

QUANTIFYING PLANT COMMUNITY SHIFTS IN
RESPONSE TO FIRE ACROSS TOPOGRAPHIC
GRADIENTS

by

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A THESIS

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Southwestern Oregon is characterized by complex patterns of plant communities across environmental gradients. Previous research has found the structure and composition of vegetation to be related to the complex geology of this region. In this study, we explore the relation between topography and plant communities by asking if and how vegetation changes across ridgelines of varying steepness. We selected six ridgelines with a gradient of slope steepness (steep to gentle) in Rabbit Mountain, Riddle, Oregon, and used quadrat and line-point intercept techniques to quantify vegetation cover by species at each site. We assessed the differences and similarities between plant communities with NMDS (non-metric multidimensional scaling) analysis. We found plant communities on steep ridgelines are significantly different than communities on gentle ridgelines. Plant habit varied significantly across topographical gradient, as abundance of woody species was greater on steep ridgelines while herbaceous plants occurred more frequently on gentle ridgelines. Studying how landscapes exist in relation to vegetation deepens our understanding of the connectedness of Earth's processes, emphasizes the interdisciplinary nature of environmental science, and further informs forestry management practices in a time of increasing climate change.

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Background

A. Framing

This thesis aims to illuminate the inherent value of interdisciplinary natural sciences by operating within the partnership of two lab groups at the University of Oregon: the Earth Surface Processes Lab and the Soil-Plant-Atmosphere Lab. With the support of and in contribution to these two groups, we are essentially studying how topography shapes vegetation, and in turn, how vegetation shapes topography. We are studying how rock and life shape one another.

The STEM (science, technology, engineering, mathematics) world is highly categorized. With infinite ground to cover, this style of organization is often thought of as logical, as general fields are defined and further sorted into specialized studies. When we delegate like this, we discover more—or at least that is one way to consider this highly categorized approach. Although STEM tends to operate this dissected way, it is critical to investigate all parts of a system to truly understand it. Due to the need to connect multiple disciplines, science is innately collaborative. Environmental science is an interdisciplinary field. When it comes to understanding Earth, physical and natural processes are inextricable. We discover more and gain more detailed insight when we utilize integrated, multidisciplinary approaches.

This project is an examination into how landscape and topography are related to vegetation. Soil, as an interface between vegetation and rock, essentially serves as the connecting piece in this puzzle – soil properties are influenced by landscape dynamics. For example, the steepness of a hill influences speed of erosion. This project will thus

operate by combining plant surveying, soil science, and earth science data collection/analysis. Exploratory projects like this offer insight into the mechanisms and importance of the diversity of landscapes and life we see. Studying how a landscape exists in relation to its vegetation not only deepens our understanding of the connectedness of Earth's processes and helps demystify the "black box of community ecology", but also is crucial to land management decisions. Land management and conservation practices are only increasing in importance in the face of climate change and bringing together these disciplines will help inform solutions

B. Introduction

The Klamath Mountains ecoregion is well known as a unique landscape of diverse topography and exceedingly diverse flora (Whittaker 1960, Skinner 2006, Halofsky 2022). Situated between the Oregon Coast Range, the Cascade Range, and the Sierra Nevada, the Klamath Mountains are distinctly heterogeneous—as they tie together a multitude of geomorphological processes and ecosystems, the region is sometimes referred to as the "Klamath Knot" (Skinner 2006). Previous studies have found the complex geology of this region to be related to the structure, composition, and productivity of vegetation (Whittaker 1960, Zald & Dunn 2017, Barton & Poulos 2021). As an area of ecological interest, southwestern Oregon is characterized by complex patterns of plant communities across environmental gradients, such as parent material, climate, and topography (Skinner 2006).

Here at the University of Oregon, current research in the Earth Surface Processes Lab explores how long-term soil production and erosion rates in mountainous landscapes influence soil properties, which determine soil carbon and soil fertility. As

this thesis operates within both Earth Sciences and Biology, erosion refers to two very different timelines and processes—geomorphological processes occur on the timescale of thousands of years, whereas vegetation growth occurs a much shorter timeline (Wondzell et. al 1996, Roering 2003). Geomorphological erosion rates determine thickness of soil and its residence time. As seen below, when hillslopes are steeper and have steeper ridgelines, the geomorphological erosion rate which shapes the landscape, is faster and soils are shallower and rockier. Gentle ridgelines are characterized by thicker soil horizons with more highly weathered soil (Patton et. al 2018).

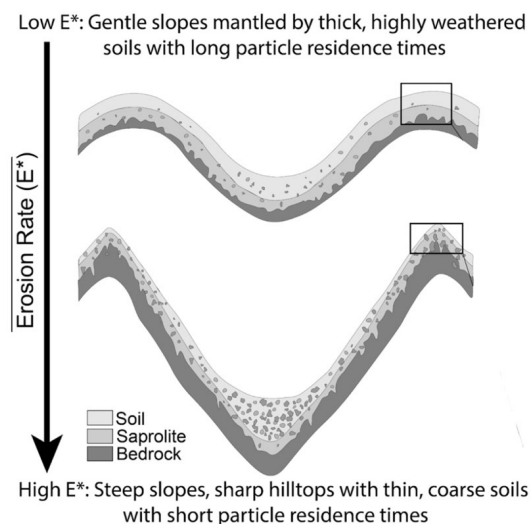
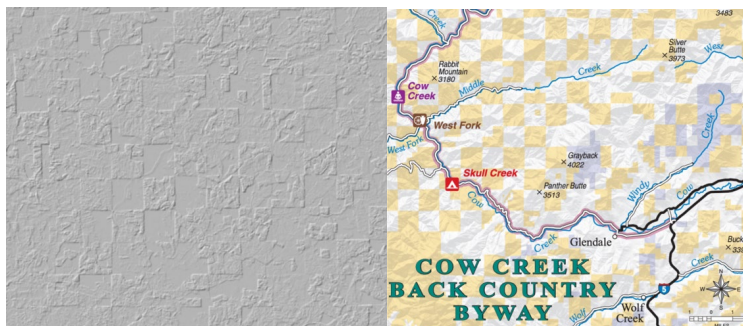


Figure 1. Steep and gentle ridgelines have different soil properties.

A visual comparison of gentle and steep ridgelines and their associated soil properties and horizons. Geomorphological erosion rate increases as ridgeline steepness increases. The steeper ridgelines have rocky and coarse soils compared to the highly weather soils of gentle ridgelines. Figure credit: Brooke Hunter.

In 2013, the Douglas Fire complex burned nearly 20,000 ha of southwestern Oregon forests in the Klamath Mountains (Zald & Dunn 2018). The climate of this

region is Mediterranean, with hot, dry summers and wet winters (Zald & Dunn 2018, Skinner et al. 2002). The fire burned across both federally and privately owned land, as much of Oregon's forests' ownership is divided up in a checkerboard pattern. The Douglas Fire complex began as multiple small fires from lightning strikes, and eventually merged into two larger fires: Rabbit Mountain and Dads Creek. The region's unique geology, paired with the massive burn scar and multi-owner landscape, has left this area as a case study system that researchers have used explored fire effects on this style of land management (Zald & Dunn 2018). The Relative differenced Normalized Burn Ratio (RdNBR), a satellite-imagery-based metric of pre- to post-fire change, has been used to quantify fire severity and analyze it in relation to variables of the fire behavior triangle: weather, fuel, and topography (Zald and Dunn 2018).



Figures 2 & 3. Checkerboard multi-owner landscape of Oregon forests.

Two images of the checkerboard pattern of Oregon land near Cow Creek in Riddle, OR. Left: image captured from the Oregon Lidar viewer website. Right: image from a Cow Creek BLM recreational brochure.

Vegetation is not randomly assembled across space (Rosenzweig 1995); the biosphere is a dynamic system and vegetation diversity and composition is influenced by atmosphere, soil, and water processes (Moura et al. 2016). One of the major

endeavors of ecology is understanding how spatial patterns relate to species diversity and distribution (Stein 2014). Research supports the notion of a positive relationship between environmental heterogeneity and species richness (Stein 2014). Multiple studies have found patterns of topography, soil, and microclimate linked with plant biodiversity (Woodward 1987, Opedal et al. 2015, Deak et al. 2021). Plants assemble in communities depending on various temporal and spatial patterns and variables (Zhang et al. 2017). Community ecology is an important field of research as it largely informs land management strategies and practices; landscape ecology, ecohydrology, and biogeomorphology are all examples of disciplines which pivot on not only how organisms respond to their physical environment, but also how they shape and modify their physical environment (Reinhardt 2009).

Fire regimes structure plant communities worldwide (Metlen et al. 2018). Fire is critical in influencing species composition, forest structure, and ecosystem processes (Bond et al. 2005, Krawchuk et al. 2009, Pausas & Keeley 2009, Archibald et al. 2018, Bowman et al. 2020). Globally, historical fire regimes have been disrupted due to increasing climate change. For example, summers in Oregon are projected to become increasingly warmer and dryer (Marlon et al., 2013). Further, especially in the United States, settler colonialism dismantled and forcibly removed and displaced Indigenous peoples and cultures from their land. Fire suppression policies replaced Indigenous Fire Stewardship practices, such as cultural burning, which had fostered and maintained a strong relationship between fire and ecosystems (Lake & Christianson 2019). In order to reinstate the long cultivated beneficial role of fire, it is critical to understand how these ecosystems fire regimes have changed and how vegetation is responding.

Further research into the relationship between topography, fire, and vegetation is critical to building our understanding of the connection between these realms. Fire suppression paired with intense management in the face of climate change has increased the risk of more frequent and more intense wildfire (Perry et al. 2011, Driscoll et al. 2012). There are gaps in the literature when it comes to pairing geomorphology and ecology. We need more studies to observe the response and recovery of landscapes to forest fire in order to better predict the response of landscapes to human activity and climate change (Reinhardt 2009). The complicated, dynamic interplay of biological, physical, and chemical processes in soil formation and hillslope erosion constricts our ability to interpret landscape dynamics (Roering 2010). In this study, we do not aim to draw definite conclusions of causation between vegetation and landscapes shaping one another other. Rather, we will contribute research to fill the knowledge gap and paucity of interdisciplinary research that involves geomorphology and ecology.

We selected six ridgelines in Douglas County as study sites to explore how vegetation changes with both terrain steepness and wildfire burn severity. We measured vegetation on both steep and gentle ridgelines, as well as burned and unburned ridgelines as our controls. We asked 1) does vegetation differ across fire-disturbed topographic gradients, and (2) if so, how does vegetation differ in terms of community composition and biodiversity?

C. Research Questions and Hypotheses

1. Does plant community assemblage differ on ridgelines of differing fire-disturbance (burn versus unburn) and topographic gradient (steep versus gentle)?

2. If so, how does vegetation differ? How are plant communities different?
 - a. Which plants dominate each site? What are the patterns in the plant communities?
 - b. Does species diversity differ?

Topography

Topography strongly affects the state and distribution of vegetation (Woodward 1987, Opedal et al. 2015, Bunyan et al. 2015, Deak et al. 2021) via regulation of solar radiation, redistribution of water, and soil properties such as soil pH, soil texture, and soil moisture. Differences in spatial distributions of soil properties within and between landscapes are reflections of geomorphic control (Chases et al. 2012). Because of the importance of geomorphic control on soil properties, we hypothesized that **(1) species community composition will differ between steep and gentle ridgelines** and **(2) diversity will be different between steep and gentle ridgelines.**

Commented [HRD1]: I don't know if first person singular or plural is more common in theses, but in the above sections you were using plural. Consistency, I suspect, is the key.

Fire

High-intensity, large-scale fire can homogenize landscapes; however, low to moderate-severity fire can increase heterogeneity, which in turn can increase species diversity (Richter et al. 2019). Studies have reported species richness decreases as time since fire increases (Strand et al 2019); specifically, species richness increases rapidly during the first five years post-fire, and then levels off to increase slowly (Romme et al. 2016). From this, we hypothesized that not only will **(3) species diversity be different between burned and unburned ridgelines**, but further, that **(4) differences in community composition will be detectable between unburned and burned sites in**

that burned sites will greater species richness.

Synergistic Effects of Topography and Fire on Diversity

Ecological theory (i.e. the Intermediate Disturbance Hypothesis; Huston 1979) supports increased levels of local diversity at moderate levels of disturbance. We hypothesized that **(5) species diversity will be greatest among communities in sites of with one level of disturbance as representing moderate disturbance** (i.e. *steep* unburned sites and gentle *burned* sites) **compared to high disturbance sites** (i.e. both steep and burned) **and low disturbance sites** (i.e. gentle and unburned).

Methods

A. Site Characterization

Our study took place in southwestern Oregon in Douglas County on Rabbit Mountain. Rabbit Mountain (elevation 3,200 feet) is a peak within the Cow Creek Recreation Area, southwest of Riddle, Oregon. The climate is mild Mediterranean with a mean daily high temperature below 55°F in January and a mean daily high temperature above 80°F in July. Mean annual rainfall is 35 inches, falling mainly from October through May (National Weather Service). Vegetation data was collected during two fieldwork outings: June 24-25, 2021 and July 19, 2021. The topographical heterogeneity and various burn history of this region, paired with unique flora and various parent materials, host a variety of forest types from coastal temperate rainforest to semi-arid oak woodlands. Our field sites consisted of mixed-evergreen forests, including *Pseudotsuga menziesii* (Douglas-fir), *Arbutus menziesii* (Pacific madrone), and *Pinus ponderosa* (ponderosa pine).

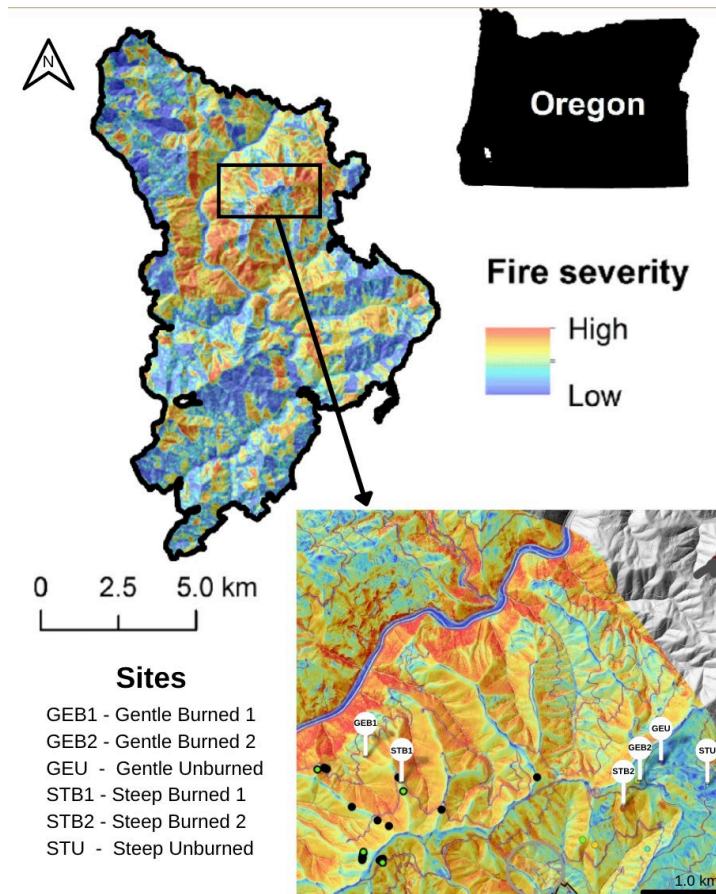


Figure 4. Study location within Rabbit Mountain burn scar in Douglas County, OR.

Figure adapted from Zald & Dunn 2017. Fire severity varies across topographical gradients. The location of the six selected ridgelines for this study are noted in the bottom right map. Unburned sites border the edge of the fire scar.

We chose the sampling region within Cow Creek Recreational Area on Rabbit Mountain because it contained both unburned and burned forest across steep and gentle ridgelines, all within the same general area (Table 1). Steep hillslopes are associated with sharp, rocky ridgelines, indicating fast erosion rates on the millennial timescale. In

contrast, gentle hillslopes have rounded ridgelines with lower angle slopes and well-developed thick soils, associated with slower long-term erosion rates on the millennial timescale (Hurst et al 2013). The proximity of these diverse topographic sites ensured a consistent climate. Within Rabbit Mountain, we selected ridgeline sites that represented the four treatments of study in order to compare burn history and topographical gradient: sharp unburned ridgelines, gentle unburned ridgelines, sharp burned ridgelines, and gentle burned ridgelines. Estimates of burn severity were achieved using relativized differenced Normalized Burn Ratio (RdNBR) by way of satellite sensor imagery. To ensure we sampled both extremes of sharp and gentle hilltops, we looked at the curvature of hilltops through topographic LiDAR analysis of a digital elevation model (Hunter et al, in prep). To categorize hilltops as fast and slow eroding, we tried to find sharp ridgelines with similar curvature values in both burned and unburned areas as well as gentle ridgelines with similar curvature values in both burned and unburned areas.

<i>Burn History</i>	<i>Topography</i>	<i>Site Name</i>	<i>Latitude (°N)</i>	<i>Longitude (°W)</i>	<i>Elevation (ft)</i>	<i>E*</i>	<i>Soil pH</i>
Burned	Steep	STB1	42.84843	-123.58968	2657 ± 11	32.500	4.590000
	Steep	STB2	42.84620	-123.55856	2306 ± 13	5.290	5.547500
	Gentle	GEB1	42.85105	-123.59460	2982 ± 20	0.674	5.903333
	Gentle	GEB2	42.84875	-123.55648	2616 ± 13	1.590	5.293333
Unburned	Steep	STU	42.84847	-123.54687	1730 ± 18	9.990	5.330000
	Gentle	GEU	42.85077	-123.55334	2473 ± 20	1.531	5.496667

Note: Data from sites STB1, STU, GEB1, GEU were collected on June 24th-25th 2021. Data from sites STB2, GEB2 were collected on July 19th 2021.

Table 1. Site summary of the six selected ridgelines of study.

Coordinates and elevation obtained vis GPS on site. E* values are a metric of ridgeline curvature, where positive values for convex hilltops and negative values of concave hilltops.



Figures 5 & 6. Steep burned sites.

Left: Steep burned 1. Right Steep burned 2.



Figures 7 & 8. Gentle burned sites

Left: Gentle burned 1. Right: Gentle burned 2.



Figures 9 & 10. Unburned sites.

Left: Steep unburned. Right: Gentle unburned

B. Data Collection

We created a sampling design that used multiple metrics to record plant communities (figure 11).

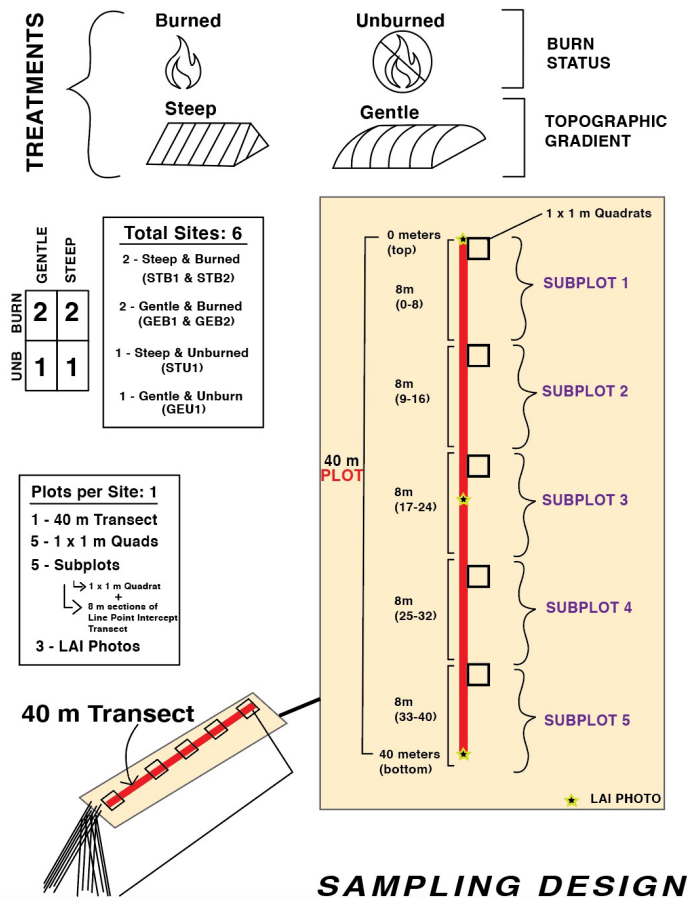


Figure 11. Sampling Design.

Diagram of sampling technique per ridgeline, as well as treatment categories. Credit to Cade Hole of the University of Oregon Department of Art & Design for assistance in the digital production of this figure.

I. Line-point Intercept (LPI)

We laid a 40 meter transect on top of each hillslope, directly on the ridge at each site (methods adapted from Herrick et al. 2009). Transects were taut and placed as close to the ground as possible, secured with pin flags on each end. Beginning at the 0 m mark, a pin flag was dropped from chest height every 1 m. We recorded the substrate of each flag drop was recorded as either soil, rock, dead wood, or duff (litter layer). Each species intercepted by the flag was recorded using the PLANTS database species codes (USDA, 2021), moving from the top of the flag (first touch) to the base of the flag (final touch). Contacts on dead plants were not recorded. If the flag fell and was caught by vegetation, data was recorded from that position. If the flag fell entirely over, it was placed perpendicularly into the substrate and data was recorded from this upright position. Each flag drop occurred on the left side of the transect tape.

II. Quadrat

Along each transect, we recorded species cover data with a 1 m² PVC pipe quadrat. Facing downslope from the top of the transect, the bottom right corner of the quadrat was aligned at the 0 m mark on the left side of the transect. Percent cover of each unique species was estimated and recorded using the PLANTS database species codes. Percent cover of exposed bare ground, soil, or duff was estimated and recorded. This process was repeated five times per transect; one quadrat placed every 10 meters (0 m, 10 m, 20 m, 30 m, 40 m; at the 40 m mark, the quadrat extends beyond the length of the transect).

III. General Site Survey, Specimen and Soil Collection, Leaf Area Index

After LPI and quadrat data were collected, we collected specimens of all unknown plants for later identification. Then, the site was surveyed and other plants that were not encountered by the transect or quadrat were collected for later identification.

To calculate leaf area index (LAI), we took true hemispherical photos at each site utilizing a Nikon fisheye lens to capture a 180 degree photo of the canopy. Three photos were taken along the 40 m transect. The LAI camera was positioned to face North before each photo.

C. Data Analysis

I. Plant Data Processing

Plant specimens were pressed and processed in the 24 hours following fieldwork. Photos of plant specimens were uploaded to iNaturalist, a community science platform with one of the largest databases.

II. Soil pH

We tested soil pH by combining 5 g soil and 10 mL deionized water in 50 mL cylindrical Falcon tubes. Samples were placed in a shaker for ten minutes and then left to sit for five minutes (Maxwell 2017). The pH values were obtained using SevenCompact S220 pH meter by Mettler Toledo. Per measurement, the pH electrode was submerged into sample solution without touching the bottom of the container until the sample's pH value was indicated. We rinsed the electrode with deionized water and dabbed lightly with a Kimwipe between sample measurements to prevent contamination and maintain standardization.

III. Statistical Analysis

We conducted all statistical analysis in R using R Studio (R version 4.0.2). Non-metric Multidimensional Scaling (NMDS) was used to determine statistical significance between communities. In R Studio, the following figures and metrics were produced and calculated: Rarefaction curves, Shannon Diversity, NMDS, Whittaker plots, Species Cover (Auguie 2017, Wickham et al. 2019, Chao et al. 2020, Hsieh et al, 2020, Oksanen et al. 2020, Wickham et al. 2020).

Diversity metrics including Shannon Diversity, Species Richness, and Species Evenness were calculated by summing data from the 5 quadrats per site. NMDS figures were produced using quadrat data.

Results

A. Non-metric Multidimensional Scaling–Community Comparison

The NMDS ellipses for steep and gentle communities do not overlap, indicating statistical difference (Figure 13). The larger ellipse for steep sites indicates there was more variation and spread among steep communities than gentle communities. A key takeaway from this ordination is the pattern of the habits of each plant within these communities. The three steep sites are dominated by woody and shrubby plants, such as *Arbutus menziesii* (Pacific madrone), *Symphoricarpos mollis* (creeping snowberry), *Quercus vacciniifolia* (huckleberry oak), and *Rosa gymnocarpa* (wood rose). In contrast, the three gentle sites are dominated by grasses and perennial forbs, including *Veronica reginivalis* (snow queen – perennial herb), *Whipplea modesta* (whipplevine), *Viola* spp (viola), *Galium triflorum* (bedstraw), and various grasses within the Poaceae family.

Our results indicate steep burned landscapes favor woody vegetation. When synthesizing comparisons of topographical gradient with burn history, we found greater similarity between plant communities at steep ridgelines and burned ridgelines than gentle and burned ridgelines. The area of overlap between steep and burned ellipses is greater than overlap between gentle and burned ellipses (Figure 13).

B. Diversity

We found plant species diversity was not significantly different between sites (Table 3), although community composition was significantly different across topography (Figure 13), and observational data indicated differences between sites.

While species richness of burned sites was not consistently greater than the species richness of unburned sites, the richness of sites that were steep and burned exceeded that of steep and unburned sites (Table 3). Similarly, species richness of gentle burned sites exceeded that of gentle unburned sites (Table 3).

We found all three gentle ridgelines, regardless of burn history, had greater species evenness than all three steep ridgelines (Table 3).

In terms of species evenness, we found the most even site was steep burned site 2 (with an evenness index closest to 1) and the least even site was the gentle unburned site (Table 3). There is not an evident trend between species evenness when we look at burn history, and there is not a strong trend between species evenness when we look at topography. However, as seen (supplementary) Figure 15, the E star values for steep sites are more dissimilar than the E star values of gentle sites (E star is a metric of steepness of ridgelines, with positive values indicating greater steepness and negative values indicating concavity). Specifically, steep burn 1 had the greatest E star value, indicating it was the steepest site. The steep unburned and steep burn 2 sites had significantly lower E star values (Figure 15), and had the greatest species evenness of all sites (Table 3).

<i>Species Field Code</i>	<i>Genus/Species Identification</i>	<i>Common Name</i>
ABI GRA	<i>Abies grandis</i>	grand fir
ARB MEN	<i>Arbutus menziesii</i>	Pacific madrone
ARC COL	<i>Arctostaphylos columbiana</i>	hairy manzanita
BRO SP1	<i>Bromus sp.</i>	brome grass
CAL DEN	<i>Calocedrus decurrens</i>	California incense-cedar
ERI CAL	<i>Eriodictyon californicum</i>	California yerba santa
FRA SPP	<i>Frangula sp.</i>	buckthorn
GAL TRI	<i>Galium triflorum</i>	fragrant bedstraw
GOO REP	<i>Goodyera repens</i>	lesser rattlesnake plantain
HEI BOL	<i>Hieracium bolanderi</i>	Bolander's hawkweed
HOL DIS	<i>Holodiscus discolor</i>	oceanspray
IRI SPP	<i>Iris sp.</i>	iris
KOP STR	<i>Kopsiopsis strobilacea</i>	California ground-cone
LAP COM	<i>Lapsana communis</i>	common nipplewort
LIT DEN	<i>Lithocarpus densiflorus</i>	tanbark-oak
LYS BOR	<i>Lysimachia borealis</i>	starflower
LYS LAT	<i>Lysimachia latifolia</i>	starflower
LYS SP1	<i>Lysimachia sp.</i>	starflower
MAD SP1	<i>Madia sp.</i>	tarweed
MAH REP	<i>Mahonia repens</i>	creeping Oregon grape
MOSS	moss	moss
NOT LIT	<i>Notholithocarpus densiflorus</i>	tanbark-oak
OSM SP1	<i>Osmorhiza sp.</i>	sweetcicely
PAX MYR	<i>Paxistima myrsinites</i>	Oregon boxwood
POA SP1	<i>Poaceae sp.</i>	poaceae grass
POA SPP	<i>Poaceae sp.</i>	poaceae grass
PSE MEN	<i>Pseudotsuga menziesii</i>	Douglas-fir
QUE CHY	<i>Quercus chrysolepis</i>	canyon live oak
QUE VAC	<i>Quercus vaccinifolia</i>	huckleberry oak
RIB SP1	<i>Ribes sp.</i>	currant
RIB SPP	<i>Ribes sp.</i>	currant
ROS GYM	<i>Rosa gymnocarpa</i>	baldhip rose
RUB LEU	<i>Rubus lecuodermis</i>	blackcap raspberry
RUB PAR	<i>Rubus parviflorus</i>	thimbleberry
RUB SPP	<i>Rubus sp.</i>	blackberry/raspberry
RUB URS	<i>Rubus ursinus</i>	Pacific blackberry
SYM MOL	<i>Symphoricarpos mollis</i>	creeping snowberry
TOX RAD	<i>Toxicodendron diversilobum</i>	poison-oak
UNK AST	<i>Aster sp.</i>	aster
UNK BRO	<i>Bromus sp.</i>	brome grass
UNK BRO2	<i>Bromus sp.</i>	brome grass
UNK POA	Poaceae sp.	poaceae grass
UNK SP1	Montiaceae	chickweed
VER REG	<i>Veronica regina-nivalis</i>	snow queen
VIC SP1	<i>Vicia sp.</i>	common vetch
VIO SPP	<i>Viola sp.</i>	violet
WHI MOD	<i>Whipplea modesta</i>	modesty
XER TEN	<i>Xerophyllum tenax</i>	bear-grass

Table 2. Species names list

Each species 6-character field code name used during data collection, as well as each species corresponding Latin and common name. The following species were encountered during quadrat or line-point intercept data collection.

Table 3 provides the diversity calculations of each site, including Shannon Diversity Index, the Species Richness, and Species Evenness.

<i>Burn History</i>	<i>Topography</i>	<i>Site Name</i>	<i>Shannon Diversity (H)</i>	<i>Species Richness (R)</i>	<i>Species Evenness (E)</i>
Burned	Steep	STB1	1.832588	12	0.737488
	Steep	STB2	1.957155	10	0.8499816
	Gentle	GEB1	2.324544	14	0.7894692
	Gentle	GEB2	1.604724	19	0.7303414
Unburned	Steep	STU	2.223413	9	0.8425027
	Gentle	GEU	1.267236	12	0.5099733

Table 3. Diversity metrics per site

Shannon Diversity was not significantly different between sites. Species richness was greatest at GEB2. All gentle sites had greater species richness than steep sites. Species richness was lowest at STU. Species evenness was greatest at STB2. Species evenness was lowest at GEU

Whittaker Plot / Rank-Abundance Curve
 Ranked Relative Abundance of Plant Species Per Site

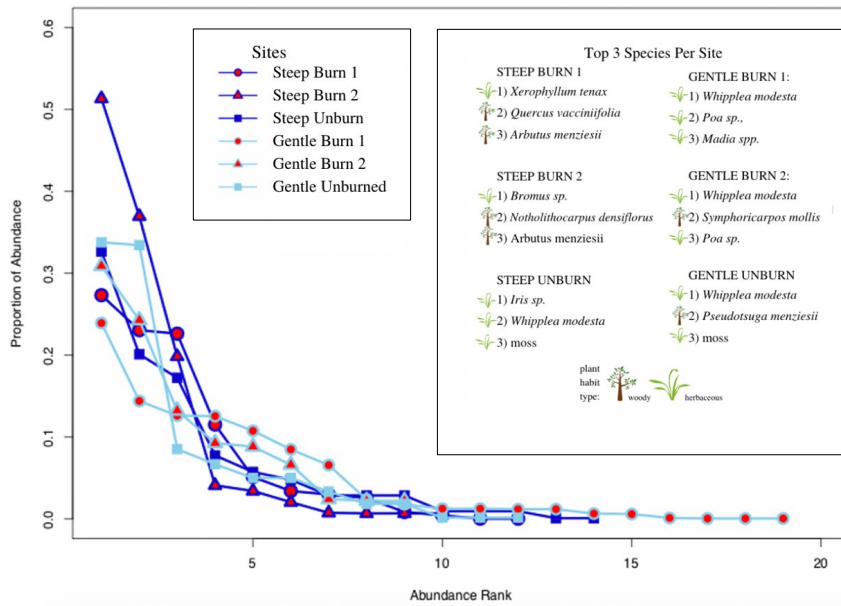


Figure 12. Whittaker Plot / Rank-Abundance Curve

The x axis represents rank, with the most abundant species per site being rank 1, the second most as rank 2, etc. The y axis represents percent relative abundance, summing to a total of 1.0, or 100% per site. Steeper curves represent lower species evenness. Top 3 species per site are listed next to a symbol indicating their plant habit as either woody or herbaceous.

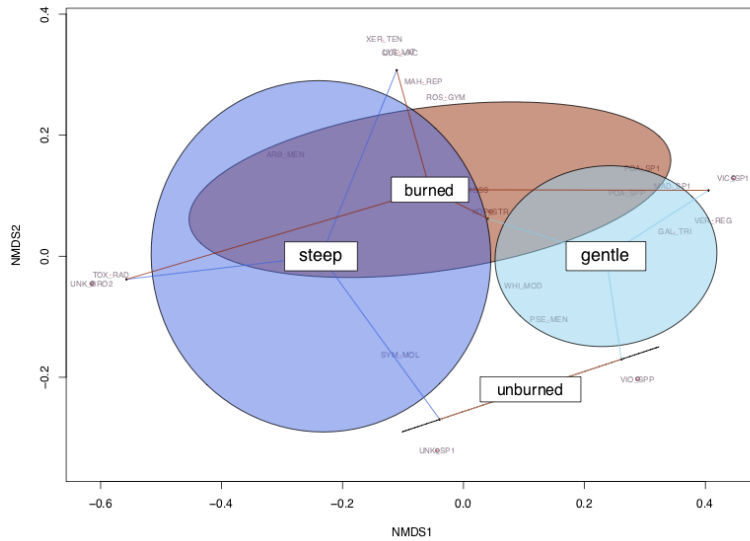


Figure 13. Non-metric Multidimensional Scaling (NMDS) Comparison of Plant Communities.

NMDS ellipses representing four different ridgeline treatments (steep, gentle, burned, unburned). Dark blue ellipse represents steep, light blue represents gentle, orange represents burned, and the light orange line represents unburned (due to lack of sample size, unburned ellipse could not be produced). Steep communities are statistically different from gentle communities. NMDS represents the original position of communities in multidimensional space as accurately as possible using a reduced number of dimensions that can be easily plotted and visualized. The function “ordiellipse” creates ellipses that pass through the outermost site scores of each group and define the maximum area of each group’s site scores in the two-dimensional ordination space. The less overlap between the ellipses, the more statistically dissimilar those groups are. Conversely, overlapping ellipses are more similar.

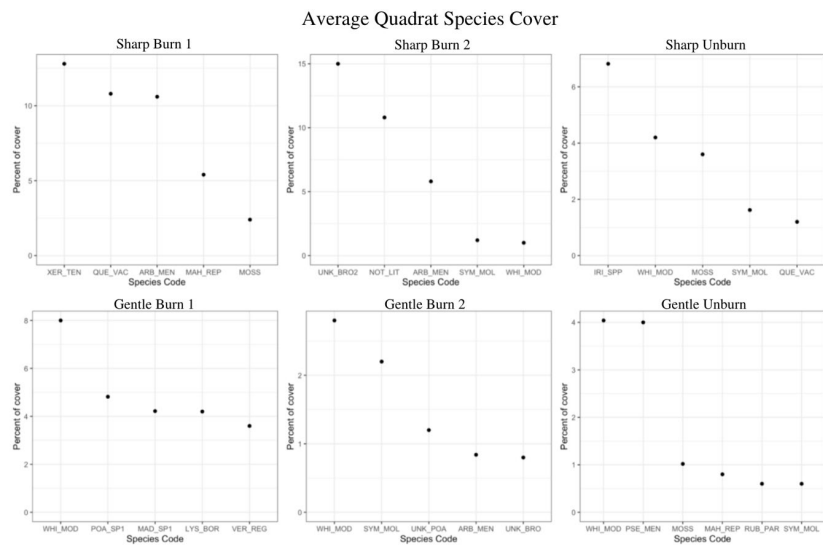


Figure 14. Average Quadrat Species Cover.

Average Vegetation Cover per site by species based on quadrat measurements. Sharp burned sites had greatest vegetation cover at 13%. Gentle Burn 2 had the least vegetation cover at 4%.

Discussion

A. Non-metric Multidimensional Scaling–Community Comparison

The data supported our first hypothesis that plant community composition was significantly different between steep and gentle ridgelines. Abundance of woody species was greater at steep ridgelines, and abundance of herbaceous species was greater at gentle ridgelines.

As found in the literature, we observed positions on landscapes most likely to burn at high severity tend to favor plants with adaptations that allow them to persist with such a fire regime (Estes et al. 2022). *Arbutus menziesii* is plotted approximately halfway between the centroid of the steep burned 1 and steep burned 2 sites (Figure 12), representing this species as equally present and abundant in both of these steep burned sites. This observation aligns with the life history strategy and growing conditions of this tree. *A. menziesii* is most abundant at rocky sites with well-drained soils and is considered an early-successional hardwood following disturbance (FEIS 2022). Many shrub and hardwood species, including *A. menziesii*, resprout vigorously, especially after high severity fire (Cocking et al. 2014). *A. menziesii* are able to recolonize rapidly following fire by resprouting from intact or lightly burned vegetative burls, rather than germinating from seed (FEIS 2022). In addition to resprouting mechanisms, other plants with fire adaptations, including *Arctostaphylos columbiana*, a common shrub in this region observed throughout our burned sites, are stimulated to germinate by fire (Keeley et al. 2005). *A. columbiana* have the ability to produce viable seeds that persist in the soil for many years (Hibbs 2011).

These results share findings with the research regarding habitat and fire regime of hardwoods and shrubs of the Klamath Mountains ecoregion (Hibbs 2011, Perry et al. 2011, Cocking et al. 2014, Estes et al. 2022). Our data indicates hardwoods, like *A. menziesii*, *Notholithocarpus densiflorus*, and *Quercus chrysolepsis*, and shrubs, such as *A. columbiana*, are favored on steep and burned ridgelines due to their adaptation to persist in the face of fire. The distinguished diversity of vegetation in the Klamath Mountains is a product of the relationship between landscape and fire and illustrates the importance of mixed-severity fire in shaping vegetation in this region (Skinner et al. 2006, Perry et al. 2011, Estes et al. 2022).

We found that burned communities were different from unburned communities, supporting hypothesis 2 (Figure 12); however, analysis and conclusion cannot exceed much beyond this because our sample is too small. We can extract less from the NMDS plots in terms of burn treatment due to limited sampling—only 2 of the 6 sites were unburned, which limits the robustness of our ordinated NMDS ellipses analysis as the unburned sites produce a linear line rather than an ellipse.

While in the field, we observed a visibly stark contrast between burned and unburned sites, as burned sites had a significantly sparser overhead canopy. When fire reduces canopy cover, light available to the understory increases, which permits heterogeneity and new growth (Abella & Springer 2015, Bohlman et al. 2016). In a region where fire is a prominent component to ecosystem structure and function, fire in low to moderate severities tends to burn understory species, leaving the canopy intact (Skinner et al. 2006). In high severity burns, crown fires are common, which can replace stands or open up large portions of the canopy to allow sunlight in (Hibbs et al.

2011). After fire moves through a system, it can transform vegetative communities by altering environmental variables. Unburned sites had denser canopy cover and thus less available sunlight to understory plants at the forest floor. There is a trend in greater understory species cover at sharp burned sites than at sharp unburned sites due in part to the intact canopy at unburned sites (Figure 14). While our NMDS data is inconclusive due to limited sampling, we observed differences in forest structure, including insolation changes related to canopy cover, and can infer a high likelihood of statistically differing plant communities at burned and unburned sites.

The greater overlap of steep and burned ellipses compared to gentle and burned ellipses indicates greater similarity in abundance and frequency of species found on steep sites and burned sites than between gentle sites and burned sites. Our results indicate steep burned landscapes favor woody vegetation. As discussed prior, the finding that burned landscapes favor woody vegetation relates to the adaptations of hardwoods and woody shrubs to persist on landscapes of disturbance (Estes et al. 2022). The underdeveloped thin, rocky soils of steep ridgelines are harsh environments for many plants, but not for our hardwoods like *A. menziesii*, *Q. chrysolepsis*, and *N. densiflorus* (FEIS 2022). These hardwoods, plus woody shrubs, like *A. columbiana*, are well adapted to recolonize rapidly following fire. In combination, these plants have adaptations that explain their prevalence in disturbed communities, with both steep ridgelines and burned landscapes each functioning as unique forms of disturbance.

B. Diversity

I. Shannon Diversity Index

The initial hypotheses (2 and 3) that species diversity would differ between steep and gentle ridgelines, and burned and unburned ridgelines, respectively, was not supported by statistical analyses. Strand et al. found climatic variables are the most important predictors for alpha diversity, which perhaps explains why the Shannon Indices across our sites were generally similar (Strand et al. 2019).

Our hypothesis (5) that species diversity will be greatest among communities in sites of moderate disturbance – steep unburned sites and gentle burned sites – compared to high disturbance sites (steep burned) and low disturbance sites (gentle unburned) was not significantly supported by our findings. Among sites of greater topographical disturbance (i.e. steep sites), diversity is greatest when burn disturbance is low (i.e. unburned); among sites of lower topographical disturbance (i.e. gentle sites), diversity is greatest when burn disturbance is high. In agreement with our hypothesis, our data suggests when layering disturbance, such as topography and burn history, diversity is greatest at moderate levels. Species diversity was greatest at the steep unburned site (hypothesized as moderate disturbance), and species diversity was relatively high at the gentle burned sites (hypothesized as moderate disturbance; Table 3); however, species diversity at the steep burn 2 site was also relatively high. Despite this pattern, no strong relationships were evident between site treatment and Shannon Diversity. The observed relationship between topography, burn history, and diversity is therefore likely more complex or stochastic than hypothesized, or more samples are needed to find significance between this relationship (Perreault et al. 2016). There may be some

influence of the Intermediate Disturbance Hypothesis here, but we likely need more samples to find any significant results. Rather than in alpha diversity metrics, we found statistical differences between communities was in community composition.

II. Richness

Following an analysis of alpha diversity, we explored other diversity metrics including species richness and species evenness. Our hypothesis (4) regarding burned sites having greater species richness than unburned sites was not supported by the data. We did, however, find a trend in richness related to burn history when topography was accounted for. Species richness of burned sites was not consistently greater than the species richness of unburned sites, the richness of sites that were steep and burned exceeded that of steep and unburned sites (Table 3). Similarly, species richness of gentle burned sites exceeded that of gentle unburned sites (Table 3). The pattern in this data suggests species richness increases along both steep and gentle ridgelines following burn, when compared to their respective unburned sites. Ecological literature supports the notion that greater pyrodiversity (defined by Stephens et al. as variability in fire severity, season, size, frequency) produces greater landscape heterogeneity and thus greater biodiversity than fire-suppressed areas (Martin & Sapsis 1992, van Wagtendonk & Lutz 2007, Boisramé et al. 2017a, Stephens et al. 2021, Steel et al. 2021). Although our burned ridgelines boasted greater diversity than unburned ridgelines when comparing sites of the same topographical level, our analyses did not find strong significance within this pattern which is likely due to limited sampling size.

We expected gentle ridgelines, as less disturbed habitats with deeper, more well-developed soils, to be more homogenous and thus, have a lower level of species

richness (Stephens et al. 2021); however, we found the reverse. Barton and Poulos (2021) suggests that topography is an intrinsic regulator of diversity, regardless of the effects of fire. There is good documentation of associations with environmental gradients at the landscape level (Strand, Bunyan et al. 2015, Moura et al. 2016), but there's limited information or agreement on how patterns on the community-level, like species richness, change in relation to structural variation of forests and topography (Wolf 2005). While our data suggests topography may be the stronger factor in influencing species richness, we cannot yet make statistically backed conclusions.

III. Evenness

When considering the Intermediate Disturbance Hypothesis, our results suggest that species evenness increases with increasing steepness until a certain degree of steepness is reached. This supports our expectations that topography would function as a form of disturbance when analyzing community composition.

The curves of the unburned sites are more similar to each other than the burned sites (Figure 14). Potentially, the variation observed among the burned sites indicates that these communities are responding to burn in unique ways and on different timelines. This variation may also be due to our burned sites being non standardized in terms of severity. The Klamath Mountains are characterized by a mixed-severity fire regime, and while most of the sites experiences moderate burn severity, some of the burned sites experiences low burn severity (Halofsky et al. 2011). In order to draw more significant conclusions, we suggest future studies should collect more samples across more ridgelines. Then, our binary burned/unburned analysis could be transformed into a burn gradient analysis that takes into account the mixed-severity nature of this

landscape. Further, since topographic variance exists more along a gradient, rather than two distinct categories explicitly, there is some variance within the fast and slow groups. We could examine a true topographic gradient instead of classifying our sites in the binary fashion of steep or gentle, as there is uneven variation among the steepness of the steep sites compared to that of the gentle sites (Figure 15).

Conclusion

The effects of climate change on hydrology in southwest Oregon will be significant, and lead to increased frequency of extreme climate events and ecological disturbance (Halofsky 2022). Forested systems dominate this region, and frequency of high-severity wildfire is expected to accelerate. The diverse topography and geology of the Klamath Mountains ecoregion posits this landscape as vulnerable and sensitive to change. There is a significant need of thinning and low-severity fire treatments in alleviate this region from impending dangers posed by a changing climate (Metlen et al. 2018, Halofsky 2022).

Informed land management has a critical need for studies like this one that are interdisciplinary and bridge multiple natural and physical science perspectives. We know vegetation does not occur randomly throughout space. Studies that merge research on plant communities, topography, and fire will contribute significantly and aid in making lucid the complex relationship between these realms. This study indicated steep ridgelines favor woody species, while gentle ridgelines favor herbaceous species. Our results suggest burned and steep ridgelines are more similar in community composition than burned and gentle ridgelines, but further research is needed to determine the role of topography as a form of disturbance and how it relates to vegetative assemblage and diversity.

Future research should examine ridgelines and fires more robustly by increasing sampling size and analyzing both topography and burn treatment as true gradients. In doing so, future studies can further develop the understanding of fire and topography as forms of disturbance proposed here. Nature does not exist within a binary.

Condensing it to fit within a binary both shrinks and distorts the inherent complexity of this system and its many parts that have been in relation since time immemorial.

Supplementary Materials

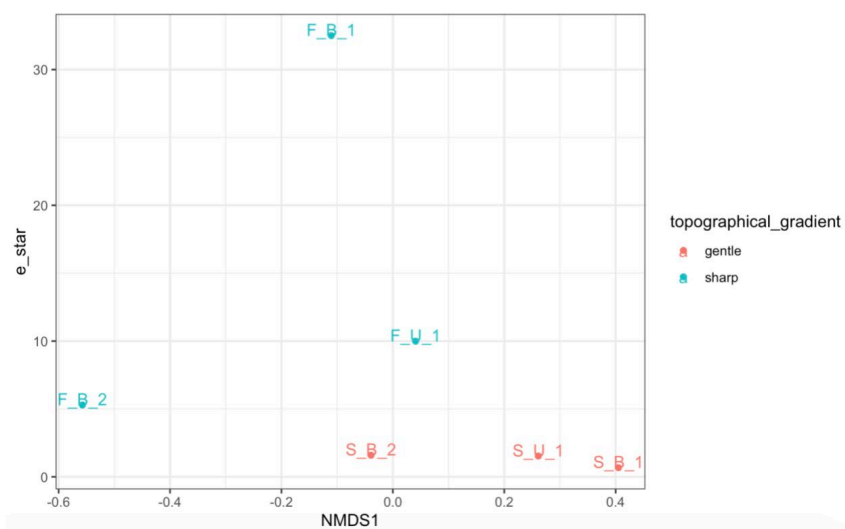
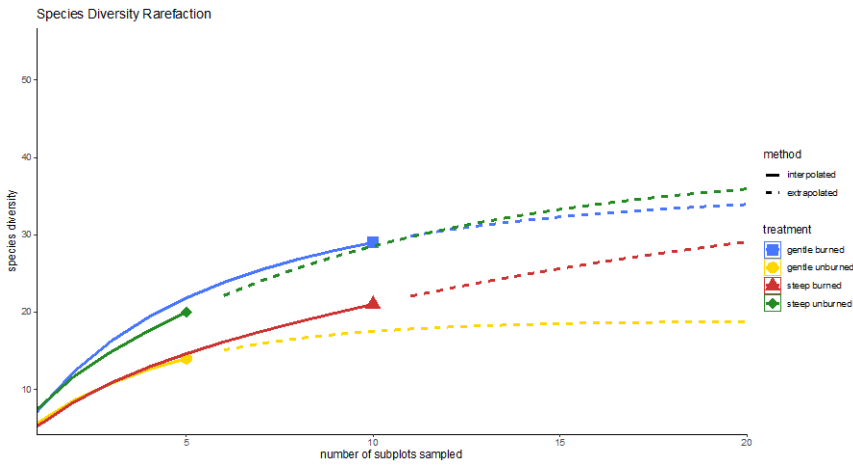
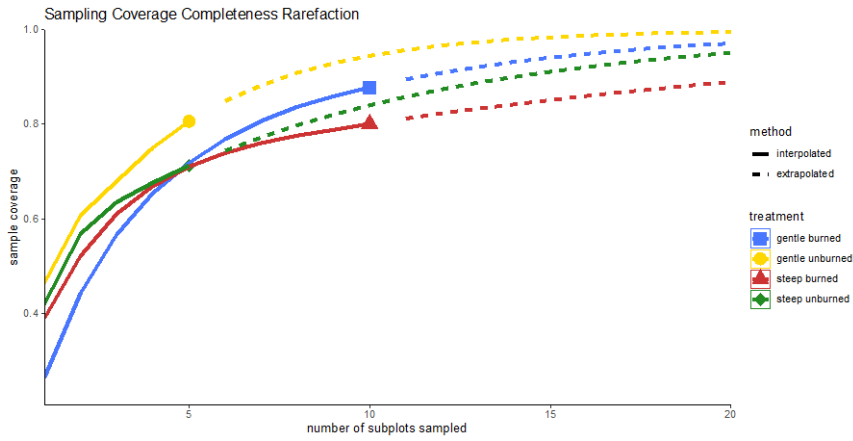


Figure 15. Estar values of 6 ridgelines plotted against NMDS1 axis.

This figure was generated to observe the variation amongst ridgeline topography.

Gentle sites are plotted in red, while steep sites are plotted in blue. This figure was generated before we changed the naming system of our ridgelines – “F” as in “fast” represents our steep ridgelines while “S” as in “slow” represents our gentle ridgelines.



Figures 16 and 17. Rarefaction curves to quantify species diversity accuracy and sampling completeness.

The sample coverage curves indicate how close to a complete sample our efforts were and the species diversity curves indicates how many more species we expect to see as our sampling effort increased. Interpolated refers to what we measured, and extrapolated refers to the projected data based off what we measured.

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