metrics and cover by undesirable species. This result means that areas with more litter tend to have slightly lower species richness and higher cover by undesirable species.

4.5 Discussion

The first overarching goal of this study was to identify the spatial scales of heterogeneity in range indicators and what inherent factors drive that variation. The second goal was to identify grazing conditions, locations, and indicators to focus future monitoring and management actions on to achieve more desirable conditions across this range. Broadly, I found that undesirable range conditions—bare ground and undesirable species cover—vary at moderate

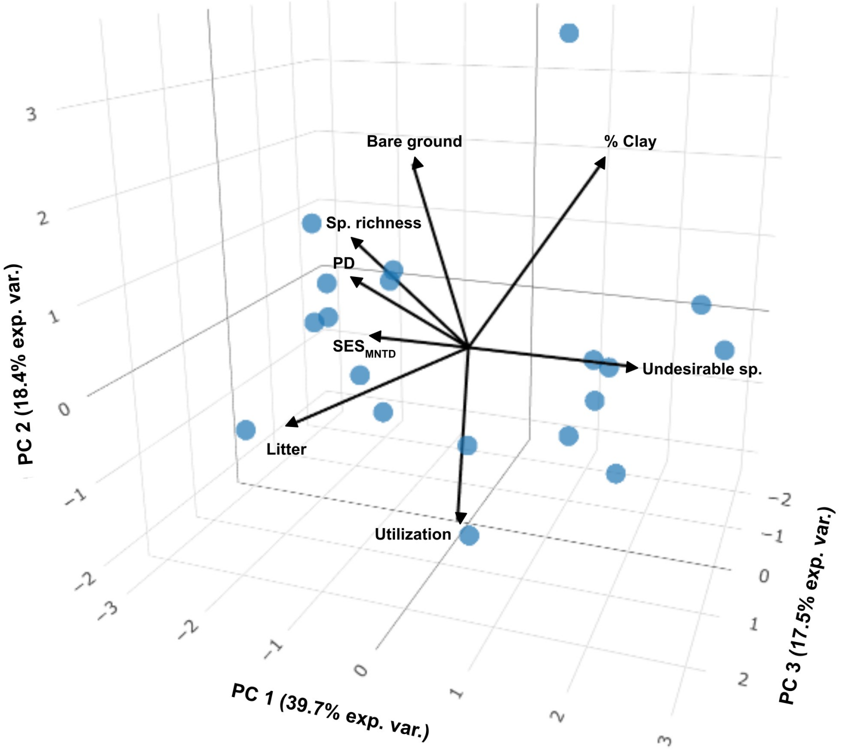

Fig. 4.5: **Range condition indicators associate with PC axis of variation defined by relationships between diversity and undesirable species (PC 1) and indicators of utilization (PC 2).** Each arrow shows one of the indicators assessed in nineteen plots in 2020 (Figure 4.1). Coverage by undesirable species negatively correlated with all diversity-related indicators (and litter cover) and loaded onto PC 1 which explained 39.7% of the variation in the data. Utilization, bare ground, and the amount of clay in the soil loaded onto PC 2 (18.4% of explained variation), with a negative correlation between utilization and both bare ground and clay (%). Litter loaded most strongly onto PC 3 (17.5% of explained variation).

spatial scales, while desirable range conditions—good forage cover and biodiversity—vary at the smallest spatial scale. Inherent variation in topography mainly drove compositional (and phylogenetic) differences in plant communities but did not strongly impact other range indicators. Bare ground increased as slope steepness increased and cover by undesirable species increased as elevation increased, in plots grazed by cattle. Cover by undesirable species was especially high in the Mud Flat pasture. Finally, undesirable species are related to with lower biodiversity and litter cover. Based on these results I make two overarching recommendations about which spatial scales, environmental conditions, and indicators to monitor and manage undesirable and desirable range conditions.

Recommendation 1: Monitor and manage undesirable range conditions, like bare ground and undesirable species cover, at a one-km^2 spatial scale, in pastures grazed by cattle.

Two undesirable range condition indicators partitioned variance across the two moderate spatial scales—bare ground and undesirable species. Combined, the 0.91-km^2 and 0.021-km^2 spatial scales partitioned 33% of the variance in bare ground and 52% of the variance in undesirable species cover (Figure 4.2). The co-occurrence of higher amounts of variation in these indicators at the same spatial scales indicates that similar factors impact these indicators or that these indicators interact. If bare ground results from livestock disturbance, the cumulative effects of vegetation removal and trampling by livestock can work in tandem with acute disturbances, like fire and drought, to produce more bare ground (Danvir et al., 2018; Weber et al., 2009). Without management, undesirable species (*i.e.* poor forage and noxious weeds) often grow and spread in bare ground and also act in an amplified cycle with acute disturbances (Morrow & Stahlman, 1984; USDA Forest Service, 2003). While we did not directly assess whether heavy grazing in the last quarter century led to large patches of bulbous bluegrass and mule-ears, high cover by these species typically indicates heavy grazing throughout Utah and other rangelands (Davis et al., 1996; Kachergis et al., 2014).

Bare ground increased as slope increased, but only in plots grazed by cattle (Figure 4.4). This indicates that in plots grazed by cattle, bare ground may be interacting with livestock disturbance and leading to degraded soil stability on steep slopes (Pellant et al., 2020). Even though bare ground did not change across topography in plots grazed by sheep, both of these grazers had similar numbers of plots above the 15% threshold of concern (USDA Forest Service, 2003). However, the plots above this threshold (22/80) may not currently be a concern. Almost half of the variation in good forage cover (48%) occurred at the smallest spatial scale in the sampling design (Figure 4.2). This indicates high heterogeneity in desirable range conditions and nutrition for cattle, even though, more broadly, undesirable conditions are a concern. While it would require more direct study and monitoring, high heterogeneity in good forage means that there are likely native propagules near current bare soil that could provide a seed source for revegetation. Leveraging current management practices in these pastures, like rotation grazing (USDA Forest Service, 2022a), and resting pastures, especially at times that are critical for plant reproduction, may help reduce bare ground as long as bare soil is not too compacted.

Even without changing the current grazing rotational schedule or stocking rates, this range would benefit from more attention to moving cattle away from areas with bare ground that is directly connected to livestock disturbance (*e.g.* near water and shade resources) and forage areas that visually appear to have greater than 15% bare ground. This action could be implemented using active herding, salt blocks, and other strategies already suggested in the annual operating instructions for this allotment (USDA Forest Service, 2022a). However, this strategy only has the potential to help reduce bare ground if it is consistently applied over a longer time frame or may require more active intervention like resting pastures (10+ years, Danvir et al., 2018). Management actions to reduce cover by bulbous bluegrass and mule-ears must account for the tradeoff between the benefit of stabilization and poor forage quality these species provide. A combination of mechanical and herbicide-based removal applications can reduce mule-ears cover (Maxwell et al., 2021; Mueggler & Blaisdell, 1951). Overall, I recommend that bare ground and undesirable species cover continue to be monitored to directly assess if these indicators change (1) in response to each other, (2) as a result of livestock disturbance (or lack there-of, *i.e.* rest from grazing) and (3) environmental conditions like drought. Since the Mud Flat pasture had a particularly high cover by undesirable species (Figure 4.4), this may be a good location to study the potential interaction of undesirable species and bare ground. Additionally, bare ground can be monitored via remote sensing and other aerial techniques, so it may be a good candidate for assessing rangeland conditions at larger spatial scales in WCNF (Breckenridge & Dakins, 2011; Rigge et al., 2020; Weber et al., 2009).

Recommendation 2: Monitor and manage desirable range conditions, like good forage cover and vegetation biodiversity, at smaller spatial scales to address undesirable species cover.

High heterogeneity of (graminoid) forage species at small spatial scales indicates that nutritious forage for livestock is well dispersed across this range (Figure 4.2). Biodiversity metrics—species richness, Faith's PD, and SES_{MNTD}—also significantly varied at this spatial scale. Like the undesirable range conditions that varied at the same spatial scales, this co-occurrence of significant variance suggests that similar factors impact these indicators or that these indicators interact. Inherent topographic differences supported greater differences in both plant community composition and phylogenetic difference and categorical information about grazing does not affect biodiversity-environment relationships (Figure 4.4). This means that landscape heterogeneity supports vegetation heterogeneity and currently, grazing regimes do not appear to impact good forage cover or biodiversity.

Additionally, there was a negative correlation between all three diversity metrics and undesirable species (Figure 4.5). This relationship means that species richness can be used as a monitoring tool and management objective, because it has the same relationship with the management concern as more complex metrics, like Faith's PD or SES_{MNTD}. This result indicates a strong constraint on species richness (and thereby phylogenetic diversity) related to the presence and abundance of undesirable species, which is surprising given that we did not see a constraint on species richness (but did see a constraint on phylogenetic diversity and structure metrics) on south-facing slopes with more harsh conditions (Simpson & Pearse, 2021c).

Overall, heterogeneous vegetation provides opportunities for management that focuses on maintaining more functional, diverse vegetation patches and increasing cover and species richness in patches that have high amounts of bare ground and/or undesirable forage species. Existing heterogeneity in biodiverse vegetation can support revegetation by desirable forage species (Mangold et al., 2015). Maintaining diverse vegetation patches (as opposed to restoring) better sustains populations of reproducing individuals that act as a seed source for non-restored, degraded patches of vegetation and bare ground (Davies & Sheley, 2011; Hulvey et al., 2017; Landeen et al., 2021). It will be important to continue to monitor and maintain the current cover of both native and introduced perennial bunchgrasses to potentially promote natural revegetation in bare soil (Davies et al., 2021). Based on the frequency of grasses found within the plots (Appendix D), I suggest that bluebunch wheatgrass (*Psuedoroegneria spicata*) and blue wildrye (*Elymus glaucus*) would be good native candidates to monitor and manage, while smooth brome (*Bromus inermis*) and crested wheatgrass (*Agropyron cristatum*) would be good introduced candidates.

Maintaining and restoring vegetation heterogeneity can promote greater biodiversity across the range as a whole, improves wildlife habitat, and can help with managing undesirable species (Fuhlendorf et al., 2017; McGranahan et al., 2012). Adaptive changes to the current grazing rotational schedule and stocking rates (year-to-year) may help maintain and restore vegetation heterogeneity, increase the cover of desirable forage species, and decrease the presence of undesirable species. Rotational grazing that varies the seasonality of grazing helps promote overall vegetation health in rangelands. Adjusting stocking rates and the timing of grazing depending on current climate conditions and forage production can enhance vegetation heterogeneity (Jakoby et al., 2015). This strategy is especially important in rangeland with high climate variability. Additionally, since species richness follows similar patterns to phylogenetic diversity (at least, in terms of predicting undesirable species) and phylogenetic and functional diversity are conserved (see the previous chapter), strategies that protect and increase plant species richness will also likely support a more functional and stable ecosystem across this range (Tucker et al., 2019).

4.6 Conclusion

Maintaining the desired conditions of working landscapes will be critical to supporting both human livelihoods and ecosystem health. While complex, interacting factors make it hard to assess rangeland conditions, these factors also provide opportunities to enhance complexity (*i.e.*, heterogeneity) across space and environments. Based on the results, I make two overarching recommendations for improving the range conditions in this location, and potentially the Bear River range more generally. (1) Monitor and manage undesirable range conditions, like bare ground and undesirable species cover, at a one-km^2 spatial scale in pastures grazed by cattle. (2) Monitor and manage desirable range conditions, like good forage cover and vegetation biodiversity, at smaller spatial scales to address undesirable species cover. These recommendations serve as a starting point for improving and maintaining range conditions and demonstrate how methods that assess the spatial scale of range indicator heterogeneity and the impact of inherent and management-based variation should continue to be used in rangeland monitoring whenever possible. Applying these recommendations in the context of managing adaptively will help maximize rangeland functionality for humans while also supporting the health of ecosystems both now and in the future.

CHAPTER 5

CONCLUSION

Broadly, I found that phylogenetic and functional diversity shifted across aspect-driven variation in near-surface soil temperature, even though taxonomic diversity metrics did not. In this arid, Northern Hepmisphere location, hotter, more variable south-facing slopes (in contrast to north-facing slopes) support more closely related assemblages, with lower functional dispersion, shorter stature, and more conservative resource acquisition (leaf) traits. The spatially-explicit analysis of these metrics also indicates an overall environmental filter at this site, which may result from the combined effect of changing and interacting abiotic and biotic conditions across aspect (Cadotte & Tucker, 2017). However, when I applied this research framework to investigate rangeland management concerns, I found that non-phylogenetic and functional trait-related indicators were the best candidates to focus future management actions on. Overall, I recommended management actions that reduce bare ground cover and undesirable species (by increasing species richness in these areas) and maintain diverse vegetation in areas where that already occurs. Below, I discuss four themes that reoccurred throughout this dissertation and how they inform future observations and experiments aimed at collaboratively monitoring and managing healthy ecosystems.

5.1 Assess both phylogenetic and functional diversity for the best representation of ecological risk. (Ch. 2, 3 & 4)

Research that assesses phylogenetic diversity without looking at functional diversity (or at least whether traits are phylogenetically conserved), risks making an assumption that does not always hold true (Mazel et al., 2018). The relationship between phylogenetic and functional diversity can inform how at risk of losing important ecosystem functions an assemblage is, especially when both traits that respond to environmental stressors and traits that affect ecosystem processes are assessed (Díaz et al., 2013). If the assumption of traits being phylogenetically conserved is met and there is a strong correlation between response and effect traits, the ability for an assemblage to maintain ecological function is most at risk. However, many traits both respond to environmental conditions and affect ecosystem processes/services, so I assumed that current variation in functional trait strategies across environment represents a unified functional strategy of response and effect traits, without directly measuring ecosystem function (Elmqvist et al., 2003; Reich, 2014; Suding et al., 2008).

Both phylogenetic and functional diversity shifted across aspect-defined near-surface soil temperature gradients. The more closely-related communities on south-facing slopes were less functionally dispersed and had shorter stature and more conservative leaf traits than north-facing slopes. This relationship between phylogenetic and functional diversity demonstrates an environmental and evolutionary constraint on species in the harsher environment on south-facing slopes. Knowing that the link between phylogeny and function exists under these conditions provides support for just using phylogenetic metrics to understand how communities are shifting across similar nearby environments. Additionally, functional dispersion only evaluated two traits that provide information about plant function and are likely to correlate with resource availability and lack thereof—(1) height and (2) leaf economic strategy. It would be interesting to see whether the trend of functional dispersion changes if traits related to functions that I might expect to have more variation in them (*e.g.*, dispersal) were collected and included.

Species richness and Simpson's diversity did not respond to environmental gradients at the fieldsite, whether these were defined by topography, near-surface-soil temperature, and/or texture. However, phylogenetic diversity metrics—like Faith's PD and SES_{MNTD}—shifted across aspect and allowed me to make inferences about the ecological processes shaping this difference. Future studies in this area must continue to carefully consider the questions a metric can help answer and I encourage the comparison of different metrics that provide contrasting information about assemblages' evolutionary history. For example, I found that SES_{MNTD} and Faith's PD were more predictive than species richness.

Specifically, Faith's PD provided more information about how assemblages respond to environmental gradients than species richness, likely because it includes information about the total evolutionary history of species in an assemblage. These findings provide support for the use of phylogenetic metrics in conservation work, one of the initial purposes of these metrics (Faith, 1992; Gerhold et al., 2008), but only in conjunction with the assessment of phylogenetic diversity (Tucker et al., 2019)

5.2 Include aspect in range-shift studies. (Ch. 2 & 3)

Many studies about how species might move, or shift their ranges, in response to climate change, focus on species moving uphill or poleward to cooler elevations and latitudes (Parmesan & Yohe, 2003; Rubenstein et al., 2020). Within these broader trends many different processes—both physiological (*e.g.*, functional) and demographic (migration, persistence, extinction)—direct potential species range shifts (Thuiller et al., 2008). My work focused on functional traits, which provide indirect insight into physiological dynamics that are occurring in different environmental and spatial conditions. Based on the shifts in diversity across aspect that I found; I suggest that future range studies target aspect as a potential moderator of increasingly warm and variable climate. This provides a mechanistic link for how I expect species traits to vary across aspect, which may help make traits more useful for understanding range shifts (Beissinger & Riddell, 2021).

For example, I found a 6°C mean temperature difference across south- to north-facing slopes and if the variance in temperature tracks this shift in the mean, like it did across the plots, this differentiation holds promise for supporting species if they can migrate and persist on the opposite slope. In arid environments where water is limited, less evapotranspiration on cooler south-facing slopes supports taller more resource-acquisitive assemblages, which I also saw (Albrich et al., 2020; Yang et al., 2020). In more humid environments, vegetation dynamics and composition are often still different on north- versus south-facing slopes, even though heat-regulated water limitation is not necessarily driving (Ackerly et al., 2020; Elliott & Cowell, 2015). Mobile organisms may even be able to take advantage of the temperature differentiation provided by aspect on shorter timescales than plants (Feldmeier et al., 2020).

5.3 Leverage methodology to determine the influence of spatial scale. (Ch. 2 & 4)

Ecologists know that ecological processes operate at and across different spatial scales (Chave, 2013; Levin, 1992). By coupling the fractal-based sampling design I used with a variance components analysis, I pinpointed the spatial scales where diversity and range-health metrics varied the most. The flexibility of the sampling design allowed me to add a smaller-scale level of sampling in the second year of surveys because the results from the first year suggested that processes might be driving patterns at smaller spatial scales. Indeed, I captured more variance in phylogenetic structure metrics (SES_{MNTD} and SES_{MPD}) at this smallest spatial scale (81 total plots); however, I detected these patterns at the next largest spatial scale (27 plots). This indicates that these 27 plots are good candidates for long-term monitoring if a researcher or manager wants to understand long-term trends in plant biodiversity across aspect at this fieldsite.

We suggest that spatially-explicit designs like this can serve a similar role to sampling curves, but instead of sampling until little or no species are added, additional and fewer spatial scales can be used, as needed, to understand ecological dynamics. I also identified the spatial scale(s) that range health indicators varied at in the fourth chapter, which allowed me to make scale-specific recommendations about how to focus management actions to improve range health. The tool of spatially explicit sampling designs will help ecologists account for the effect of spatial scale in patterns they observe and can directly inform more efficient allocation of research and management resources (Ewers et al., 2011; Jackson & Fahrig, 2015; Marsh & Ewers, 2013; Wheatley & Johnson, 2009).

Fractal designs perform especially well in periodically-variable environments, like mountains, where the many interacting ecological processes shaping observed patterns are unknown. I knew that a similar fractal-based design effectively detected turnover in diversity (β-diversity) in variable landscapes (Marsh & Ewers, 2013). The simulation I did to compare the fractal-based design to classic sampling designs—random, grid, and transects—showed that in periodically variable environments the fractal design detects changes in α-diversity across environment as well or better than the other three designs. This theoretical work validates the empirical results in a broader context and builds on a body of work supporting equilateral-triangle-fractal-based sampling designs as efficient, flexible tools for assessing ecological patterns and processes (Albert et al., 2010; Halley et al., 2004; Kallimanis et al., 2002; Luzuriaga et al., 2012).

5.4 Assess manager concerns to generate unique, complementary insights. (Ch. 4)

In translational ecology, the process of making usable science involves academic researchers coproducing knowledge with land managers, users, and other stakeholders. This framework centers on good communication and long-term engagement to help different individuals collaborate and better understand the context that frames the challenges research and management seek to address (Enquist et al., 2017). Ideally, all individuals are part of understanding the many interacting parts of a system and co-designing research questions and studies from the beginning. Even though my initial questions and study system were not developed with this translational framework in mind I was still able to apply the principles and goals of translational ecology to assess manager and range user concerns at the fieldsite I worked in. I accomplished this by having listening-focused conversations with managers, learning about and helping out with range monitoring, and centering my research within their perspectives and concerns. This helped me understand that we have a common goal of understanding, maintaining, and improving the quality and health of vegetation across this landscape. Within this context, I am well-positioned to help managers navigate new metrics and tools that may or may not help them address their concerns.

For example, as described in the first theme, one of my main findings is that phylogenetic and functional diversity metrics better capture differences in assemblages across topography and temperature gradients. However, when I focused on coverage by two species that managers and range users are concerned about —bulbous bluegrass and mule-ears—I found a negative correlation between species richness and the amount of cover by these species. This provides support for using species richness, instead of more complicated phylogenetic diversity metrics, in the context of understanding and managing potentially increasing poor forage species. While looking at evolutionary history and structure could continue to provide interesting insights about plant assemblages at this site, especially over long periods of time, I found evidence that it is not necessary to measure it to understand manager and user concerns.

The rangelands across the Bear River Range provide a unique context in which to study ecosystem health and how management actions can improve and support that. The presence of large patches of bulbous bluegrass and mule-ears provides an opportunity to develop and implement experiments that test the efficacy of different treatments aimed at increasing the diversity and overall cover of higher-quality forage. It will be especially important to study these treatments in the context of environmental variability, like near surface soil temperature, because that affects the establishment of plants in reseeding projects (Landeen et al., 2021), is an overall concern for managers (Maczko et al., 2016), and I found variation in diversity across temperature gradients. However, projects like this will require collaborative, communication-based relationships with academic researchers who often have more resources to contribute toward something like this. Applying these projects in the context of adaptive management will develop rangeland functionality for humans while also supporting the health of ecosystems both now and in the future.

5.5 Final thoughts

In an increasingly hot and variable global climate, innovative tools, collaborations, and diverse knowledge systems will all be critical to understanding how to manage ecosystems to sustain their health and the services they provide to humans (Díaz et al., 2018). In this dissertation, I focused on understanding the effect of spatial scale on relationships between vascular land plant diversity and environment at a mountainous fieldsite in northeastern Utah. In the context of an active rangeland, I demonstrate and discuss the complementary efficacy of phylogenetic and functional diversity to detect shifts in diversity, and underlying ecological processes, that taxonomic diversity metrics did not always detect. I show how near-surface soil-temperature-defined microenvironments support distinct functional and phylogenetic assemblages, especially across aspect. Finally, by having discussions with local managers about their goals and objectives for this area, I adapted my data collection and analysis to focus on their concerns and provide recommendations for how to prioritize management actions. This thesis was informed by a wide range of disciplines—community, Indigenous, restoration, spatial, and translational ecology, evolutionary and invasion biology, and sampling theory, among others. Drawing expertise from diverse fields and perspectives allowed me to ask more holistic questions about the intertwined nature of ecosystem wellbeing and, ultimately, humans' wellbeing as members of ecosystems.

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APPENDICES

APPENDIX A

Supplementary tables and figures for chapter 2: Fractal triads efficiently sample ecological diversity and processes across spatial scales

Table A.1: **Source-pool definitions affect the overall value of SES_{MNTD} but not SES_{MPD} at the 4th triad level.** Each column shows the summary statistics of a paired t-test for a given phylogenetic structure metric (row 1) calculated with two different source-pool definitions (row 2, as defined in the main text, Figure 2.1a). For each paired t-test, we compared the smaller source-pool definition to the next largest source-pool definition to demonstrate how the overall values of the metrics shift across source-pool definitions. When the mean of the differences is positive (row 3), this indicates a shift toward a comparatively more overdispersed metric when we use a smaller source-pool definition. Conversely, when the mean of the differences is negative, this indicates a shift toward a comparatively more clustered metric when we use a smaller source-pool definition. For SES_{MNTD}, both smaller source-pool definitions caused the overall metric to become significantly more overdispersed (albeit, still exhibiting overall patterns of clustering, shown in columns 1 and 2, both p-values <0.001). Smaller source-pool definitions did not significantly affect the overall value of SES_{MPD} (both p-values > 0.05).

Metric	SES_{MNTD}		SES_{MPD}	
Source-pool comparison	Major, Total	Minor, Major	Major, Total	Minor, Major
Mean of the differences	0.215	0.282	0.021	-0.043
SE of the mean of the differences	0.034	0.049	0.033	0.046
t_{77}	6.258	5.758	0.624	-0.936
p-value	<0.001	<0.001	0.535	0.352

Table A.2: **Source-pool definitions also affect the overall value of SES_{MNTD} but not SES_{MPD} at the 3rd triad level.** Rows and columns as described in Table A.1. For SES_{MNTD}, a smaller source-pool definition caused the overall metric to become significantly more overdispersed (albeit, still exhibiting overall patterns of clustering, shown in column 1, p-value = 0.001). A smaller source-pool definition did not significantly affect the overall value of SESMPD (shown in column 2, p-value > 0.05)

Metric	SES_{MNTD}	SES_{MPD}
Source-pool comparison	Major, Total	Major, Total
Mean of the differences	0.195	0.012
SE of the mean of the differences	0.054	0.055
t_{25}	3.636	0.218
p-value	0.001	0.829

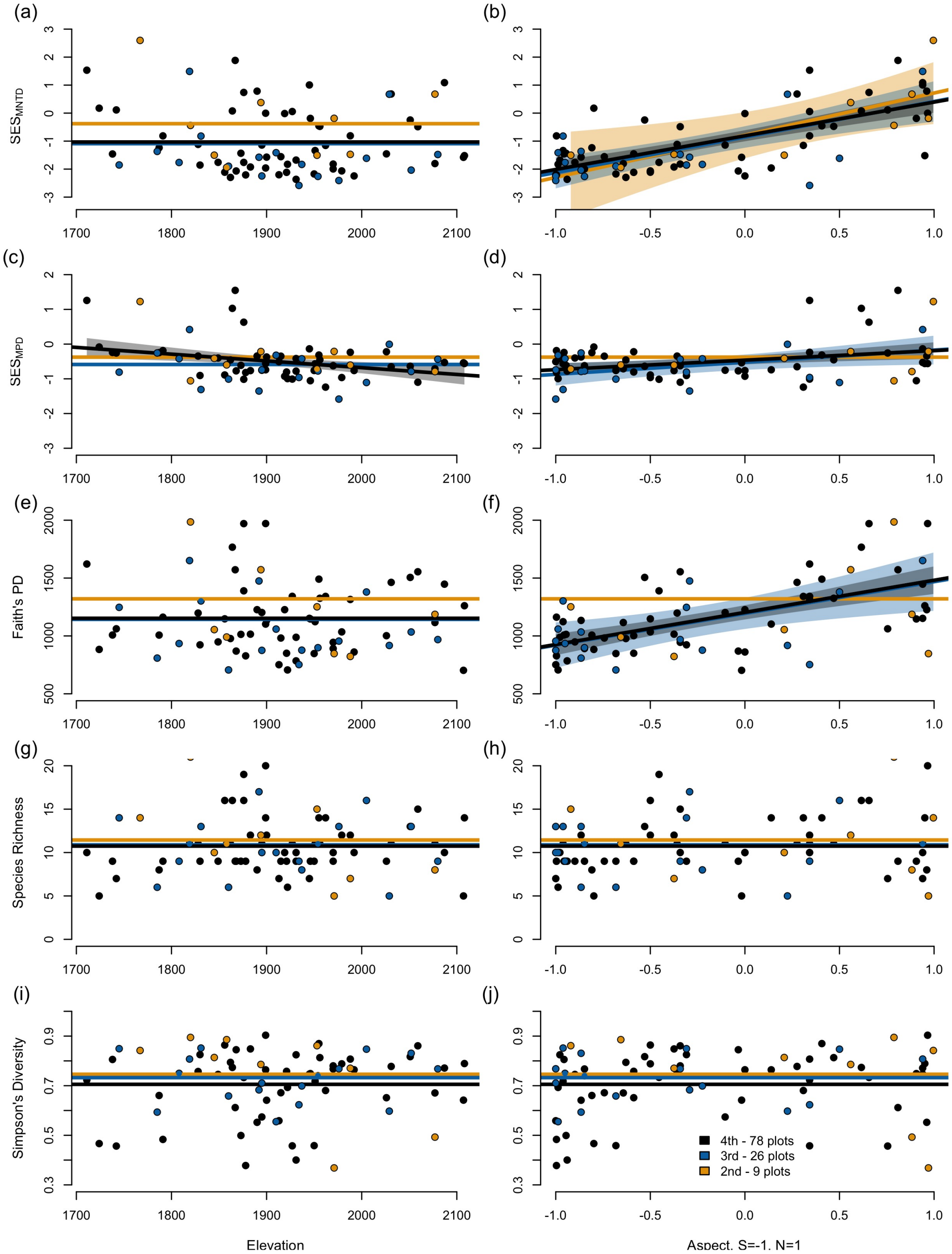

Fig. A.1: **A number of the diversity metrics we assessed did not change across aspect or elevation.** Calculating these metrics (as done in Figure 2.3) at different triad levels (Figure 2.1b) can affect the overall mean of these metrics, as shown. Left column shows change (or lack thereof) in diversity across elevation while the right column shows the same diversity metrics across aspect. Each row shows the results for one biodiversity metric; (a, b) SES_{MNTD}, (c, d) SES_{MPD}, (e, f) Faith's PD, (g, h) species richness, and (i, j) Simpson's diversity. Color scheme and models plotted as described in Figure 2.3 caption and panels (b), (c), (d), and (f) match the results plotted in Figure 2.3.

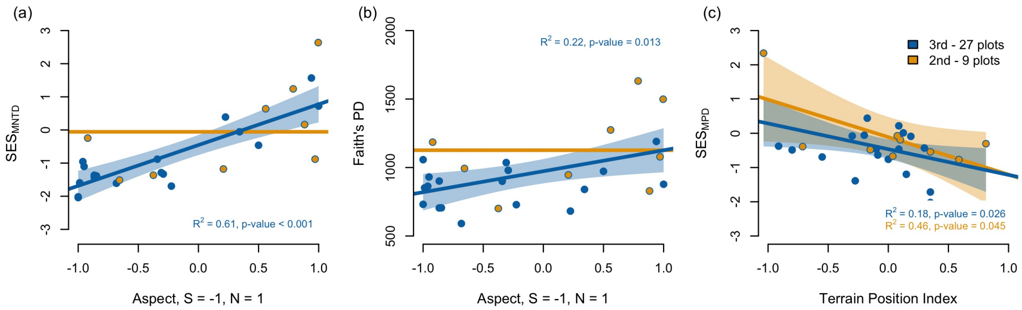

Fig. A.2: **We found significant changes in diversity across environment in 2017, which motivated us to add a 4th triad level in 2018.** Each panel shows change in (a) SES_{MNTD} across aspect, (b) Faith's PD across aspect, and (c) SES_{MPD} across Terrain Position Index. Color scheme and models plotted as described in Figure 2.3 caption.

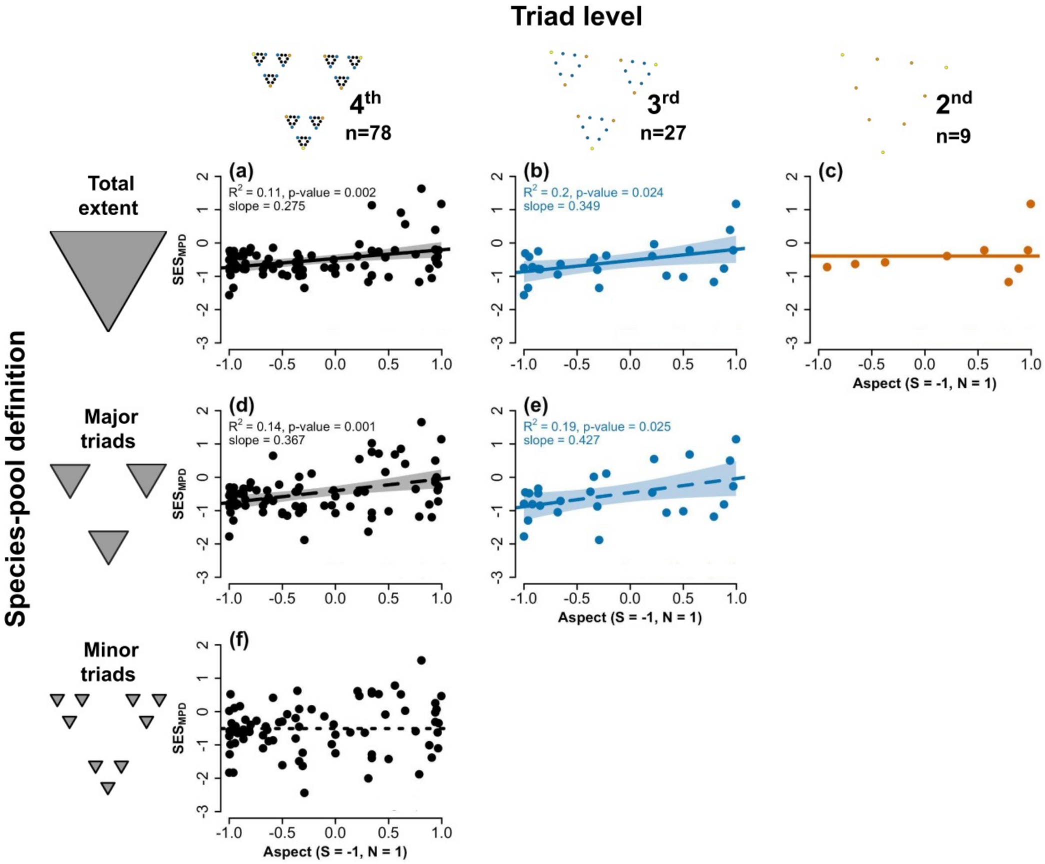

Fig. A.3: **When the source pool for an assemblage is defined as the major triad group it is in, we observe a similar trend in SES_{MPD} across aspect as when the source pool is the total extent of the study.** However, when the source pool for an assemblage is defined as the minor triad group it is in, we no longer detect a relationship between SES_{MPD} and aspect. This indicates that environmental filtering at larger spatial scales within our study, drives changes in SES_{MPD} across aspect. Explanation of plot in the main text (Figure 2.4 caption).

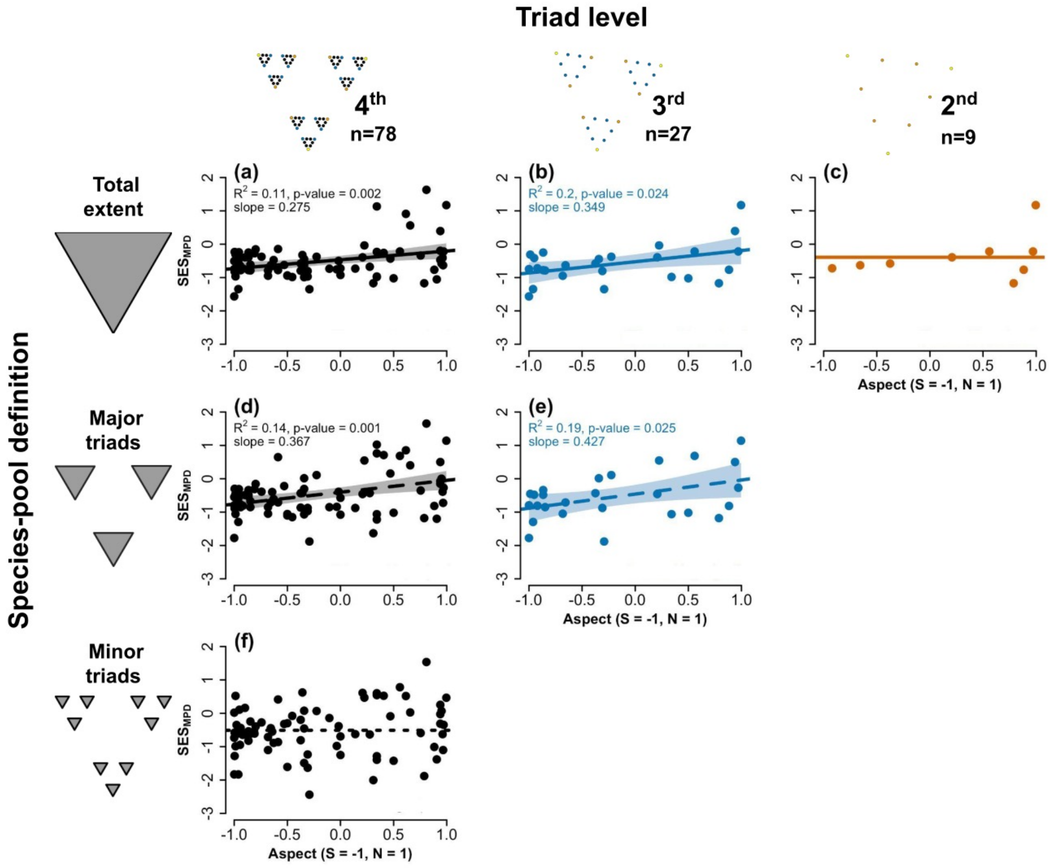

Fig. A.4: **When the source pool for an assemblage is defined as the major or minor triad group it is in, we no longer detect a relationship between SES_{MPD} and aspect.** This indicates that environmental filtering, at the largest spatial scale in our study extent, drives changes in SES_{MPD} across elevation. Explanation of plot in the main text (Figure 2.4 caption).

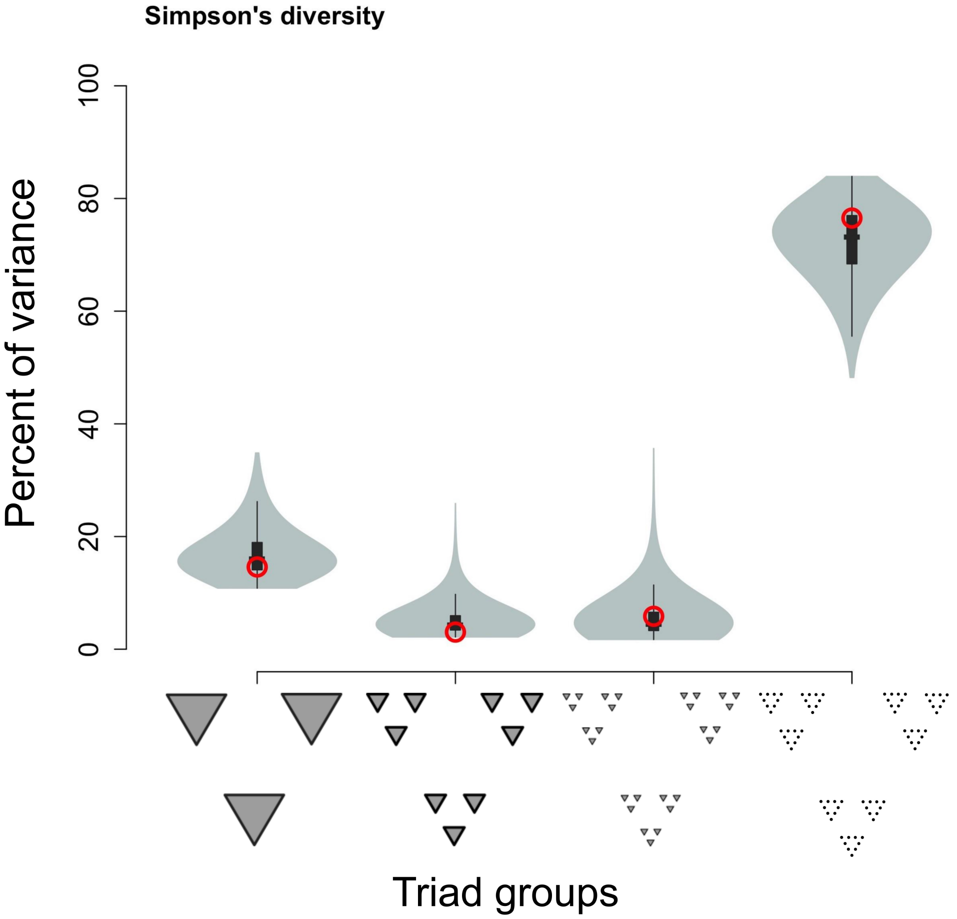

Fig. A.5: **None of the triad groupings, which define spatial scales, accounted for a significant portion of the variance in Simpson's diversity at Right Hand Fork.** Explanation of plot in main text (Figure 2.5 caption.)

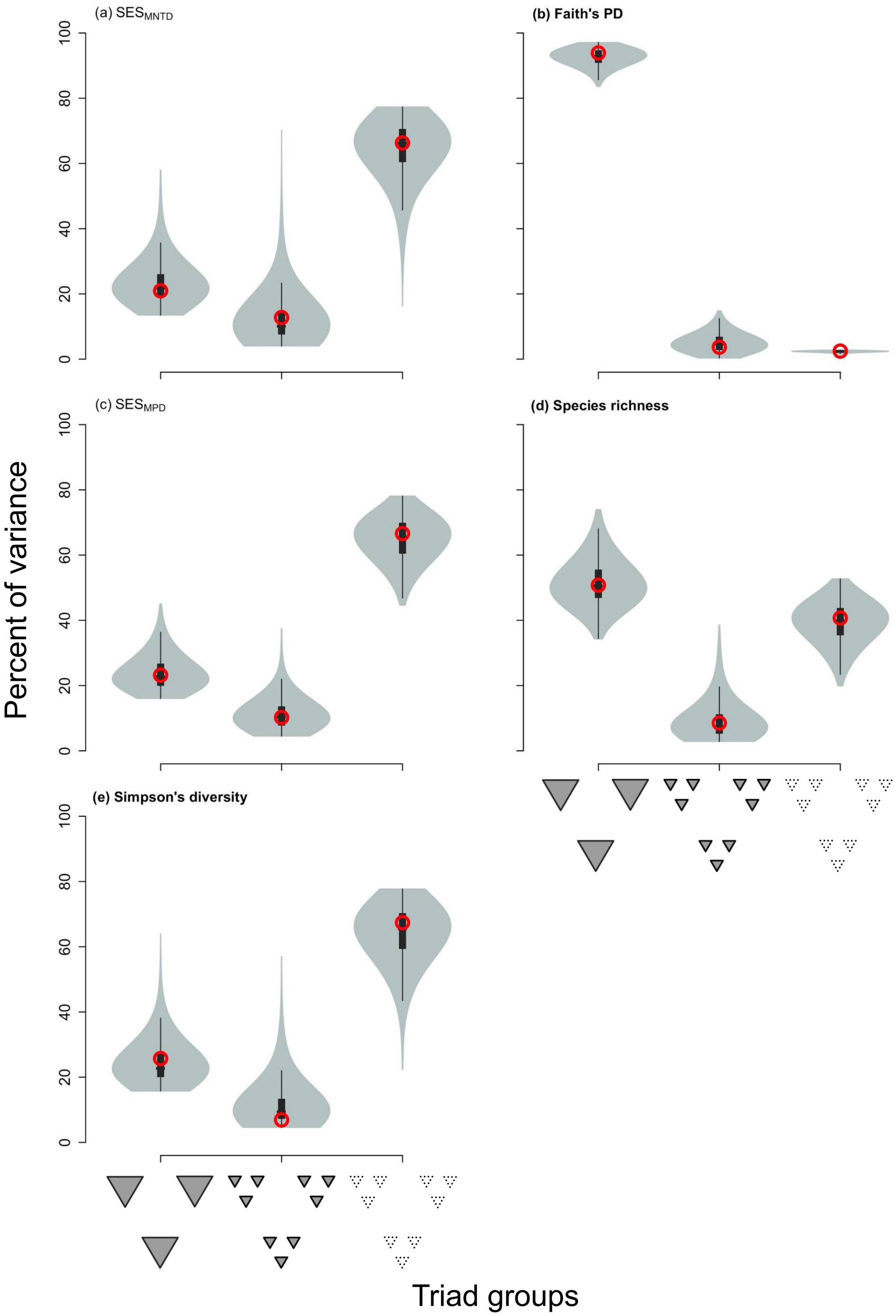

Fig. A.6: **When we surveyed with only three triad levels in 2017, none of the triad groupings accounted for a significant portion of the variance in the five diversity metrics we calculated.** Explanation of plot in main text (Figure 2.5 caption.)

APPENDIX B

Fractals sample diversity-environment relationships in periodically variable landscapes as well or better than classic sampling designs: a simulation

B.1 Introduction

The best sampling design to answer a given ecological research question depends on many factors, including what is being assessed at each sampling point, whether the question requires cross-scale sampling, and how much time and resources are available. We are interested in the potential of fractal designs to effectively answer cross-scale questions about how diversity changes across environment. A previous simulation study found that comparing fractal, grid, transect, and random sampling designs, only fractal designs partition diversity across all of the spatial scales they were interested in looking at (Marsh and Ewers 2013). They looked at sampled turnover (β-diversity) across randomly-oriented linear environmental gradients, and found that fractal designs slightly underestimate β-diversity across spatial scales but but capture similar diversity-environment relationships to that of the control design. They also looked at how well these different designs capture α-diversity and found that the proportion of diversity was consistently sampled by all designs.

We implemented the fractal design we propose in mountainous terrain in Northeastern Utah. Like many mountainous landscapes, this environment is highly heterogeneous and undulating at both fine and broad spatial extents. Visually, from an aerial view, this natural landscape's topography repeats in a self-similar pattern across spatial scales. Marsh and Ewers recommend that ecological surveys looking at β-diversity should use sampling designs with clustered points, to determine accurate estimates across spatial scales. We hypothesize that self-similar sampling designs will work especially well at accurately capturing diversity-environment relationships in mountainous, self-similar landscapes.

We only used a fractal sampling design to assess plant assemblage structure in the field.

But, we wanted to understand how different sampling designs perform in a mountainous environment. To do this, we assessed the ability of the fractal sampling design we used in the field to detect changes in simulated α-diversity across a periodically variable landscape. Specifically, we contrasted our fractal design to three commonly used sampling designs—grid, random, and transect—with the same or as near-same as possible number of sampling locations. We tested these designs across a wide range of landscapes generated using two equations which make more mountainous landscapes (N=2916, Figures B.1 and B.2) and a wavy-linear gradient (N=2916, Figures B.3 and B.4). We parameterized each set of landscapes with varying degrees of amplitude, periodicity, and noise in environment, and slope, intercept, and additional noise in the diversity-environment relationship and sampled them with two fractal driven numbers of points (N=27, 3 triads and N=9, 2 triads). We emphasize that we looked at these different designs' ability to detect α-diversity across a periodically variable landscape and not these designs' ability to effectively partition diversity across spatial scales, which has already been theoretically demonstrated (Marsh and Ewers 2013).

We predicted that all of the sampling designs will have a similar ability to detect the true slope of the relationship between diversity and environment. But, the fractal sampling design will only be significantly able to detect this relationship when the spacing of the points matches that of the periodicity of the landscape. This would demonstrate that the fractal sampling design we use detects diversity-environment relationships equally as well as other classic ecological sampling designs and has especial use in mountainous environments. In tandem with the Marsh and Ewers' simulation, this outcome would support the use of fractal sampling designs for both detecting changes in α-diversity across environment and partitioning that diversity across spatial scales (2013).

B.2 Methods

We used simulations to compare how often each sampling design – random, fractal, grid, transect (Figure B.5) – captured periodic variation in diversity (or structure).

We calculated the environment in each cell using the equation $M_{ij} = A_i(cos(B_i(i))) +$

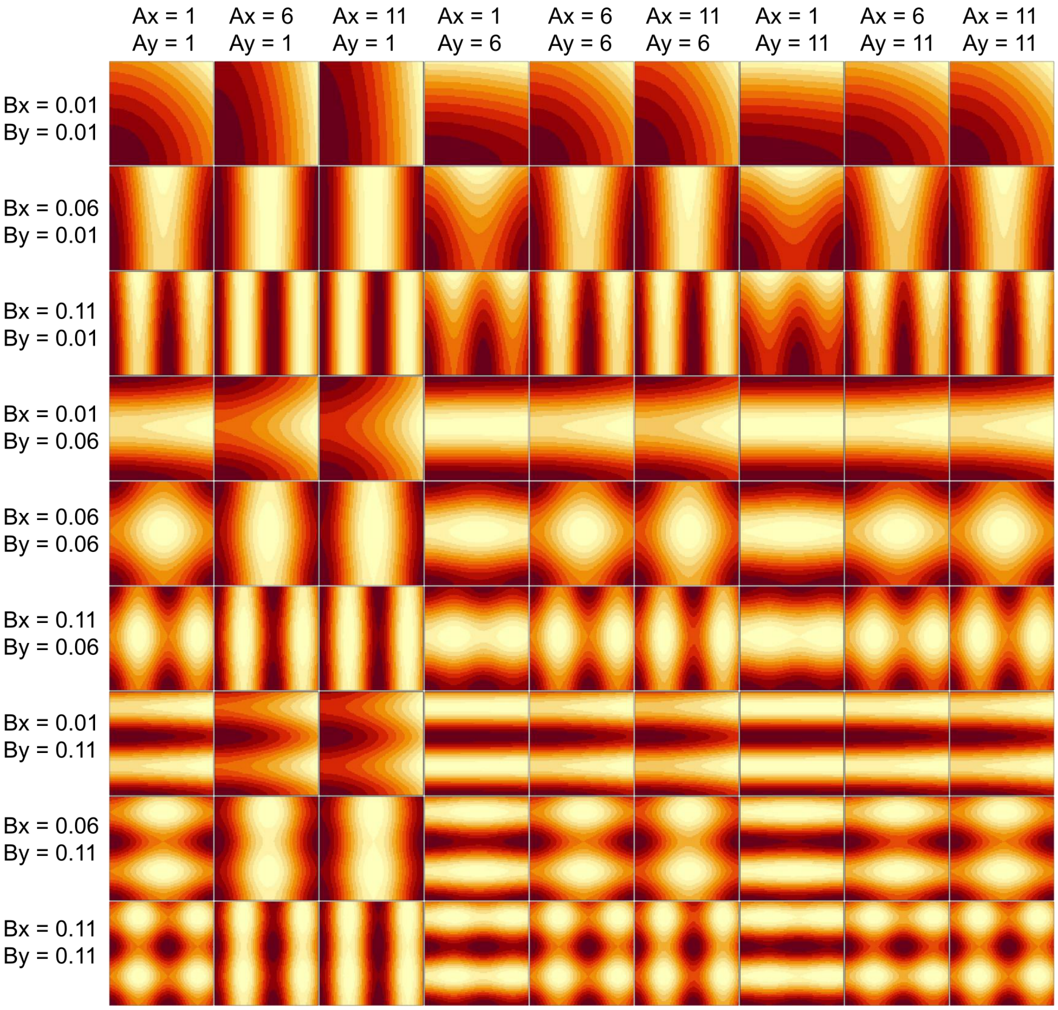

Fig. B.1: **Mountainous periodic environments with no noise.** Parameter values along the top and left size show how changes in amplitude and the coefficient that drives period affect the pattern of the landscape. The standard deviation of the noise parameter equals zero.

$A_j(cos(B_j(j))) + e_M$ where A_i and B_i determine the amplitude and period of M_{ij} in the i dimension and A_j and B_j determine the amplitude and period of M_{ij} in the j dimension. e_M is a random error term drawn from a normal distribution centered on 0 with a standard deviations as designated by our parameter array. Then we distributed diversity across that environment using the equation $D_{ij} = m(M_{ij}) + e_D$ where m controls the strength of the relationship between diversity and environment and e_D is a random error term drawn

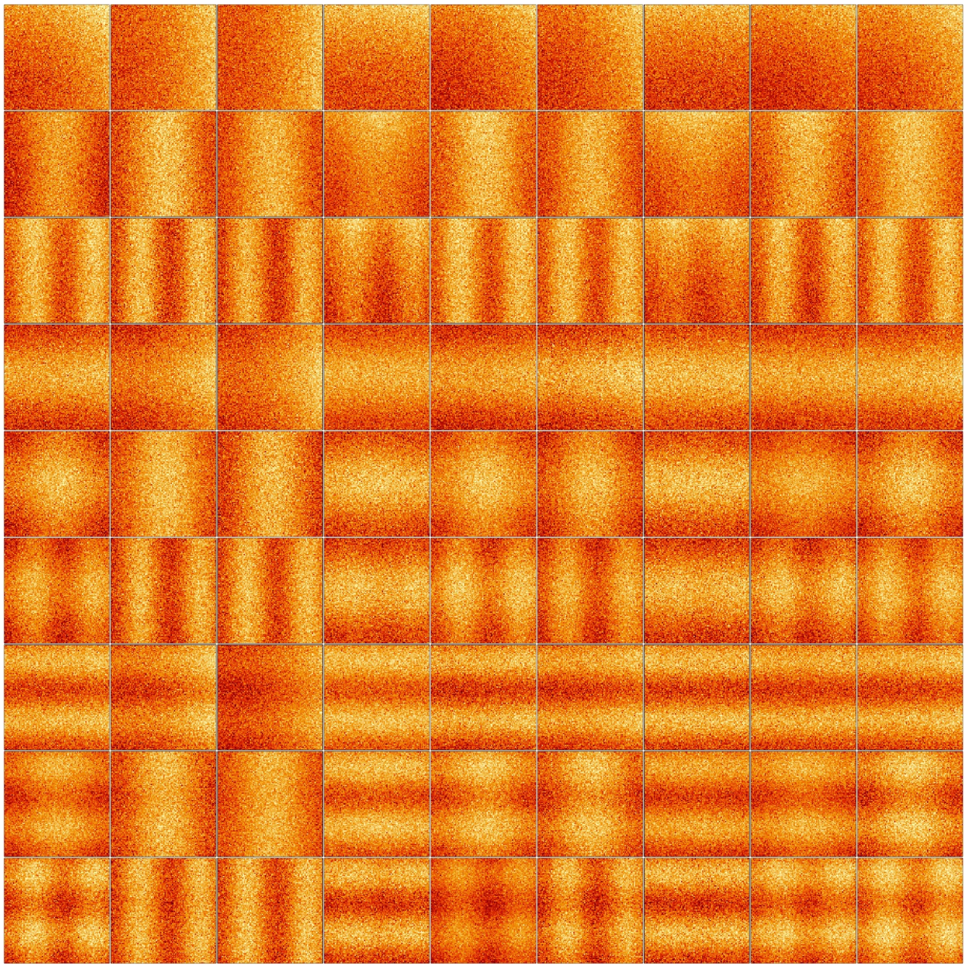

Fig. B.2: **Mountainous periodic environments with maximum noise** The standard deviation of the noise parameter equals 1.

from a normal distribution centered on 0 with a standard deviations as designated by our parameter array. We used combinations of the seven parameters to make 2916 paired diversity-environment landscapes (Figures B.1 and B.2). Then we sampled each of these with the four sampling designs – random, fractal, grid, and three transects and two different triad levels of points (N=27 and N=9). Each landscape was sampled with a different random sampling design.

We evaluated the effectiveness of each designs's ability using a generalized linear model of each set of sampled diversity values (N=2916) across the same set of sampled environment values (N=2916) for each sampling design (N=4). From these models we extracted the

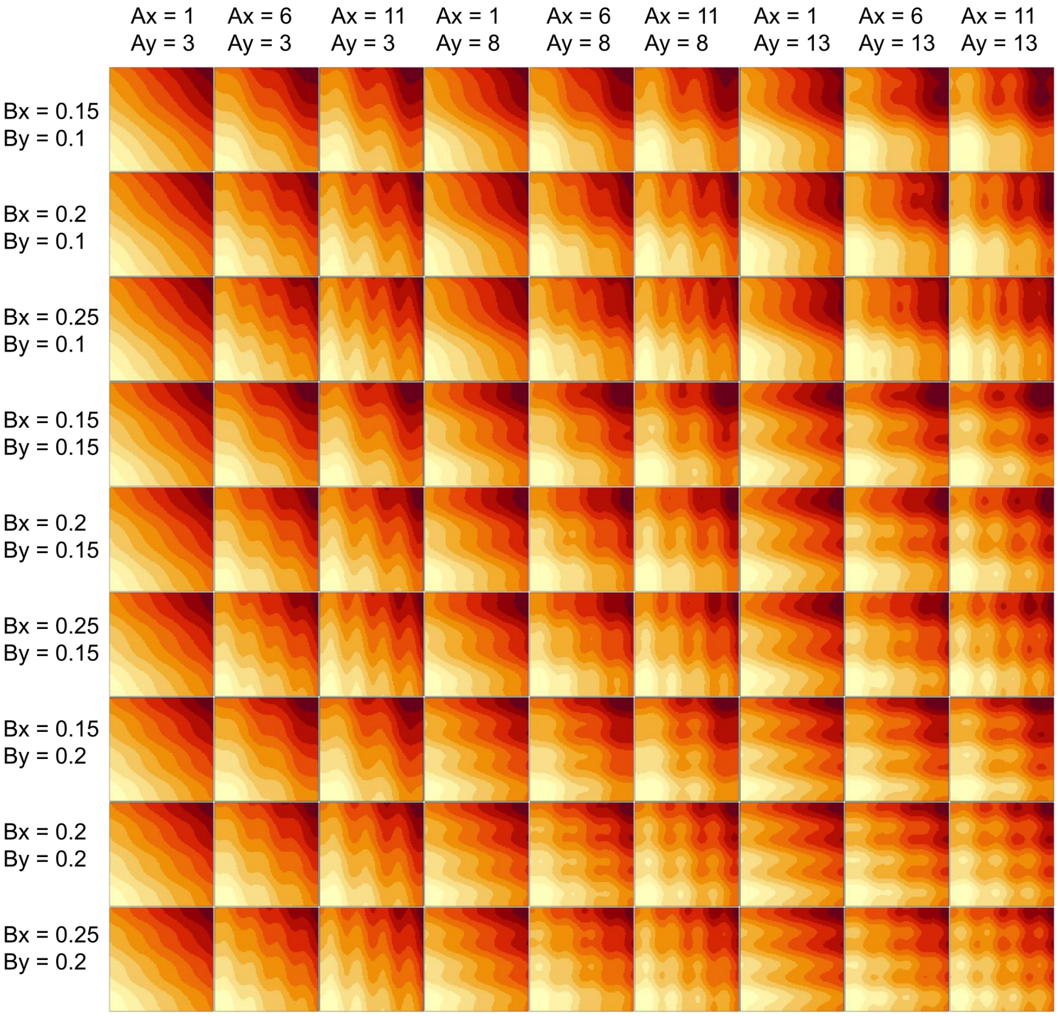

Fig. B.3: **Wavy-linear periodic environments with no noise.** Parameter values along the top and left size show how changes in amplitude and the coefficient that drives period affect the pattern of the landscape. The standard deviation of the noise parameter equals zero.

confidence interval for the estimated slope value from the sampled diversity and environment and assessed whether it contained the true slope value. Then, we used a generalized linear model, with the logit link, to model whether or not sampled diversity and environment captured the true slope of this relationship across all parameter values used to build the landscape and which sampling design was used. We set random sampling as the reference design to compare all systematic designs to. By calculating the contrasts and using an

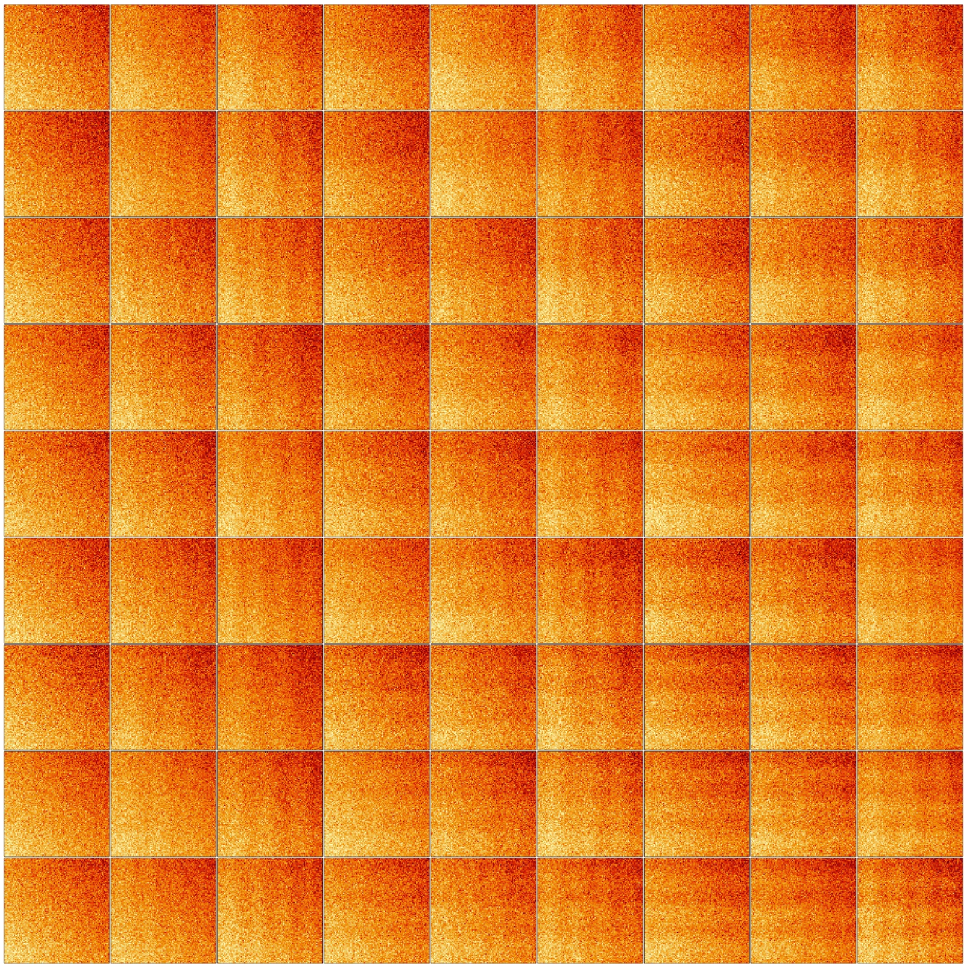

Fig. B.4: **Wavy-linear periodic environments with maximum noise.** The standard deviation of the noise parameter equals 1.

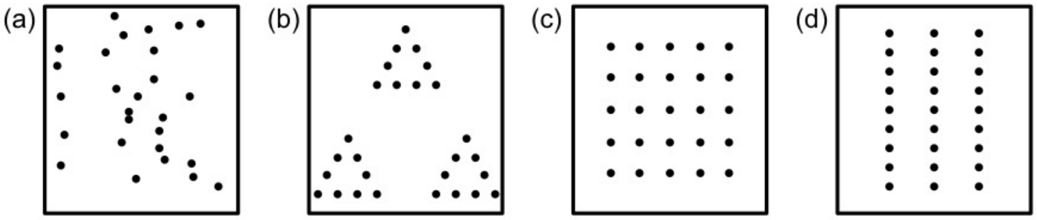

Fig. B.5: **The four sampling designs with 27 plots (25 for the grid design)**

inverse logit function to transform the coefficient values, we can determine the probability that each coefficient influences whether the true diversity-environment slope parameter is captured by a give sampling design.

We repeated this process with a different set of paired diversity-environment landscapes (N=2916), to investigate the same questions in a more linear environmental gradient that also contains fine-scale periodic variation. We used the equation $W_{ij} = (i+A_i(cos(B_i(i))))+(j + A_j(cos(B_j(j)))) + e_W$ to generate the environment, W_{ij}, and the equation $D_{ij} = m(W_{ij}) + e_D$ to distribute diversity across that environment (Figures B.3 and B.4). The parameter definitions for this landscape generation are the same as in the other set of landscapes, however, we did use slight different parameter values to achieve higher fine scale variation in these landscapes. All simulations were conducted in R (R Core Team 2020) and we release all code for this simulation (Simpson & Pearse, 2021b).

B.3 Results

This simulation assesses what landscape parameters and sampling designs influence whether or not we are able to assess a known diversity environment across two types of diversity-environment landscapes—mountainous and wavy-linear—with two levels of sampling intensity, 27 and 9 points. Across all models, the noise in environment and noise in diversity significantly determined whether or not a sampling design was able to assess the true slope parameter.

For the mountainous landscapes, sampled with 27 points, we found that all sampling designs assessed the true slope parameter around 91% of the time and random and fractal sampling had a significant effect (Table B.1). When we sampled the same landscape with 9 points, all designs correctly sampled the true slope value 94-95% of the time, but instead the random and grid/transect design had a significant effect. The latter model (9 points) accounted for about a third of the variance that the former (27 points) did (Table B.2).

For the wavy-linear landscapes, sampled with 27 points, we found that all sampling designs assessed the true slope 92-94% of the time and the random and transect sampling designs had a significant effect (Table B.3). When sampled with 9 points, the sampling designs assessed the true slope 95-96% of the time and the random on grid/transect designs had a significant effect (Table B.4).

Table B.1: **Statistical model of the environmental parameters that may drive whether four different sampling designs accurately detect the true slope of the relationship between diversity and a mountainous environment (Figures B.1 and B.2) sampled with 27 points (or 25 for the grid design).** This model accounts for around 30% of variation in the data. The parameters that determine the periodic patterns of diversity include amplitude (A) and the coefficient that determines the period (B) in the x and y dimension. The slope parameter determines the relationship of the landscape between diversity and environment and both diversity and environment are influenced by random noise. The first coefficient is the overall intercept and represents how well random sampling captures the true relationship between diversity and environment. The last three coefficients are contrasts for each of the other sampling designs—fractal, grid, and transect sampling. Probability that each coefficient influences whether the true diversity-environment slope parameter is captured by a given sampling design per unit increase in that coefficient: 0.908, 0.908, 0.908, 0.653, 0.863, 0.904, 0.998, 0.511, 0.893, 0.905, 0.917.

	Estimate	Std. Error	z value	Pr(>|z|)
Reference—random sampling	2.2945	0.1014	22.63	<0.001
Ax	0.0004	0.0060	0.06	0.9521
Ay	0.0031	0.0060	0.51	0.6093
Bx	1.6629	0.6017	2.76	0.0057
By	0.4519	0.6013	0.75	0.4523
slope	0.0482	0.0439	1.10	0.2724
Noise in environment	-3.9247	0.0763	-51.42	<0.001
Noise in diversity	2.2516	0.1043	21.59	<0.001
Contrast—fractal sampling	0.1675	0.0697	2.40	0.0163
Contrast—grid sampling	0.0433	0.0694	0.62	0.5323
Contrast—transect sampling	-0.1026	0.0691	-1.48	0.1376

B.4 Discussion

In the main text, we demonstrate a fractal sampling designs' ability to detect diversity-environment relationships across spatial scales. In this supplement we simulate two sets of diversity-environment landscapes to assess how well four sampling designs—random, fractal, grid, and transect—capture periodic fluctuations in α-diversity. This simulation builds on theoretical work that demonstrates fractal designs effectiveness at detecting β-diversity and partitioning that diversity across spatial scales (Marsh and Ewers 2013).

We find that all four sampling designs similarly assess the true relationship between diversity and environment across these landscapes. The pattern of when we have evidence that there is a difference between these and other designs indicates that when the spatial

Table B.2: **Statistical model of the environmental parameters that may drive whether four different sampling designs accurately detect the true slope of the relationship between diversity and a mountainous environment (Figures B.1 and B.2) sampled with 9 points.** Note that grid and transect designs are identical with this particular number of plots. This model accounts for around 9.2% of variation in the data. All parameters as described in Table B.1. Probability that each coefficient influences whether the true diversity-environment slope parameter is captured by a given sampling design per unit increase in that coefficient: 0.937, 0.937, 0.938, 0.950, 0.695, 0.936, 0.991, 0.898, 0.935, 0.947, 0.947

	Estimate	Std. Error	z value	Pr(>|z|)
Reference—random sampling	2.7027	0.1090	24.79	<0.001
Ax	0.0038	0.0063	0.60	0.5483
Ay	-0.0140	0.0063	-2.21	0.0271
Bx	-0.2396	0.6319	-0.38	0.7046
By	1.8768	0.6325	2.97	0.0030
Slope	0.0133	0.0461	0.29	0.7730
Noise in environment	-2.0104	0.0716	-28.06	<0.001
Noise in diversity	0.5291	0.1056	5.01	<0.001
Contrast—fractal sampling	0.0365	0.0750	0.49	0.6261
Contrast—grid sampling	-0.1722	0.0729	-2.36	0.0181
Contrast—transect sampling	-0.1722	0.0729	-2.36	0.0181

scaling of the points, aligns with patterns in the landscape, fractal designs do better. In the mountainous environment, where the landscape is more self-similar at moderate scales, the fractal design with smaller spacing (3 triads, 27 points) performs better. Conversely, in the wavy-linear environment, where the landscape is more self-similar at finer scales, and overall, follows a linear gradient, the more linear aligned designs (transect and grid/transect) do better.

These results support the use of nested fractal designs as an effective tool for assessing α-diversity in self-similar, periodic environments. While other designs may perform as well at assessing α-diversity, across an array of landscapes, fractals perform equally well and provide particular strength in periodic environments with self-similarity at different spatial scales.

Table B.3: **Statistical model of the environmental parameters that may drive whether four different sampling designs accurately detect the true slope of the relationship between diversity and a wavy-linear environment (Figures B.3 and B.4) sampled with 27 points (or 25 for the grid design).** This model accounts for around 28% of variation in the data. All parameters as described in Table 1. Probability that each coefficient influences whether the true diversity-environment slope parameter is captured by a given sampling design per unit increase in that coefficient: 0.923, 0.923, 0.923, 0.970, 0.915, 0.924, 0.998, 0.481, 0.923, 0.928, 0.941

	Estimate	Std. Error	z value	Pr(>|z|)
Reference—random sampling	2.4881	0.1763	14.11	<0.001
Ax	-0.0007	0.0060	-0.12	0.9050
Ay	0.0107	0.0060	1.79	0.0735
Bx	-0.9970	0.5969	-1.67	0.0948
By	0.1068	0.5967	0.18	0.8579
Slope	-0.0147	0.0436	-0.34	0.7356
Noise in environment	-3.6243	0.0744	-48.70	<0.001
Noise in diversity	2.5654	0.1045	24.56	<0.001
Contrast—fractal sampling	0.0072	0.0694	0.10	0.9170
Contrast—grid sampling	-0.0647	0.0692	-0.93	0.3502
Contrast—transect sampling	-0.2890	0.0687	-4.21	<0.001

Table B.4: **Statistical model of the environmental parameters that may drive whether four different sampling designs accurately detect the true slope of the relationship between diversity and a wavy-linear environment (Figures B.3 and B.4) sampled with 9 points.** Note that grid and transect designs are identical with this particular number of plots. This model accounts for around 9.3% of variation in the data. All parameters as described in Table 1. Probability that each coefficient influences whether the true diversity-environment slope parameter is captured by a given sampling design per unit increase in that coefficient: 0.953, 0.953, 0.954, 0.984, 0.984, 0.953, 0.993, 0.886, 0.952, 0.964, 0.964

	Estimate	Std. Error	z value	Pr(>|z|)
Reference—random sampling	3.0177	0.1848	16.33	<0.001
Ax	-0.0010	0.0062	-0.15	0.8769
Ay	-0.0127	0.0062	-2.04	0.0410
Bx	-1.0939	0.6197	-1.77	0.0776
By	-1.0747	0.6197	-1.73	0.0829
slope	-0.0000	0.0452	-0.00	1.0000
Noise in environment	-1.9250	0.0692	-27.83	<0.001
Noise in diversity	0.9692	0.1042	9.30	<0.001
Contrast—fractal sampling	0.0331	0.0743	0.45	0.6557
Contrast—grid sampling	-0.2573	0.0716	-3.60	<0.001
Contrast—transect sampling	-0.2573	0.0716	-3.60	<0.001

APPENDIX C

Supplementary tables and figures for chapter 3: Variation in near-surface soil temperature drives plant assemblage insurance potential

Table C.1: **Near-surface soil temperature does not significantly correlate with soil texture.** This table shows the correlation coefficients (Pearson's r) and p-values for each temperature variable with the three soil texture components.

	Sand	Silt	Clay
Mean temp.	-0.15	0.03	0.27
p value	0.48	0.88	0.20
SD temp.	-0.09	-0.02	0.23
p value	0.66	0.92	0.28
Max temp.	-0.13	0.03	0.23
p value	0.54	0.89	0.26
Mean temp.	0.24	-0.10	-0.37
p value	0.25	0.65	0.07

Table C.2: **Near-surface soil temperature most strongly and significantly correlates with aspect, while soil texture components most strongly and significantly correlate with elevation.** This table shows the correlation coefficients (Pearson's r and p-values for each temperature and texture variable in relation to three topographic variables—aspect, elevation, slope. The coefficient for the most strongly correlated topographic variable is bolded.
Here, * means that $p < 0.05$.

	Aspect	Elevation	Slope
Mean temp.	**-0.827**	-0.025	-0.250
p value	<0.001*	0.906	0.227
SD temp.	**-0.677**	0.134	-0.322
p value	<0.001*	0.524	0.116
Max. temp.	**-0.595**	0.023	-0.291
p value	0.002*	0.914	0.159
Min. temp.	0.240	0.319	0.027
p value	0.248	0.120	0.896
% Sand	0.278	**0.450**	-0.091
p value	0.178	0.024*	0.666
% Silt	-0.278	-0.344	-0.072
p value	0.179	0.092	0.733
% Clay	-0.205	**-0.477**	0.291
p value	0.326	0.016*	0.158

Table C.3: **The CWM of leaf traits and functional dispersion significantly and most strongly correlates with mean soil temperature, while the CWM of height traits significantly and most strongly correlate with inter-annual variation in soil temperature**. Leaf traits and functional dispersion calculated from four traits correlated most strongly with the amount of clay in the soil while height traits and functional dispersion calculated from the CWM of SLA and maximum height correlated most strongly with the amount of sand in the soil. All functional metrics were logged to improve normality in resulting models. For each functional metric, this table shows the correlation coefficients (Pearson's r) and p-values between that metric and seven soil temperature and texture environmental variables. Since the temperature and texture variables exhibit co-linearity and we can only use two predictor variables in each multiplicative and additive linear model, we chose the temperature and texture variables that was were most correlated with each functional metric (bolded).
Here, * means that $p < 0.05$.

	Mean temp.	SD temp.	Max. temp.	% Sand	% Clay
ln(CWM of LA)	**-0.825**	-0.695	-0.536	0.059	**-0.105**
p value	<0.001*	<0.001*	0.006*	0.779	0.617
ln(CWM of SLA)	**-0.539**	-0.485	-0.381	0.026	**-0.028**
p value	0.005*	0.014*	0.060	0.903	0.893
ln(CWM of max. height)	-0.666	**-0.698**	-0.683	**-0.144**	0.113
p value	<0.001*	<0.001*	<0.001*	0.493	0.591
ln(CWM of mean height)	-0.643	**-0.679**	-0.666	**-0.092**	0.069
p value	0.001*	<0.001*	<0.001*	0.662	0.741
ln(FDis - 4 tr.)	**-0.750**	-0.699	-0.603	<0.001	**-0.033**
p value	<0.001*	<0.001*	0.001*	0.998	0.877
ln(FDis - 2 tr.)	**-0.748**	-0.709	-0.614	**-0.055**	-0.015
p value	<0.001*	<0.001*	0.001*	0.792	0.942

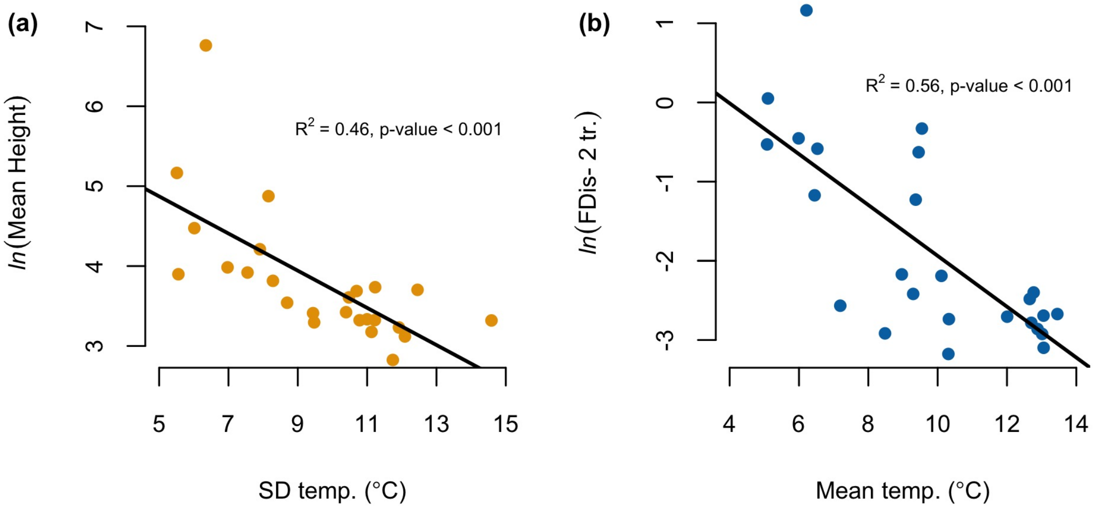

Fig. C.1: **Increases in soil temperature variation and mean soil temperature predict a decrease in the CWM of mean height and functional dispersion, calculated with two traits, respectively.** (a) Plots with less variation in soil temperatures support taller assemblages [higher logged CWM of mean height (cm), slope = -0.233, $F_{1,23} = 19.67$]. (b) Even when FDis is calculated from only two traits—maximum height and SLA—plots with lower mean temperatures support assemblages with more functional variation [*i.e.* more biological insurance; higher FDis, slope = -0.321, $F_{1,23} = 29.19$]. Color coding described in Figure 3.1 in the main text.

Table C.4: **Functional dispersion and the CWM of traits vary for different life history strategies when aggregated across all twenty-five plots at Right Hand Fork.** Most species across the site were herbaceous perennials 54/84. Woody perennials had a functional dispersion over four times higher than herbaceous perennials or annuals/biennials. Herbaceous perennials had the most acquisitive leaves (highest SLA), followed by woody perennials and then annuals/biennials; however, they had much higher leaf area than either of the other groups. Woody perennials were much taller than other life history groups, whether measured as maximum or mean height.

	Sp. richness	FDis	CWM SLA	CWM LA	CWM max. height	CWM mean height
Annual/biennials	17	0.11	23.48	0.27	41.47	22.48
Herbaceous perennials	54	0.81	73.83	15.01	61.89	40.02
Woody perennials	13	4.20	34.96	3.33	1046.43	687.19

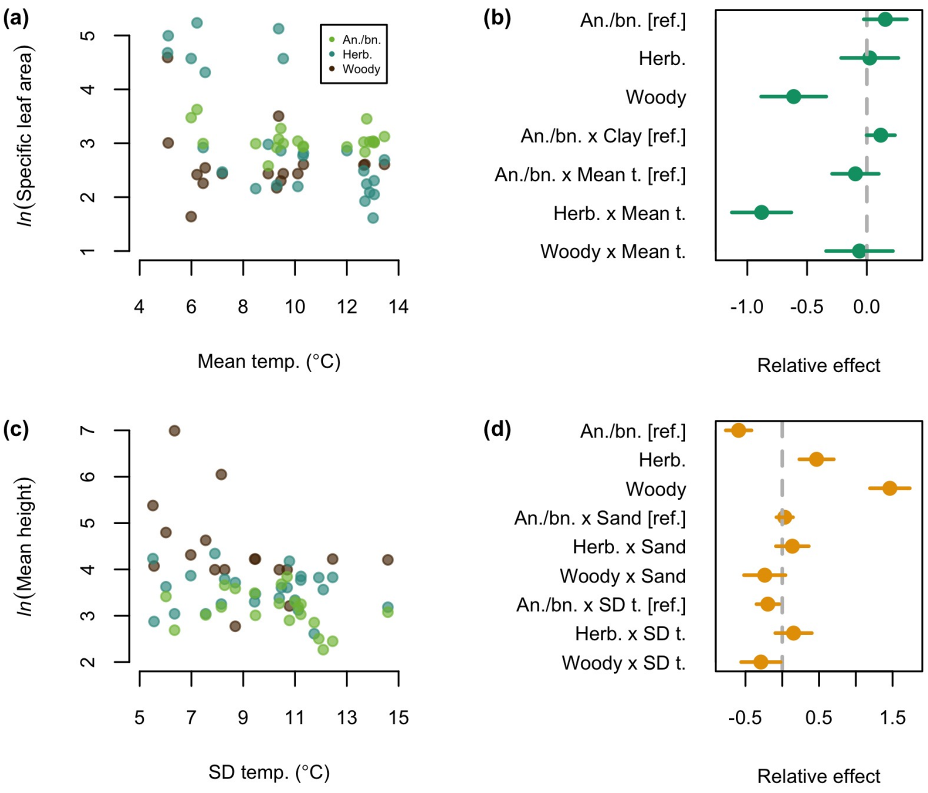

Fig. C.2: **Life history strategies affect the relationship between additional functional diversity metrics and microenvironment.** Plots in the left column show how the logged CWM of (a) specific leaf area and (c) and mean height, vary across the temperature variable they were most correlated with when subset by life history strategy — annuals/biennials (green), herbaceous perennials (blue), and woody perennials (brown). Plots in the right column show the relative effect of each explanatory variable in models that look at how these life history strategies affect the relationship between each functional metric (in the left column) and both the soil temperature and texture variable most correlated with that functional metric. Coefficient values are reference contrasts from those labeled as such. Values further from zero indicate that a variable or interaction between variables has a greater effect on a functional metric.

APPENDIX D

Supplementary tables for chapter 4: Quantifying range indicator heterogeneity supports management of range conditions.

Table D.1: **All sixteen good quality forage species found in the eighty plots across Right Hand and Temple Fork in 2019 are cool-season, perennial grasses.** Origin and forage quality from Utah State University Extension: Range Plants of Utah <https://extension.usu.edu/rangeplants/>. Frequency is the number of plots each species occurred in.

Species	Origin	Livestock/wildlife forage quality	Frequency
Agropyron cristatum	Introduced	Good/Fair	3
Bromus carinatus	Native	Excellent/Good	14
Bromus catharticus	Native	Excellent/Good	2
Bromus inermis	Introduced	Excellent/Excellent	3
Elymus glaucus	Native	Good/Good	21
Elymus lanceolatus	Native	Good/Good	3
Elymus smithii	Native	Good/Fair	1
Elymus trachycaulus	Native	Excellent/Excellent	3
Festuca idahoensis	Native	Excellent/Excellent	3
Koeleria macrantha	Native	Excellent/Good	6
Leymus cinereus	Native	Good/Good	6
Melica bulbosa	Native	Excellent/Excellent	9
Poa pratensis	Introduced	Good/Good	15
Poa secunda	Native	Good/Good	12
Pseudoroegneria spicata	Native	Excellent/Excellent	25
Stipa lettermanii	Native	Good/Good	1

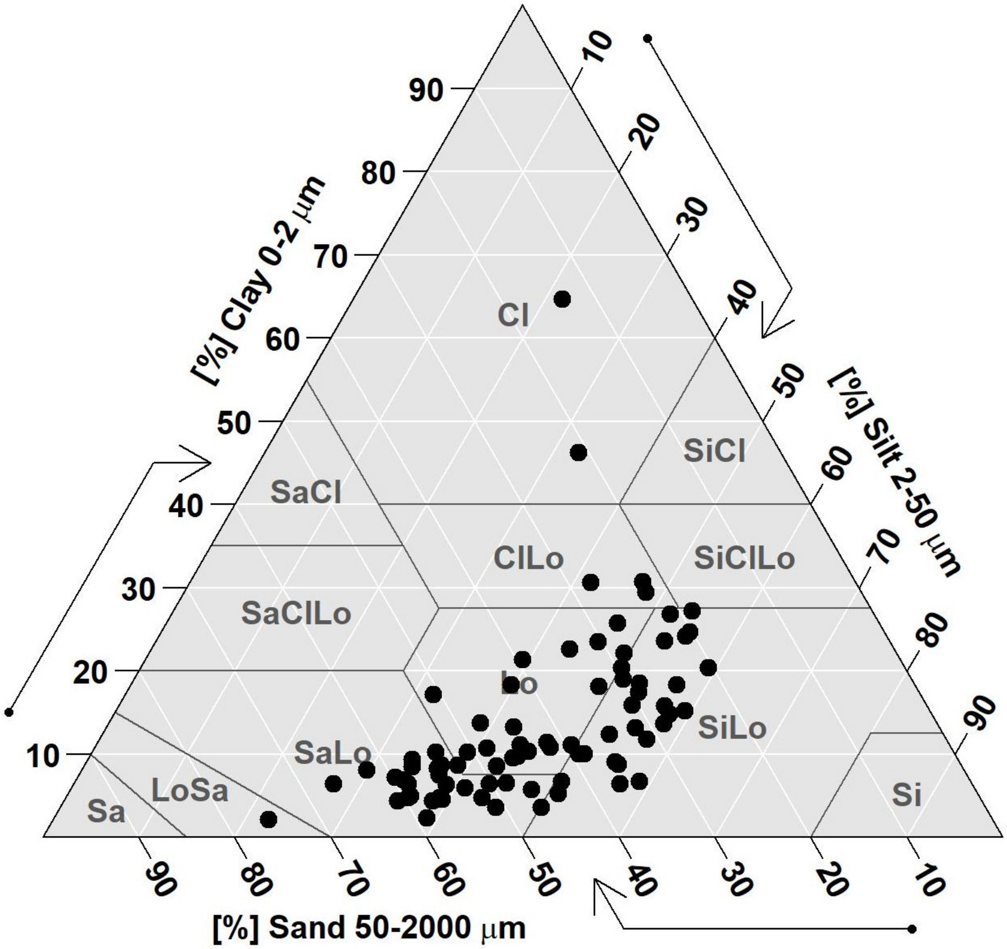

Fig. D.1: **Most of the soils at Right Hand and Temple Fork are loams with lower amounts of clay (0 - 30 %), moderate amounts of silt (20 - 60 %), and moderate to high amounts of sand (20 - 70%).**

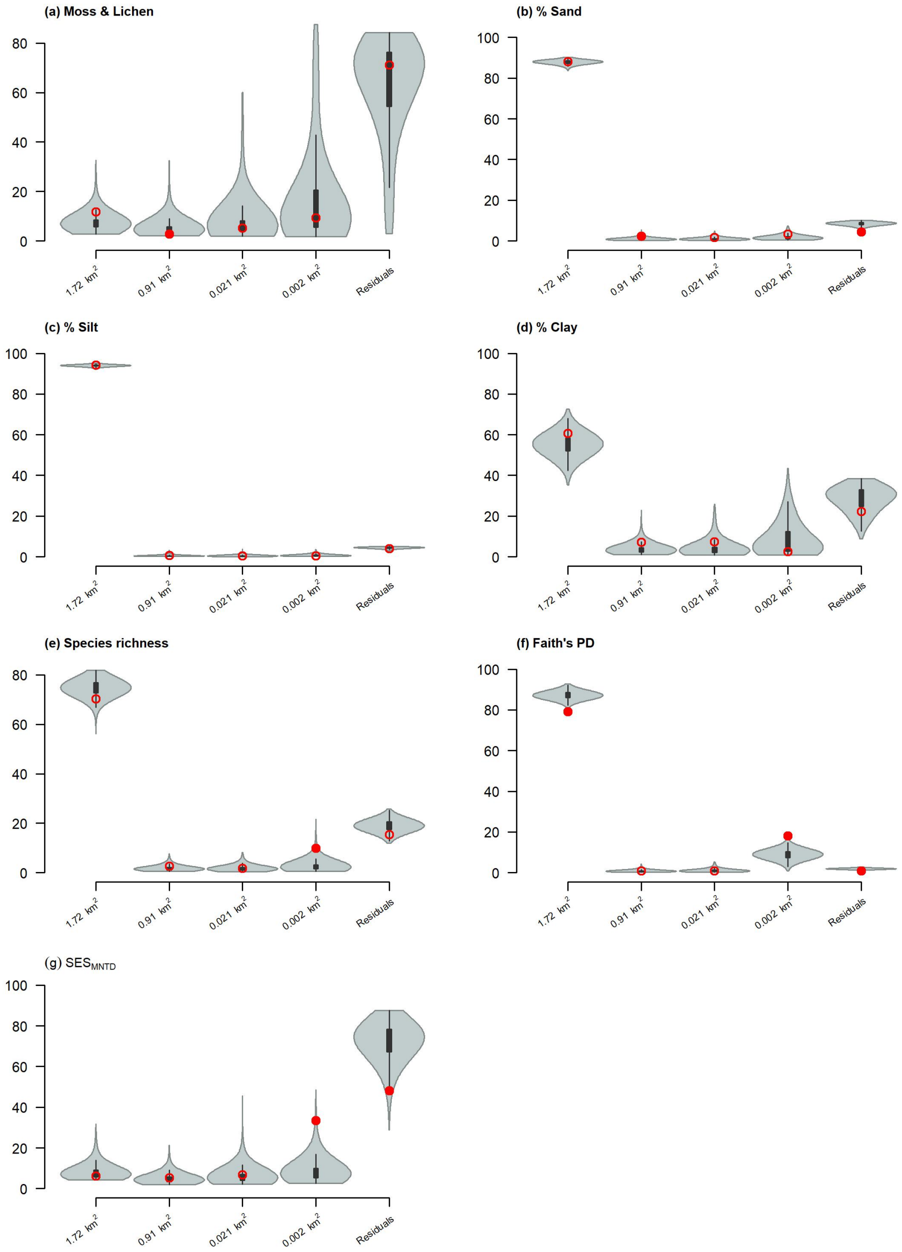

Fig. D.2: **Biodiversity indicators vary at the smallest spatial scale in the sampling design.** For each indicator, a red point shows the observed amount of variation at a given spatial scale in contrast to a distribution of randomized diversity values at each spatial scale (999 iterations, gray violin plots). Filled red points indicate observed values that are significantly different from the randomized distribution. Spatial scale groupings as shown in the main text. P-values of spatial scales with significantly different observed variance than the null distribution—moss and lichen cover: 3% at 0.91-km^2 ($p = 0.049$); amount of sand: 2% at 0.91-km^2 ($p = 0.036$), 4% in residuals ($p = 0.001$); species richness: 10% at 0.002-km^2 ($p = 0.012$); Faith's PD: 80% at 0.91-km^2 ($p = 0.001$), 18% at 0.002-km^2 ($p < 0.001$), 1% in residuals ($p = 0.001$); SES_{MNTD}: 34% at 0.002-km^2 ($p = 0.006$), 48% in residuals ($p = 0.016$).

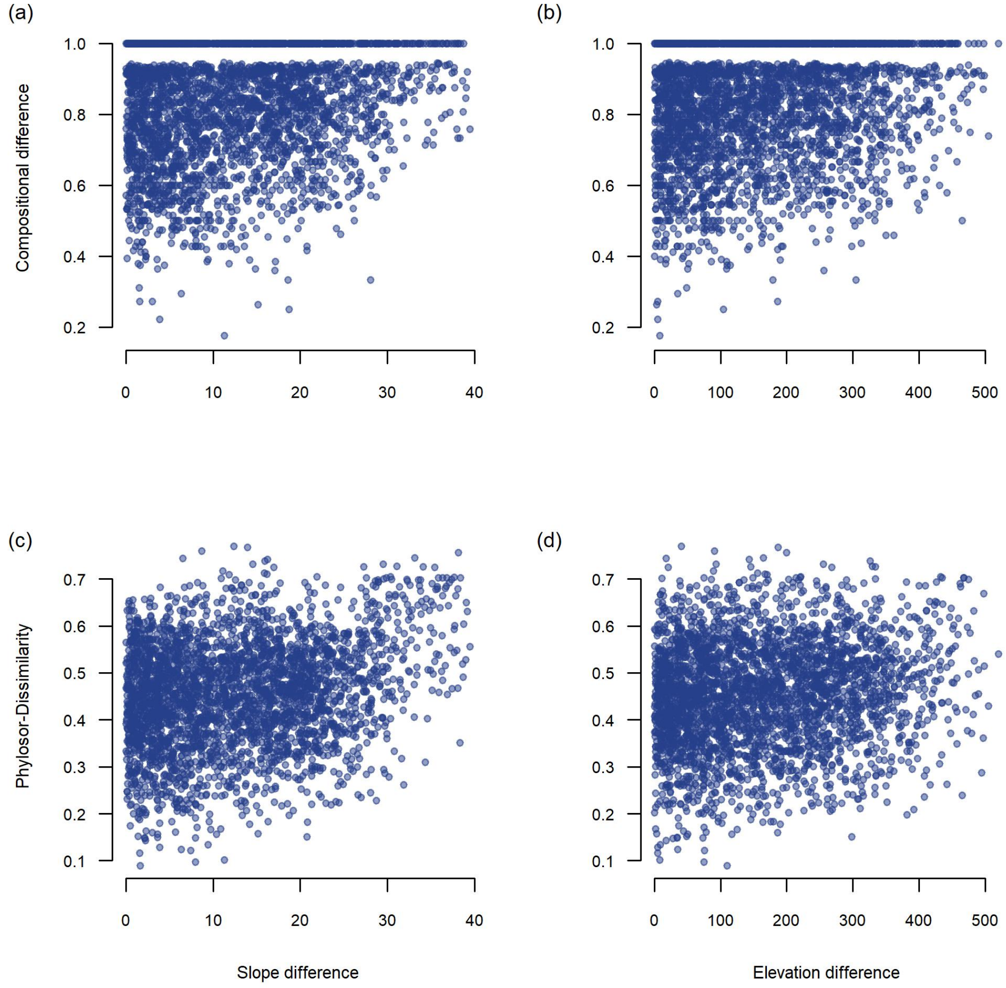

Fig. D.3: **Differences in topography support compositional differences in plant communities.** On the most different slopes (maximum = 40°difference) plant communities have (a) 11% more different species compositions (as measured by Sørenson's Index, slope = 0.003, p-value < 0.001) and (c) 11% more phylogenetic difference (as measured by PhyloSor, slope = 0.003, p-value < 0.001). At the most different elevations (maximum 500 meters) plant communities have (b) 9% more different species compositions (as measured by Sørenson's Index, slope = 0.0002, p-value < 0.001) and (c) 5% more phylogenetic difference (as measured by PhyloSor, slope = 0.0001, p-value < 0.001).

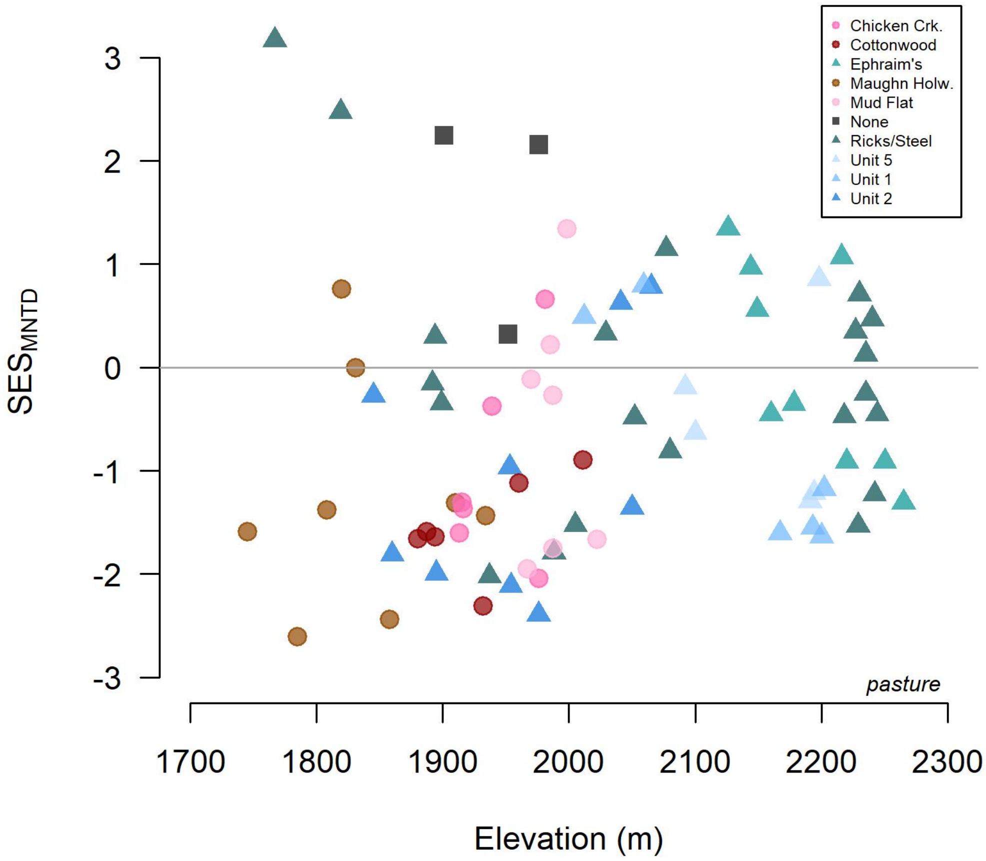

Fig. D.4: **The relationship between SES_{MNTD} and elevation is also impacted by which pasture plots are located in.** Overall, SES_{MNTD} is higher at lower elevations than higher ones and plots that are not in a pasture (black squares) have an overall higher SES_{MNTD} ($r^2 = 0.69$, $F_{38,41} = 2.370$, $p = 0.004$). Communities above the horizontal gray line at zero are less related than expected by chance while communities above the gray line at zero are more related than expected by chance.

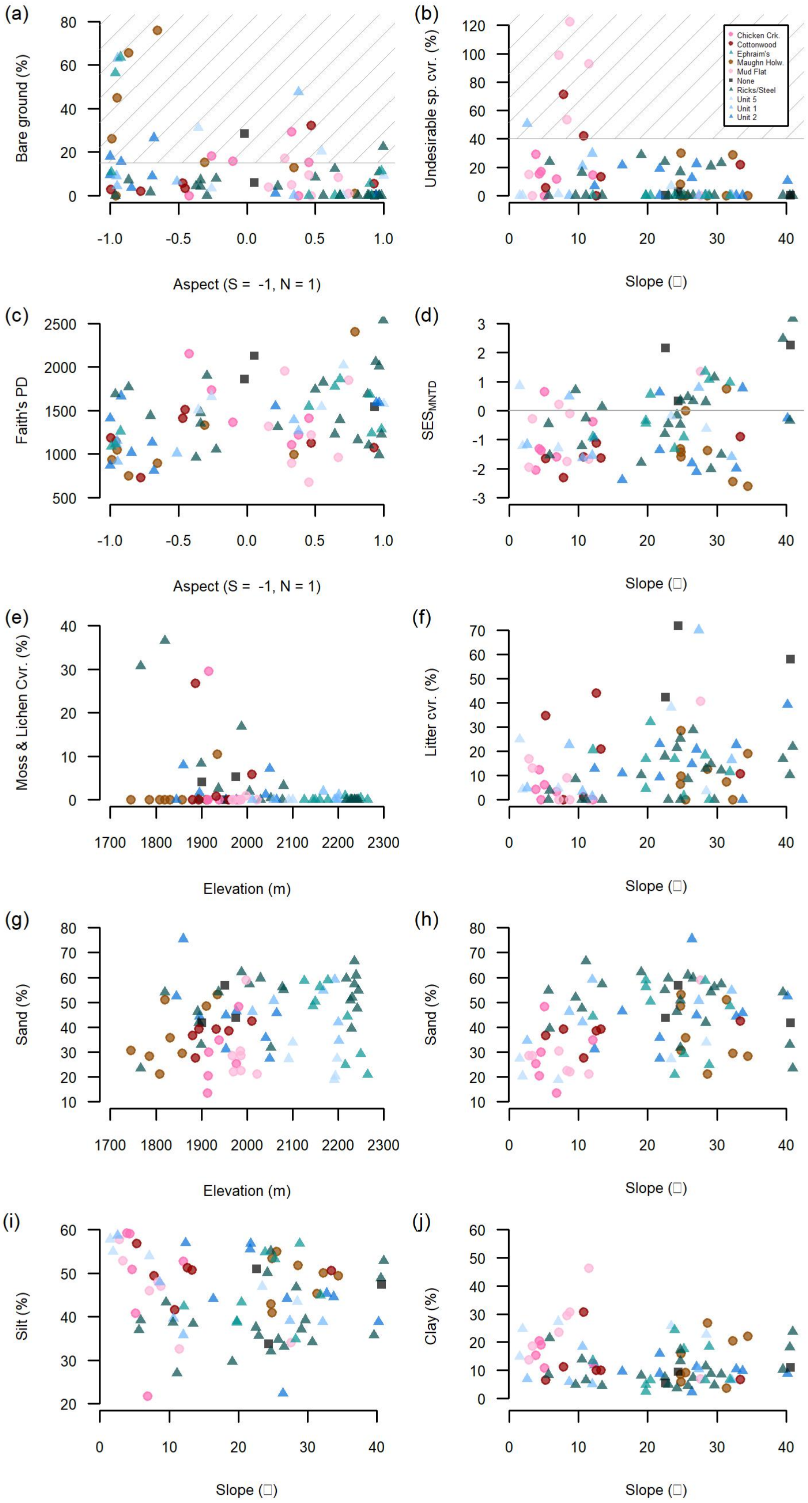

Fig. D.5: **Many indicators varied across topography, but were not affected by categorical management strategies, livestock or pasture.**
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Table D.2: **Differences in topography support subtle differences in range indicators ($<$ 5% more different at maximum topographic difference than zero topographic difference)**. For each indicator, the first row shows the slope of difference in that indicator across difference in the topographic variable at the top of the column. P-values shown in parentheses below each slope value. Significant relationships ($alpha = 0.05$) are bolded.

Indicator	Elevation difference	Slope difference	Aspect difference
Bare ground	**0.007**	-0.015	0.379
	(0.003)	(0.590)	(0.412)
Litter cover	-0.004	**0.005**	-0.657
	(0.067	**(0.034)**	(0.106)
Moss & Lichen cover	-0.0004	**0.035**	0.032
	(0.185)	**(< 0.001)**	(0.619)
% Sand	**0.008**	**0.090**	-0.199
	(0.002)	**(0.007)**	(0.697)
% Silt	**0.006**	-0.003	0.258
	(< 0.001)	(0.864)	0.410
% Clay	0.002	**0.046**	-0.400
	(0.167)	**(0.022)**	(0.195)
Undesirable sp.	**-0.017**	**0.084**	0.893
	(< 0.001)	**(0.048)**	(0.230)
Forage sp.	-0/002	-0.0003	-0.327
	(0.244)	(0.986)	(0.211)
COMDIST	**0.016**	**0.119**	**4.463**
	(< 0.001)	**(0.010)**	**(< 0.001)**

CURRICULUM VITAE

Elizabeth G. Simpson

Biology & Ecology Ph.D. — Utah State University — *elizabeth.g.simps@gmail.com*

Education

Utah State University, Logan, UT (2017-2022 Ph.D. - Biology Ecology Research - Ecoevolutionary ecology, phylogenetic functional diversity, spatial scaling

Cornell University, Ithaca, NY (2010-2014) B.S. - Plant Science Natural Resources, Distinction in research

Research Experience

- Graduate Research Assistant, Utah State University, Logan, UT, Sept. 2017 - Apr. 2022

  —Developed protocols and collected, processed, and analyzed data including plant community composition and functional traits, soil temperature and texture each summer.

  —Trained and mentored undergraduate researchers in conducting independent lab work.

- Undergraduate Research Assistant, Cornell University - Ecology and Management of Invasive Plants Program, Ithaca, NY, Jan 2011 - May 2012, Aug. 2012 - May 2014

  —Assisted with projects studying deer herbivory, native seedling germination and survival, earthworm prevalence, and introduced and invasive plants.

  —Trained undergraduates in research techniques and data management.

- Biology Research Fellow, Cornell Office of Undergraduate Biology - Summer Institute for Life Sciences, Ithaca, NY, June - Aug. 2013

—Developed and conducted an investigation of the interaction between white-tail deer and invasive earthworms in Northeastern forests.

—Contacted and worked with landowners in three states to access deer fences and obtain information about land use history and deer management practices.

- Student Research Fellow, Punta Cana Ecological Foundation - Cornell Biomedicine and Control of Tropical Diseases and Vectors Program, Dominican Republic, June - July 2013

  —Learned the medicinal uses of tropical plants from a traditional healer and performed assays to investigate the bioactivity of plants used to treat inflammation.

  —Monitored a Ridgeway Hawk nest, sea turtle beaches, and fish-catch surveys.

Teaching Experience

- Teaching Assistant, Utah State University - Biology I and II Laboratory (BIOL 1615 and 1620), Logan, UT, Aug. 2020 - Apr. 2022

  —Guided students through learning and doing the process of discovery-based science via online and in-person classes and consistent feedback.

- Lead Facilitator Instructor, Native American in STEM Mentorship Program, Logan, UT, Jan. 2020 - Nov. 2021

  —Advocated for and led the transition a typically in-person research experiences into a completely remote rotational research program. Included development of synchronous and asynchronous learning opportunities.

  —Coordinated all aspects of the program including budget, hiring facilitators, and developing coursework.

  —Worked directly with research mentors to help them develop and implement hands-on research experiences in a remote context.

- Facilitator, Native American in STEM Mentorship Program, Logan, UT, Feb. - June 2018, Feb. - June 2019

—Organized a month-long rotation of research experiences for undergraduate students from Utah State University's Blanding Campus. Mentors and supports student's writing and presentation skills. Acts as liaison between students and the research faculty.

- Environmental Educator Naturalist, Exploring New Horizons at Sempervirens, Boulder Creek, CA, Sept. 2015 - June 2016, Sept. 2016 - June 2017

  —Developed and implemented student-driven, inquiry-based lessons according to Next Gen. Science standards at a week-long residential outdoor program for 5th and 6th graders.

  —Mentored high school students in group management techniques and teaching strategies, created interpretational signage, helped maintain organic garden.

- Naturalist Intern, San Mateo County Outdoor Education, La Honda, CA, Sept. 2014 - May. 2015

  —Learned and actively practiced experienced-based learning in all subjects at a week-long residential outdoor program for 5th and 6th graders.

- Environmental Educator, New York State Parks, Recreation and Historic Preservation, Trumansburg, NY, May - Aug. 2014

  —Led interactive tours for general public, which covered a range of topics from local geology, natural history and medicinal plants.

  —Created interpretive materials and signage for tours, bike routes and native species ID.

- Curriculum Developer Teaching Assistant, Cornell University - The Art of Horticulture (HORT 2010), Jan - May Sept - Dec 2013, Ithaca, NY

  —Developed and facilitated hands-on creative and reflection-based learning activities.

  —Presented lectures on natural plant dyes, cordage, and making clothing.

Publications

- **Simpson, E.G.**, Pearse, W.D. 2021. Fractal triads efficiently sample ecological diversity and processes across spatial scales. Oikos 130 (12), 2136-2147.

- Lembrechts, J. J., Aalto, J., Ashcroft, M. B., De Frenne, P., Kopecký, M., Lenoir, J., ...**Simpson, E.G.**...& Rocha, A. 2020. SoilTemp: A global database of near-surface temperature. Global Change Biology, 26(11), 6616-6629.

- Dávalos, A., **Simpson, E.G.**, Nuzzo, V., Blossey, B. 2015. Non-consumptive Effects of Native Deer on Introduced Earthworm Abundance. Ecosystems 18, 1029-1042.

Presentations

- **Simpson, E.G.**, Pearse, W.D. 2020. Understanding the Interaction Between Ecological Diversity and Land-Use Across Spatial Scales, Utah State University Department of Biology Seminar, Logan, UT.

- **Simpson, E.G.**, Pearse, W.D. 2019. Variance and redundancy of functional trait assemblages in seasonally variable environments, Ecological Society of America Annual Meeting, Louisville, KY, Contributed Oral Presentation.

- **Simpson, E.G.**, Pearse, W.D. 2019. Sampling ecological diversity and process across scales using fractal triads. Utah State University Student Research Symposium, Logan, UT, Oral Presentation.

- **Simpson, E.G.**, Pearse, W.D. 2018. Uncovering ecosystem heterogeneity across spatial scales using a new fractal-based sampling design. Ecological Society of America Annual Meeting, New Orleans, LA, Contributed Oral Presentation.

- **Simpson, E.G.** 2016. Tricky Topics: Incorporating Math and Physics with Traditional Teaching Methods. California Association for Environmental and Outdoor Education Conference, Malibu, CA, Discussion and Practice Based Workshop

- **Simpson, E.G.** 2014. Interaction Between Forest Ecosystem Stressors: Whitetail Deer and Earthworms. Cornell Department of Natural Resources Honors Thesis Symposium, Ithaca, NY, Oral Presentation
- **Simpson, E.G.**, Blossey, B. 2013. Interactions Between Whitetail Deer and Earthworms in Northeastern Forests, Summer Institute for Life Sciences Undergraduate Research Symposium, Ithaca, NY, Poster.
- **Simpson, E.G.** 2012. Plant-derived Blood Disease Treatments in Hispaniola. Cornell Undergraduate Research Board Fall Poster Session, Ithaca, NY, Poster.
- **Simpson, E.G.** 2012. Examination of Traditional Plant-derived Blood Disease Treatments on the Island of Hispaniola. Medicinal Plants Research Symposium, MHIRT Cornell, Punta Cana, DR, Oral Presentation.

Funding & Awards

- K. Patricia Cross Future Leaders Award Finalist, Association of American Colleges Universities, 2019, 2020 —Recognizes graduate students who show exemplary promise as future leaders of higher education and who are committed to academic innovation in the areas of equity, community engagement, and teaching and learning.
- Presidential Doctoral Research Fellowship, Utah State Office of Research, Sept 2017 - Present —Full tuition award and contribution toward annual stipend supports focus on research and mentoring fellow graduate and undergraduate students.
- Utah State Biology Graduate Student Association Travel Award, Aug 2019 —Supported travel to present a talk at the 2019 Ecological Society of America meeting. —Shared benefits and learning from this travel via two local outreach events: An interactive 4H Girl's Science Club Lesson titled: "Observing, classifying, and documenting the natural world " and hands-on booth about seed diversity and function at an elementary school science night.

- Pi Alpha Xi - Honors Society for Horticulture, 2014
- NSF Undergraduate Research and Mentoring in Biology Grant, Cornell Office of Undergraduate Biology, Summer 2013
- Dextra Undergraduate Research Fund, Cornell College of Agriculture Life Sciences, 2012
- Department of Plant Biology Grant, Cornell College of Agriculture and Life Sciences, 2012

Servie & Outreach

- Donation Organizer Mask Sewer, NavajoStrong, April – July 2020 — Collects and delivers essential items for non-profit that works to directly meet Navajo family's needs in response to the COVID-19 pandemic. Sews masks to donate.
- Editorial Board Member, Curiosity: The Undergraduate Research Journal of Utah State University, Dec 2020 - Present —Provide feedback on journal structure, submission process, and editing help as needed.
- Grant Reviewer, Judge, Panelist, Utah State U. - Office of Research, Sept. 2017 - Present —Reviews and provides feedback for undergraduate proposals for the Undergraduate Research and Creative Opportunities grant each semester. Interviews and judges undergraduate students at fall and spring research symposium. Has sat on panel to provide insight about how to be a good mentor and mentee
- Fundraising Chair Secretary, Utah State U. - Biology Graduate Student Association, Jan - Dec 2018 —Planned, organized and implemented annual plant scale fundraiser, recruitment weekend events for prospective graduate students, outreach programs, and advocated for graduate students
- Programmer, Utah State U. - Biology Nerd Herd: Programming Club, Sept 2017 - May 2018 —Participated in weekly meetings to build hardware and program software to

support researchers in USU's Biology Department and seminars to learn new, related skills.

- Art Committee Member, for Surface Tension, an art installation at Utah State U. —Organized and curated images from Biology Department labs according to artist's specifications.

Relevant Skills

- Programming - Proficient in algorithm design and implementation in R and Python.
- Statistics - Hierarchical/mixed effects modeling, biodiversity and phylogenetic metrics and models, and spatial analysis in R. Mark-recapture analysis in MARK.
- GIS - Familiar with spatial analysis in ArcGIS and R.
- Taxonomy/botany - Proficient use of microscopes and dichotomous keys to identify invertebrates and plants in geographic regions throughout the US and eastern coast of the Dominican Republic
- Grant writing - Attended Planning Writing Successful Proposals: Starting Out workshop by the AtKisson Training Group, LLC. during Fall 2017

Relevant Outdoor Experience & Certifications

- Wilderness First Responder with Standard First Aid and CPR, Sausalito, CA Salt Lake City, UT, June 2021, 2018, 2016 —80 hours of initial hand-on training in backcountry decision making and medicine two 16 hour recertification courses.
- Long Distance Backpacker, Summer 2015, 2016, 2017 —Developed excellent stamina, planning, and gear organization skills via two-week to two-month long trips including 1,200 northern miles of the Appalachian Trail, the 273 mile Long Trail in VT, as well as shorter trips in Iceland, the Eastern Sierra and throughout California.

- Ultrarunner, Oct 2015 - Present —Have successfully finished multiple 50k, 50 mile, 100k and 100 mile trail races and solo efforts as well as numerous off-trail orienteering events. Paced (ran with and supported) three different runners during 25 and 33 mile night sections of rugged Utah mountain races (Fall 2017, 2018).
- Gear Seamstress, April 2011 - Present —Designed and sewed equipment for research projects as an undergraduate. Creates patterns for, sews and sells lightweight backpacking gear including fleece jackets, flat tarps, sleeping bags and gaiters.