

Assessing Plant Community Attributes Along Environmental Gradients in two Critical Landscapes

A Thesis

Presented in Partial Fulfillment of the Requirements for the
Degree of Master of Science

with a

Major in Natural Resources and Society

in the

College of Graduate Studies

University of Idaho

by

Amy Thorson

Major Professor: Mark Wolfenden, Ph.D.

Committee Members: Lee Vierling, Ph.D.; David C. Tank, Ph.D.

Department Administrator: Lee Vierling, Ph.D.

December 2019

ProQuest Number: 27541654

All rights reserved

INFORMATION TO ALL USERS

The quality of this reproduction is dependent on the quality of the copy submitted.

In the unlikely event that the author did not send a complete manuscript and there are missing pages, these will be noted. Also, if material had to be removed, a note will indicate the deletion.



ProQuest 27541654

Published by ProQuest LLC (2020). Copyright of the Dissertation is held by the Author.

All Rights Reserved.

This work is protected against unauthorized copying under Title 17, United States Code
Microform Edition © ProQuest LLC.

ProQuest LLC
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106 - 1346

Authorization to Submit Thesis

This thesis of Amy Thorson, submitted for the degree of Master of Science with a Major in Natural Resources and titled "Assessing Plant Community Attributes Along Environmental Gradients in two Critical Landscapes" has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

Major Professor: _____ Date: _____
Mark Wolfenden, Ph.D.

Committee Members: _____ Date: _____
Lee Vierling, Ph.D.

_____ Date: _____
David C. Tank, Ph.D.

Department Administrator: _____ Date: _____
Lee Vierling, Ph.D.

Abstract

"The wilderness and the idea of wilderness is one of the permanent homes of the human spirit"

Joseph Krutch (1995)

"Wilderness itself is the basis of all our civilization. I wonder if we have enough reverence for life to concede to wilderness the right to live on?"

Margaret Murie

Human activities contributing to the accumulation of greenhouse gasses in the atmosphere have created a rapid spike in surface temperatures leading to major shifts in ecological processes (Walther et al., 2002). Changes to abiotic cycles are affecting biological communities however, not all species will respond the same way. Changes to colonization and extinction rates are leading to novel communities and functional compositions, further altering ecosystem processes. (Díaz, S., & Cabido, M., 1997). Our current state of urgency regarding climate change mitigation demands a better understanding of ecosystem responses.

Relative to other landscapes, wilderness areas offer a rare opportunity to study ecological processes in a setting affected little by direct human manipulation. Studying naturally functioning systems provides a frame of reference for addressing baseline ecosystem health and can inform better management decisions (Sharman, Landres, & Boudreau, 2007). Protected under the wilderness act, wilderness areas also provide the opportunity for long-term landscape-level studies (Six et al., 2000).

Wilderness areas are critical landscapes not only as the last living laboratories to study natural ecological processes but, as a necessity to the human spirit. Research shows that more life-sustaining, intrinsic, future, and spiritual values are associated with wilderness areas than outside of these areas (Cordell et al., 1998; Cordell, Bergstrom & Bowker, 2005). Based on a survey of 5,000 Americans by Cordell, Tarrant and Greene (2003), the level of importance placed on wilderness values has increased in the 21st century compared to a 1995 survey. Beyond engaging in research on natural systems, we have a responsibility to protect our remaining wilderness areas.

The first two studies of this thesis take place in the heart of the Frank Church- River of No Return (RNR) Wilderness at one of the most remote research stations in the country. Taylor Wilderness Research Station was first established as a homestead by Dave Lewis in 1879 (Dave Lewis Papers). Prior to that, the area was a piece of the homeland inhabited by the Tukudeka (Frey & McCarl, 2014). Overtime, the rugged mountainous terrain, carved out by swift rivers, under a semi-arid climatic regime has shaped both social and ecological attributes of the communities existing within this landscape. A baseline study of plant community dynamics was conducted from the Taylor

Ranch Wilderness Research station at an elevation of 3,800 ft to the summit of Dave Lewis Peak at 9,200 ft. This study aims to provide a snapshot of the current state of vegetation communities to help better understand how this biologically and culturally rich landscape will adapt and transform in our changing climate.

The third study takes place in a remote valley on the island of Kauai, HI under preservation by the National Tropical Botanic Gardens. This landscape is critical due to its conservation of rare, threatened and, culturally significant plant species in addition to its reputation as the longest remaining biocultural unit managed under the traditional Hawaiian system of land management. After a severe rainstorm event in April of 2018, flooding and landslides devastated the valley and isolated the community of Ha'ena. During this unique time in history, I had the opportunity to observe the social and ecological community dynamics after a major disturbance driven by climate change.

Together, these chapters comprise an exploration of community dynamics from a social and ecological perspective in the midst of climate change. In the first chapter, we analyze plant community characteristics in addition to phylogenetic and functional diversity patterns along an elevation gradient in a remote wilderness setting. The second chapter adds to this baseline study an investigation of floral scent composition from *Penstemon* species, an endemic North American taxon. In the final chapter, plant community composition and functional diversity during early succession are compared to intact communities after a recent landslide within a highly manipulated system. Woven into these chapters are aspects of my personal experiences, observations of cultural dynamics and historical accounts. With these underlying notes of human interactions with the natural world, the aim of this thesis is to explore plant community dynamics in critical landscapes from a perspective recognizing that changing landscapes will shift both social and ecological aspects of communities. The overarching goals of this project include: 1. To continue to understand these critical landscapes by collecting baseline data in order to be better stewards of the land. 2. Expose some of the cultural ties to these landscapes which are equally important with ecological aspects when considering conservation strategies.

Acknowledgements

First, I would like to thank my committee. Mark Wolfenden has a unique ability to inspire creative ways to see and study the world. I am so thankful to have Mark as my major advisor. Through his guidance and trust, Mark has allowed my own curiosity to lead the way. For that reason, I have felt engaged and passionate through the entirety of this endeavor. Thank you to Lee Vierling for all his hard work, especially with the MOSS program as I would not be here otherwise. Lee has been encouraging and supportive throughout. I want to thank Dave Tank for his knowledge and ideas. Also, for his time and dedication to the Stillinger Herbarium. The majority of this work has been funded through the Stillinger herbarium expedition grant. I could not be more thankful for Tom Revely for his contributions to the department of Natural Resources and for funding my research assistantship at Limahuli Gardens. This was a unique, lifechanging experience that I could never have imagined. I thank everyone at Limahuli Gardens for sharing their knowledge and culture and providing a holistic experience. I want to thank Armando Macdonald for allowing me to use only the best Mass Spec machine and for giving me a crash course in GCMS analysis. I want to thank Jim Kingery for all his knowledge and wisdom. Jim is not only a plant guru but a mentor to me. I have learned so much from Jim that no textbook could ever convey. I want to give a big thank you to Pete, Meg, Teyha and Bitzer Gag for giving so much to ensure that Taylor Wilderness Research Station is a place that fosters scholarship and personal growth alike. I will never forget my days spent at Taylor Ranch. The Gags are largely responsible for the positive experience I had there. Last but not least, thank you to the many Professors with an open door that helped along the way and to the administrative staff for being the glue that holds everything together.

Dedication

I want to thank my friends and family for being a source of inspiration, creativity, love and, joy. You are the reason for my success and happiness

Table of Contents

Authorization to Submit Thesis.....	ii
Abstract	iii
Acknowledgements	v
Dedication	vi
Table of Contents	vii
List of Tables.....	ix
List of Figures	x
Chapter 1: Assessing Plant Community Dynamics Along an Elevation Gradient in the Frank Church Wilderness	11
1.1 Introduction	11
1.2 Methods and Materials	16
1.3 Results	19
1.4 Discussion	31
Chapter 2: <i>In Situ</i> Analysis of Floral Scent Composition from <i>Penstemon</i> Along an Elevation Gradient in the Frank Church Wilderness	36
2.1 Introduction	36
Methods and Materials	37
Results	40
Discussion	47
Chapter 3: A Baseline Assessment of Early Succession Vegetation Regeneration after a Landslide in Limahuli Valley, Kauai, Hawaii	50
Introduction	50
Methods and Materials	52
Results	55
Discussion	59

Chapter 4: Conclusion	63
References	66

List of Tables

Table 1.1: Full species list with occurrences by elevation band	23
Table 2.1 Species of populations sampled with elevation	40
Table 2.2: Chemical species identified by functional group.....	41
Table 2.3: Number of samples placed in each cluster in k-means and hierarchical cluster analysis...	44

List of Figures

Figure 1.1: Community assemblage theories	16
Figure 1.2: Study area inside Frank Church-RNR boundary with transect locations.....	18
Figure 1.3: Example of 50m line transect spanning across slope.....	18
Figure 1.4: Percent foliar cover	20
Figure 1.5: Percent foliar cover by life form by elevation band.....	21
Figure 1.6: Percent ground cover	22
Figure 1.7: Percent cover of a) bare soil b) bare rock.....	22
Figure 1.8: Species richness along an elevation gradient.....	23
Figure 1.9: Linear regression of Phylogenetic and Functional trait diversity	29
Figure 1.10: Phylogenetic and Functional trait diversity SES.....	30
Figure 1.11: Percent composition of seven seed dormancy classes by elevation band.....	31
Figure 1.12: Community weighted mean of seed mass by elevation band.....	31
Figure 2.1: Study area with VOC collection sites.	39
Figure 2.2: Pearson's correlation test for a) 1-Heptanol, b) Decanal; and c) Nonenal vs. elevation (ft) and d) Temperature (°F) vs. relative humidity (%).	42
Figure 2.3: Pearson's correlation test for a) Total emission vs. Total flowers and b) Total pollinator visits in 1 hr. vs. the number of open flowers.....	42
Figure 2.4: Dendrogram of hierarchical cluster.....	43
Figure 2.5: Diagram of K-means cluster	44
Figure 2.6: Diagram of silhouette plots for a) k-means cluster and b) hierarchical cluster	45
Figure 2.7: Spatial distribution of k-means cluster analysis.....	46
Figure 3.1: Image of two parallel landslides with transect locations	54
Figure 3.2: a) Mean soil temperature and b) mean soil moisture landslide (L) vs. control (C).....	55
Figure 3.3: Percent composition of soil textures landslide (L) vs. control (C).	56
Figure 3.4: Mean soil moisture of landslide by elevation band.....	56
Figure 3.5 a) Percent foliar cover and b) Species richness for landslide (L) vs. control (C).....	57
Figure 3.6: Mean foliar cover landslide (L) vs. control (C)	57
Figure 3.7 Average percent composition of a) seed dormancy class; b) vegetative reproductive potential; c) dispersal mode and; d) seed mass landslide (L) vs, control (C).....	58

Chapter 1: Assessing Plant Community Dynamics Along an Elevation Gradient in the Frank Church Wilderness

1.1 Introduction

Amid rapid climate change, wilderness areas will serve as critical landscapes for research in order to observe and predict natural ecological responses (Arcese & Sinclair, 1997; Gillson *et al.*, 2011). Not only do we have the responsibility of protecting our remaining wilderness areas, but natural systems less affected by human disturbances can serve as “a base datum of normality, a picture of how healthy land maintains itself as an organism” (Leopold, 1949). The study was conducted in the center of the Frank Church- RNR Wilderness encompassing the Salmon River Mountains of Central Idaho (Figure 1.2). A suite of plant community attributes and biological indicators was collected including plant foliar cover, ground cover, plant species inventory and plant species richness within communities along the elevation gradient. In addition to community characterization, phylogenetic and plant trait analysis was conducted to better understand changes in community assemblage processes along an elevation gradient.

Elevation gradients have a correlation with other environmental factors such as temperature, moisture, pressure, and weather. Due to rapid abiotic changes, an elevation gradient is often used as a proxy for studying the effects of environmental gradients. The moist adiabatic lapse rate models a temperature gradient of approximately 0.6 °C per 100 m of elevation (Barry, 2008). Precipitation generally increases with elevation but is less predictable and more climate dependent than the temperature gradient. Although precipitation increases with elevation, available moisture in the alpine zone is limited due to sustained temperatures below freezing. Increasing temperature as a result of climate change has led to changes in these typical abiotic patterns along the elevational gradient.

While the overall precipitation has increased across the United states, this is primarily due to more intense single precipitation events rather than sustained precipitation throughout the season (Klos *et al.*, 2015). The ratio of precipitation falling as snow versus rain has decreased in the last several decades which affects the timing of available moisture. Nayak *et al.*, 2010, looked at 45 water years (1962-2006) of temperature, precipitation, snow and streamflow data along an elevation gradient at the Reynolds Creek Experimental Watershed in the Owyhee mountains. Their study addresses the effects of changing precipitation patterns on the empirical relationship between Snow Water Equivalent (SWE) and stream discharge. Their results show that although total precipitation and stream discharge have remained relatively constant, the amount of snow versus rain has decreased at all elevations and most significantly at mid to low elevations. Reduced SWE was

correlated with higher early season stream discharge and reduced late season stream discharge. Bales *et al.*, 2011 found that soil dries out quicker after rain than snow in a study assessing the response of soil moisture to snowmelt and rainfall in a mixed conifer forest in the Sierra Nevadas. Their study reveals the temporal differences in the timing of soil dry out which, was strongly correlated to timing of snowmelt. Low and mid elevations, where the shift from snow to rain is most pronounced, will be more affected by changing soil moisture regimes.

As a result of these recent climatic shifts, increasing evidence supports the upwards migration of species distribution giving reason to believe that species occurring at the highest elevations are at the greatest risk of extinction (Pauli *et al.*, 2001; Pauli *et al.*, 2012; Matteodo *et al.*, 2013). With nowhere left to go, species at high elevations may be most susceptible to extinction however, plant communities at lower elevations will also respond to changing climate affecting community composition and ecological function. For example, A study conducted by Crimmins *et al.*, 2011, in the California mountains shows a greater percentage of plant species has a downward shift in the optimum elevation verses plant species with an upwards shift in optimum elevation. This study is based on over 10,000 plots of plant data from studies conducted in the 1930's compared to later studies in the 2000's. In order to understand local scale changes, baseline data is a necessity. In this study we use a combination of plant community attributes with phylogenetic and functional trait analysis to better understand plant community dynamics along an elevation gradient in a remote area of the Frank Church-RNR Wilderness. The primary purpose of this study is to characterize the existing vegetation, have a look into current plant community assemblage processes and provide a robust compilation of baseline data. By using a standardized protocol widely applied throughout the west, this data is compatible to a high volume of datasets and is applicable to further studies in order to better understand how our local natural landscapes are reacting to climate change.

Combining phylogenetic and functional trait analysis is becoming more common as a method to infer community assemblage processes (Ackerly, 2003; Diaz *et al.*, 2007; Webb *et al.*, 2010; Pavoine & Bonsall, 2010; Lopez *et al.*, 2016). Three main theories driving community assemblage processes have been derived based on three patterns of phylogenetic and functional trait diversity, as illustrated in Figure 1, from Lopez *et al.*, 2016. The term phylogenetic clustering describes a plant community comprised of species more closely related than by chance. Thus, the average phylogenetic distance is less than the null model derived from the regional species pool as in community A (Figure 1.1b). Phylogenetic overdispersion describes a plant community comprised of species more distantly related than by chance with an average phylogenetic distance that is greater than the null model as in community C (Figure 1.1b). A neutral or random assemblage pattern explains a community of species

which are no more or less related than compared to the null model as in community B (Figure 1.1b). Environmental filtering suggests that environmental variables are driving community assemblage processes, filtering out unequipped species. In theory, environmental filtering results in a phylogenetically clustered community of functionally similar species because the necessary traits for survival are only expressed by a group of closely related species (Figure 1.1a). When competition dominates the assemblage process, the result is phylogenetic overdispersion and functional dissimilarity. This theory suggests that closely related species compete against each other while more distantly related species cohabitate due to trait differentiation and niche partitioning (Figure 1.1a). Finally, a neutral or random assemblage theory is based on environmental stochasticity resulting in a community with a random composition of traits and a phylogenetic distance that does not differ from the randomly generated null model (Figure 1.1a).

A suite of indices exists to choose from for calculating phylogenetic diversity however, besides choosing the most appropriate index, calculating phylogenetic diversity is straight forward. (For a more in-depth discussion on the different indices available and their applications see *Measuring Phylogenetic Biodiversity*, Chapter 14). Here, we use an approach first introduced by Webb *et al.*, 2002 which uses a distance matrix generated from a phylogeny to calculate Mean Nearest Taxon Distance (MNTD), Mean Pairwise Distance (MPD) and, Standardized Effect Size (SES) for hypothesis testing. Calculating functional diversity requires much greater meticulousity. In addition to choosing the most appropriate index, careful consideration must be given to the traits chosen for analysis. Furthermore, a sound framework for jointly analyzing numeric and discrete traits does not yet exist. Aside from choosing the right traits, conducting multivariate or single variable analysis is also critical. Although multiple traits may contribute to a single function, using a multivariate approach can mask competition or environmental filtering if not all traits are under equal constraint (Lopez *et al.*, 2016). Lopez *et al.*, 2016 illustrates some of the prominent sensitivities in functional trait analysis, supporting claims with multiple simulated datasets. In our study we analyze two traits individually by generating a distance matrix based on converting the Gower (1971) similarity index into a dissimilarity index. The distance matrix is then used to calculate MPD, MNTD and SES in each community.

Violle, *et al.*, 2007 defines functional traits as “Morpho-physio-phenological traits, which impact fitness directly or indirectly via their effects on growth, reproduction and survival”. Lavorel and Garnier, 2002 provide a more ecological definition: “Plant traits that contribute to the responses of species to changes in the environment and/or the contribution of species to ecosystem functions” Functional traits were chosen based on the hypothesis that moisture and temperature are likely abiotic

factors that will impact community assemblage patterns along the elevation gradient. Due to elevational driven changes in snow cover, temperature and growing season, seed dormancy class was considered an important trait. Seed dormancy class describes the mechanism used by a plant to delay seed germination under otherwise optimal conditions (Baskin and Baskin, 2004). In terms of genetic expression, Van der Schaar, 1997 calls seed dormancy one of the most complicated traits in nature due to a large amount of genetic variation and the fact that gene expression is strongly impacted by environmental factors during seed development.

Six classes of seed dormancy are defined based on the seed dormancy classification scheme outlined in Baskin and Baskin, 2004. There are subclasses within each class. For the scope of this study, dormancy was identified only to the class level. No Dormancy (ND), describes seeds that do not undergo dormancy. Dust classifies the smallest seeds in angiosperms with highly reduced embryos of only a few cells. Dust seeds require an external nutrient source to break dormancy. Physiological Dormancy (PD) is dependent on time and temperature and depending on the subclass, seeds may require a period of cold or warm stratification. The amount of time to dormancy break will affect the optimal germination temperature requirements. Morphological dormancy (MD) is dependent on time. Embryos are underdeveloped and require several days to weeks to fully develop. Morphophysiological dormancy (MPD) is dependent on time and temperature. Embryos are underdeveloped and require time to fully develop in addition to a dormancy-breaking pretreatment. Physical dormancy (PD), is characterized by a seed coat that is impermeable to water requiring chemical or mechanical scarification to allow water to pass through. Physical + Physiological dormancy (PYPD), is dependent on scarification to break the impermeable seed coat and a temperature dependent pretreatment to break physiological dormancy in the embryo. Analysis of seed dormancy class will help determine if environmental filtering is driving plant community assemblage.

Seed mass is known to be correlated with interspecific competition, germination and establishment. It takes less energy for smaller seeded species to develop many seeds than larger seeded species however, larger seeded species are better equipped for successful germination and establishment in harsh conditions (Moles *et al.*, 2005). Additionally, seed mass is correlated with other characteristics including life cycle, height, and dispersal mode all of which are involved in competition (Westboy *et al.*, 1996). Seed mass was chosen as a functional trait to inquire competition related assemblage process however, it may be associated with both environmental filtering and competition.

Assemblage processes are less predictable at lower elevations however, hot and dry conditions at the lowest elevations may also lead to clustering. Clustered or over-dispersed functional trait diversity will support phylogenetic analysis. Because extreme heat is a common form of mechanical scarification, PY and PYPD are less likely to occur at high elevations where fires are less frequent. A shorter growing season at higher elevations may select against MD while favoring PD or ND. Harsh conditions at high elevations are expected to select for relatively larger seeded species. Due to strong environmental gradients associated with elevation and generally harsher conditions in the alpine zone, our hypothesis is that species assemblages will be driven by environmental filtering with increasing elevation and thus show phylogenetic and functional trait clustering at the highest elevations.

The purpose for this study is to add to the existing body of data that exists at TWRS by taking a novel approach of studying plant communities along an elevation gradient. Because of the correlation between elevation and other environmental gradients that are directly linked to climate change, we believe an elevation gradient will be an effective way to detect subtle changes in plant communities to changing climate. We aim to provide baseline data in order to assess changes over time in three primary areas of focus: 1. The distribution of invasive species. 2. Dominant vegetation types 3. Individual species shifts. However, we collected a wide-ranging dataset so that it would not limit future studies. Additionally, we aim to understand patterns of plant community assemblage along an elevation gradient through phylogenetic and functional trait analysis by addressing two questions: Is there is evidence of phylogenetic clustering at higher elevations? 2. If so, what functional traits are possibly being selected for? By analyzing the data in multiple ways, we aim to reveal evidential processes without masking cooperating processes.

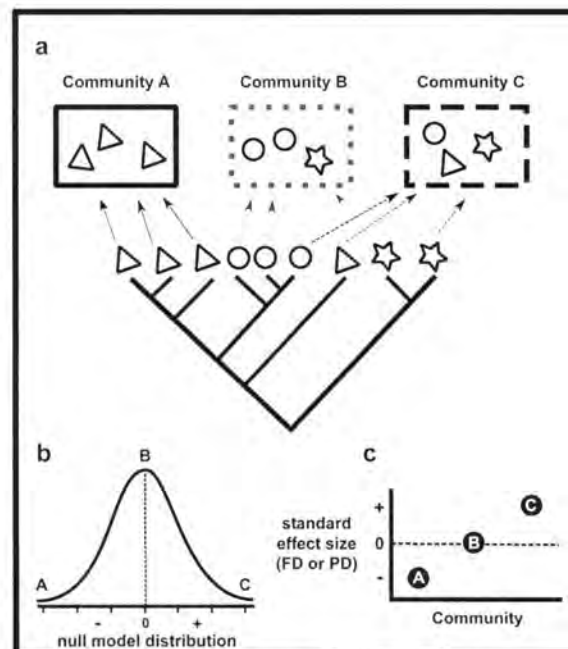


Figure 1.1: Community assemblage theories-
a) Shapes represent traits in species. Community A illustrates the theory of clustering by environmental filtering. Community B illustrates a random assembly theory based on environmental stochasticity. Community C illustrates the overdispersion by competition assembly theory. **b)** The null distribution of phylogenetic or functional trait diversity based on the regional species pool is centered at zero. **c)** Standard effect size is derived based on the difference in observed vs. null model. SES below the null model suggests clustering while SES above the null model suggests overdispersion. (Figure from Lopez et.al., 2016)

1.2 Methods and Materials

Study area

The study area is located east of Ellensburg, ID in the center of the Frank Church-RNR Wilderness, 32 miles from the nearest road. Situated on Big Creek at 1,178m, the Taylor Wilderness Research Station (TWRS) served as the base for this project. The study was conducted along 44 latitudinal transects spanning the NW slope of Dave Lewis Peak, typical of the rocky slopes of the Salmon River Mountain Region in Central Idaho (Figure 1.2). This area is characterized by a network of steep ridgelines severed by deep river canyons. The vegetation is dominated by shrub-steppe rangelands at lower elevations, transitioning into tree dominated communities near 2,000m and reaching alpine communities above 2,500m (Peek, 2005). The Snake River, the Salmon River and their tributaries form a hydrologic network traced by dense riparian vegetation. At 2,800m, Dave Lewis Peak forms the apex of the pioneer creek watershed which drains into Big Creek, a major

tributary of the Middle Fork Salmon river. Soils in the area are nutrient poor, comprised of decomposed granites of the Idaho Batholith (Peek, 2005; Finklin, 1988). Soil types have not been described for this region by the Natural Resource Conservation Service (NRCS) due restricted access in wilderness areas. The climate is driven by a semi-arid desert system of hot and dry summers and wet winters. Based on data acquired from the TWRS weather station at 1178m, an average 38 cm of precipitation falls annually, the wettest months occurring in December and January. The mean minimum temperature occurs in January at -10°C and the mean maximum temperature occurs in July at 31°C (Peek, 2005).

Study design

A stratified random sample design was used to generate a total of 44 plots distributed evenly between 11 elevation bands on a NW facing slope. Beginning at 1,220m, 11 bands were drawn in 152m increments. The summit was reached in the last band terminating at 2,835m (Figure 1.2).

Samples were collected June 5th – July 21st. The line-point intercept (LPI) method was used to collect vegetation and ground cover composition using a single line transect design (Herrick *et al.*, 2017, pp.7-8). A 25 m transect was extended latitudinally in each direction from the center point to create a single 50 m transect (Figure 1.3). The LPI method is considered the least biased and most objective method for sampling community level vegetation (USDA-ARS; Elzinga, 1998; Karl & Colson, n.d.; Godínez-Alvarez *et al.*, 2009). Additionally, the line-point intercept method is becoming a standard for all federal agencies collecting rangeland health indicators. Therefore, this data is compatible with a large regional pool of samples. In order to amplify the presence of herbaceous species which, can be hard to detect using LPI, the quadrat frequency method was employed using 1m^2 quadrats every 2.5 m. A plot level species inventory was conducted at every plot by walking the length of the transect, extending 1 m in width on each side of the transect, creating a 100m^2 rectangle. The rectangle was systematically searched for a total of 15 minutes. LPI and plot level species inventory methods are outlined in Herrick, 2017 (pp. 27-28; 55). The Quadrat frequency method can be found in Volume II of Herrick, 2009 (p. 79).

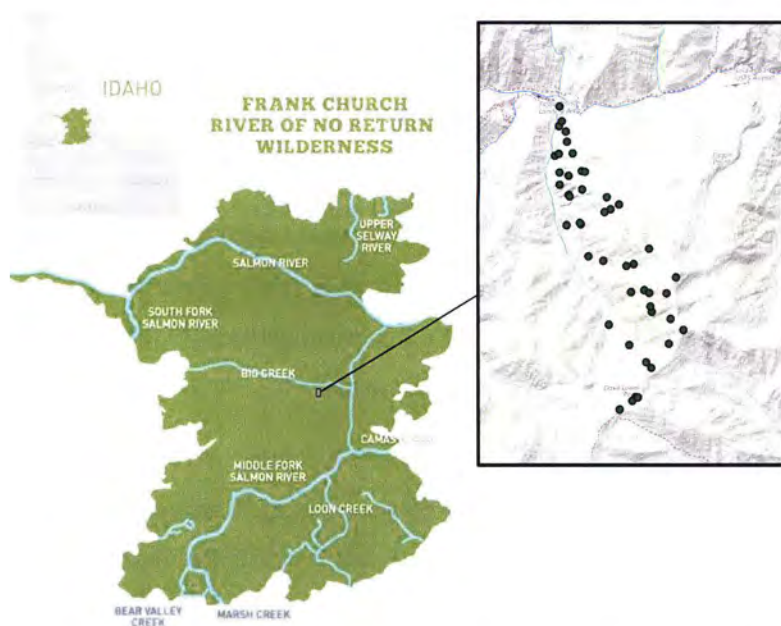


Figure 1.3: Study area inside Frank Church-RNR boundary with transect locations.



Figure 1.2: Example of 50m line transect spanning across slope.

Analytical methods

R statistical software was used for statistical analysis. Percent composition of ground cover types and foliar cover was calculated on the plot level and by elevational band in which case the plot level data was averaged across each elevational band. Linear regression analysis was used to determine the relationship between variables along the elevation gradient. Pearson's correlation

analysis was used to test for correlation between patterns of phylogenetic and functional diversity and environmental variables. Data was transformed for normalization using Tukey's ladder of powers.

The mega-phylogeny of spermatophyta (seed plants) derived from public gene repositories and phylogenies from the open tree of life project by Smith and Brown, 2018 was pruned to the regional species pool. Some species present in the study were missing from the mega-phylogeny in which case the accepted method of choosing a closely related species occurring in the same genus as a replacement was used (Qian, & Jin, 2016). Six unknown species, which accounted for less than 1% of the total abundance, were removed from the data.

Phylogenetic distances and functional trait distances were computed using the *picante* package in R (Kembel *et al.*, 2010). Mean Nearest Taxon Distance (MNTD) and Mean Pairwise Distance (MPD) measures were calculated on a species basis and functional trait basis for observed communities. MNTD is the average distance based on tree branch lengths of a species to the nearest relative for all species in the community. MPD is the average distance based on tree branch lengths of a species to all other species for all species in the community. To test for statistical significance of clustering or overdispersion, null communities were generated based on 10,000 random draws from the regional pool to calculate Standardized effect sizes (SES) of MNTD and MPD. SES are calculated by standardizing the mean MNTD and MPD values of the null communities. MNTD is more sensitive to branch tips while MPD is more useful for deeper branching patterns. Both can be important detectors of assemblage process. Phylogenetic and functional trait patterns were analyzed for all species in spermatophyta and for herbaceous forbs only weighted by abundance. MNTD and MPD values were compared for the full community analysis to illustrate the difference in results.

1.3 Results

Foliar Cover

Total foliar cover ranged from 14% to 88%. A negative trend in percent foliar cover with increasing elevation was significant ($R=-0.68$; $P=3.4e-07$) (Figure 1.4a). Foliar cover of graminoids showed a negative linear trend with elevation which was statistically significant ($R=-0.60$; $P=1.6e-05$) (Figure 1.5). Foliar cover of shrubs showed a unimodal distribution below 2,000 m, the maximum percent shrub cover occurring between 1,600-1,900 m. Above 2,200 m, shrub cover was negligible to absent (Figure 1.5). Tree cover did not have a linear relationship with elevation, however trees became the dominant foliar cover type above 2,210 m. No significant patterns in foliar cover of forbs, sub-shrubs or succulents were evident (Figure 1.5). Foliar cover of perennials showed a significant negative trend with increasing elevation ($R=-0.63$; $P=4.6e-06$) while annual foliar cover showed a

weakly bimodal distribution and were present mostly below 2,000 m (Figure 1.4b). Maximum foliar cover of invasive species occurred at 1,635 m with 15% cover. Above 2,000 m invasive species cover abruptly declined with foliar covers of 0-2% (Figure 1.4d). Slopes ranged from 16%-44%. Foliar cover of stabilizing species had a weak positive correlation with slope however, it was not significant. A peak of 49% foliar cover of stabilizing species occurred on a slope of 33% (Figure 1.4c).

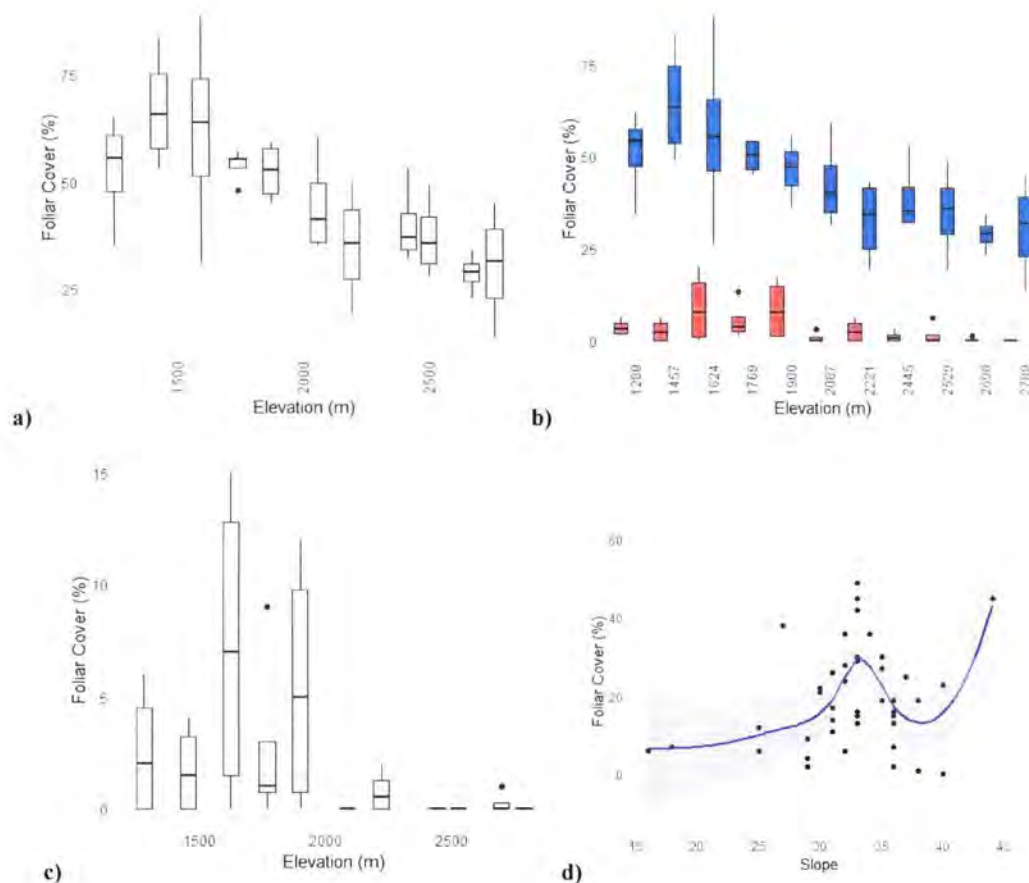


Figure 1.4: Percent foliar cover of **a)** total vegetation, **b)** perennial (green) and annual (red), **c)** invasive species by elevation and, **d)** stabilizing species by % slope.

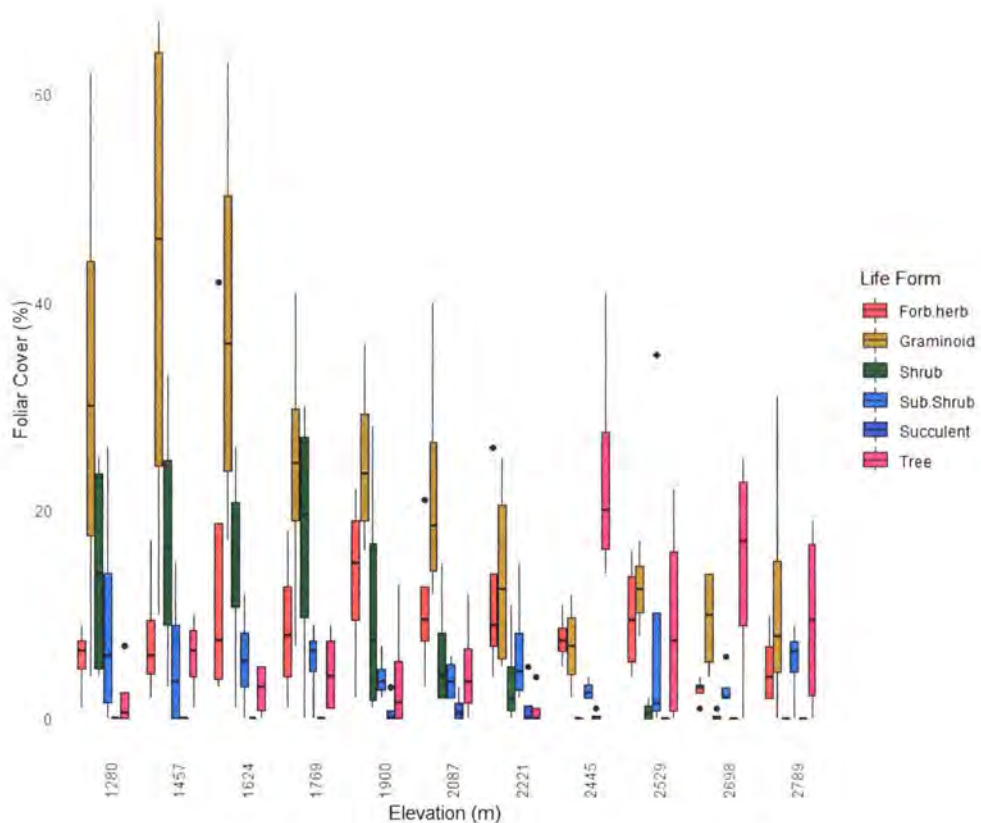


Figure 1.5: Percent foliar cover by life form by elevation band.

Ground cover

Herbaceous litter cover ranged from 10% to 71% and had a weak negative linear relationship with elevation that was significant ($R=-0.29$, $P=0.049$) (Figure 1.6a). Woody litter (2mm-3cm diameter) ranged from 0-18 % cover and had a positive linear relationship with elevation ($R=0.36$, $P=0.015$) (Figure 1.6b). Large diameter woody litter (>3cm diameter) ranged from 0-22% cover. Large diameter woody litter did not have a significant linear relationship with elevation (Figure 1.6c). Litter amount was most strongly correlated to percent cover of graminoids. Bare rock cover ranged from 0-69% while bare soil cover ranged from 0-28% (Figure 1.7). Bare rock cover increased with elevation having only a weakly significant linear relationship ($R=0.30$, $P=0.049$). Soil cover had a strong positive relationship with increasing elevation that was significant ($R=0.47$, $P=0.001$)

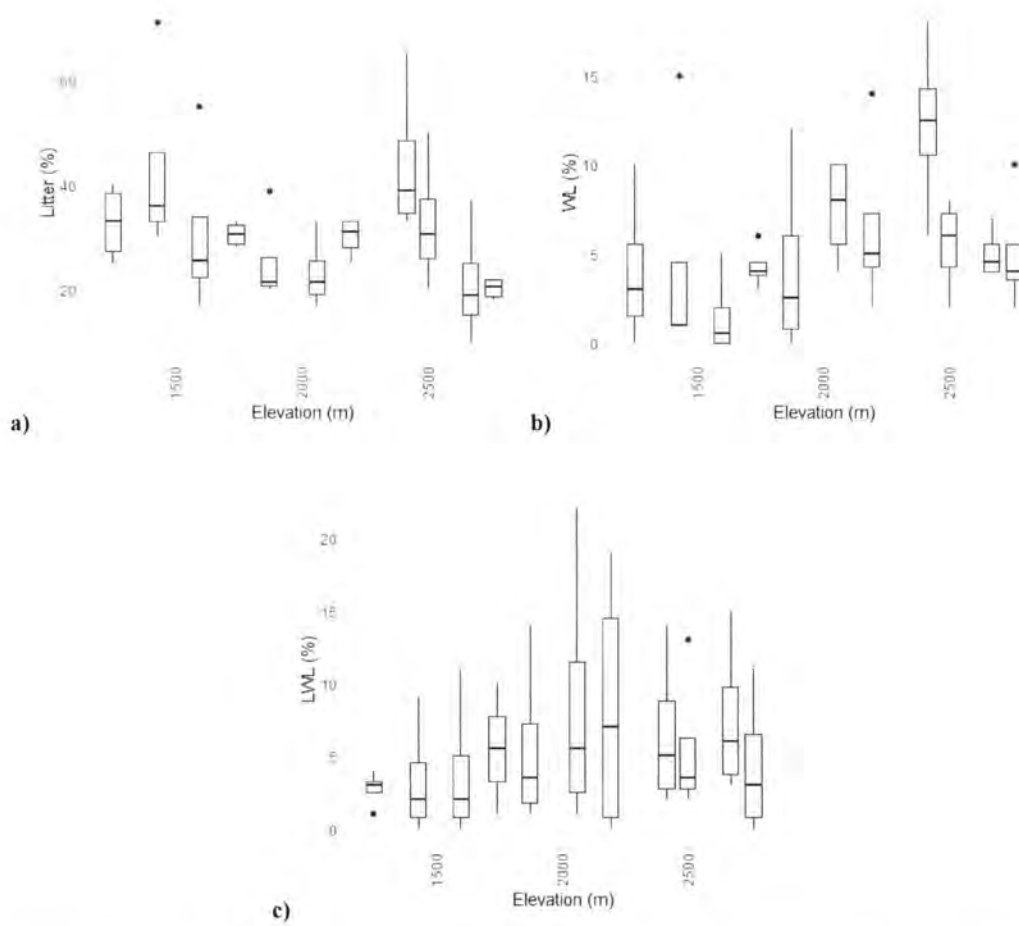


Figure 1.7: Percent ground cover of **a)** herbaceous litter, **b)** small diameter (≤ 3 cm) woody litter; **c)** large diameter (> 3 cm) woody litter.

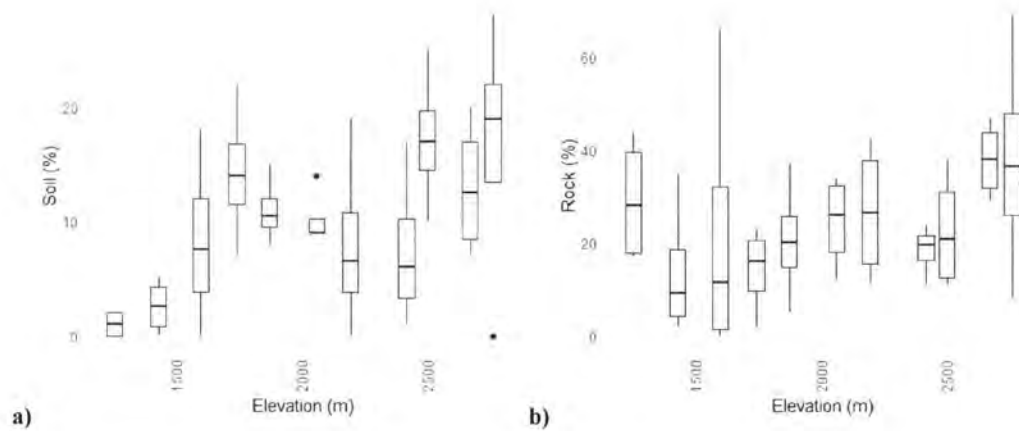


Figure 1.6: Percent cover of **a)** bare soil **b)** bare rock.

towards overdispersion in all analyses except MPD on spermatophyta (Figure 1.9). The degree of overdispersion was stronger for MNTD analysis than MPD and in unweighted herbaceous forb analysis vs. weighted (Figure 1.9). Herbaceous forb weighted and unweighted communities showed significant evidence for overdispersion in dormancy class from 1608-1975 m and clustering from 2583-2761m (Figure 1.9).

Seed mass ranged from .002-12.2 g/1000 seeds. Community weighted values ranged from .068-1.69g/1000 seeds. There was a significant negative correlation between seed mass and elevation ($R=-0.65$; $P=1.71e-06$)(Figure 1.12). Seed mass trended towards clustering in all diversity analyses except MNTD of spermatophyta (Figure 1.9). Seed mass showed significant clustering in herbaceous forbs weighted and unweighted communities between 2461-2687 m (Figure 1.9).

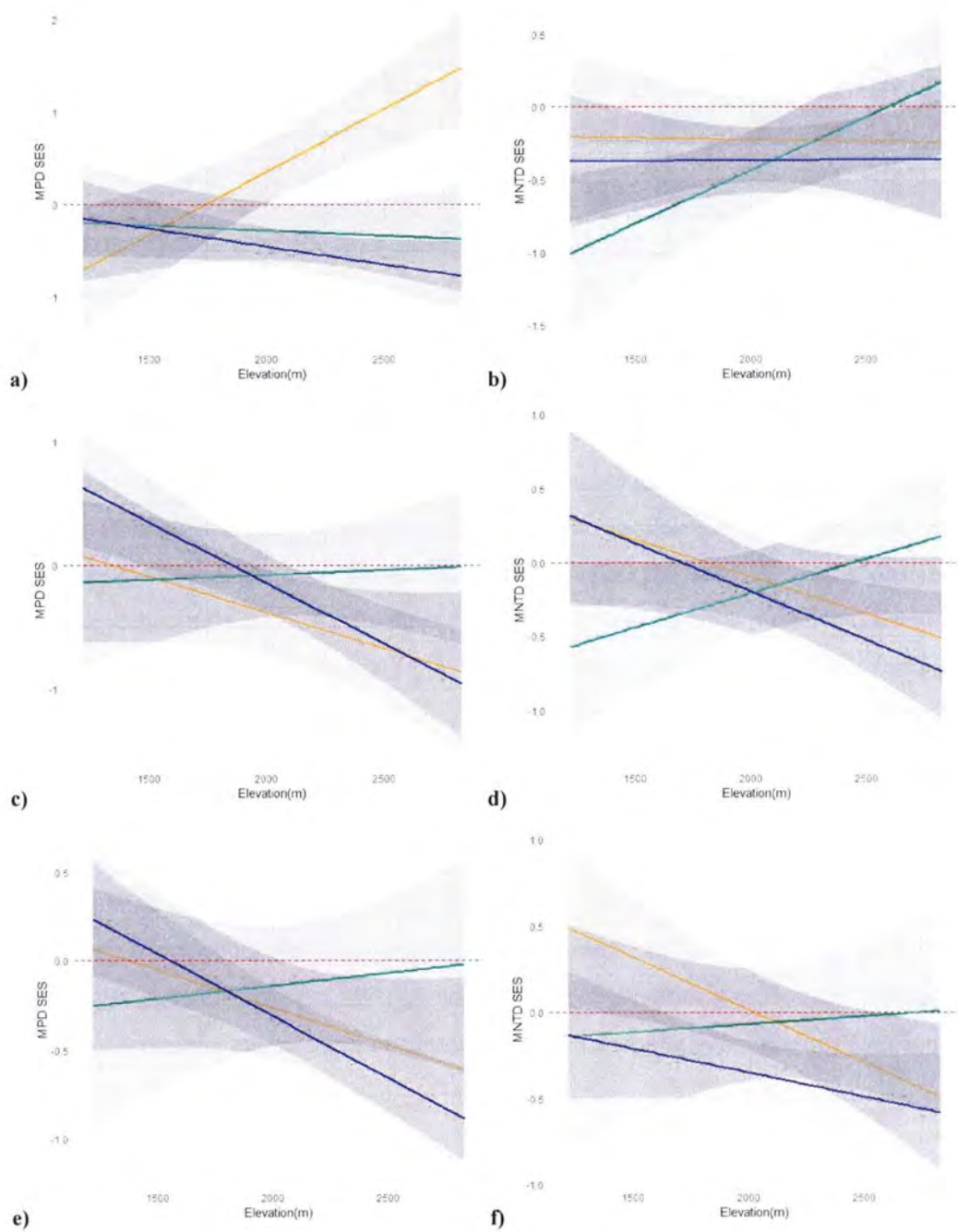


Figure 1.9: Linear regression of Phylogenetic and Functional trait diversity standard effect sizes for mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) versus elevation. Phylogenetic distance (orange); Seed dormancy class (green); Seed mass (blue); Spermatophyta (**a-b**), herbaceous forbs unweighted (**c-d**), and herbaceous forbs weighted (**e-f**); Null-distribution (Red-dashed).

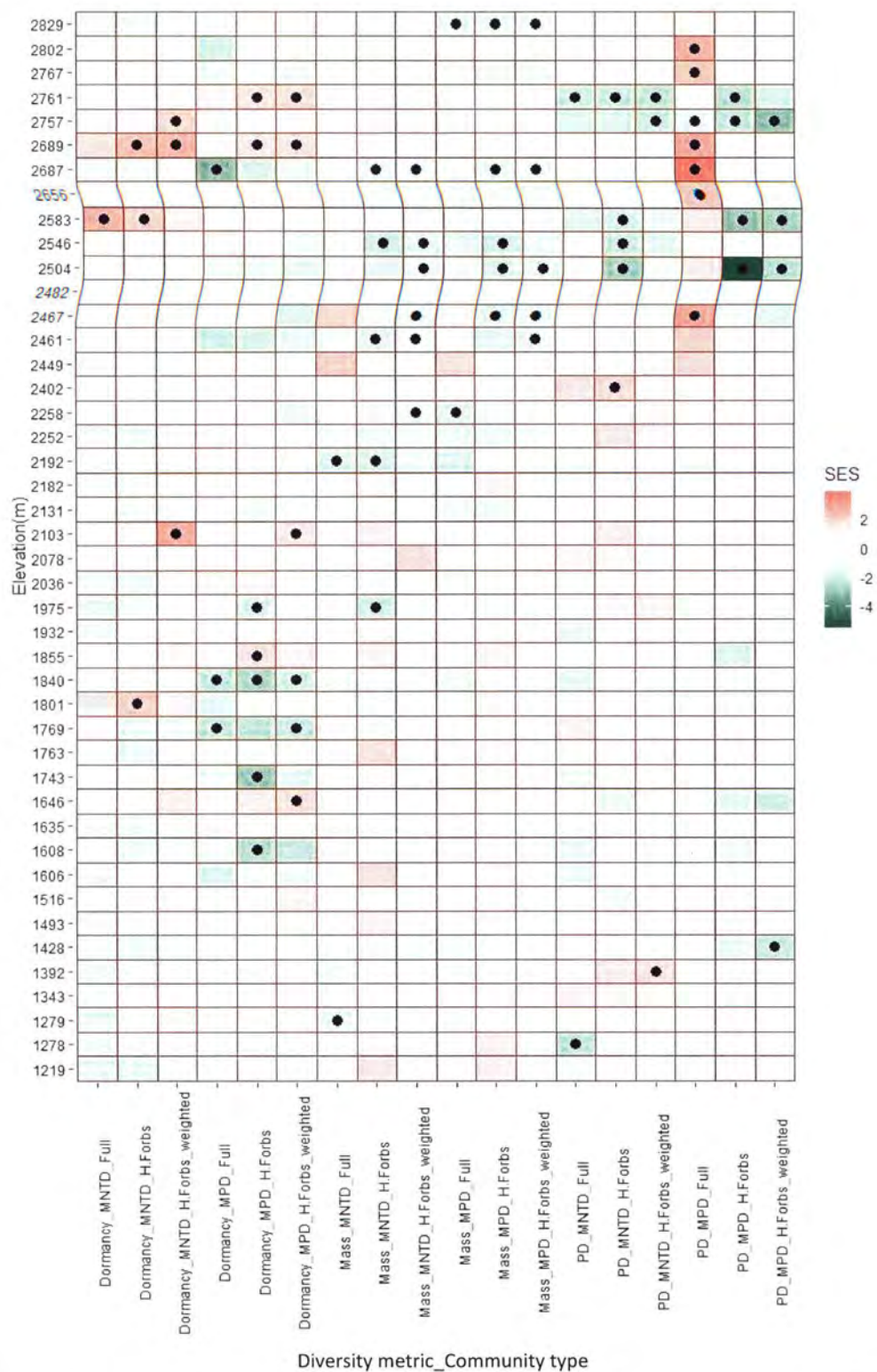


Figure 1.10: Phylogenetic and Functional trait diversity standard effect sizes using mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) by elevation and community type. Black dots represent significance ($P > 0.95$ =overdispersion; $P < 0.05$ =clustering)

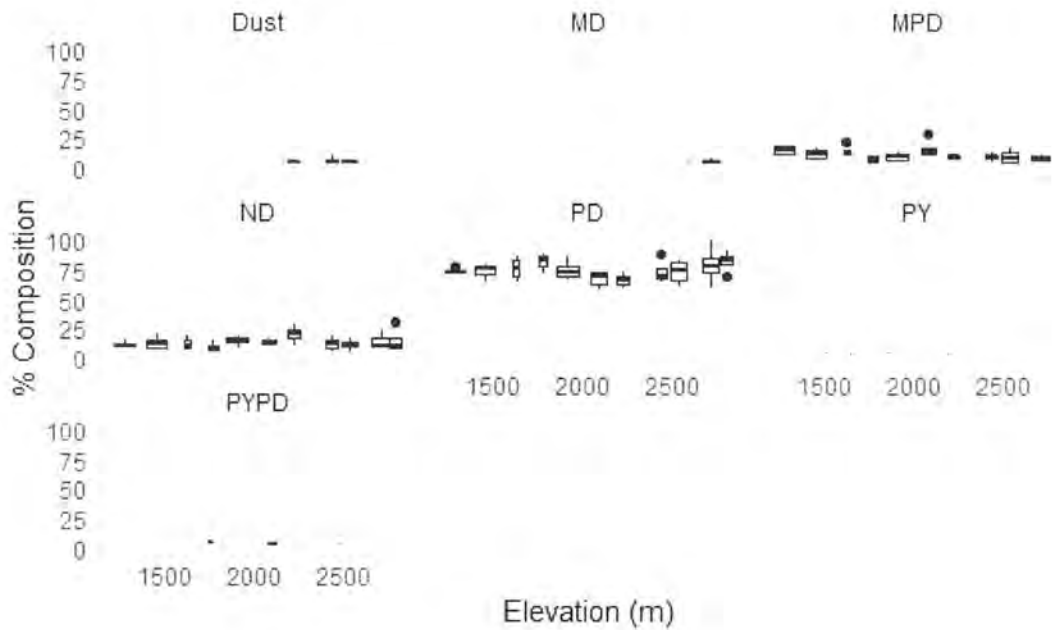


Figure 1.11: Percent composition of seven seed dormancy classes by elevation band.

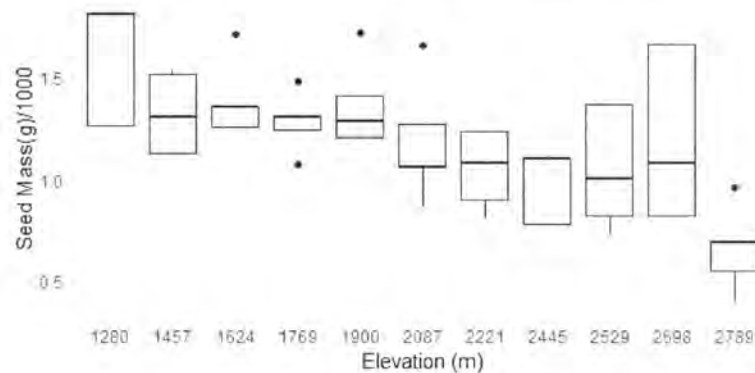


Figure 1.12: Community weighted mean of seed mass by elevation band. ($R=-0.65$, $P=1.71e-06$)

1.4 Discussion

Community attributes

A decrease in foliar cover with increasing elevation is common. At low elevations grasses and shrubs are the dominant species contributing to a large amount of foliar cover. Shrubs and grasses are reduced when transitioning into forested zones which are dominated by trees in the overstory and herbaceous forbs in the understory. Above tree line, foliar cover will significantly decline as communities are dominated by herbaceous forbs and a much reduced overstory. In our study shrub cover was sub-dominant until approximately 1,800 m. Former wildlife professor, Jim Peek, who contributed to much of the existing plant research in the area surrounding TWRS, speculated an

increase in shrub cover and an upwards migration of shrub species with climate change (Peek, personal communication, July, 2017). There is much evidence to support Dr. Peek's speculation, specifically in the Alaskan tundra (Strum *et al.*, 2001; Naito *et al.*, 2011; Meyers-Smith *et al.*, 2015), but also in the Southwest dryland systems (Munson *et al.*, 2011; Anderegg, *et al.*, 2013). In the Alaskan tundra a positive feedback between dense and tall shrub communities and snow drifts may be the contributing factor to an increase in shrub cover as a result of greater insulation and available moisture (Strum *et al.*, 2001). On the contrary, in the arid and semi-arid systems, increase in shrub cover may be driven by drought mortality of grasses and trees (Winkler *et al.*, 2019). During a field expedition near TWRS in June of 2017, personal observations were made leading to the speculation of a douglas-fir (*Pseudotsuga menziesii*) dominated community transitioning into a ponderosa pine (*Pinus ponderosa*) dominated community, a more drought tolerant community type. An increase in shrub cover could have major impacts on biotic integrity and ecosystem function. Bighorn sheep rely heavily on bunch grasses, *Pseudoroegneria spicata* in particular (Tilton, 1997). Eldridge *et al.*, 2011 found that increasing shrub cover is correlated to a decrease in graminoid cover, and an increase in soil carbon and nitrogen in ecosystems world wide. An increase in shrub dominance alters aboveground net primary production (ANPP) thus, altering the carbon storage potential of the site (Knapp *et al.*, 2008).

Invasive species is another major cause for concern. In the west, cheatgrass, (*Bromus tectorum*) is perhaps the greatest threat to rangeland ecosystems. Peterson, 2005, estimated 13.3 million ha of continuous cheatgrass cover in Nevada alone. Fortunately, in our study no more than 15% foliar cover of cheatgrass was detected on any plot. Just 3 other species considered to be invasive according USDA plants database were detected (*Bromus inermis*, *Symbrium altissimum*, *Cirsium vulgare*) These species contributed to less than 10% foliar cover. Above 2,000m invasive species were nonexistent in our samples. Due to wilderness protections and limited human disturbances, invasive species have not yet fully displaced native communities in our study area. However, other areas in the Frank Church-RNR suffer from more intense invasions of cheatgrass and other noxious weeds such as spotted knapweed (*Centaurea maculosa*). Highly invaded sites are most often linked to areas concentrated by human and stock use (personal observations, 2017-2018).

Phylogenetic and Functional diversity

Plant community assemblage process theories based on phylogenetic and functional trait dispersion are logical however, a number of assumptions must be made. Perhaps the most controversial assumption is that competition and environmental filtering are alternative processes. Research shows that the two can be independent or may work in concert (Gerhold, *et al.*, 2015).

Additionally, choosing the most informative traits is difficult as many traits may interact and be subject to both competition and filtering. By analyzing plant communities in several ways, using several metrics, our goal was to uncover some of the patterns of plant community assemblage without masking alternative processes.

When including all spermatophyta in phylogenetic analysis MPD increased linearly with elevation while functional trait distances slightly decreased (Figure 1.9). This would counter theories of competitive exclusion and environmental filtering. Based on SES values, MPD analysis detected 7 significantly overdispersed communities above 2,400m (Figure 1.10). However, this information should be considered carefully before drawing conclusions. Conifers belonging to *coniferophyta* are more distantly related than all other species in the study which belong to *magnoliophyta*. Conifers occupy the overstory, a different niche space than most other species in our study, therefore, are less likely to compete against them. For this reason, when including a broader range of taxa in phylogenetic analysis the phylogenetic distance metric should be highly considered. In our study, MNTD is a more appropriate metric for detecting phylogenetic signal. MNTD was stagnant along the elevation gradient but detected two communities that were significantly clustered at 1,278m and 2,761m which, supports our hypothesis because the method is more appropriate (Figure 1.10).

Analyzing herbaceous forbs only was of interest based on the fact that forb diversity accounted for a majority of species richness and was the only growth form to show a strong unimodal distribution. Whether to use MNTD or MPD is a little more obscure in this case. Additionally, we were able to weight the samples based on forb frequency data. SES values for PD trended from overdispersion towards clustering with elevation for all metrics weighted and unweighted. Weighted values most strongly affected MNTD PD increasing the degree of negative correlation. While SES values for seed mass trended in the same direction as PD, seed dormancy showed the opposite, trending from more clustered to overdispersed (Figure 1.9). Several communities that were significantly clustered phylogenetically showed significance for overdispersion based on dormancy class. Again, this disputes the theories of community assemblage based on functional trait analysis.

Seed dormancy is one of the first traits expressed in the plant lifecycle therefore it has a major role in competition and establishment, plant distribution and speciation (Willis *et al.*, 2014). PD was the dominant seed dormancy class at all elevations. PD is the broadest class of dormancy, containing five subclasses based on different temperature and moisture requirements and timing of dormancy break. MD and ND were sub-dominant to PD at all elevations. ND allows germination to happen at any time provided the optimal conditions. This may be advantageous at higher elevations do to the short growing season. Alternatively, J.E. Pelton found twelve of eighteen high altitude species studied

in Colorado required a dormancy phase (Pelton, 1956). ND is the most versatile of the dormancy classes. Willis et al., (2014) hypothesized that plants classified as ND may have an advantage in novel environments. It is therefore logical that as climate change leads to novel ecosystems, ND will be advantageous. The versatility of ND holds true in our study as most of the species with the broadest elevation range are classified as ND. Dust seeds, the smallest seeds among angiosperms, most likely evolved to maximize fecundity at a low cost (Eriksson and Kainulainen, 2011). Dust seeds are so reduced that an external carbon source is required for initial growth. In our study, species with dust seeds occurred between a narrow elevation range (2,220m-2,530m). Only two species expressed dust seed dormancy. *Chimaphila umbellata* and *Pyrola asarifolia* are myco-heterotrophic, relying on fungi in the soil for nutrients. Tree cover creates a moist, cool microclimate fostering a vigorous fungal community. The occurrence of these two species was highly correlated to tree cover, however the occurrence of these species was not enough to detect significance. It is possible that the mutualism between dust seed species and fungal host will be highly susceptible to climate change in regards to increasing temperatures and more frequent wildfire. PY was expressed by two species (*Lupinus sericeus*, *Trifolium repens*) and PYPD by two species (*Lupinus argenteus*, *Ceanothus velutinus*). All species expressing PY in the form of PY or PYPD have the ability to fix nitrogen with root nodules. These species are associated with wildfire as they are often the first to establish in newly burned areas. This poses an interesting question regarding the evolutionary sequence of nitrogen fixation capacity and physical seed dormancy. Perhaps the most surprising result is the expression of MD in a species occurring only above 2,000 m. *Cymopterus nivalis*, has the common name Snowline spring-parsley as it is often the first to appear after snowmelt. MD requires a developmental period prior to dormancy break however, in a species that is one of the first to begin growth, this is unexpected. Perhaps the period of development happens underneath the snow in cool conditions.

Although larger seeds are generally more viable, resistant to adverse conditions and produce more robust seedlings, larger seeds can be very energetically expensive. Therefore at high elevations in harsh growing conditions, larger seeds may require too much energy. Murray, *et al.*, 2004 found a significant correlation between solar radiation and seed mass. Their theory suggests that increased photosynthates leads to excess energy to spend on seed size. Our study shows support for half of this theory. According to Blumthaler, *et al.*, 1997, there is a positive correlation between total solar irradiance increases and elevation. In our study there was a statistically strong negative correlation between seed mass and elevation (Figure 1.12). However, if seed mass is correlated to excess energy then it is possible that the higher elevation communities in our study have little excess energy based on harsh habitat conditions therefore, smaller seed masses. Based on our results, it is apparent that

herbaceous forbs are trending towards phylogenetic clustering at high elevations along with seed mass however, seed dormancy class is trending towards overdispersion.

Overall, our study provides a wide range of baseline data to complement future studies in addition to some insight into plant community assemblage processes. Currently, invasive species are not a major threat at any elevation and foliar cover significantly declines above 2,000 m. Plant species ranges are outlined in Table 1.1. By updating this table over time, we can reveal how individual species ranges are shifting in relation to climate. Figure 1.5 shows the dominant vegetation types along the elevation gradient. Again, addressing foliar cover by lifeform over time will reveal changes in our dominant vegetation types. Finally, there was evidence for phylogenetic clustering with increasing elevation which may suggest environmental filtering. Seed mass may be a trait that is affected by environmental filtering as suggested by the linear trend in decreasing seed mass with increasing elevation. Seed dormancy class does not seem to be involved in environmental filtering however, ND was revealed as a potential climate change advantageous trait, while Dust seeds may be negatively impacted.

Chapter 2: *In Situ* Analysis of Floral Scent Composition from *Penstemon* Along an Elevation Gradient in the Frank Church Wilderness

2.1 Introduction

Originating in the Rocky Mountains, the genus *Penstemon* is the largest genus endemic to North America containing almost 300 known species (Straw, 1956; Wolfe *et al.*, 2002). Diversity is strongest in the intermountain region of the Southwest however; every U.S. state contains at least one species of *Penstemon*. Such rapid speciation makes this group a rare example of continental evolutionary radiation (Wolfe *et al.*, 2006a). Adaptation to a wide range of ecosystems has occurred as species evolve to take advantage of distinct pollinators and ecological niches (Castellanos *et al.*, 2003; Wilson *et al.*, 2008). Pollination specialization has played a major role in speciation events within the genus *Penstemon* (Wolfe *et al.*, 2006b).

A pollination syndrome describes a distinct set of phenotypic floral traits specialized to attract a specific pollinator or group of pollinators (Fenster *et al.*, 2004). *Penstemon* are pollinated by a variety of pollinators including hymenopterans, lepidopterans, dipterans and hummingbirds. Although visual traits seemingly play the primary role in pollination specialization, recent discoveries have revealed that chemical expressions may be just as important. Parachnowitsch *et al.*, 2012, concluded that floral scent emission had a greater effect on pollinator visitation than did flower color or size. Although little is known about olfactory cues, it is likely a combination of the olfactory and visual characteristics that form a complete syndrome (Leonard *et al.*, 2011; Burger & Ayasse, 2010). Furthermore, it is possible that both visual and olfactory cues are regulated by the same genes. Cna'ani *et al.*, 2015, discovered that PH4, a transcription factor in petunia, is a key floral regulator for both color and scent.

Because pollination specialization is a primary driver of speciation in *Penstemon*, and much of the nuances associated with visual cues have already been described, identifying and quantifying floral scents to support the evolutionary storyline of *Penstemon* is important. In addition to understanding evolutionary history, plant-pollinator interactions are highly sensitive to changing climate. Hegland *et al.* (2009) provides an extensive review on how increasing temperatures may affect the phenology and distribution of plants and pollinators. Their findings suggest that phenological responses to climate change between plants and pollinators may be linear however, several cases have detected temporal mismatches between mutualistic partners with increasing temperature. In conclusion, more extensive research is a necessity to understand drivers of plant-pollinator mutualisms. Most of the available research on plant-pollinator mutualism responses to

climate change have again, been focused on visual cues regarding the onset of flowering. Less studied is the impact that increasing temperature may have on the composition and emission of floral scents which, we have learned, is an important facet of pollination syndrome.

Floral scents are made up of a suite of volatile organic compounds (VOCs) often referred to as a bouquet. VOCs are classified as secondary plant metabolites meaning they do not serve a purpose in primary metabolic processes. However, VOCs play a dominant role in a plethora of ecological functions including defense, inter or intraspecific communication and attraction (Vivaldo *et al.*, 2017). VOCs can be released in almost any part of the plant. Floral VOCs are a type of plant VOC released specifically in the flower. It is believed that the chemical constituents making up a bouquet function in concert rather than independently therefore, caution should be taken when analyzing a single compound versus composition. Constituents are most commonly classified into groups based on biosynthetic pathways. Knudsen *et al.*, 2006 created seven classes for floral VOCs. Aliphatics, benzenoids and phenylpropanoids, C5-branched compounds, terpenoids, nitrogen-containing compounds, sulfur-containing compounds, and miscellaneous cyclic compounds (Knudsen *et al.*, 2006).

Although a few studies have focused on the effects of temperature (Scaven and Rafferty, 2013), drought (Burkle, and Runyon, 2016) and nutrient availability (Majetic *et al.*, 2017) on floral scent, no studies currently exist along an elevation gradient. Furthermore, very little studies on floral scents are conducted *in situ*. Our study characterizes floral scent *in situ* in several species of *Penstemon* that inhabit the Salmon River mountains in the Frank Church-RNR wilderness. One of the primary objectives of this study was to collect inventory of VOCs from *Penstemon* species that have not yet been sampled. Additionally, this study aimed to answer three primary questions: 1. Does total scent emission have a positive relationship with pollinator frequency? 2. Is VOC composition constrained within a species? 3. Is there a spatial pattern of similar VOC composition along the elevation gradient suggesting environmental factors influence VOC composition?

Methods and Materials

Study design

The study is an addition to the baseline study conducted at TWRS. The study area was expanded to include the adjacent ridgeline on the west side of pioneer creek leading up the Dave Lewis Peak and area across Big Creek to the north on south facing slopes (Figure 2.1). Refer to chapter one Methods and Materials section for climatic and biogeographical details of the study area.

17 communities of *Penstemon* were identified along the east and west ridgelines leading up to Dave Lewis Peak ranging from 4400-9000 feet in elevation. Two additional populations on adjacent

ridgelines on the north side of Big Creek were sampled (Figure 2.1). The majority of the populations are from *P. attenuatus* var. *attenuatus* and *P. attenuatus* var. *pseudoprocera* for intraspecific analysis; however, the study was not limited to one species. Samples from *P. wilcoxii*, *P. payettensis*, and *P. salmonensis* were also included (Table 2.1). A total of 80 samples were analyzed from 17 different communities.

Three to nine individuals of the same species per population were sampled. Populations were sampled on the same day between the hours of 7am-9pm. Time of day, relative humidity and associated species were recorded at the beginning of collection. The methods used to collect VOCs including a visual, are outlined in Burkle, *et al.*, 2017. We used a portable volatile assay collection system (Volatile Assay Systems, Rensselaer, NY, USA) to collect VOCs using the dynamic headspace technique. One inflorescence per individual was enclosed in a clear polyethylene plastic cup with a clear dome lid attached to a glass Volatile Collection Trap (VCT) lined with 30 mg of HayeSep-Q absorbent material (Restek, Bellefonte, PA, USA). Air was pulled at a rate of 0.5 L min⁻¹ for 1 hr. through a plastic hose attached from the VCT to the collection system. VCTs were sealed and stored for further analysis. Exact specifications for VCTs and the portable VAS machine can be found online at vassays.com. Pollinator visitation was recorded by functional group based on 1 hr. observations immediately prior to VOC collections for 21 samples. Finally, for each inflorescence sampled, the total number of flowers was recorded by stage: bud, flower, or seed.

Volatiles were eluted from traps using 500 μ L of hexane solution. 100 μ L of naphthalene was added to each sample as an internal standard. Samples were analyzed using gas chromatography paired with mass spectrometry (GC-MS) using an ISQ7000 instrument and separation was performed on a ZB1 column (0.25 mm x 30 m) with a temperature profile of 40°C (2 min) to 200°C (10 min) at 5°C/min. Chemical compounds were identified based on a comparison between the mass spectrometer and Arithmetic Retention Index (RI) using Adams, 2017 and The Pherobase. For the scope of this study, only monoterpenes and low molecular weight compounds were identified. Chemical compounds were quantified based on the known concentration of internal standard. Volatile emissions were recorded on a per inflorescence basis (g inflorescence⁻¹ hr⁻¹).

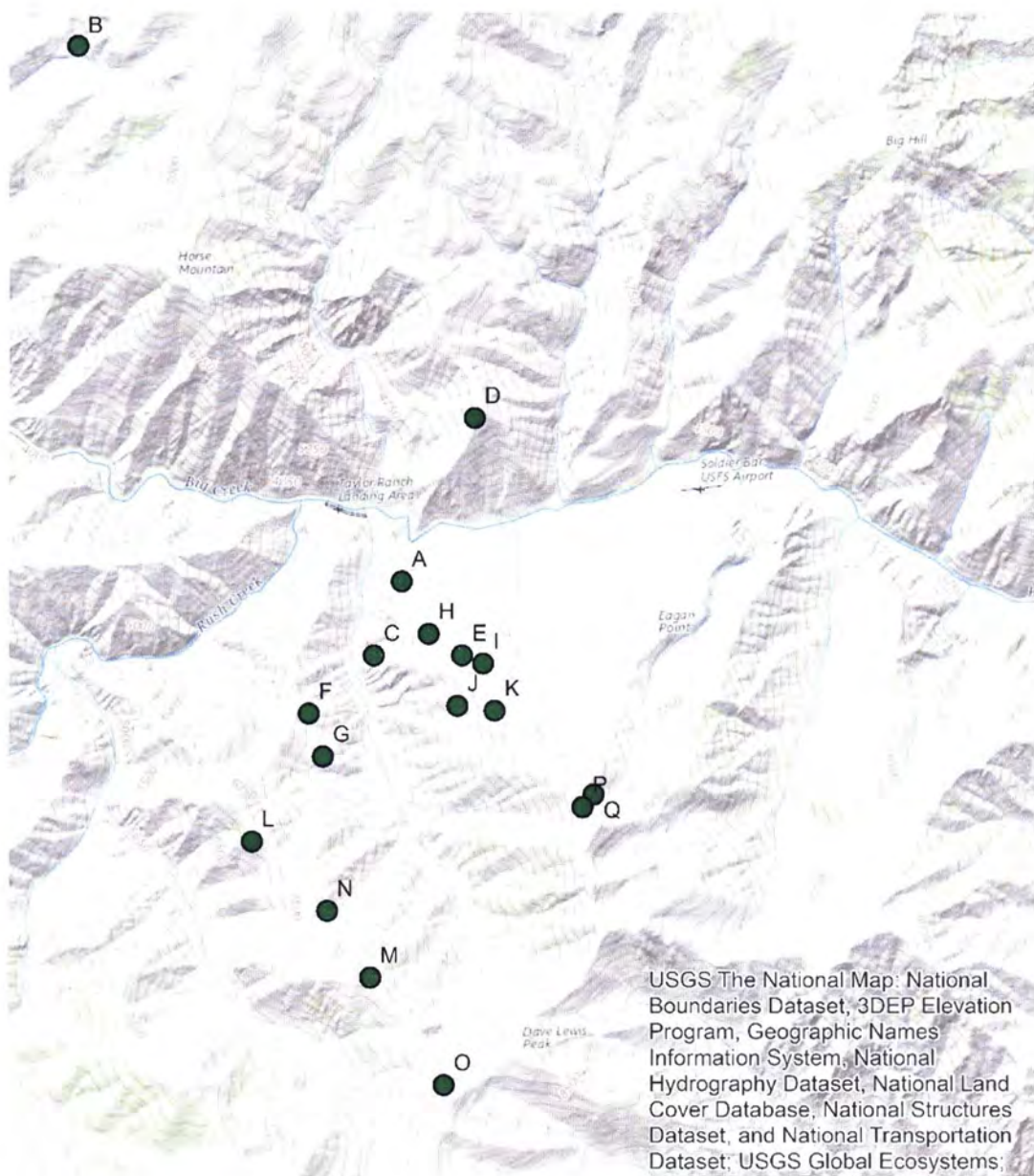


Figure 2.1: Study area with VOC collection sites.

Table 2.1 Species of populations sampled with elevation.

Population	Species	Elevation(ft)
A	<i>P. attenuatus</i> var. <i>attenuatus</i>	4400
B	<i>P. payettensis</i>	6280
C	<i>P. attenuatus</i> var. <i>attenuatus</i>	5880
D	<i>P. attenuatus</i> var. <i>attenuatus</i>	5900
E	<i>P. attenuatus</i> var. <i>attenuatus</i>	6000
F	<i>P. wilcoxii</i>	6000
G	<i>P. payettensis</i>	6000
H	<i>P. attenuatus</i> var. <i>attenuatus</i>	6300
I	<i>P. attenuatus</i> var. <i>attenuatus</i>	7000
J	<i>P. attenuatus</i> var. <i>attenuatus</i> (possible hybrid w. <i>P. wilcoxii</i>)	6500
K	<i>P. attenuatus</i> var. <i>pseudoprocerus</i>	7300
L	<i>P. salmonensis</i>	7250
M	<i>P. attenuatus</i> var. <i>pseudoprocerus</i>	8375
N	<i>P. attenuatus</i> var. <i>attenuatus</i>	7700
O	<i>P. attenuatus</i> var. <i>pseudoprocerus</i>	9200
P	<i>P. attenuatus</i> var. <i>attenuatus</i>	8750
Q	<i>P. attenuatus</i> var. <i>pseudoprocerus</i>	8750

Analytical Methods

11 chemical species were identified in the study. Quantity and composition of chemical species was calculated based on the known amount of the internal standard. Pearson's correlation analysis was used to determine the correlation between quantity of chemical species, pollinator visitation and environmental variables. A complete hierarchical and a k-means cluster analysis was performed using `eclust()` from the 'factoextra' package in R (Kassambara & Mundt, 2017). Four was the optimal number of clusters determined based on the within groups sum of squares. Distance matrices were derived based on euclidean distances. A silhouette analysis was used to determine the validity of both cluster methods.

Results

11 VOCs were identified from five functional groups (Table 2.2). There was no correlation between total mass emitted vs. elevation, however, several individual chemical species had a significant correlation in mass emitted vs. elevation. 1-heptanol had a negative correlation with elevation (Figure 2.2a) while Decanal and 2-Nonenal showed a positive correlation (Figure 2.2b,

2.2c). Expectedly, temperature and relative humidity had a significant strong negative correlation (Figure 2.2d). There was no correlation between total emissions and temperature or relative humidity. Likewise, there was no correlation between total emission and time of day or date or collection. Total pollinator visits per hour ranged from 0-24. There was a positive correlation between the number of open flowers and total number of pollinators (Figure 2.3b) however, there was no correlation between the number of pollinators and total emission. There was a positive correlation in total number of flowers and total emissions (Figure 2.3a).

Table 2.2: Chemical species identified by functional group.

Species	Functional Group
1-heptanol	Aliphatic
Decanal	Aliphatic
2-Nonenal	Aliphatic
Cis 3-hexenal	Aliphatic
Octanal	Aliphatic
Cis 3-hexenyl acetate	Aliphatic
2-ethylhexyl acetate	Aliphatic
4-ethyl acetophenone	Benzenoid and Phenyl Propenoid
Linalool	Terpene
Ocimene	Terpene
Myrcene	Terpene

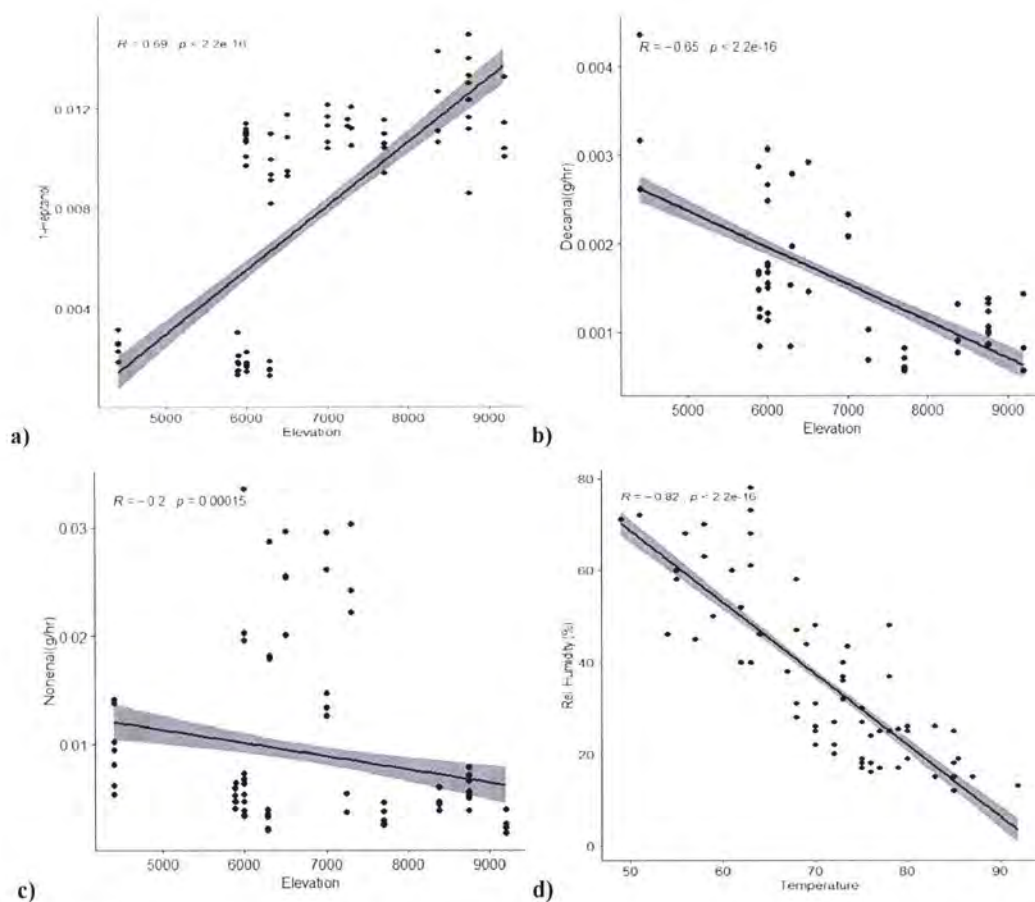


Figure 2.2: Pearson's correlation test for **a)** 1-Heptanol, **b)** Decanal; and **c)** Nonenal vs. elevation (ft) and **d)** Temperature (°F) vs. relative humidity (%).

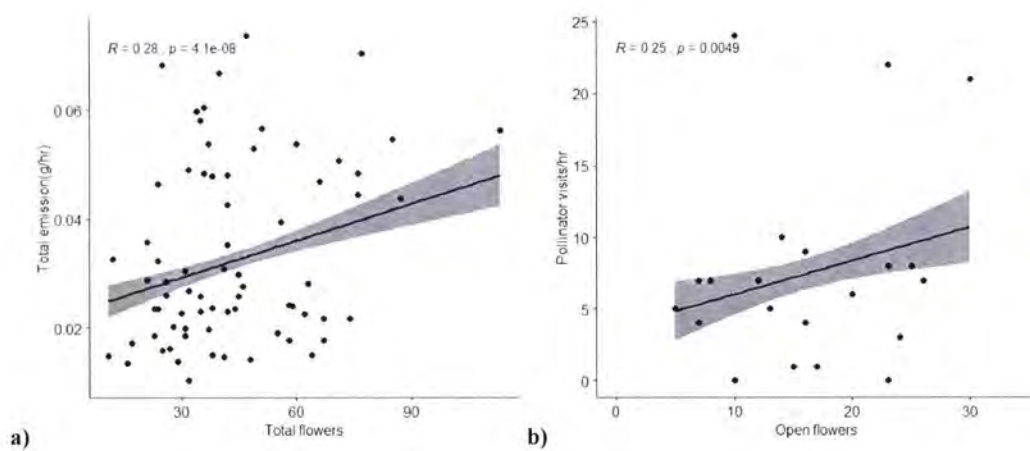


Figure 2.3: Pearson's correlation test for **a)** Total emission vs. Total flowers and **b)** Total pollinator visits in 1 hr. vs. the number of open flowers.

Cluster analysis

The number of samples per cluster are more evenly dispersed in the k-means cluster than the hierarchical cluster (Table 2.3). Based on the silhouette analysis, the k-means cluster outperformed the hierarchical cluster (Figure 2.6) The average width of the silhouette was higher for k-means and only one sample was misplaced. In the hierarchical cluster, the silhouette analysis shows 15 samples may be misplaced (Figure 2.6).

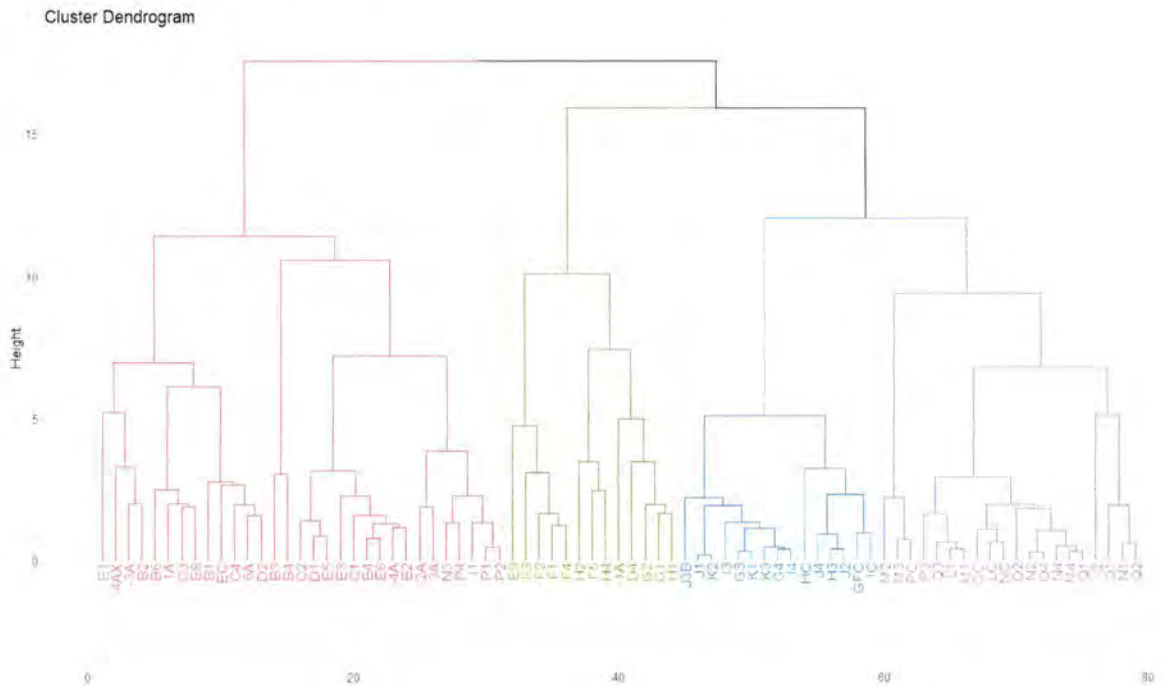


Figure 2.4: Dendrogram of hierarchical cluster (method=complete; k=4).

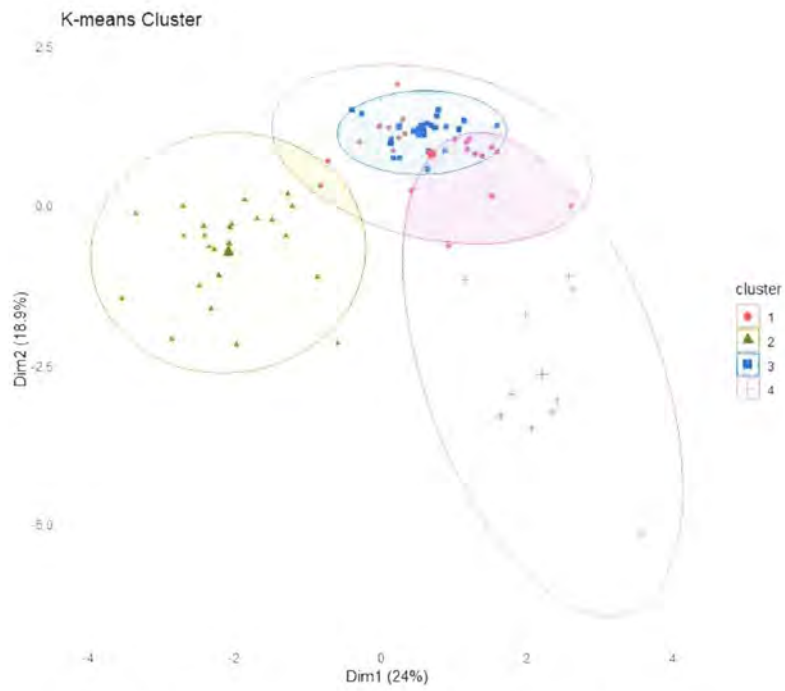


Figure 2.5: Diagram of K-means cluster (method=complete; k=4).

Table 2.3: Number of samples placed in each cluster in k-means and hierarchical cluster analysis.

Cluster	k-means	hcluster
1	22	13
2	23	31
3	23	15
4	10	20

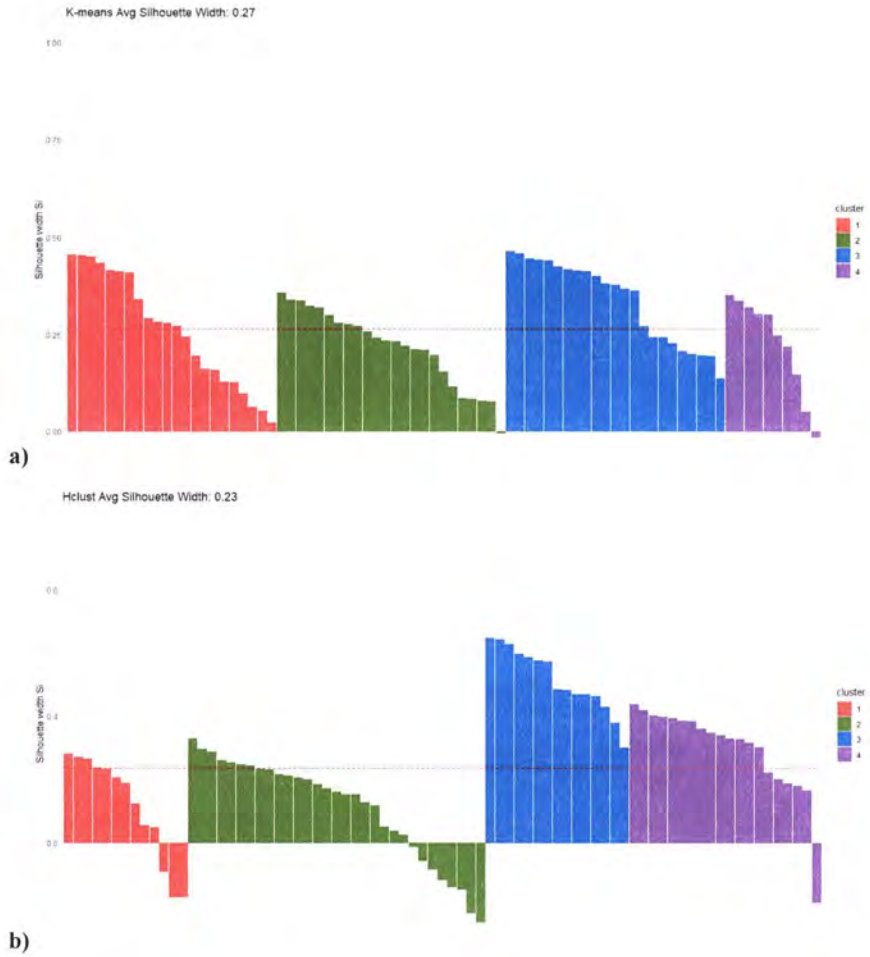


Figure 2.6: Diagram of silhouette plots for **a)** k-means cluster and **b)** hierarchical cluster. Mean silhouette width shown as red dashed line. Negative values indicate misplaced samples.

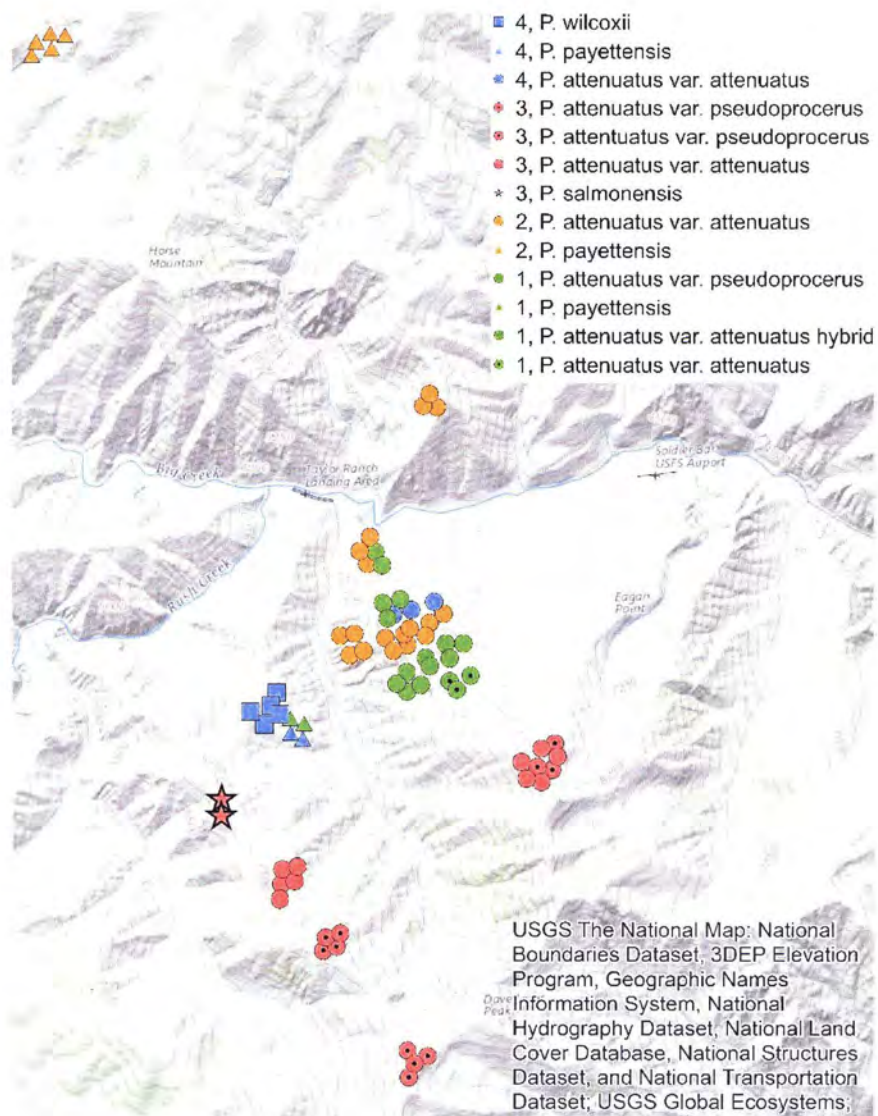


Figure 2.7: Spatial distribution of k-means cluster analysis. Shapes represent species, color represents cluster category based on k-means.

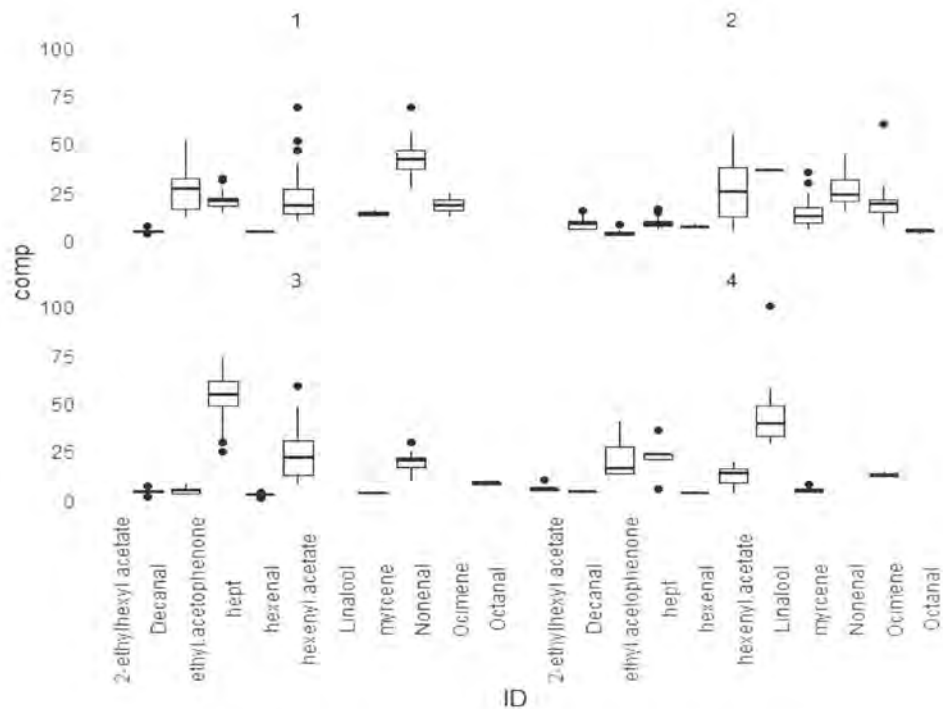


Figure 2.8: Average composition (%) of chemical species by K-means cluster.

Discussion

The critical roles that VOCs play in plant communication is gaining more awareness within the research community. Although these are secondary compounds not directly involved in primary metabolism, VOCs serve a variety of purposes including defense, attraction, and mutualisms that a plant relies on for survival. Now that the importance of VOCs is becoming clearer, it is important to collect and characterize VOCs from as many species as possible. Knudsen *et al.*, 2006 provides the most recent inventory of all plant species sampled for VOCs in the literature. Based on his paper, in 2006, 991 flowering plants had been sampled in just 270 published papers. *Penstemon* do not occur on the 2006 list. Since then, several species of *Penstemon* have been sampled. Although *Penstemon* do not have a strong fragrance to the human nose, much of their diversity is related to pollinator niche specialization therefore, it would be logical to expect floral VOCs have played a role in species evolution (Wolfe, *et al.*, 2006; Parachnowitz, *et al.*, 2012).

Knudsen (2006) classifies VOCs into 7 chemical classes based on structure. In our study 11 chemical species were identified representing 3 classes. We sampled from four species of *Penstemon* including 2 subspecies for a total of 5 taxa. According to the inventory, floral VOCs seem to vary widely within the order level and often the family level therefore, VOCs are not phylogenetically distinct from a broad taxonomic scale. Some floral VOCs are ubiquitous occurring in over half of

plant species on record. In our study Linalool, (*E*)-Ocimene and Myrcene occur in $\geq 70\%$ of species on record (Knudsen *et al.*, 2006). Our study shows however, that VOC composition may somewhat distinct at the species level or potentially within populations in the *Penstemon* species we sampled. (Figure 2.7).

Cluster analysis

Based on our cluster analysis individuals at high elevations on north facing slopes were clustered together into group 3. Group 3 can be explained by higher concentrations of 1-heptanol (Figure 22). This group contains mostly *P. attenuatus* var. *pseudoprocerus* with the exception of some higher elevation samples of *P. attenuatus* var. *attenuatus* which may be hybrids and *P. salmonensis*. Group 1 consist of mid-low elevation species of *P. attenuatus* (both varieties) and 2 samples of *P. payettensis*. This group contains the highest level of species diversity. Considering it is the middle of the elevation gradient it is possible that this is a transition zone. In Group 2, species are grouped at low elevations from *P. attenuatus* var. *attenuatus* and some higher elevation samples on south facing slopes including one population of *P. payettensis*. Group 2 can be characterized by higher levels of 4-ethyl acetophenone and Nonenal. 4-ethyl acetophenone is a benzenoid which are generally believed to be more involved in pollinator attraction than plant defense (Junker *et al.*, 2011). Unfortunately, the samples in this group did not receive pollinator surveys therefore, we cannot test for a correlation between 4-ethyl acetophenone and pollinator visitation. Finally, Group 4 contains the most variability within the cluster. This makes sense when considering that the group contains *P. wilcoxii* and *P. payettensis* and only 3 samples of *P. attenuatus*. Group 4 can mostly be explained by the expression of Linalool (Figure 2.9). Linalool was only expressed in 11 samples, 7 of which came from *P. wilcoxii* and *P. payettensis*. Research suggests that monoterpenoids mostly function in plant defense (Junker & Blüthgen, 2008). Linalool in particular is known to be involved in defense against nectar thieving ants (Galen, 1983; Irwin and Dorsett, 2002) What is interesting is that *P. wilcoxii* and *P. payettensis* both prefer sandier coarser soils which may see a higher concentration of ants therefore would benefit from Linalool production however, this is speculative at this point. .

Pollinator attraction

21 samples were selected for a 1-hour pollinator observation. All species were represented in pollinator samples from populations E, F, G, P, and Q (Table 2). Total pollinator visitation was not significantly correlated with total emission. Total emission was positively correlated with total number of flowers on the inflorescence (buds, flowers, seed) (Figure 19a). This would suggest that VOCs are not necessarily coming from reproductive organs but from the corolla, stem and leaves as

well. The more plant material, the more VOCs were emitted. Furthermore, total pollinator visitation was correlated with number of open flowers (Figure 19b) however, the data was not normally distributed. The samples with the most pollinators were among those with the most open flowers which may suggest these species of *Penstemon* may rely more heavily on floral display than chemical bouquet however, further studies are needed to this potential relationship.

Chapter 3: A Baseline Assessment of Early Succession Vegetation Regeneration after a Landslide in Limahuli Valley, Kauai, Hawaii

Introduction

On April 15th, 2018, rain gauges caught record highs on the island of Kauai. On the northwest side of the island, an area which receives approximately 80-100 inches of rainfall per year, close to 50 inches of rain fell in one day (National Oceanic and Atmospheric Administration, 2018). Flooding and landslides devastated the landscape. Severe damage to infrastructure isolated the communities of Waineha and Ha'ena. The Limahuli Garden and Preserve, in Ha'ena, is of critical concern based on its preservation of imperiled and culturally significant plants, and traditional system of land management. Over 20 landslides have been reported in the Limahuli Valley (NTBG, 2018a).

The unique history of the Kauai has created a complex ecosystem developed by overlapping stories of land use and resource management. From initial settlement to statehood, land management has transitioned from a place-based holistic system to a centralized bureaucracy. The ahupua'a system, one of the earliest systems of resource management implemented during the ali'i era, divided the islands into self-sustaining communities to create a decentralized system focused on adaptive management for species abundance. For centuries, the ecosystem flourished with native and culturally significant species ("Canoe" species) brought by early settlers from the Polynesian islands (Minton & Ka'imikaua, 2000). During the kingdom era, the arrival of Captain James Cook in 1778 initiated colonization by missionaries and an array of new species. Overtime, a flood of immigrants from all over the world lead to major land transformations. Much of Kauai was transformed to pineapple, coffee and sugarcane plantations. When a group of plantation owners overthrew the king in 1893, followed by the U.S. Annexation, the territorial era began. During this time, resource management objectives shifted dramatically from abundance to exploitation. The contemporary era began when Hawaii became a state in 1959. New taxes and fair labor laws cause plantations to plummet with the last plantation in Waimea closing in 2001. Under U.S. government control, a centralized bureaucratic system of resource management was solidified.

Situated in Limahuli valley on the North side of Kauai, Limahuli Garden and Preserve, is within the ahupua'a of Ha'ena, known as the longest functioning ahupua'a on the island (Winter & Lucas, 2017). Ahupua'a is a division of land in the traditional system of land management herby referred to as the Moku system. Ha'ena continued to be managed in the traditional way into the contemporary era by a group of Hawaiian natives known as the HUI. Eventually it was transferred to the state as conservation lands in 1960 which was then donated to Ms. Juliet Riche Wichman. Ms.

Wichman recognized the value of the Limahuli valley and recognized the need for conservation therefore, in 1967, she began to build the garden to preserve rare and endangered species. The garden was passed down to her son Chipper Wichman who eventually donated it to the National Tropical Botanic Garden in 2007. Currently, “Limahuli NTBG adapts ancestral resource management practices to address contemporary conservation challenges and restore health, function, and resilience to the valley. This approach is known as biocultural conservation.” (NTBG, 2018b).

Colonization of peoples and plants, land use changes, and climate change are among the most threatening aspects to native ecosystem conservation (Minerbi, 1999; Benning *et al.*, 2002). Contemporary conservation challenges include invasive species, extreme weather events, increased recreation and resource use, and loss of pollinators for endemic species. Several recent extreme weather events have caused severe damage to Limahuli Garden & Preserve. It has been documented that Pacific islands are experiencing more frequent storm events as a result of climate change (Taylor & Kumar, 2016). The April flooding event was a pivotal moment in the Limahuli Valley, fueling a renaissance of cultural values and determination to build a more resilient community. In order to continue serving the mission of the garden, research is critical to develop best management practices.

Restoration often begins with the question, “What is natural?” or, “What is native?”. Typically, the goal is to restore natural ecosystem functions and a native community that most closely resembles its pre-colonial potential. The overlapping history of Kauai, exemplifies the complexities of the social-ecological system. Determining what is natural in a system that has been highly manipulated and managed since the first Polynesians arrived, is a complex question. For this reason, determining restoration goals and outcomes can be difficult. According Burnett *et al.*, 2019, cultural objectives are just as important as biological objectives. Burnett *et al.*, (2019) aims to optimize restoration by quantifying cultural and biological objectives and applying various restoration scenarios to determine the most effective scenario. The findings suggest that a hybrid system of restoration including both native and non-native species is the most effective restoration scenario for meeting a suite of objectives. This would classify as a biocultural approach.

This study is phase one of a long term multi-scaled study to identify barriers and outcomes of landslide restoration in the Limahuli valley using a biocultural approach. Landscape level monitoring using remote sensing technology and drone imagery will be combined with small scale targeted monitoring to better understand the successional trajectories of landslides in Limahuli Valley under various treatments and manipulations. Additionally, this research will further investigate the effectiveness of a hybrid system of restoration. Phase one of this study provides a baseline assessment of early successional plant communities through plant species and functional trait analyses. Early

successional species composition can dictate secondary plant community composition, therefore assessing early colonizing plant communities will set a baseline for temporal studies addressing the effects of early species composition on future plant communities (Walker and Del Moral, 2003). There were two primary objectives for this project. By identifying colonization and establishment traits of early plant colonizers, our goal was to reveal colonization and establishment barriers of desired species. Seed dormancy class, seed mass, maximum height and vegetative reproductive potential is analyzed for early landslide communities vs. intact communities. Our second goal was to contribute baseline data in order to track the outcomes of various restoration treatments to the landslide area.

Methods and Materials

Study area

This study was conducted on two parallel landslides in the lower preserve of Limahuli valley. Limahuli valley is part of the Ha'ena ahupua'a located on the North side of Kauai, HI. Steep cliffs flank the valley which is carved out by Limahuli stream. The highest point is approximately 3500 feet, sharply declining to sea level. Each landslide measures approximately 0.2 hectares in area and approximately 250 m in length. Elevation of the northern most landslide ranges from 410-635 feet. Elevation of the southern most landslide ranges from 495-805 feet. Soils are composed of Hihimanu, silty clay loam, 40-70% slopes at higher elevations transitioning to Hanamaulu, stony silty clay, 10-35% slopes at lower elevations. (Web Soil Survey, 2018) These soils are deep, well-drained, derived by basic igneous rock with an erosion T-factor of 5 indicating low potential for erosion (Web Soil Survey, 2018). This area receives 80-100 inches of rain annually (Ha'ena fisheries committee, 2011). Average temperatures remain relatively stable throughout the year ranging from 54-77°F (NOAA, 2018).

The study area is within the wao nāhele zone of biocultural management which, consist of dry and mesic forested ecosystem types that were passively managed (Winter & Lucas, 2017). Intact vegetation communities are a mixture of species including indigenous, endemic, Polynesian-introduced and other introduced species. The overstory is dominated by Kukui (*Aleurites moluccanus*), Coffee (*Coffea arabica*), Guava (*Psidium guajava* and *Psidium cattleianum*) and Mountain apple (*Syzygium malaccense*). The understory is dominated by mostly invasive grasses and ferns including Basket grass (*Oplismenus hirtellus*) and Christella (*Thelypteris parasitica*). Several noxious weeds have taken hold such as Clidemia (*Clidemia hirta*), Himalayan ginger (*Hedychium gardnerianum*), Job's tears (*Coix lacryma-jobi*) and Elephantopus (*Elephantopus mollis*).

An ungulate-proof fence surrounds the study area to keep out mostly feral pigs (*Sus scrofa*), originally brought over by the Polynesians as early as the fourth century A.D., and feral goats which were introduced during the kingdom era upon the arrival of Captain James Cook (Stone, 1990). Feral pigs have contributed to the demise and reduction of several indigenous and endemic species on Kauai in addition to overall landscape degradation (Burney et.al., 2005). Even more ubiquitous than the feral pig, black rats (*Rattus rattus*), are not protected by the fence and continue to wreak havoc (Shiels, 2011). Both landslides in the study extend below the fence line however, the majority of the landslide area remains inside the fenced restoration area.

A variety of vegetation treatments have been implemented in the study area, inside the fence, beginning in 2009 (Figure 3.1). These fenced restoration projects began with selective thinning of the existing canopy and understory with a goal of eradicating invasive species such as Coffee, Guava, and Schefflera and thinning of Kukui and Mountain apple. Some of these areas have remnant populations of culturally important species including Papala kepau (*Pisonia umbellifera*), Lama (*Diospyros sandwicensis*) and Ohia'a lehua (*Metrosideros polymorpha*) which, are treated with targeted intensive weeding. One of the more intensive restoration efforts occurred in 2010 that focused on removing large expanses of invasive ground cover and replacing with native ferns and sedges.

Current restoration activities now focus on removing invasive shrubs and saplings, and outplanting native species. Invasive ground cover may be removed immediately surrounding recent shrub and tree plantings. Most invasive plants are pulled by hand but, some must be removed with the use of herbicide via direct application to the plant. Broadcast methods for herbicide application are prohibited. Native plant outplanting focuses on hardy shrubs and small trees.

Study design

We used a random stratified sample design to establish 15 line transects in two strata, landslide area vs. intact vegetation (Figure 3.1). Three transects were randomly located in surrounding intact vegetation for a control while, 12 transects were randomly established spanning the width of the landslide. One of the 12 landslide transects lies outside the fenced area. Depending on the width of the landslide, transects ranged from 14 m to 25 m in length. The first five meters of each transect, extended into intact vegetation on the edge of the landslide. Three to five quadrats were randomly distributed along the transect depending on the length. The first quadrat was placed in the intact region within the first five meters and analyzed as control.

Data was collected between the months of September-October in 2018. The line-point intercept method was used as outlined in Canfield, 1941, to detect canopy and groundcover. The top layer of

cover was recorded at each meter along the entire length of the transect. Total overstory canopy cover was recorded for trees and shrubs along the transect. Height and width of species contributing to overstory canopy cover along the transect was recorded. Percent foliar cover by species and ground cover was recorded within each transect using ocular estimates. Ocular estimates of foliar cover for each species and ground cover were recorded. Within each quadrat soil temperature ($^{\circ}\text{C}$) and soil moisture (%) were recorded using a LabQuest on three separate days yielding three readings per quadrat. The mean value for soil moisture and temperature was taken for each quadrat. Additionally, soil texture of the top 6" of soil within each quadrat was recorded. Functional trait data for seed dormancy class and seed mass was obtained from the Baskin & Baskin, 2014 and Royal Botanic Gardens Kew, respectively. Vegetative reproduction potential and dispersal mode data was obtained from Wagner *et al.*, 1999 and field observations.

Landslide monitoring in Lower Limahuli Preserve

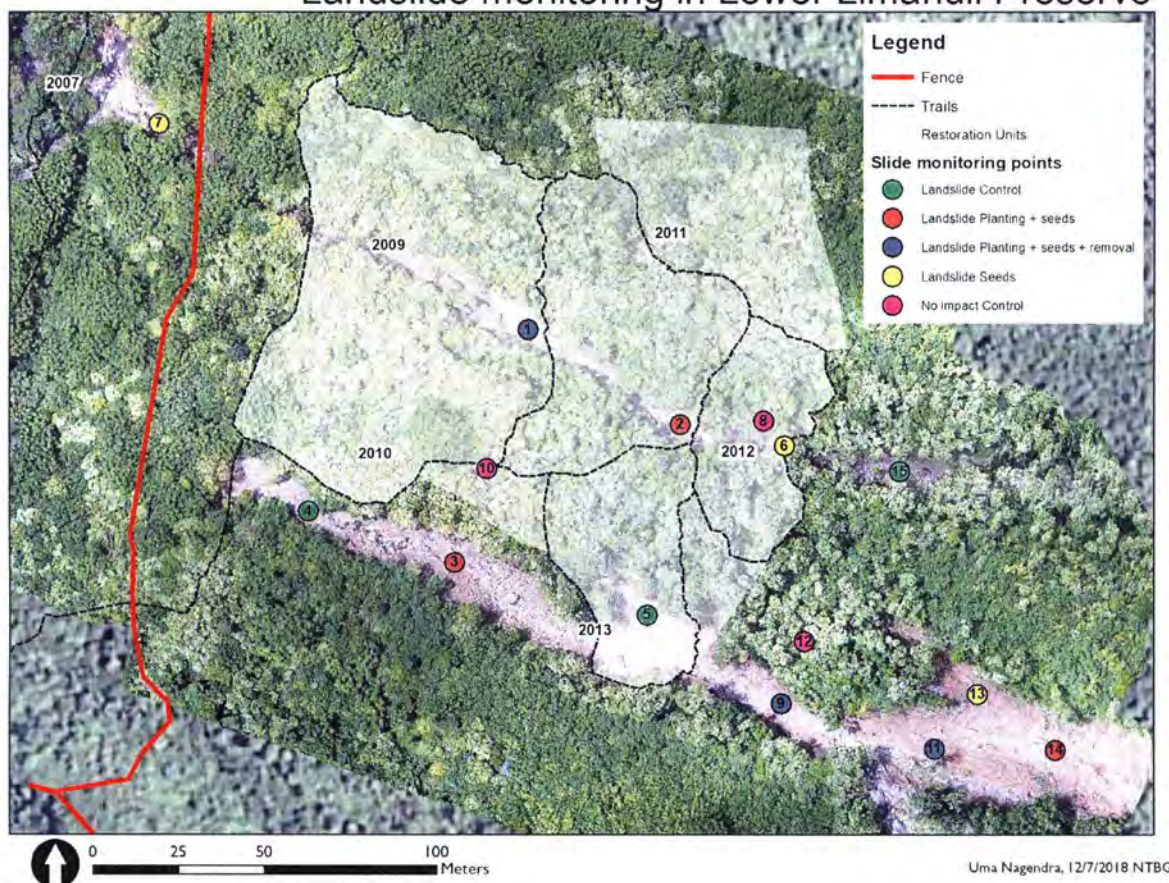


Figure 3.1: Image of two parallel landslides with transect locations. Historical restoration sites and ungulate proof fence are outlined.

Analytical Methods

Total percent cover by species and ground cover type was calculated from linepoint data. Quadrat data was transformed using Tukey's ladder of powers and mean values for percent cover, soil moisture, soil temperature and soil texture were calculated for all quadrats in the landslide area vs. quadrats in the intact control area. Functional trait composition was calculated based on foliar cover and averaged for all landslide plots vs. control plots. A two-sampled t-test was used to compare means between the landslide area and the control area and detect any significant differences.

Results

Baseline statistics

A total of 62 species were identified within the study area, however 15 of these were unidentified. Species richness in the landslide area versus the control was 56 and 33 respectively. Soil moisture was significantly greater in the control area versus the landslide (Figure 3.2b). Soil temperature was not significantly different in the landslide area vs. the control (Figure 3.2a). Soil texture was more clayey in the control area while soil texture in the landslide area was sandier and coarser (Figure 3.4). There was a positive correlation between soil moisture and elevation in the landslide area (Figure 3.3). Total foliar cover based on ocular estimates of quadrats was significantly greater in the control than the landslide area (Figure 3.5) however, total shrub cover was greater in the landslide area (Figure 3.6a). Graminoids and ferns dominated understory foliar cover in the control, while the landslide area was dominated by shrubs. Overall bare soil and rock cover was greater in the landslide area. Species richness of introduced species and unknown species was greater in the landslide area while species richness for native species was greater in the control area (Figure 3.6b).

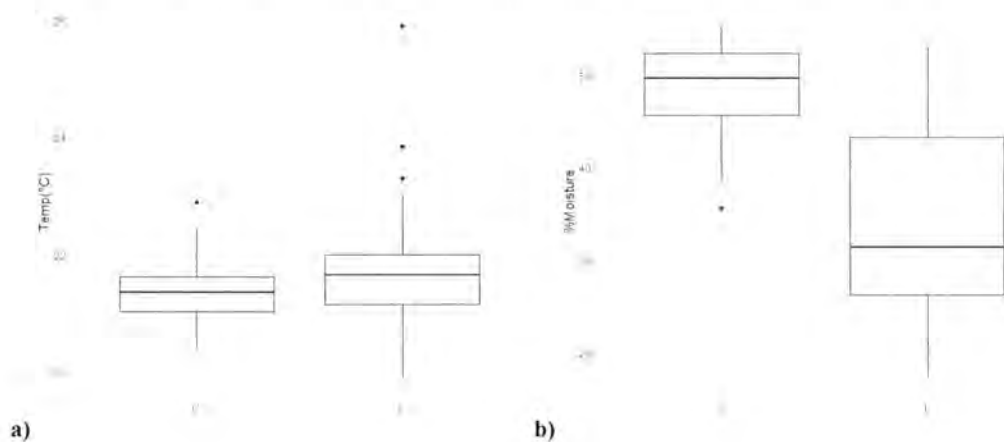


Figure 3.2: a) Mean soil temperature ($t=-1.70$; $P=0.093$) and b) mean soil moisture ($t=6.82$; $P=4.21e-09$) of landslide (L) vs. control (C).

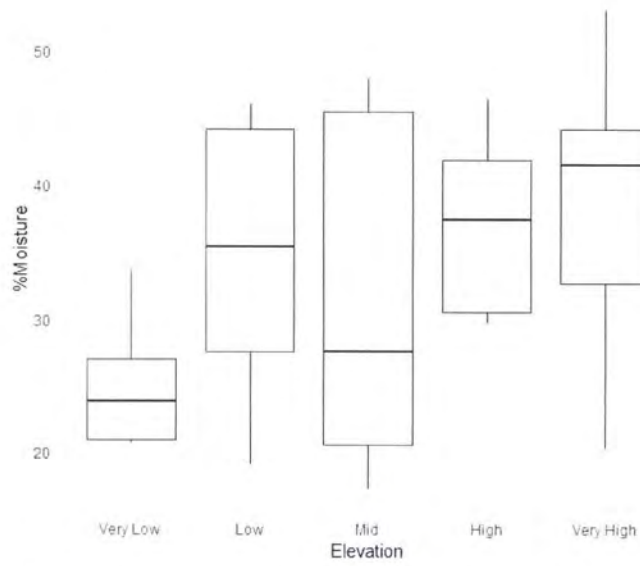


Figure 3.4: Mean soil moisture of landslide by elevation band.

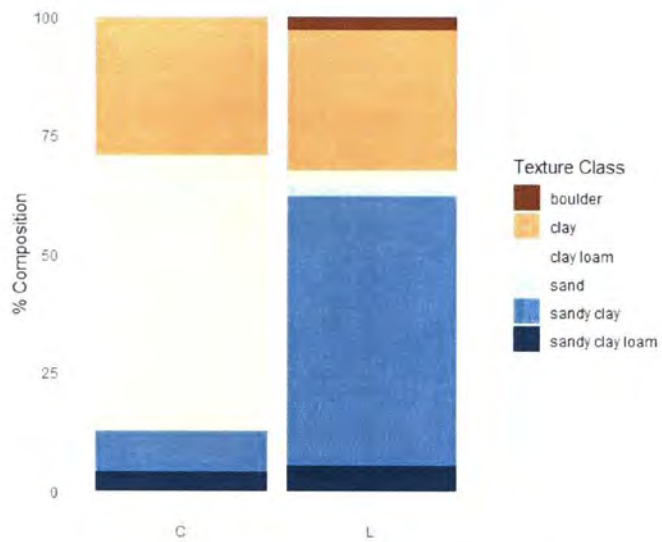


Figure 3.3: Percent composition of soil textures in landslide (L) vs. control (C).

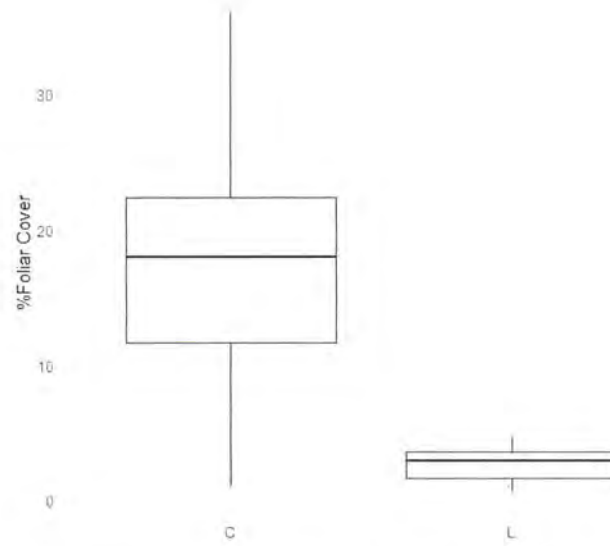


Figure 3.6: Mean foliar cover of landslide (L) vs control (C) ($t=7.876$; $P=6.42e-08$).

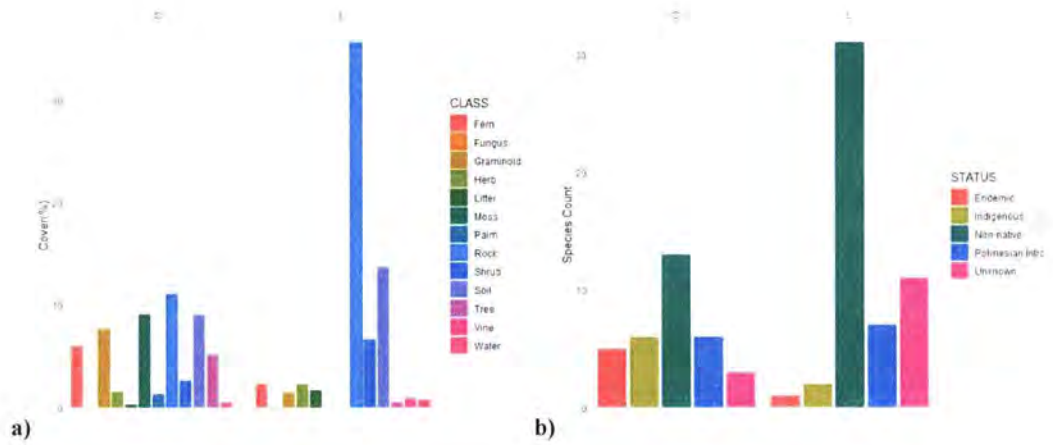


Figure 3.5 a) Percent foliar cover by growth habit class. **b)** Species richness by native status for landslide (L) vs. control (C)

Functional traits

Five classes of seed dormancy were detected in the study area in addition to spores. No dormancy (ND) was the dominant class in the landslide area while spores dominated the control area, with ND as the next dominant class (Figure 3.7a). More than 90% of the species are capable of vegetative reproduction therefore many species inhabiting the landslide and control area are capable of vegetative reproduction (Figure 3.7b). Wind was the single dominant dispersal class of species inhabiting the landslide area while wind and animal dispersal were co-dominant in species inhabiting the control area (Figure 3.7c). The average seed mass was significantly higher in the control area versus the landslide area (Figure:3.7d).

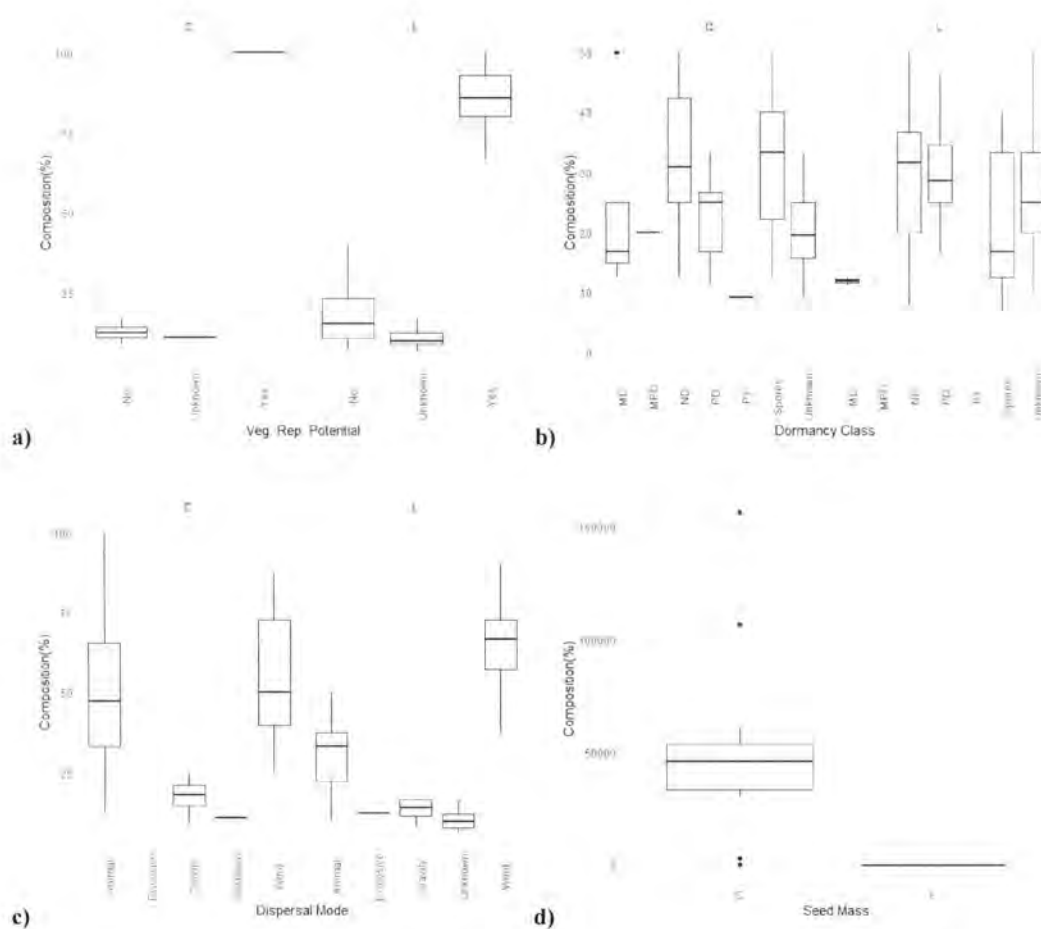


Figure 3.7 Average percent composition of **a)**seed dormancy class; **b)**vegetative reproductive potential; **c)**dispersal mode and; **d)**seed mass ($t=5.66$; $P=3.52e-05$) in landslide (L) vs control (C).

Discussion

Landslide characterization

Although mean soil temperature was not significantly different in the landslide area versus the intact control, mean soil moisture was significantly lower in the landslide area. Soil moisture in the landslide trended from low to high with increasing elevation. Low soil moisture can affect seed germination and may prohibit seed germination in some species (Holl, 1999; Traveset *et al.*, 2007). Additionally, soil textures varied greatly between the landslide and the control. Currently, the landslide area is much coarser while the intact control area is higher in clay. This difference in soil texture can have a significant impact on long term successional patterns. Clay particles are the smallest size class particles with the largest relative surface area full of cation exchange sites which are important for binding to cations (Troeh & Thompson, 2005). Cations are essentially, the nutrients that plants can uptake through their root system. Additionally, clay particles have a high water holding capacity. Low amounts of clay in the landslide area results in a lower water holding capacity and limited nutrient supply which may filter out unequipped species. In fact, shrub cover is the dominant growth habit in the landslide area which may be a result of coarse soils and increased infiltration. Shrubs have a root system that can extend lower down to reach the water table. Six months after the landslide when data was collected, average % foliar cover is still significantly greater in the intact communities versus control however, a large percentage of foliar cover in the intact regions is comprised of non-native, mat-forming, ground cover. Species richness was greater in the landslide area however, most species were non-native. The intact areas have greater species richness of indigenous and endemic species. Although species richness on the landslide area is much higher than the intact area and high species richness may be an indicator of competition related assemblage processes, it is unlikely that competition is influencing the current plant community assemblage process. Species richness is typically high during early plant community succession due to abundant resources (Pykälä, 2004; Catford *et al.*, 2012). Environmental filtering and stochastic processes would thus be the main drivers of current assemblage processes.

Functional traits

Seed mass is correlated to dispersal distance and may be a direct measure of a plants potential to reach the landslide area (Foster & Janson, 1985; Jongejans & Schippers, 1999). Additionally, seed mass is known to be correlated with dispersal by black rats (*Rattus rattus*) (Shiels, 2011). Black rats are considered a highly problematic invasive species throughout Kauai. Rats can act not only as dispersal barriers but dispersal agents (Shiels & Drake, 2011). Shiels & Drake (2011) suggest that small seed masses close to zero can be effectively dispersed by rats while larger seeds have the

potential to be dispersed or destroyed depending on the species. Shiels (2011) showed that black rats are not attracted to Kukui seed and therefore have no effect on its dispersal. *Alyxia*, *Psydrax*, and *Diospyros* are three native species found in the intact area that showed less than 50% of seed mass remaining after experimental trials with black rats. *Psidium*, also found in the intact community, is also susceptible to frugivory of black rats however, *Psidium* is considered an invasive in which case a dispersal barrier could be potentially beneficial. Invasive species that Shiels found to be spread by black rats include *Clidemia*, *Buddleia* and *Rubus*. All three of these species are present in the landslide area and intact communities. Additionally, seed mass is often correlated with dispersal mode. Seeds of larger masses are typically animal, or gravity dispersed traveling shorter distances, while smaller mass seeds travel further, usually through wind dispersal. Therefore, the large seed mass of Kukui and Mountain apple may inhibit colonization into the landslide area. In some areas, where the width of the landslide is relatively small, this may not be an issue. A majority of the invasive and non-native species present in our study have smaller seed masses, which have no dispersal barriers.

As discussed in Chapter 2, seed dormancy is one of the first traits to be expressed and serves as an important role in germination and establishment. Due to changes in light and soil moisture and texture, seed dormancy class may be an important factor to consider for colonization potential. The dominant dormancy class in the landslide area was ND. ND is often a characteristic of invasive species colonizing novel communities (Willis *et al.*, 2014). The dominant seed dormancy classes in the intact control area was ND and spores. Most of the desirable species do not classify as ND. Pepala keapu (*Pisonia umbellatum*), Alahe'e (*Pydrax odorata*), and Kopiko (*Psychotria*) have PD which is more dependent on timing of temperature and moisture. Wili wili (*Erythrina sandwicensis*) falls under PY. Unless scarification happened as a result of the landslide Wili wili may have a hard time germinating and establishing in the landslide area. This may be true for the PD species as well due to changes in soil moisture and light in the landslide area.

Restoration

Currently, the landslide area is still in early succession and species that arrive first have different characteristics than species arriving in later succession (Eviner & Chapin 2003). However, the composition of early successional species plays a role in determining later successional communities (Walker *et al.*, 2010). Walker *et al.*, 2010 found that scrambling ferns can inhibit forest development while early colonizing woody species and tree ferns promote forest development based on observations made over 7 years on 10 landslides in Puerto Rico. Our study shows that total shrub cover is twice as high as scrambling fern cover in the landslide area (Figure 3.6a). Shrub cover in the

landslide area is dominated by *Pluchea*, (*Pluchea carolinensis*), an introduced species. Although a non-native species, it is not known to be highly invasive compared to other shrubs like *Clidemia*. *Clidemia* is the dominant shrub in the intact communities. It is listed in Hawaii as a noxious weed (USDA plants database, 2019). It can form thick monocultures and displace native vegetation (Wester & Wood, 1997). There will be several treatments implemented in the landslide area including a combination of broadcast seeding, out planting, intensive weeding and target weeding. Weeding should target scrambling ferns and noxious species. As an early colonizing woody species, *Pluchea* has the potential to foster forest development and resist a *Clidemia* monoculture. Despite its non-native status, *Pluchea* and other naturalized woody species may have positive effects on later succession.

Dalling, 1994 finds that soil temperature, moisture and nutrient availability, over dispersal barriers, have the biggest impact on landslide colonization in the blue mountains of Jamaica. Although not measured in this study, soil nutrients are expected to be lower in the landslide area than controls due to soil texture and loss of topsoil. Soil characteristics strongly affect germination potential (Baskin & Baskin, 2014). Coarse soils in the landslide area may be the biggest barrier to restoration. Coarse soils typically have greater infiltration, lower nutrient levels and reduced stability. It can take over 50-500 years for the soil profile to resemble that of a mature forest after a landslide (Dalling, 1994; Walker *et al.*, 1996) Dalling, 1994 found that transplanted seedlings on landslides were more successful with the addition of organic fertilizers. Thus, out planting in the landslide area may benefit from organic fertilizers.

One of the biggest barriers to restoration is deriving common goals. As previously discussed, a popular goal of restoration is to reinstate natural ecological processes which leads to the greater question, “what is natural?”. In Limahuli Valley, this question is complex. Although pre-contact Hawaii had almost 8,150 endemic species, there were very few food plants or sustenance to support human existence (Anderson-Fung & Maly, 2002). When the first inhabitants came from the Polynesian islands bringing with them flora and fauna from their homeland, diversity expanded. The island was managed under the traditional system, managing for abundance. It wasn’t until thousands of years later that the rest of the world began to flood the island with a plethora of new species, some intentionally and some accidentally. In Hawaii, “What is native” will yield a variety of answers. At Limahuli Garden & Preserve, Polynesian introduced plants are not considered invasive. However, some species are not utilized like they were during ancient times and can overextend their boundaries. Rather than aiming for site conditions based on a snapshot in time, restoration is discussed based on current desired cultural and biological outcomes. However, despite the desired outcomes, factors such

as land use changes, climate change and invasive species make these objectives unreasonable. Therefore, prioritizing desired outcomes becomes a necessity.

Aside from the initial devastation, Ha'ena locals often regard "the flood" as "the best thing that ever happened to this place" (personal communications, 2019). Before the flood, the volume of tourists in Ha'ena had reached approximately 3,000 visitors per day (Azambuja, 2019; Chang, 2019). On April, 18th, this number dropped dramatically. Flood damage led to the closing of Ha'ena State Park and tourist restrictions were enforced beyond the town of Hanalei. When I arrived at Limahuli, it had been nearly six months without tourists. This would go on for an entire year. After the flood, native Hawaiians were able to reconnect with their land and tend to the many relationships that had been neglected. Special places, fishing spots in particular, were previously overrun by tourists. This massive disturbance reset the community, providing space to reclaim the valley and reinstate cultural practices. Currently, the community is taking steps to manage for abundance and promote resilience. For example, daily visitors will be restricted from 3,000 to 900 per day. The Limahuli staff and community are combining science, culture, and creativity to rebuild the garden to be more resistant and resilient to future weather events.

Chapter 4: Conclusion

The overarching goal of this thesis is to investigate the current community characteristics of critical landscapes to better understand how communities react to climate change. The study areas are considered critical for their protected status as wilderness and/or cultural significance. The main focus is plant community attributes along environmental gradients including elevation and disturbance. An underlying theme of human connections to landscapes and reactions to climate change aims to tie together humans and the environment.

Elevation gradients, which are correlated with environmental variables such as temperature and moisture, provide an effective way to study trends in plant community attributes along environmental gradients. Temperature and precipitation regimes are changing as a result of climate change therefore, studying plant community dynamics along an elevation gradient can help us understand how plant community dynamics will shift under future climate predictions. Chapters 1 and 2, take place along an elevation gradient in the Frank Church-RNR.

In Chapter 1, Phylogenetic and functional trait analysis revealed that herbaceous forb communities trended from overdispersion towards clustering with increasing elevations. This suggests environmental filtering has a greater effect at higher elevations while competition may be at work towards the base. Diversity of seed mass showed a similar pattern as phylogenetic diversity suggesting larger seeded species are filtered out at high elevations. Dormancy class showed a different trend with neutral to slight overdispersion trending towards greater overdispersion with increasing elevation. It is uncertain whether climate changes progression will enhance or alter these patterns. For this reason, recurrent analysis is needed in the future.

Recent research continues to confirm floral scent as an important functional trait for pollination success in some species. Chapter 2 looks at floral VOC composition in *Penstemon*. Total emission and composition are analyzed in several communities along an elevation gradient along with pollinator visitation observations. For the species in our study, VOC emission does not seem to have an impact on pollinator visitation rates thus, VOCs may be less important in the pollinator syndrome unlike some *Penstemon* species. Our study also showed that chemical composition of floral VOCs is relatively distinct between species and elevation. Our cluster analysis based on chemical composition showed clusters by species and elevation. Elevation seems to have an effect on floral VOC composition however, additional research is needed to determine what is driving these changes to determine the impacts of climate change. For example, looking at how the expression of individual compounds is impacted by temperature and moisture.

Chapter 3 takes place in an entirely different ecosystem. In a remote valley on Kauai, plant community attributes are assessed between a disturbed and intact community after a recent landslide. We found that although vegetation attributes were different in the landslide area versus the intact area, soil characteristics are most likely the greatest area of concern. Species richness was much higher in the landslide area suggesting competition is not a major driver in early successional community assemblage. Shrub dominance in the landslide area suggests that coarse soils with low moisture in the upper rooting zone may be acting as an environmental filter. The intact community has a greater composition of large seeded species which may be inhibited by dispersal barriers such as distance and black rats. ND was the dominant dormancy class in both areas which was largely due to the presence of non-native species. Indigenous and endemic species in the intact area had PY and PD dormancy. It is possible that germination in these species will be inhibited by landslide soil conditions however, more research is needed. From a restoration standpoint, soil characteristics and noxious species are the biggest concern. *Applying different restoration treatments will help in determining how early successional species affect future successional communities.*

Humans are a part of the ecological community and are reacting to climate change as well. At Limahuli, I was able to witness this first hand while working with the local community including *some decedents of the original inhabitants. Over the period of my stay, I witnessed a community of people reconnect with their land and culture in a way that has already begun to reshape their future.* Returning to old fishing spots, gathering from the forest, and sharing stories of their ancestors has *fueled an effort towards biocultural restoration. This major disturbance triggered by climate change provided space and time for the community to reclaim Hawaiian values and stewardship. Moving forward, the community is working towards rebuilding a more stable and resilient community by identifying cultural and biological priorities and optimizing restoration.*

I do not represent the indigenous people however, I believe it is important to acknowledge a major part of the ecosystem that was lost over a century ago. The Tukudeka are the traditional landowners of the middle fork of the salmon river including the big creek tributary (U.S. Department of Agriculture, 2006). Tukudeka translates to Sheepeater (Frey McCarl, 2014). Bighorn sheep served as one of the staples in their diet however, the Tukudeka were considered hunter-gathers, relying on different food sources at different times of the year. Weather and phenology dictated migration (E. Galindo, personal communication, June, 2017). Because of a lifestyle dependent on seasonal shifts, the Tukudeka were once intertwined into the complex ecological network of the middle fork corridor. *During the Sheepeater wars in 1879, the U.S. military forcibly removed the Tukudeka from their home and from the ecological network. Unfortunately, much history and centuries of knowledge was*

left behind. Most of the remaining Tukudeka now live on the Fort Hall reservation and continue to live their culture through stewardship of the land (Archaeological Legacy Institute, 2017).

Wilderness areas make up some of the last remaining landscapes that represent, as Murie states “the basis for all our civilization”. These critical landscapes withhold the history of our ancestral lands. As baseline datum, these areas can teach us about natural processes and the effects of climate change on the most basic level which can then be applied to more complex systems. In order to see the effects, additional data is required to observe change over time. Therefore, this information is presented in hopes to inspire future investigations at TWRS and on other critical landscapes.

References

- Abatzoglou, J. T. (2011). Influence of the PNA on declining mountain snowpack in the Western United States. *International Journal of Climatology*, 31(8), 1135-1142.
- Ackerly, D. D. (2003). Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Sciences*, 164(S3), S165-S184.
- Adams, R. P. (2017). Identification of essential oil components by gas chromatography/mass spectrometry. 5 online ed.
- Anderson-Fung, P. O., & Maly, K. (2002). Hawaiian Ecosystems and Culture; Why Growing Plants for Lei Helps to Preserve Hawaii's Natural and Cultural Heritage.
- Arcese, P., & Sinclair, A. R. (1997). The role of protected areas as ecological baselines. *The Journal of wildlife management*, 587-602.
- Archaeological Legacy Institute. (2017, March). *Middle Fork Salmon River Tukudeka*
<https://www.archaeologychannel.org/video-guide/strata-portraits-of-humanity/2574-strata-march-2017>
- Bales, R. C., Hopmans, J. W., O'Geen, A. T., Meadows, M., Hartsough, P. C., Kirchner, P., ... & Beaudette, D. (2011). Soil moisture response to snowmelt and rainfall in a Sierra Nevada mixed-conifer forest. *Vadose Zone Journal*, 10(3), 786-799.
- Barry, R. G. (1992). *Mountain weather and climate*. Psychology Press.
- Barry, R. G. (2008), *Mountain Weather and Climate*, 3rd ed., Cambridge Univ. Press, Cambridge, U. K
- Baskin, C. C., and Baskin, J. M. (2014). *Seeds: ecology, biogeography, and evolution of dormancy and germination*. Second Edition. San Diego: Academic Press
- Baskin, J. M., & Baskin, C. C. (2004). A classification system for seed dormancy. *Seed science research*, 14(1), 1-16.
- Benning, T. L., LaPointe, D., Atkinson, C. T., & Vitousek, P. M. (2002). Interactions of climate change with biological invasions and land use in the Hawaiian Islands: modeling the fate of endemic birds using a geographic information system. *Proceedings of the National Academy of Sciences*, 99(22), 14246-14249.

- Blumthaler, M., Ambach, W., & Ellinger, R. (1997). Increase in solar UV radiation with altitude. *Journal of photochemistry and Photobiology B: Biology*, 39(2), 130-134.
- Burger, H., Ayasse, M., Häberlein, C. M., Schulz, S., & Dötterl, S. (2010). Echium and Pontechium specific floral cues for host-plant recognition by the oligolectic bee *Hoplitis adunca*. *South African Journal of Botany*, 76(4), 788-795.
- Burkle, L. A., & Runyon, J. B. (2016). Drought and leaf herbivory influence floral volatiles and pollinator attraction. *Global Change Biology*, 22(4), 1644-1654.
- Burkle, L. A., & Runyon, J. B. (2017). The smell of environmental change: Using floral scent to explain shifts in pollinator attraction. *Applications in plant sciences*, 5(6), 1600123.
- Burnett, K. M., Ticktin, T., Bremer, L. L., Quazi, S. A., Geslani, C., Wada, C. A., ... & Wolkis, D. (2019). Restoring to the future: Environmental, cultural, and management trade-offs in historical versus hybrid restoration of a highly modified ecosystem. *Conservation Letters*, 12(1), e12606.
- Burney, D. A., & Burney, L. P. (2016). Monitoring results from a decade of native plant translocations at Makauwahi Cave Reserve, Kauai. *Plant ecology*, 217(2), 139-153.
- Burney, D. A., Bender, D., Perlman, S., Salvador, C., & Wichman, C. (2005). The National Tropical Botanical Garden: creating a Genetic Safety Net for Hawaii's vanishing flora. *BGjournal*, 2(1), 17-19.
- Canfield, R.H. (1941). Application of the line interception method in sampling range vegetation. *Journal of Forestry* 39:399-394.
- Castellanos, M. C., Wilson, P., & Thomson, J. D. (2003). Pollen transfer by hummingbirds and bumblebees, and the divergence of pollination modes in *Penstemon*. *Evolution*, 57(12), 2742-2752.
- Catford, J. A., Daehler, C. C., Murphy, H. T., Sheppard, A. W., Hardesty, B. D., Westcott, D. A., ... & Hulme, P. E. (2012). The intermediate disturbance hypothesis and plant invasions: Implications for species richness and management. *Perspectives in Plant Ecology, Evolution and Systematics*, 14(3), 231-241.
- Cna'ani, A., Spitzer-Rimon, B., Ravid, J., Farhi, M., Masci, T., Aravena-Calvo, J., ... & Vainstein, A. (2015). Two showy traits, scent emission and pigmentation, are finely coregulated by the MYB transcription factor PH 4 in petunia flowers. *New Phytologist*, 208(3), 708-714.
- Cordell, H. K., Bergstrom, J. C., & Bowker, J. M. (2005). The multiple values of wilderness. In: *The Multiple Values of Wilderness*: 1-6.

- Cordell, H. K., Tarrant, M. A., & Green, G. T. (2003). Is the public viewpoint of wilderness shifting. *IJW*, 9(2), 27-32.
- Cordell, H. K., Tarrant, M. A., McDonald, B. L., & Bergstrom, J. C. (1998). How the public views wilderness. *International Journal of Wilderness*, 4(3), 28-31.
- Cordell, S., Ostertag, R., Rowe, B., Sweinhart, L., Vasquez-Radonic, L., Michaud, J., ... & Schulten, J. R. (2009). Evaluating barriers to native seedling establishment in an invaded Hawaiian lowland wet forest. *Biological Conservation*, 142(12), 2997-3004.
- Crimmins, S. M., Dobrowski, S. Z., Greenberg, J. A., Abatzoglou, J. T., & Mynsberge, A. R. (2011). Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science*, 331(6015), 324-327.
- Dalling, J. W. (1994). Vegetation colonization of landslides in the Blue Mountains, Jamaica. *Biotropica*, 392-399.
- Daubenmire, R.F. (1959). Canopy coverage method of vegetation analysis. *Northwest Science* 33:43-64.
- Díaz, S., & Cabido, M. (1997). Plant functional types and ecosystem function in relation to global change. *Journal of vegetation science*, 8(4), 463-474.
- Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., & Robson, T. M. (2007). Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences*, 104(52), 20684-20689.
- Eldridge, D. J., Bowker, M. A., Maestre, F. T., Roger, E., Reynolds, J. F., & Whitford, W. G. (2011). Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecology letters*, 14(7), 709-722.
- Elzinga, C. L., Salzer, D. W., & Willoughby, J. W. (1998). *Measuring & Monitoring Plant Populations*.
- Eriksson, O., & Kainulainen, K. (2011). The evolutionary ecology of dust seeds. *Perspectives in Plant Ecology, Evolution and Systematics*, 13(2), 73-87.
- Eviner, V. T., & Chapin III, F. S. (2003). Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. *Annual Review of Ecology, Evolution, and Systematics*, 34(1), 455-485.

- Fenster, C. B., Armbruster, W. S., Wilson, P., Dudash, M. R., & Thomson, J. D. (2004). Pollination syndromes and floral specialization. *Annu. Rev. Ecol. Evol. Syst.*, 35, 375-403.
- Finklin, A. I. (1988). Climate of the Frank Church-River of No Return Wilderness, central Idaho. Gen. Tech. Rep. INT-240. Ogden, UT: US Department of Agriculture, Forest Service, Intermountain Research Station. 221 p., 240.
- Foster, S., & Janson, C. H. (1985). The relationship between seed size and establishment conditions in tropical woody plants. *Ecology*, 66(3), 773-780.
- Frey, R., & McCarl, R. (2014). The Confluence of Rivers: the Indigenous Tribes of Idaho.
- Galen, C. (1983). The effects of nectar thieving ants on seedset in floral scent morphs of *Polemonium viscosum*. *Oikos*, 245-249.
- Gerhold, P., Cahill, J. F., Winter, M., Bartish, I. V., & Prinzing, A. (2015). Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Functional Ecology*, 29(5), 600-614.
- Gillson, L., Ladle, R. J., & Araújo, M. B. (2011). Baselines, patterns and process. *Conservation biogeography*. Oxford: Wiley-Blackwell. p. 31-44.
- Godínez-Alvarez, H., Herrick, J. E., Mattocks, M., Toledo, D., & Van Zee, J. (2009). Comparison of three vegetation monitoring methods: their relative utility for ecological assessment and monitoring. *Ecological indicators*, 9(5), 1001-1008.
- Gower, J. C. (1971). A general coefficient of similarity and some of its properties. *Biometrics*, 857-871.
- Hā'ena Fisheries Committee. (2011). Proposed management plan and fishing regulations for the Hā'ena community-based subsistence fishing area, Kaua'i. Hā'ena Fisheries Committee: A partnership between the community members of Hā'ena, the Hui Maka'āinana o Makana, and Limahuli.
- Hegland, S. J., Nielsen, A., Lázaro, A., Bjerknes, A. L., & Totland, Ø. (2009). How does climate warming affect plant-pollinator interactions?. *Ecology letters*, 12(2), 184-195.
- Herrick, J. E., Van Zee, J. W., McCord, S.E., Burkett, L. M., Karl, J.W. & Courtright, E.M. (2017). Monitoring Manual for Grassland, Shrubland and Savanna Ecosystems. 2nd Edition. Volume I: Core Methods. 86 pp., USDA-ARS Jornada Experimental Range, Las Cruces, NM

- Herrick, J.E., Van Zee, J. W., Havstad, K. M., Burkett, L. M., & Whitford, W. G., (2009) Monitoring Manual for Grassland, Shrubland and Savanna Ecosystems. 1st Edition. Volume I: Quick Start and Volume II: Design, Supplementary Methods and Interpretation, 236 pp., USDA-ARS Jornada Experimental Range, Las Cruces, NM
- Holl, K. D. (1999). Factors Limiting Tropical Rain Forest Regeneration in Abandoned Pasture: Seed Rain, Seed Germination, Microclimate, and Soil I. *Biotropica*, 31(2), 229-242.
- Irwin, R. E., & Dorsett, B. (2002). Volatile production by buds and corollas of two sympatric, confamilial plants, *Ipomopsis aggregata* and *Polemonium foliosissimum*. *Journal of chemical ecology*, 28(3), 565-578.
- Jongejans, E., & Schippers, P. (1999). Modeling seed dispersal by wind in herbaceous species. *Oikos*, 362-372.
- Junker, R. R., & Blüthgen, N. (2008). Floral scents repel potentially nectar-thieving ants. *Evolutionary Ecology Research*, 10(2), 295-308.
- Junker, R. R., Gershenzon, J., & Unsicker, S. B. (2011). Floral odor bouquet loses its ant repellent properties after inhibition of terpene biosynthesis. *Journal of chemical ecology*, 37(12), 1323-1331.
- Karl J, Colson K. Line-Point Intercept (n.d.). https://wiki.landscapetoolbox.org/doku.php/field_methods:line_point_intercept. Accessed April 5, 2019.
- Kassambara, A., & Mundt, F. (2017). Package 'factoextra'. Extract and visualize the results of multivariate data analyses.
- Kassambara, A., & Mundt, F. (2017). Package 'factoextra'. *Extract and visualize the results of multivariate data analyses*, 76.
- Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., ... & Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26(11), 1463-1464.
- Klos, P. Z., Abatzoglou, J. T., Bean, A., Blades, J., Clark, M. A., Dodd, M., ... & Jansen, V. S. (2015). Indicators of climate change in Idaho: an assessment framework for coupling biophysical change and social perception. *Weather, Climate, and Society*, 7(3), 238-254.

- Knapp, A. K., Briggs, J. M., Collins, S. L., Archer, S. R., BRET HARTE, M. S., Ewers, B. E., ... & Cleary, M. B. (2008). Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inp
- Knudsen, J. T., Eriksson, R., Gershenzon, J., & Ståhl, B. (2006). Diversity and distribution of floral scent. *The botanical review*, 72(1), 1.
- Krutch, J. W. (1995). best nature writing of Joseph Wood Krutch. University of Utah Press.
- Lavorel, S., & Garnier, É. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional ecology*, 16(5), 545-556.
- Leonard, A. S., Dornhaus, A., & Papaj, D. R. (2011). Why are floral signals complex? An outline of functional hypotheses. *Evolution of plant-pollinator relationships*, 261-282.
- Leopold, Aldo, 1886-1948. (1949). A Sand County almanac, and Sketches here and there.
- Loope, L. L., Hamann, O., & Stone, C. P. (1988). Comparative conservation biology of oceanic archipelagos: Hawaii and the Galapagos. *BioScience*, 272-282.
- Lopez, B., Burgio, K., Carlucci, M., Palmquist, K., Parada, A., Weinberger, V., & Hurlbert, A. (2016). A new framework for inferring community assembly processes using phylogenetic information, relevant traits and environmental gradients. *One Ecosystem*, 1, e9501.
- MacArthur, R. H. (1984). Geographical ecology: patterns in the distribution of species. Princeton University Press.
- Majetic, C. J., Fetters, A. M., Beck, O. M., Stachnik, E. F., & Beam, K. M. (2017). Petunia floral trait plasticity in response to soil nitrogen content and subsequent impacts on insect visitation. *Flora*, 232, 183-193.
- Matteodo, M., Wipf, S., Stöckli, V., Rixen, C., & Vittoz, P. (2013). Elevation gradient of successful plant traits for colonizing alpine summits under climate change. *Environmental Research Letters*, 8(2), 024043.
- Merlin, M. D., & Juvik, J. O. (1992). Relationships among native and alien plants on Pacific islands with and without significant human disturbance and feral ungulates. Alien plant invasions in native ecosystems of Hawai'i: Management and research, 597-624.
- Minerbi, L. (1999). Indigenous management models and protection of the ahupua'a. *Soc. Process Hawai'i*, 39, 208-225.

- Minton, N., & Ka'imikaua, J. K. (2000). A Mau A Mau: To Continue Forever. *Oshita, R., Minton, N., Eds.*
- Munson, S. M., Belnap, J., Schelz, C. D., Moran, M., & Carolin, T. W. (2011). On the brink of change: plant responses to climate on the Colorado Plateau. *Ecosphere*, 2(6), 1-15.
- Murray, B. R., Brown, A. H. D., Dickman, C. R., & Crowther, M. S. (2004). Geographical gradients in seed mass in relation to climate. *Journal of biogeography*, 31(3), 379-388.
- Myers-Smith, I. H., Forbes, B. C., Wilkening, M., Hallinger, M., Lantz, T., Blok, D., ... & Boudreau, S. (2011). Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters*, 6(4), 045509.
- Naito, A. T., & Cairns, D. M. (2011). Patterns and processes of global shrub expansion. *Progress in Physical Geography*, 35(4), 423-442.
- National Oceanic and Atmospheric Administration (April, 2018) *April 13-15, Flash Flooding on Kauai and Oahu* <https://www.weather.gov/hfo/RecordKauaiandOahuRainfallAndFlooding-April2018>
- National Oceanic and Atmospheric Administration, United States Department of Commerce. *Kauai Weather Averages*. Available online. Accessed [October/10/2018].
- National Tropical Botanical Gardens *Historic Flooding Affects Limahuli Valley* (2018) <https://ntbg.org/news/historic-flooding-affects-limahuli-garden>
- National Tropical Botanical Gardens *Limahuli Garden and Preserve* (2019) <https://ntbg.org/gardens/limahuli>
- Nayak, A., Marks, D., Chandler, D. G., & Seyfried, M. (2010). Long term snow, climate, and streamflow trends at the Reynolds Creek experimental watershed, Owyhee Mountains, Idaho, United States. *Water Resources Research*, 46(6).
- Parachnowitsch, A. L., Raguso, R. A., & Kessler, A. (2012). Phenotypic selection to increase floral scent emission, but not flower size or colour in bee pollinated *Penstemon digitalis*. *New Phytologist*, 195(3), 667-675.
- Pauli, H., Gottfried, M., & Grabherr, G. (2001). High summits of the Alps in a changing climate. In *"Fingerprints" of climate change* (pp. 139-149). Springer, Boston, MA.

Pauli, Harald, Michael Gottfried, Stefan Dullinger, Otari Abdaladze, Maia Akhalkatsi, José Luis Benito Alonso, Gheorghe Coldea et al. "Recent plant diversity changes on Europe's mountain summits." *Science* 336, no. 6079 (2012): 353-355.

Pavoine, S., Baguette, M., & Bonsall, M. B. (2010). Decomposition of trait diversity among the nodes of a phylogenetic tree. *Ecological Monographs*, 80(3), 485-507.

PBS, Nature. (2012, April 13) Frank Church-River of No Return Wilderness Map.

<https://www.pbs.org/wnet/nature/river-of-no-return-frank-church-river-of-no-return-wilderness-map/7652/>

Peek, J. M. (2005). Shrub-steppe vegetation of the East Fork and the Middle Fork of the Salmon River Drainages. Department of Fish & Wildlife Resources, University of Idaho.

Pelton, J. (1956). A study of seed dormancy in eighteen species of high altitude Colorado plants. *Butler University Botanical Studies*, 13(1), 74-84

Pykälä, J. (2004). Immediate increase in plant species richness after clear cutting of boreal herb rich forests. *Applied vegetation science*, 7(1), 29-34.

Qian, H., & Jin, Y. (2016). An updated megaphylogeny of plants, a tool for generating plant phylogenies and an analysis of phylogenetic community structure. *Journal of Plant Ecology*, 9(2), 233-239.

Royal Botanic Gardens Kew. (2019) Seed Information Database (SID). Version 7.1. Available from: <http://data.kew.org/sid/> (January 2019)

Scaven, V. L., & Rafferty, N. E. (2013). Physiological effects of climate warming on flowering plants and insect pollinators and potential consequences for their interactions. *Current zoology*, 59(3), 418-426.

Sharman, L. C., Landres, P., & Boudreau, S. (2007). Developing a framework for evaluating proposals for research in wilderness: science to protect and learn from parks. *Small*, 7, 11.

Shiels, A. B. (2011). Frugivory by introduced black rats (*Rattus rattus*) promotes dispersal of invasive plant seeds. *Biological Invasions*, 13(3), 781-792.

Shiels, A. B., & Drake, D. R. (2011). Are introduced rats (*Rattus rattus*) both seed predators and dispersers in Hawaii?. *Biological Invasions*, 13(4), 883-894.

- Six, D. L., Alaback, P., Winfree, R. A., Snyder, D., & Hagele, A. (2000). Wilderness for science: pros and cons of using wilderness areas for biological research. *Wilderness Science in a Time of Change*, 3, 271-275.
- Smith, S. A., & Brown, J. W. (2018). Constructing a broadly inclusive seed plant phylogeny. *American Journal of Botany*, 105(3), 302-314.
- Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Web Soil Survey. Available online. Accessed [October/10/2018].
- Stone, C. P. (1990). Biological Invasions: A Global Perspective. *BioScience*, 40(11), 846-848.
- Straw, R. M. (1956). Floral isolation in *Penstemon*. *The American Naturalist*, 90(850), 47-53.
- Strum, M., Pielke SR, R.A. & Chapin III, F.S. (2001). Interactions of shrubs and snow in arctic tundra: measurements and models. In *Soil-vegetation-atmosphere Transfer Schemes and Large-scale Hydrological Models: Proceedings of an International Symposium (Symposium S5) Held During the Sixth Scientific Assembly of the International Association of Hydrological Sciences (IAHS) at Maastricht, The Netherlands, from 18 to 27 July 2001* (No. 270, p. 317). IAHS.
- Taylor, S., & Kumar, L. (2016). Global climate change impacts on pacific islands terrestrial biodiversity: a review. *Tropical Conservation Science*, 9(1), 203-223.
- Tilton, M. E. (1977). Habitat selection and use by bighorn sheep (*Ovis canadensis*) on a northwestern Montana winter range.
- Traveset, A., Robertson, A. W., & Rodríguez-Pérez, J. (2007). A review on the role of endozoochory in seed germination. *Seed dispersal: theory and its application in a changing world*, 78-103.
- Troeh, F. R., & Thompson, L. M. (2005). *Soils and soil fertility* (Vol. 489). Ames: Blackwell.
- U.S. Department of Agriculture, Forest Service. (2006, March). *The Mountain Sheepkeeper People* https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fsbdev3_029427.pdf
- Van Der Schaar, W., Alonso-Blanco, C., Léon-Kloosterziel, K. M., Jansen, R. C., Van Ooijen, J. W., & Koornneef, M. (1997). QTL analysis of seed dormancy in *Arabidopsis* using recombinant inbred lines and MQM mapping. *Heredity*, 79(2), 190.
- Vaughan, M. B. (2018). *Kaiaulu: Gathering Tides*. Oregon State University Press.

- Vellend, M., Cornwell, W. K., Magnuson-Ford, K., & Mooers, A. O. (2011). Measuring phylogenetic biodiversity. *Biological diversity: frontiers in measurement and assessment*. Oxford University Press, Oxford, 194-207.
- Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional!. *Oikos*, 116(5), 882-892.
- Vivaldo, G., Masi, E., Taiti, C., Caldarelli, G., & Mancuso, S. (2017). The network of plants volatile organic compounds. *Scientific reports*, 7(1), 11050.
- Wagner, W. L., Herbst, D. R., & Sohmer, S. H. (1999). Manual of the flowering plants of Hawaii. Bernice pauahi bishop museum special publication.
- Walker, L. R., & Del Moral, R. (2003). *Primary succession and ecosystem rehabilitation*. Cambridge University Press.
- Walker, L. R., Landau, F. H., Velazquez, E., Shiels, A. B., & Sparrow, A. D. (2010). Early successional woody plants facilitate and ferns inhibit forest development on Puerto Rican landslides. *Journal of Ecology*, 98(3), 625-635.
- Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J., ... & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, 416(6879), 389.
- Webb, C. O., Ackerly, D. D., McPeck, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual review of ecology and systematics*, 33(1), 475-505.
- Webb, C. T., Hoeting, J. A., Ames, G. M., Pyne, M. I., & LeRoy Poff, N. (2010). A structured and dynamic framework to advance traits based theory and prediction in ecology. *Ecology letters*, 13(3), 267-283.
- Wester, L. L., & Wood, H. B. (1977). Koster's curse (*Clidemia hirta*), a weed pest in Hawaiian forests. *Environmental Conservation*, 4(1), 35-41.
- Westoby, M., Leishman, M., & Lord, J. (1996). Comparative ecology of seed size and dispersal. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 351(1345), 1309-1318.
- Willis, C. G., Baskin, C. C., Baskin, J. M., Auld, J. R., Venable, D. L., Cavender Bares, J., ... & NESCent Germination Working Group. (2014). The evolution of seed dormancy: environmental cues, evolutionary hubs, and diversification of the seed plants. *New Phytologist*, 203(1), 300-309.

- Wilson, P., Castellanos, M. C., Wolfe, A. D., & Thomson, J. D. (2006a). Shifts between bee and bird pollination in Penstemons. *Plant–pollinator interactions: from specialization to generalization*, 47–68.
- Winkler, D. E., Belnap, J., Hoover, D., Reed, S. C., & Duniway, M. C. (2019). Shrub persistence and increased grass mortality in response to drought in dryland systems. *Global change biology*.
- Winter, K. B., & Lucas, M. (2017). Spatial Modeling of Social-Ecological Management Zones of the Ali'i Era on the Island of Kaua'i with Implications for Large-Scale Biocultural Conservation and Forest Restoration Efforts in Hawai'i. *Pacific science*, 71(4), 457-477.
- Wolfe, A. D., Datwyler, S. L., & Randle, C. P. (2002). A phylogenetic and biogeographic analysis of the Cheloneae (Scrophulariaceae) based on ITS and matK sequence data. *Systematic Botany*, 138–148.
- Wolfe, A. D., Randle, C. P., Datwyler, S. L., Morawetz, J. J., Arguedas, N., & Diaz, J. (2006b). Phylogeny, taxonomic affinities, and biogeography of Penstemon (Plantaginaceae) based on ITS and cpDNA sequence data. *American Journal of Botany*, 93(11), 1699-1713.