



Semi-arid Plant Communities of the Southern Colorado Plateau in Relation to Regional Climate Context and Local Topoedaphic Conditions

Comparing Species Abundance Patterns Across a Network of Sites to Identify Climate-Driven Vulnerabilities and Inform Hypotheses About Future Composition Shifts



Clockwise, from top-left: semi-arid plant communities in El Morro National Monument, Bandelier National Monument, Wupatki National Monument, and Petrified Forest National Park.

NPS

Semi-arid plant communities of the Southern Colorado Plateau in relation to regional climate context and local topographic conditions: Comparing species abundance patterns across a network of sites to identify climate-driven vulnerabilities and inform hypotheses about future composition shifts

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Abstract

With climate projections for increased warming and greater drought severity, the semi-arid grasslands, shrublands and pinyon-juniper woodlands occurring at lower elevations on the Colorado Plateau are likely to change in coming decades. Using shrub and herbaceous data from seven long-term study areas, I describe across-ecosite compositional gradients within the current regional climate context and compare spatial variability among assemblages. At the local scale, I model the relationship between composition and topoedaphic conditions. I use these results to develop hypotheses regarding the types of community change that may occur.

From the across-ecosite ordination, I found high similarity among three of four grassland/shrubland assemblages, and low to moderate similarity among woodland assemblages. Beta diversity is significantly higher in two of the five assemblages, denoting spatially heterogeneous composition patterns. Analysis of the relationship between the species abundance matrix and climate variables found that the three primary axes of variation accounted for 48.7% of total variation. Axis 1 separates grassland/shrubland assemblages from woodland assemblages, aligning with a gradient in annual precipitation. Axis 2, reflecting a gradient in perennial grass dominance, aligns with precipitation seasonality. Axis 3 aligns with seasonal temperature differences and Vapor Pressure Deficit.

Because topoedaphic conditions mediate soil water availability in semi-arid ecosystems, understanding their relationship to local composition patterns is essential to predicting how these communities will respond to climate change. Within-ecosite compositional gradients aligned with one to five environmental variables per ecosite. Elevation correlated with compositional gradients in all ecosites, and edaphic variables correlated with compositional gradients in four ecosites.

Compositional dominance also influences community stability. Dominance strength varied among ecosites, with abundance of the top two species ranging from 66% of total abundance for the strongest pattern to 35% for the weakest. From a functional group perspective, dominance was shared between perennial grass and shrub species for three woodland ecosites and one grassland/shrubland ecosite. Perennial grasses dominated in the other ecosites with several shrub species displaying moderate abundance.

These results contribute to comparing vulnerabilities and sources of resilience across ecosites. By considering both the strength of dominance patterns and dominant species characteristics against the backdrop of projected climate impacts, I offer hypotheses concerning future assemblage stability and propose comparisons of community change trajectories between ecosite pairs. Such comparisons complement ongoing trend analyses and may provide earlier warning of changes in dominance strength or species rank shifts than would be apparent by comparing a single assemblage to itself through time.

Acknowledgments

From the ecologists involved in developing the protocol, to the seasonal field crews who endure long days and tough field conditions, many talented individuals have contributed to the SCPN Upland Monitoring Project. No one deserves more credit for its success than its current leader, Megan Swan. Since the project's inception, her botanical expertise, ecological curiosity, and leadership skills have resulted in a consistent, high-quality record of southern Colorado Plateau plant communities. Thanks to past and current SCPN data managers for your rigorous standards, collaborative attitude, and continuing quest to make data more accessible for analysis. Thanks to SCPN and the Heartland Network for providing computer support. I appreciate the advice of two reviewers at an earlier stage of the project. Thanks also to two recent reviewers, whose thoughtful comments certainly improved this report. I want to thank Kirsten Gallo for encouraging me to begin this study as I planned my retirement from the SCPN Program Manager position. I completed most of this project post-retirement as a volunteer. After 23 years of managing NPS monitoring programs, the opportunity to directly engage in the core work that first drew me to ecological monitoring was, in my view, a fitting end to my time with NPS.



Clockwise, from left: pinyon-juniper woodland in Grand Canyon National Park, Fajada Butte amid semi-desert grassland/shrubland in Chaco Canyon National Historical Park, and pinyon-juniper woodlands in Navajo Canyon, Mesa Verde National Park. CREDITS: LEFT NPS, TOP RIGHT NPS, AND BOTTOM RIGHT © SANDY GROVES

Abbreviations Used in This Report

CE	Current Era
dbRDA	distance-based Redundancy Analysis
ENSO	El Niño-Southern Oscillation
GRTS	Generalized Random-Tessellation Stratified
MAP	Mean Annual Precipitation
NAMS	North American Monsoon System
NHP	National Historical Park
NM	National Monument
NMDS	Non-metric Multidimensional Scaling
NP	National Park
NPS-IMD	National Park Service, Inventory and Monitoring Division
NVC	National Vegetation Classification
NWR	National Wildlife Refuge
PCO	Principal Coordinates Analysis
PRISM	Parameter elevation Regression on Independent Slopes Model
RAC	Rank Abundance Curve
SCPN	Southern Colorado Plateau Network
SSURGO	Soil Survey Geographic Database
SWP	Soil Water Potential
VPD	Vapor Pressure Deficit

Ecosite Study Areas

BAND-P	Bandelier NM; pinyon-juniper woodland
CHCU-S	Chaco Culture NHP; sandy loam upland grassland
GRCA-P	Grand Canyon NP; limy upland pinyon-juniper woodland
MEVE-L	Mesa Verde NP; loamy mesa-top pinyon-juniper woodland
PEFO-C	Petrified Forest NP; clayey-fan grassland
PEFO-S	Petrified Forest NP; sandy loam upland grassland
WUPA-L	Wupatki NM; loamy & sandstone/shale upland grassland

Introduction and Background

Monitoring of biotic communities is a common theme of long-term ecological monitoring programs. Land managers are interested in many aspects of community integrity, including diversity and natural functioning, the influence of local and regional stressors, and the overarching impacts of climate change. A vital challenge for community-level monitoring is how to detect multiple aspects of biodiversity change in order to meet these varied information needs.

What types of change are most relevant from a monitoring perspective? Plant communities exhibit stochastic variation in response to environmental variability, such as fluctuations in productivity with year-to-year differences in precipitation (Knapp and Smith 2001). They may also exhibit directional change in response to pulse disturbances like wildfire, or chronic perturbations (i.e., ecological presses), such as increasing aridity (Smith et al. 2009; Hoover et al. 2017; Jones et al. 2017). The response of a community can be abrupt, as with tree mortality events (Breshears et al. 2005, 2009), or gradual, with community shifts tracking subtle change in environmental conditions (Jones et al. 2017). The eventual outcome of an ecological press could be species turnover resulting from local extinction and colonization (Collins et al. 2020). However, in communities dominated by long-lived perennial species, this process is likely to occur over decades (Collins et al. 2020). More subtle changes such as species reordering, changes in species evenness, or increasing temporal variance, are likely to precede dramatic community shifts (Avolio et al. 2014, 2019; Collins et al. 2008, 2018, 2020; Dornelas et al. 2014; Hillebrand et al. 2018). Because they could provide early warning, consideration of these more subtle types of directional change was one motivation for this study.

While community composition may shift through time in response to both pulse and press disturbances, variability in underlying topography and edaphic factors also influence patch dynamics on the Colorado Plateau (Miller 2005). Homogenous vegetation patterns are sometimes observed, with a single community occurring over large areas within a particular geomorphic setting. In other, more varied landscapes, we see a mosaic of co-occurring communities, with dominance by species or functional group (e.g., shrub, perennial grass, etc.) varying from one patch to another.

Environmental heterogeneity affects the variety and strength of abiotic conditions and competitive interactions, which govern the persistence of species in communities (Keddy 1992; Baer et al. 2015). Topographic variability is a common predictor of diversity (Lundholm 2009). It was here on the Colorado Plateau where Merriam (1890) developed the “life-zone” concept to describe shifts in dominant life-form with elevation. In dryland systems, where dynamics are tightly linked to moisture availability, soil conditions also play a strong role in mediating the relationship between climate and vegetation (Duniway et al. 2010; Munson et al. 2015; Peters et al. 2010).

This study concerns the grasslands, shrublands and pinyon-juniper woodlands common to lower elevations on the southern Colorado Plateau. Precipitation strongly regulates ecosystem processes in these semi-arid landscapes and more broadly across southwestern U.S. drylands (Noy-Meir 1973; Comstock and Ehleringer 1992; Collins et al. 2008; Knapp et al. 2015). On the Colorado Plateau, precipitation seasonality also determines dominance by life form and functional group because of its

effects on hydrologic partitioning, (Comstock and Ehleringer 1992; Schwinning et al. 2002, 2008). Climate experiments and modeling results from the Colorado Plateau indicate that perennial grass species are sensitive to rising temperatures and prolonged drought (Gremer et al. 2015; Hoover et al. 2015, 2021; Wertin et al. 2015). Recent soil water modeling for the specific ecosystems included in this study suggest that changing soil moisture patterns, as well as warmer temperatures and increased seasonal temperature variability, are key conditions likely to impact the relative abundance of grasses versus shrubs under future climate conditions (Gremer et al. 2018). These modeling results indicate contrasting climate impacts, with shrubs favored by increased seasonal temperature variability, and perennial grasses favored by decreased soil water availability in the winter. Gremer and colleagues (2018) conclude that on balance, future climate conditions will likely favor increased relative dominance by shrubs for these Colorado Plateau ecosystems.

This study explores shrub/herbaceous composition patterns and their relationship to underlying topographic characteristics using data from the first decade of monitoring. An understanding of spatial variability and its relationship to topographic factors will improve our ability to interpret composition shifts through time (Bradford et al. 2020; Collins et al. 2018; Hillebrand et al. 2018).

SCPN Upland Monitoring Project

The Southern Colorado Plateau Network (SCPN) of the National Park Service, Inventory and Monitoring Division (NPS-IMD), selected monitoring of vegetation and soils in predominant upland ecosystems as one of several vital signs for long-term monitoring (Thomas et al. 2006). Park managers emphasized monitoring in predominant ecosystems because of the influence of vegetation patterns on wildlife diversity and use, fire regimes, and ecosystem processes. For the parks with extensive grasslands, park managers ranked vegetation monitoring highly among potential vital signs because they valued these ungrazed grasslands as unique regional resources and important reference areas for more altered ecosystems. The old-growth character of some pinyon-juniper communities was cited as a reason for their inclusion. As we began developing the upland vegetation monitoring project, a wave of drought-induced pinyon pine mortality was sweeping across the Colorado Plateau, so the role of climate change in driving vegetation dynamics was prominent in our park discussions. In the intervening two decades, climate modeling projections have improved our understanding of the risks and uncertainties regarding future conditions. See Synopsis 1 below, for a brief climate summary.

As SCPN ecologists developed the monitoring project, we incorporated two foundational elements that could be further refined once the project had matured to include a sufficient temporal record. First, we based our monitoring targets on the Natural Resources Conservation Service (NRCS) concept of ecological site, which incorporates differences in climate, topography, and soil properties into ecosystem descriptions (USDA-NRCS 2003). Strong interactions between plants and soils are typical of dryland ecosystems and result in coupled spatial patterning of vegetation and soils across landscapes (Miller 2005). By defining study areas according to ecological site rather than on current vegetation types, we expected to see relatively homogenous composition patterns within a single study area. We also anticipated that a soils-based approach would be more stable over time, while plant communities might shift in response to disturbance or climate change. An added benefit of

using the NRCS ecological site concept was its linkage to state and transition models as part of the Ecological Site Description (Bowker et al. 2013).

Secondly, we worked with regional experts to develop conceptual models for dryland and montane ecosystems (Miller 2005; Vankat 2006). The initial models were admittedly generic, but we intended them to be refined for specific systems as a tool for developing hypotheses and interpreting monitoring results. Synopsis 2 provides a partial summary from Miller's report, describing the role of dominant vegetation as one of four interactive controls that influence dryland ecosystem processes.

With the conceptual models providing the underlying framework of ecosystem function, the SCPN Integrated Upland Protocol was developed to monitor two key elements in dryland ecosystems—soil stability and plant community composition and structure (DeCoster et al. 2012). We wanted the vegetation sampling methods to be comprehensive enough to address a wide range of resource-management issues, such as wildlife habitat questions, rare or endemic species occurrence and non-native species invasions. However, given their role in both controlling key ecosystem processes, and responding to changing ecosystem conditions, we viewed tracking the dominant dryland species, and the functional groups to which they belong, as fundamental objectives of this monitoring project.

With an emphasis on predominant upland ecosystems, network staff and park resource managers collaborated to select the target ecosystems in each park, based primarily on park-specific resource management needs. As a result, the study areas were not intentionally laid out along one or more climate gradients. Nevertheless, we can still ask if the relative climatic positions of the monitored study areas lend themselves to useful comparisons concerning projected compositional shifts.

SYNOPSIS 1: Current Climate Conditions and 21st Century Projections

The Colorado Plateau is a semi-arid region with cold winters, and warm, often dry summers (Comstock and Ehleringer 1992; Hereford and Webb 1992). Annual precipitation and average temperatures vary greatly across the region, mostly due to elevation (Hereford and Webb 1992). There is high interannual variability in precipitation in the Southwest, with climate model simulations suggesting that droughts lasting several years to decades are a natural occurrence (Wehner et al. 2017). Temporally variable precipitation is partially the result of El Niño-Southern Oscillation (ENSO) conditions. Warm-season precipitation is also influenced by tropical cyclones and by the North American Monsoon System (NAMS), which creates a precipitation gradient—strongest in southern Arizona and New Mexico and weakening as it extends into Utah and southwest Colorado (Hereford and Webb 1992). Seasonal moisture availability is driven by the balance of winter versus summer precipitation patterns and by evaporative demand (Comstock and Ehleringer 1992, Gremer et al. 2015).

According to the Fourth National Climate Assessment (Gonzalez et al. 2018), the average annual temperature of the Southwest has increased 1.6°F between 1901 and 2016. Increased heat has amplified drought, reduced snowpack, and advanced spring warming, resulting in extended fore-summer drying and increased wildfire frequency and severity. The result has been a decline in the integrity of Southwest ecosystems (Gonzalez et al. 2018). Large-scale tree mortality events have

been observed across the Southwest, including in Colorado Plateau ecosystems (Breshears et al. 2005; Kannenberg et al. 2021). Recent hydrological modeling combined with tree-ring reconstructions of summer soil moisture suggest that the 2000–2018 Southwest drought was the second driest period since 800 CE (Williams et al. 2020).

Future climate projections for the western U.S. indicate increased warming trends and increased drought severity (Gonzalez et al. 2018, Cook et al. 2015, Dettinger et al. 2015). Bradford and colleagues (2020) used an ecosystem water balance to estimate drought conditions across the western U.S. and Canada during the 21st century. Their results include robust projections for increasing chronic drought in much of the central and southern Great Plains, the western portion of the Great Basin, and the southern part of the Colorado Plateau. They also project drier spring soil conditions and drying earlier in the year for the Colorado Plateau. In an analysis focused on the Grand Canyon region, Tillman and colleagues (2020) combined projected temperature and precipitation data with soil water balance groundwater infiltration simulations. Their simulation results showed lower average groundwater infiltration compared to recent historical data in more than 76% of 21st-century decades.

Overall precipitation is projected to increase slightly or remain the same for the Colorado and Rio Grande basins (Bureau of Reclamation 2016). However, an important uncertainty in climate projections is the wide range in projections of future precipitation across the Southwest (Gonzalez et al. 2018). Current climate projections predict no change in the total amount of summer monsoon precipitation, but a delayed onset, thus lengthening the summer drought period (Cook and Seager 2013). Surface soil moisture deficits will be amplified because of increased evapotranspiration caused by higher temperatures (Gonzalez et al. 2018). Climate models also project an increase in extreme summer precipitation events in the Southwest (Gonzalez et al. 2018).

SYNOPSIS 2: The Structure and Functioning of Colorado Plateau Drylands

The dryland conceptual model report develops conceptual models describing functional relationships among key structural components of dryland ecosystems of the Colorado Plateau. Based on a modified version of the Jenny-Chapin model, four interactive controls—climate, soil-resource supply, major functional groups of organisms, and disturbance regime—determine ecosystem sustainability (Chapin et al. 1996). A key aspect of the Jenny–Chapin model is the associated hypothesis that interactive controls must be conserved for an ecosystem to be sustained. Large changes in any of the four interactive controls are predicted to result in a new ecosystem with different characteristics than the original system.

Vegetation is generally recognized as the dominant functional group of organisms in terrestrial ecosystems. For Colorado Plateau drylands, *Juniperus* and *Pinus* tree species, shrubs, dwarf shrubs and perennial grasses are the vegetative life forms with the greatest effect on the structure and functioning of dryland ecosystems. There are relatively large differences among dryland vegetative life forms (trees, shrubs, and perennial grasses) in terms of canopy architecture and spatial arrangement, as well as in their responses to climate, fire, and herbivory. As a result, ecosystems characterized by different proportions and spatial patterns of trees, shrubs, and grasses can be

expected to differ greatly in terms of associated ecosystem processes including nutrient cycles, hydrologic cycles, disturbance regimes, and wildlife-habitat relationships. Moreover, there is considerable functional variation within vegetative life forms and this species-level variation must also be considered on a site-specific basis.

In categorizing functional types, we emphasize the difference between *functional effect* and *functional response*. *Functional effect type* refers to organisms with similar effects on ecosystem functions such as primary production, nutrient cycling, and soil stabilization. *Functional response type* describes organisms with similar responses to environmental factors such as climate, resource availability, natural disturbances, and land use activities. The distinction between these two types is important for considering how biotic composition affects the resistance and resilience of ecosystems to climatic fluctuations and changes, natural disturbances, and anthropogenic stressors. Redundancy among organisms in terms of their effects on ecosystem processes, and diversity among organisms in terms of their responses to environmental factors, both can contribute to the buffering of ecosystem function in relation to changing environmental conditions.

Synopsis 2 is summarized from Miler, M.E. 2005. The Structure and Functioning of Dryland Ecosystems—Conceptual Models to Inform Long-Term Ecological Monitoring. U.S. Geological Survey Scientific Investigations Report 2005-5197, 73 p.

Study Objectives

This study examines plant community composition patterns across seven semi-arid study areas on the southern Colorado Plateau including grassland, shrubland, and pinyon-juniper woodland communities. The grassland/shrubland study areas include cool semi-desert scrub and grasslands confined mainly to the Colorado Plateau or also occurring in the Great Basin, desert scrub and grasslands that occur in the Chihuahuan Desert and southern Colorado Plateau, and one community that is restricted to lava and cinder substrates. The pinyon-juniper study areas exemplify the three broad physiognomic types described by Romme and colleagues (2009)—that is, persistent woodland, wooded shrubland, and savanna. The two moderately open woodland study areas have shrub-dominated understories, with one community type (or association) centered on the Colorado Plateau and the other also extending east into the southern Rockies. The more open savanna and shrubby woodland at Bandelier NM occur in the southern Rockies and extend into the southern Great Plains. I chose to focus on the shrub and herbaceous species that constitute grassland and shrubland communities and compose the understory of pinyon-juniper woodland communities.

The initial objectives were: 1) to explore the relationship between local topographic factors and species abundance patterns for each study area, and 2) to describe the spatial variability in composition (or beta diversity) among the plots within each study area. Was our initial expectation of homogenous vegetation patterns realized for each ecosite study area under consideration?

I was also interested in how the comparison of compositional patterns among assemblages could inform hypothesis development regarding projected compositional shifts in response to climate change. A first step to meet this objective, modeling the severity of climate change exposure among

the study areas, had already been accomplished through collaborative work with Dr. John Bradford (USGS), Dr. Jennifer Gremer (UC-Davis) and colleagues (see Climate Change Exposure below). Additional steps toward identifying relevant comparisons are to describe compositional gradients among the study areas within a regional climate context, and to compare compositional similarities among the monitored assemblages. These represent the third and fourth objectives of this study.

Study Approach and Emphasis

Focus on Grasslands, Shrublands and the Understory of Pinyon–juniper Woodlands

From a forest ecology perspective, it may seem unconventional to include pinyon-juniper woodlands in a study of semi-arid shrub and herbaceous composition patterns. As in other woodland ecosystems, it is well understood that overstory pinyon and juniper trees compete for resources and alter the microclimate through shading, litterfall, and the interception of light and precipitation (Breshears et al. 2006). Thus, overstory trees control key ecosystem processes and create a mosaic of canopy and intercanopy patches with differing solar radiation and soil moisture patterns (Breshears et al. 1997, 2006). Differences extend belowground as well, with higher root densities in soils underlying tree clusters (Schwinning et al. 2020). But given that pinyon-juniper vegetation occurs along a continuum (Breshears et al. 2006; Romme et al. 2009), with varying levels of coverage by trees, shrubs, and perennial grasses, it is likely that the strength of overstory control also varies.

While the influence of overstory trees on ecosystem processes must be considered when comparing woodland understory composition patterns to those of shrublands or grasslands, there are compelling reasons to examine patterns across the full grassland to woodland continuum. First, whether focused on grassland/shrubland or pinyon-juniper woodland, semi-arid Colorado Plateau vegetation is often observed as a mosaic of co-occurring communities, often with a consistent set of shrub and herbaceous species that vary in dominance from one patch to another. At this local scale, site conditions and disturbance history influence whether shrubs or perennial grasses dominate (Miller 2005; Romme et al. 2009). Secondly, both patch-scale heterogeneity and the connectivity between patches impact ecosystem processes (Breshears 2006). Examples of connectivity in pinyon-juniper woodlands include the role of intercanopy herbaceous vegetation in slowing run-off and surface erosion, or providing fine fuels to carry surface fire. (Breshears 2006). Thus, understory composition patterns may impact overstory integrity through connectivity.

Recent history and current climate projections attest to the dynamic nature of Colorado Plateau vegetation patterns. There is considerable evidence for 20th century expansion and more recent contraction of pinyon-juniper woodlands within the NPS units included in this study. In Bandelier NM, following the severe 1950s drought, Ponderosa pine mortality resulted in a rapid shift in the ecotone between Ponderosa pine forest and pinyon-juniper woodland (Allen and Breshears 1998). Late 20th century expansion of juniper into degraded grasslands in depositional valley and terrace settings has been documented in north-central New Mexico, including in Bandelier NM (Jacobs et al. 2008; Jacobs 2011). In Grand Canyon NP, 20th century decreases in tree basal area have been observed within pinyon-juniper woodlands (Vankat 2017). Nearly half of the Mesa Verde NP pinyon-juniper woodland burned in stand-replacing fires from 1972 to 2003 (Floyd et al. 2004), with no evidence to date of pinyon or juniper re-establishing in these burned areas (Floyd et al. 2021).

Bandelier NM has also lost pinyon-juniper woodland in recent fires (Jacobs et al. 2015). Finally, extreme drought conditions in the early 2000s resulted in a wave of pinyon mortality across the region, with moderate mortality rates observed for Mesa Verde NP (Breshears et al. 2005, Floyd et al. 2009, 2021). More severe mortality was seen in some stands including those of Bandelier NM, which experienced 90% mortality of mature pinyon trees (Floyd et al. 2009; Jacobs et al. 2015). Though less sensitive than pinyon, juniper species have also experienced 21st century declines (Kannenberg et al. 2021), including in Grand Canyon NP (Jackson et al. 2022).

Williams and colleagues (2013) project that by mid-century, continued increases in hot, dry warm-season conditions will force mean annual southwestern U.S. forest drought-stress levels to exceed the severity of the strongest megadroughts since 1000 CE. Given this projection, it is likely that much of the current pinyon-juniper vegetation will shift on the continuum toward wooded shrublands or savanna. Thus, understanding understory composition patterns may become increasingly relevant to effectively managing these communities.

Multivariate Analysis Paired with Description of Community Structure

A prevalent view among ecologists is that species assemblages are the best response variable available to estimate the impact of changes to ecosystems (Legendre and Gauthier 2014). Modern multivariate techniques afford a rigorous approach to analyzing community abundance data and relating it to environmental, spatial, and temporal factors (Anderson et al. 2011; Clarke et al. 2014; Legendre and Legendre 2012). But while multivariate analysis simplifies the task of detecting variability or change in community datasets, the results may seem abstract and not fully describe the exact nature of observed spatial variability or temporal change within a community (Collins et al. 2008). Distribution-based methods such as rank abundance curves (RACs) graphically depict differences in abundance among species. They provide a simple approach to look for changes in dominance structure (Matthews and Whittaker 2015) and give insight into species of intermediate abundance, a subset of interest for their roles in discriminating between sites and responding to environmental change (McGill 2011; Ulrich et al. 2010). In this study I use multivariate methods to analyze assemblage relationships but include distribution-based graphs and diversity indices to further characterize assemblage differences.

I compare functional group abundance within and among assemblages as a useful tool for generalizing about compositional patterns and use two common univariate diversity indices to summarize dominance and diversity differences. But a disadvantage of such aggregate measures is the potential for masking of complex dynamics, such as turnover and reordering of dominant species (Collins et al. 2008; Avolio et al. 2015, 2019; Hillebrand et al. 2018). Therefore, I include rank abundance curves to visualize the relative strength of dominance patterns, and a comparison of identities of dominant and moderately abundant species to further describe similarities.

In keeping with the drylands conceptual model (Miller et al. 2005), the functional effects and responses of dominant species are important themes for this study. A focus on the functional role of dominant species is consistent with the mass ratio hypothesis put forth by Grime (1998) which holds that ecosystem stability is largely controlled in the short term by dominant species, whereas

subdominant and rare species may affect stability in the long term by influencing recruitment of dominant species (Sasaki and Lauenroth 2011).

I expand the scope to include moderately abundant species because they are likely to influence the functional stability of dryland ecosystems, particularly when there are shifts in abundance among the dominant species (Walker et al. 1999; Ulrich et al. 2016). This has been demonstrated in long-term removal experiments in Chihuahuan desert grasslands, wherein the abundance of co-dominant and sub-dominant species increased in response to the removal of the dominants (Peters and Yao 2012).

Comparisons Among a Related Set of Study Areas

As is customary for long-term monitoring efforts, the SCPN Integrated Upland Protocol outlined comparing each assemblage to itself through time as the primary form of analysis (DeCoster et al. 2012). However, Avolio and colleagues (2019) remind us of a second pathway for examining differences in species composition—that is, by comparing communities that represent different environmental conditions to one another. Comparing compositional patterns across related communities (i.e., those with similar bioclimatic conditions and biogeographic histories, sharing a common species pool) can help to develop hypotheses regarding the types of temporal change we expect to see. By pursuing the four objectives outlined for this study, I hope to identify potential comparisons that could add to our understanding of community dynamics for these semi-arid Colorado Plateau ecosystems. How will communities that are initially similar in composition change with diverging climate conditions? Will communities displaying greater beta diversity be more stable through time than those with more even species abundance patterns? What impact will dominance patterns have on temporal change trajectories? Do we see perennial grass and shrub species maintaining stable co-dominance patterns in some areas, with a shift to shrub dominance in others?

Methods

Monitoring Methods

Study Areas

SCPN initiated long-term vegetation monitoring in montane and semi-arid ecosystems beginning in 2007. Study areas were chosen to represent predominant ecosystem types of interest to NPS management, using USDA Natural Resources Conservation Service's ecological site designations, which incorporate differences in climate, topography, and soil properties into ecosystem descriptions (USDA-NRCS 2003). Herein I use the terms "ecosite" or "study area" as shorthand for the selected ecological site-based study areas.

Ecological sites are not explicitly mapped in NRCS Soils Survey Geographic (SSURGO) Database spatial layers. Instead, "soil map units" are the finest spatially defined units. In general, soil map units having a high percentage of the target ecological site were selected to be part of each study area. Six of the seven study areas were rather narrowly defined to include from one to four closely related soil map units. However, for the juniper woodland study area at Bandelier NM, park resource managers and scientists preferred a broader study area delineation. Consequently, the BAND-P study area includes six soil map units representing divergent soil series. We set up more plots in the BAND-P study area (45 instead of 30), because we anticipated greater plot-to-plot variability.

Here I use data from 215 plots across seven semi-arid study areas including grassland/shrubland and pinyon-juniper or juniper woodland (Figure 1, Table 1). These study areas represent some of the least disturbed examples of their respective ecosystem types, with low level of human impact over recent decades. Figure 2 displays mean annual temperature and mean annual precipitation for plots within each ecosite study area based upon the PRISM 800-m 30-year Normal (1981–2010) dataset (PRISM Climate Group, OSU).

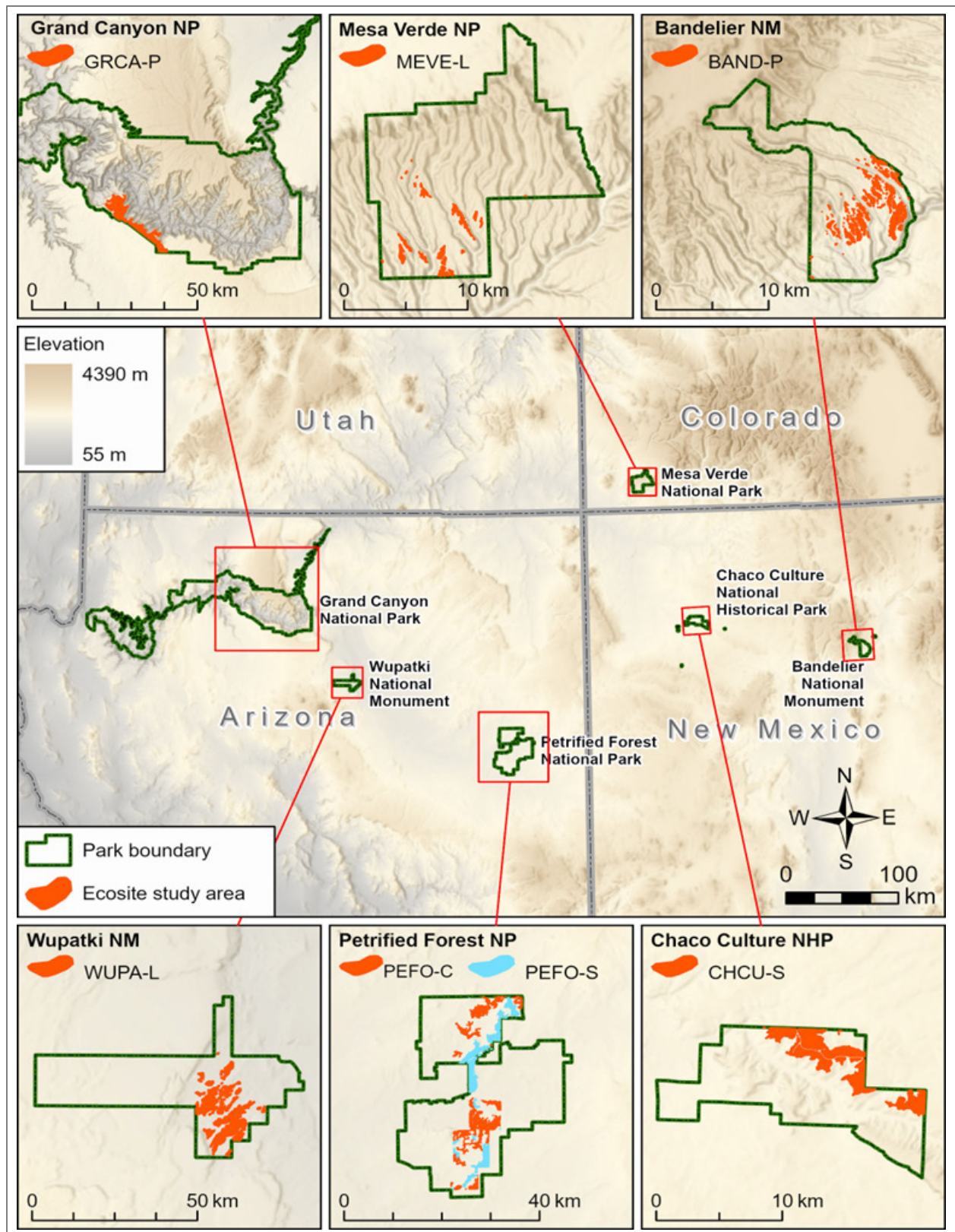


Figure 1. Overview map of the NPS units and ecosite study areas included in this report. NPS / KRISTIN STRAKA

Table 1. NPS units and ecosite study areas, number of plots, and yearly sample size for 2012–2017. Using a rotating-panel revisit design, the total number of plots is divided into three panels (A, B and C), with two of three panels sampled every other year.

Ecosite Acronym	NPS Unit; Ecosite Name	Number of Plots	Ecosite Size (ha)	Yearly Sample Size (Panels)					
				2012	2013	2014	2015	2016	2017
MEVE-L	Mesa Verde NP; loamy mesa-top pinyon-juniper woodland	28	459	–	18 (A+B)	–	18 (B+C)	–	20 (A+C)
GRCA-P	Grand Canyon NP; limy upland pinyon-juniper woodland	29	5,598	19 (A+B)	–	18 (B+C)	–	19 (A+C)	–
BAND-P	Bandelier NM; pinyon-juniper woodland	42	1,321		27 (A+B)	–	28 (B+C)	–	29 (A+C)
CHCU-S	Chaco Culture NHP; sandy loam upland grassland	29	1,725	20 (A+B)	–	19 (B+C)	–	19 (A+C)	–
PEFO-C	Petrified Forest NP; clayey-fan grassland	29	5,400	20 (A+B)	–	19 (B+C)	–	19 (A+C)	–
PEFO-S	Petrified Forest NP; sandy loam upland grassland	30	4,191	–	20 (A+B)	–	20 (B+C)	–	20 (A+C)
WUPA-L	Wupatki NM; loamy & sandstone/shale upland grassland	28	1,425	–	18 (A+B)	–	18 (B+C)	–	20 (A+C)

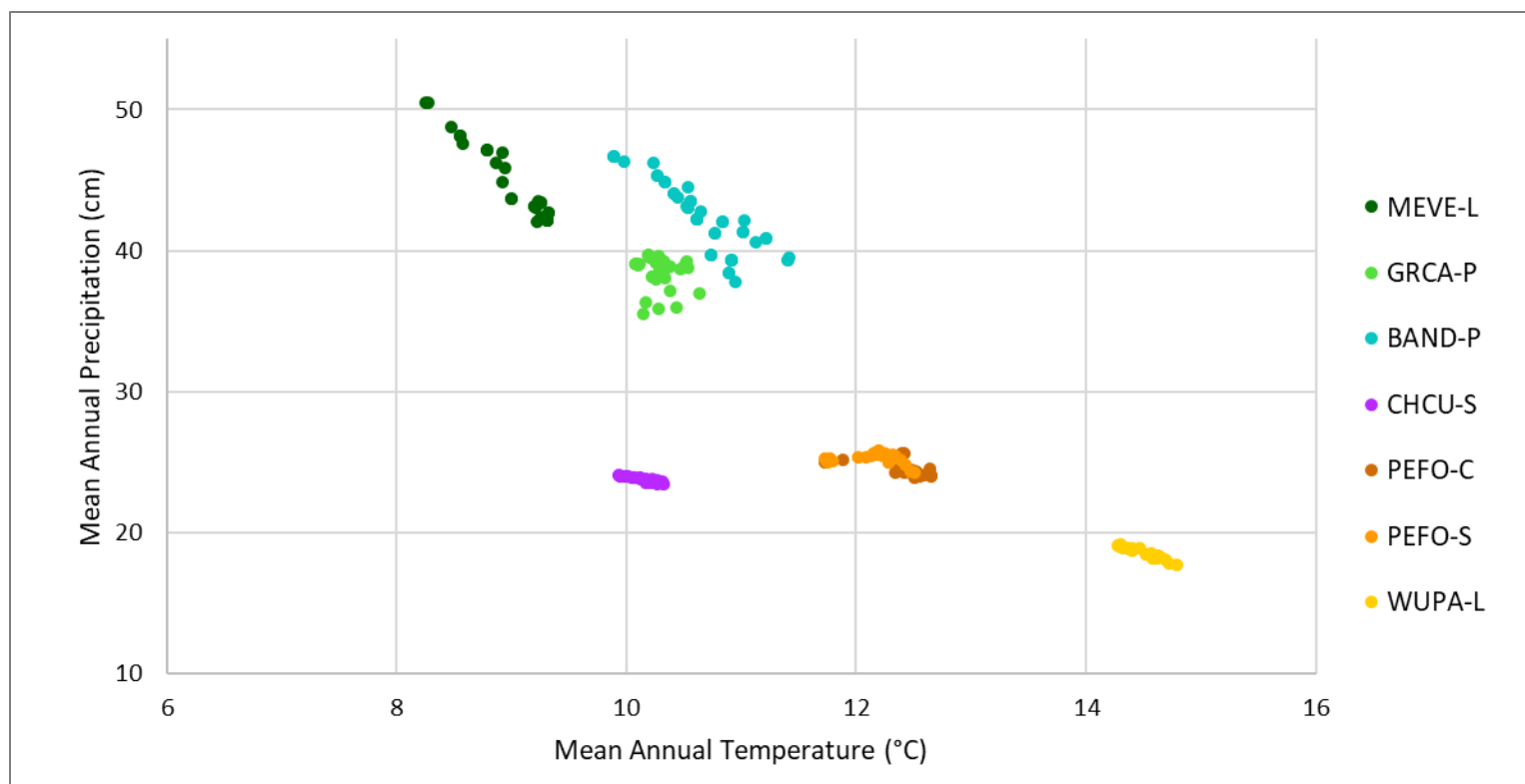


Figure 2. Mean annual temperature and mean annual precipitation for plot locations within seven southern Colorado Plateau ecosites using the PRISM 800-m dataset for the period from 1981–2010 (PRISM Climate Group, OSU). NPS / LISA THOMAS

Field Monitoring Methods

Monitoring methods are briefly summarized here; for more detail see DeCoster et al. 2012. Candidate plot locations within each target ecosite were restricted to areas removed from human disturbance (e.g., 100 m from any road) and at least 50 m from mapped ecological or soil boundaries. Permanent plot locations were selected using a generalized random-tessellation stratified (GRTS) design.

I used shrub and herbaceous foliar cover data to characterize the assemblage for each ecosite. Foliar cover is estimated for shrub and herbaceous species as well as functional groups in five 10-m² quadrats along each of three parallel 50-m transects per 0.5 ha plot (15 quadrats/plot). Designated functional groups are shrub, perennial grass, forb, cactus/succulent, and annual grass. Ocular estimates of foliar cover are made using a twelve-class cover scale (Table 12 in Appendix A) developed for use in these relatively sparse semi-arid ecosystems. Cover of ground surface features (e.g., litter, gravel, biotic crusts) is estimated using 1-m² quadrats nested within each 10-m² quadrat.

I used overstory characteristics and topographic factors to describe the local plot environment. In the pinyon-juniper woodland ecosites, I used tree canopy cover and live tree basal area (m²/ha) to describe overstory tree abundance in each plot. Tree canopy cover is measured along the three 50-m transects using line intercept methods while tree basal area is calculated from measuring overstory tree diameters (those greater than 15 cm diameter) in a 20 × 50 m subplot.

Soils data, including depth to bedrock, texture, and coarse fragment content (> 2 mm), were collected from a soil core in each plot to a maximum depth of ~1 m. Plot-level soil depth information was supplemented with tabular data linked to the SSURGO map unit components associated with the targeted ecosite (Gremer et al. 2018). Soil texture information for the top 0.5 m of the profile was converted into soil texture classes (Table 13 in Appendix A; Moeys 2018; Soil Science Division Staff 2017). Ten plots with incomplete soils data were excluded from analysis. Elevation, slope and aspect were used to describe plot topography. Slope and aspect were calculated from the 2022 National Elevation Datasets in the native datum (GCS NAD83, NAVD88) in ArcPro using quadratic surface type with adaptive neighborhood distance. The data were then extracted to the upland plot points (projected into GCS NAD83) without using bilinear interpolation. Mean elevation was similarly derived.

An index of topographic heat load was calculated for each plot using Equation 3 from McCune and Keon (2002): $0.339 + 0.808 \times \cos(L) \times \cos(S) - 0.196 \times \sin(L) \times \sin(S) - 0.482 \times \cos(A) \times \sin(S)$, where A is folded aspect in radians east of north ($|180 - |\text{Aspect} - 225||$), S is slope in radians, and L is latitude in radians north (McCune and Keon 2002; Albano 2015). I chose this measure of solar radiation effects because it accounts for the fact that a slope with afternoon sun will have higher maximum temperatures than a comparable slope with morning sun (McCune and Keon 2002).

Rotating-Panel Revisit Design and Spatial Data Summary

SCPN adopted a rotating-panel revisit design in 2012. Each ecosite is monitored every other year, with two of the three panels per ecosite (or two-thirds of the plots) visited in each year that

monitoring occurs (Table 1). Assigning GRTS points in sequential order to each of the three panels ensured spatial balance among panels. Monitoring occurs once per growing season, is approximately timed to coincide with typical peak herbaceous biomass and is repeated according to a similar sampling schedule in successive years.

Foliar cover class data were converted to cover class midpoints for all analyses (Table 13 in Appendix A). To describe spatial variability across the full complement of plots within an ecosite, I averaged species abundance data for each plot from the two initial years of sampling in the 2012–2017 time period to account for short-term temporal variability. Because of the rotating panel design, repeat visits to individual plots could be two or four years apart (Table 1). For the BAND-P ecosite, the 2013 species composition was notably distinct from other years, most likely due to extreme drought in the two preceding years (M. Swan personal communication). For that ecosite I used data from 2008–2010 as a substitute for the 2013 data (Figure 19 in Appendix B), but still basing plot averages on two visits per plot.

Statistical Analysis

Multivariate analysis summarizes the information in site-by-species abundance tables into a small number of orthogonal gradients of compositional variation (Gauch 1982). Ecologists often rely on non-parametric multivariate approaches because the assumptions of multivariate normality and homogeneity of covariance matrices are seldom met when the variables of interest are species (Legendre and Anderson 1999; Legendre and Legendre 2012). For the multivariate analyses discussed below, I selected non-parametric methods that are suitable for non-normal data and semi-quantitative measurement scales (Clarke et al. 2014). For example, non-metric multidimensional scaling (NMDS) is appropriate for semi-quantitative cover class scales because it relies upon the rank order of the distances between samples (Clarke et al. 2014).

Ordination, Ecosite Similarity and Beta Diversity

I employ two distance-based ordination techniques, NMDS and principal coordinates analysis (PCO), to describe species-based variation among plots in this study. I chose Bray-Curtis dissimilarity as the most appropriate distance measure because it is well-suited to semi-quantitative and non-normal data and because it is commonly used with ecological data (Anderson et al. 2011; Anderson and Walsh 2013; Collins et al. 2018). The Bray-Curtis measure is also less sensitive to changes in rare species than measures emphasizing proportional composition (Legendre and Gallagher 2001) and thus aligns with my focus on dominant and moderately abundant species. I used a square-root transformation of abundance data to downweigh dominant species (Clarke et al. 2014) so that the influence of moderately abundant species was more apparent. Ordinations and related analyses were run using Primer software (Clarke and Gorley 2015; Clarke et al. 2014). A few outlier plots were identified from Shepard diagrams and removed from further analyses (1 plot for GRCA-P, 2 plots for PEFO-S and 1 plot for MEVE-L).

I applied a test for homogeneity of multivariate dispersions to describe the beta diversity for each assemblage (Anderson 2006). The PERMDISP test in Permanova (Anderson et al. 2008) calculates an F-statistic to compare the average distance of observation units to their group centroid, defined in

the space identified by the chosen dissimilarity measure (i.e., Bray-Curtis). This is done using PCO to generate a new set of variables from the dissimilarity matrix in Euclidean space. A p-value is obtained by permutation of least-squares residuals.

I used the PERMANOVA test in Permanova (Anderson et al. 2008) to test the null hypothesis of no difference in composition among the seven study areas (Anderson 2001; McArdle and Anderson 2001). For the PERMANOVA model, ecosite is considered a fixed effect and plot nested in ecosite as a random effect. I made *a posteriori* pair-wise comparisons among ecosites, with p-values obtained using permutations.

Compositional Gradients in Relation to Environmental Variables

I used distance-based redundancy analysis (dbRDA) (Legendre and Anderson 1999; McArdle and Anderson 2001) to model species assemblage patterns in relation to environmental data at two spatial scales. The dbRDA performs a multivariate multiple regression of PCO axes on predictor variables. A permutational test for the multivariate null hypothesis of no relationship between the response matrix (Y) and the predictor variables (X) was performed, using the DISTLM routine in Permanova (Anderson et al. 2008). I used the AIC selection criterion with the “Best” selection procedure, which examines the selection criterion for all possible combinations of predictor variables. The environmental variables (Tables 2 and 3) were standardized as part of the routine.

Table 2. Climate variables used in distance-based redundancy analysis (dbRDA) to examine their association with compositional gradients across ecosites.

Climate Variable	Abbreviation	Description
Mean annual precipitation	MAP	Mean annual precipitation (mm)
Monsoon precipitation percentage	Monsoon % ppt	(Precipitation for Jul, Aug & Sep) / MAP
Winter precipitation percentage	Winter % ppt	(Precipitation for Dec, Jan & Feb) / MAP
Winter temperature minimum	Winter $t_{\min}$	Mean of temperature minima for Dec, Jan, Feb (°C)
Spring temperature minimum	Spring $t_{\min}$	Mean of temperature minima for Mar, Apr, May (°C)
Summer Vapor Pressure Deficit (VPD) maximum—a measure of the drying power of the air	Summer VPD _{max}	Mean of Vapor Pressure Deficit maxima for Jun, Jul & Aug (hPa)

Table 3. Environmental variables used in distance-based redundancy analysis (dbRDA) to examine their association with within-ecosite compositional gradients. Topoedaphic, overstory and ground surface variables were considered.

Environmental Category	Variable	Abbreviation	Variable Trial ^{A, B}						
			MEVE-L	GRCA-P	BAND-P	CHCU-S	PEFO-C	PEFO-S	WUPA-L
Topoedaphic	Elevation (m)	Elevation	X	X	X	X	X	X	X
	Slope (%)	Slope	X	X	X	–	–	–	–
	Topographic Heat Load	Heat Load	X	X	X	–	–	–	–
	Soil depth (cm)	Soil Depth	X	X	X	X	X	X	X
	Soil texture (top 50 cm)	Soil Texture	X	X	X	X	X	X	X
	Soil rock content (% top 50 cm)	Soil Rock %	–	X	X	X	X	–	X
Overstory Trees	Tree basal area (m ² /ha)	Tree Basal Area	X	X	X	–	–	–	–
	Tree canopy cover (%)	Canopy Cover	X	X	X	–	–	–	–
Ground Surface Cover (%)	Fine gravel	Surface Gravel	–	X	X	–	–	–	X
	Cyanobacterial crust	Surface Cyano	X	–	–	–	–	X	–
	Undifferentiated crust	Surface Undiff	X	X	X	X	X	X	–

^A dbRDA trials included ground surface cover of fine gravel and/or biotic crust in ecosites where average cover was 10% or more. Slope and topographic heat load were included in ecosites with mean slopes of 4% or more.

^B An “X” denotes that a variable was included in the variable trial for each ecosite, and an endash (“–”) indicates that it was not.

At the larger, seven-ecosite scale, I examined the association between compositional gradients and 30-year normal climate data describing average monthly conditions. For the merged species abundance dataset (211 plots across seven ecosites), I included those species accounting for 0.1% relative abundance or greater in their respective study areas. I chose climate variables to represent annual and seasonal trends, focusing on attributes most relevant or limiting to plant communities on the Colorado Plateau (Comstock and Ehleringer 1992; Holmgren et al. 2007). Climate data were acquired for the 211 plot locations from the PRISM 800-m 30-year normal dataset for the period from 1981–2010 (PRISM Climate Group, OSU). I initially considered nine candidate variables but reduced the list to six by screening out those with > 0.88 correlation to the climate variables already selected (Table 2; Figure 27 in Appendix D).

At a finer scale, to examine within-ecosite association between compositional gradients and local environmental factors, I used plot-level measures of elevation, soil factors and overstory trees (for woodland ecosites) (Table 3). Slope and topographic heat load were included for ecosites with mean slope greater than 4%. Prior to analysis, draftsman plots of the environmental variables were examined for each ecosite, resulting in the exclusion of one variable in two ecosites due to minimal variation across the plots. I included a secondary set of ground surface variables (gravel and biotic crust cover) in ecosites where these variables represented $\geq 10\%$ mean ground surface cover (Table 3). All species were retained for these within-ecosite analyses.

Cluster Analysis

I used cluster analysis to identify and characterize natural groupings based on similar composition within each ecosite assemblage. From a vegetation mapping perspective, the clusters might represent closely related plant associations. From a state and transition modeling perspective, the clusters could represent alternate states or phases within an ecological site model (Bowker et al. 2013). I used hierarchical clustering with group-average linking of Bray-Curtis similarities (Clarke and Gorley 2015; Clarke et al. 2014). Clustering results are represented as a dendrogram, linking the samples in hierarchical groups based on similarity. The Primer SIMPROF permutation routine was used to test the null hypothesis of no significant multivariate structure at successive stages in the hierarchical clustering algorithm (significance level set at 5%). Shade plots depict clustering outcomes and species abundance variation across plots for each assemblage and are displayed alongside graphs of functional group abundance. NMDS bubble plots or PCO plots are used to describe abundance gradients and/or plot clusters within ordination space.

I compared the species composition of significant plot clusters to the National Vegetation Classification (NVC) associations described in each park's Vegetation Mapping report. The comparisons were informal and based upon the map, map class keys, and association descriptions. For the two study areas exhibiting the highest beta diversity (BAND-P and WUPA-L), I compared plot-based soil variables to the Soil Map Unit descriptions in the park Soil Surveys in order to describe Soil Map Units associated with major plot clusters.

Dominance, Diversity and Species Identity

I chose two common univariate diversity metrics, Simpson Concentration and Shannon Diversity, to summarize differences in dominance and diversity across assemblages. They are directly related to Hill numbers (Hill 1973), a family of metrics that combine distinct aspects into a unified diversity profile (Jost 2006; Chao et al. 2012, 2016):

Hill Number $N_1 = \exp(\text{Shannon diversity}) = \exp(-\sum_i p_i \ln(p_i))$, or the effective number of common species, and

Hill Number $N_2 = \text{inverse Simpson Concentration} = 1/D = 1/\sum_i p_i^2$, or the effective number of dominant species,

where p_i is the proportion of total abundance arising from the i th species.

These particular indices were selected to match my focus on dominant and moderately abundant species. Expressed in effective number of species (i.e., the number of equally abundant species that would be needed to give the same value of a diversity measure), Hill numbers measure the same aspect of assemblage similarity, but differ in the parameter q , the weight given to species abundances (Jost 2006). Thus, when $q = 0$, there is no weight on abundance and species richness is returned, when q approaches 1, the exponential of Shannon entropy is returned (emphasizing common species), and when $q = 2$, the inverse Simpson (emphasizing dominant species) is returned.

I use partial dominance curves to visually compare dominance patterns among ecosites. These curves plot the abundance of each species relative to the total of its own abundance plus that of all other less-abundant species against species rank (log-scale) (Clarke et al. 2014). By removing the most abundant species, and then the next most abundant species, etc., they allow a clearer picture of dominance patterns among successively less abundant species.

To compare the identities of the more abundant species across ecosites, I classified species in each assemblage as dominant (relative abundance of 10% or greater), moderately abundant (relative abundance of 1% up to 10%) or low abundance (less than 1% relative abundance) (Avolio et al. 2019; Grime 1998; Mariotte 2014).

Climate Change Exposure

I based estimates of climate change exposure in each study area on the Soil Water Potential (SWP) modeling results from our collaborative (USGS/NPS) project with Dr. John Bradford and colleagues. SWP is a measure of how difficult water is to extract from the soil. The SOILWAT2 ecosystem water balance model was used to model plot-specific interactions between soil conditions, vegetation, and climate (Gremer et al. 2018). Model simulations were run using climate data from the past (1916–2011) to provide historical context, from recent decades (1980–2015) to provide a current baseline, and for two future time periods. The future projections were made using nine general circulation models under the 8.5 representative concentration pathway (Gremer et al. 2018). Graphs of historical and future SWP from the ecosite-specific reports are reprinted in Appendix C; modeling results are summarized in Table 4.

Table 4. Summary of SWP modeling results for the seven ecosite study areas. Model simulations were run for two future time periods: near future (2020–2059) and long-term future (2060–2099).

Ecosite Acronym	Timeframe	Projected Change in Soil Water Potential		
		Fall/Winter (October–February)	Spring (March–June)	Summer (July–September)
MEVE-L	Near Future	No change	No change	No change
	Long-Term Future	No change	Decreased SWP	No change
GRCA-P	Near Future	No change	Decreased SWP	No change
	Long-Term Future	Decreased SWP	Extreme Water Scarcity	No change
BAND-P	Near Future	No change	Decreased SWP	No change
	Long-Term Future	Decreased SWP	Extreme Water Scarcity	No change
CHCU-S	Near Future	No change	No change	No change
	Long-Term Future	No change	Extreme Water Scarcity	No change
PEFO-C	Near Future	No change	No change	No change
	Long-Term Future	Extreme Water Scarcity	Extreme Water Scarcity	No change
PEFO-S	Near Future	No change	No change	No change
	Long-Term Future	Extreme Water Scarcity	Extreme Water Scarcity	No change
WUPA-L	Near Future	Extreme Water Scarcity	Extreme Water Scarcity	No change
	Long-Term Future	Extreme Water Scarcity	Extreme Water Scarcity	No change

Soil water modeling projects late 21st century declines in spring SWP (March–June) across all seven ecosites and mid-century declines in spring SWP for the BAND-P, GRCA-P and WUPA-L ecosites. Moderate late-century declines in fall/winter SWP (October–February) were projected for the BAND-P and GRCA-P ecosites, with larger long-term declines projected for the PEFO-C, PEFO-S and WUPA-L ecosites. The most pronounced changes in SWP were projected for WUPA-L, predicting large mid-century and late-century declines in both fall/winter and spring SWP.

Results

Part 1: Across-Ecosite Composition Patterns in Relation to Climate

Ordination, Ecosite Similarity and Beta Diversity

Non-metric multidimensional scaling (NMDS) results based on the combined seven-ecosite species matrix are presented in Table 5 and Figure 3. The Bray-Curtis similarity matrix (Table 5) and accompanying NMDS plot (Figure 3) depict the similarity between ecosite centroids, as well as the multivariate dispersion among plots within each ecosite.

Table 5. Average similarity between and within ecosite assemblages, based on Bray-Curtis similarity of square-root transformed abundance data.

Ecosite Acronym	CHCU-S	PEFO-C	PEFO-S	WUPA-L	MEVE-L	GRCA-P	BAND-P
CHCU-S	56.742^A	–	–	–	–	–	–
PEFO-C	35.609	55.317^A	–	–	–	–	–
PEFO-S	49.247	39.079	59.215^A	–	–	–	–
WUPA-L	18.274	15.557	19.714	39.356^A	–	–	–
MEVE-L	3.0744	1.752	1.5161	0.523	56.194^A	–	–
GRCA-P	14.948	9.786	13.460	1.699	20.766	52.116^A	–
BAND-P	19.315	12.658	18.234	4.372	9.270	19.274	41.771^A

^A Within-ecosite similarity (also shown in **bold font**).

The WUPA-L ecosite occurs at the lowest elevation (mean = 1,427 m) and the MEVE-L ecosite at the highest elevation (mean = 2,142 m). These two assemblages displayed the lowest similarities in pairwise comparisons with the other ecosites (Table 5). The PEFO-S and CHCU-S grassland ecosites shared the highest similarity (49.2), followed by each of these ecosites paired with PEFO-C. Among the woodland study areas, the similarity between MEVE-L and GRCA-P (20.8) was comparable to that between GRCA-P and BAND-P (19.3), while MEVE-L and BAND-P shared less similarity (9.3). Within-assemblage similarity was lowest for the WUPA-L and BAND-P ecosites (39.4 and 41.8, respectively) and ranged from 52.1 to 59.2 for the other ecosites (Table 5).

The Permanova test for overall difference in group centroids among the seven assemblages was significant (Table 6), as were subsequent pairwise tests for all ecosite pairings (p-values = 0.001). Plot, as a random variable nested in ecosite, was also significant. The overall test for homogeneity of multivariate dispersion (PERMDISP) was significant ($F = 20.6$, $df_1 = 6$, $df_2 = 204$, $P\text{-value} = 0.0001$). With both the Permanova and PERMDISP tests yielding significant outcomes, this result indicates differences in beta diversity among ecosites and probable centroid location effects as well. Beta diversity across ecosites is displayed in Figure 4. In comparison to the other ecosites, beta diversity was highest for the WUPA-L and BAND-P ecosites.

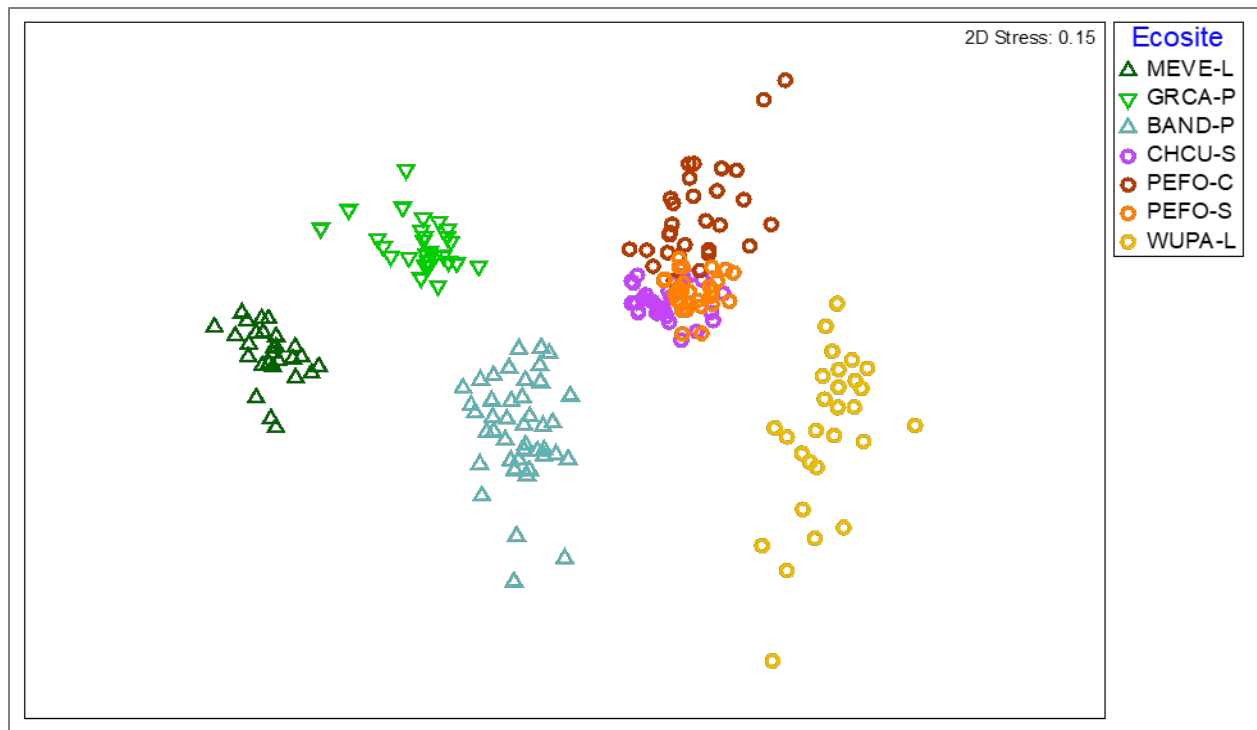


Figure 3. Non-metric multidimensional scaling (NMDS) graph depicting assemblage similarity across seven ecosites (211 plots), based on Bray-Curtis similarity of square-root transformed abundance data. Species accounting for > 0.1% relative abundance in their respective ecosites are included. The focus of a NMDS plots is on the ordering of data points relative to one another, thus axes labels are typically omitted. Woodland plots are indicated by triangle markers and grassland/shrubland plots by circles. NPS / LISA THOMAS

Table 6. Results table from the Permanova model to test for overall difference in group centroids among the seven assemblages. In the model, ecosite is treated as a fixed effect and plot nested in ecosite as a random effect.

Source	df	Sum of Squares	Mean Square	Pseudo-F	P-value	Unique Permutations
Ecosite	6	8.59E+05	1.43E+05	61.293	0.001	999
Plot (Ecosite)	204	4.76E+05	2335.6	7.5713	0.001	990
Residual	211	65088	308.48	—	—	—
Total	421	1.40E+06	—	—	—	—

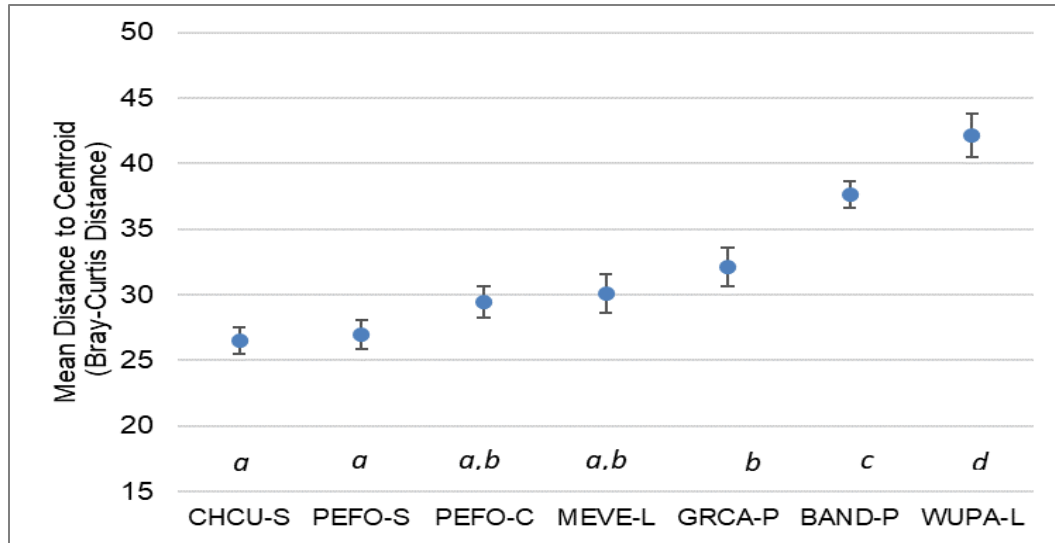


Figure 4. Beta diversity across the seven ecosites, as described by the PERMDISP test for homogeneity of multivariate dispersion. Letters indicate groups resulting from a posteriori pairwise tests ($p = 0.05$). Error bars represent ± 1 standard error. NPS / LISA THOMAS

Compositional Gradients Across Ecosites in Relation to Normal Climate Data

Results of the distance-based redundancy analysis (dbRDA) to model species assemblage patterns in relation to 30-year normal climate data (1981–2010) are shown in Figure 5 and Tables 7 and 8. The overall best solution included all six climate variables. The first three ordination axes account for 48.7% of total variation. Axis 1 of the dbRDA shows the separation of woodland ecosites from the grassland/shrubland ecosites and aligns with differences in annual precipitation. Axis 2 shows a compositional gradient within each of the woodland and grassland/shrubland groups, aligning most closely with precipitation seasonality (monsoon and winter precipitation percentage) (Figure 5a). Axis 3 separates BAND-P from the other two woodland ecosites, and WUPA-L from the other three grassland/shrubland ecosites; it is associated with differences in spring minimum temperature and summer $VPD_{\max}$ (Figure 5b).

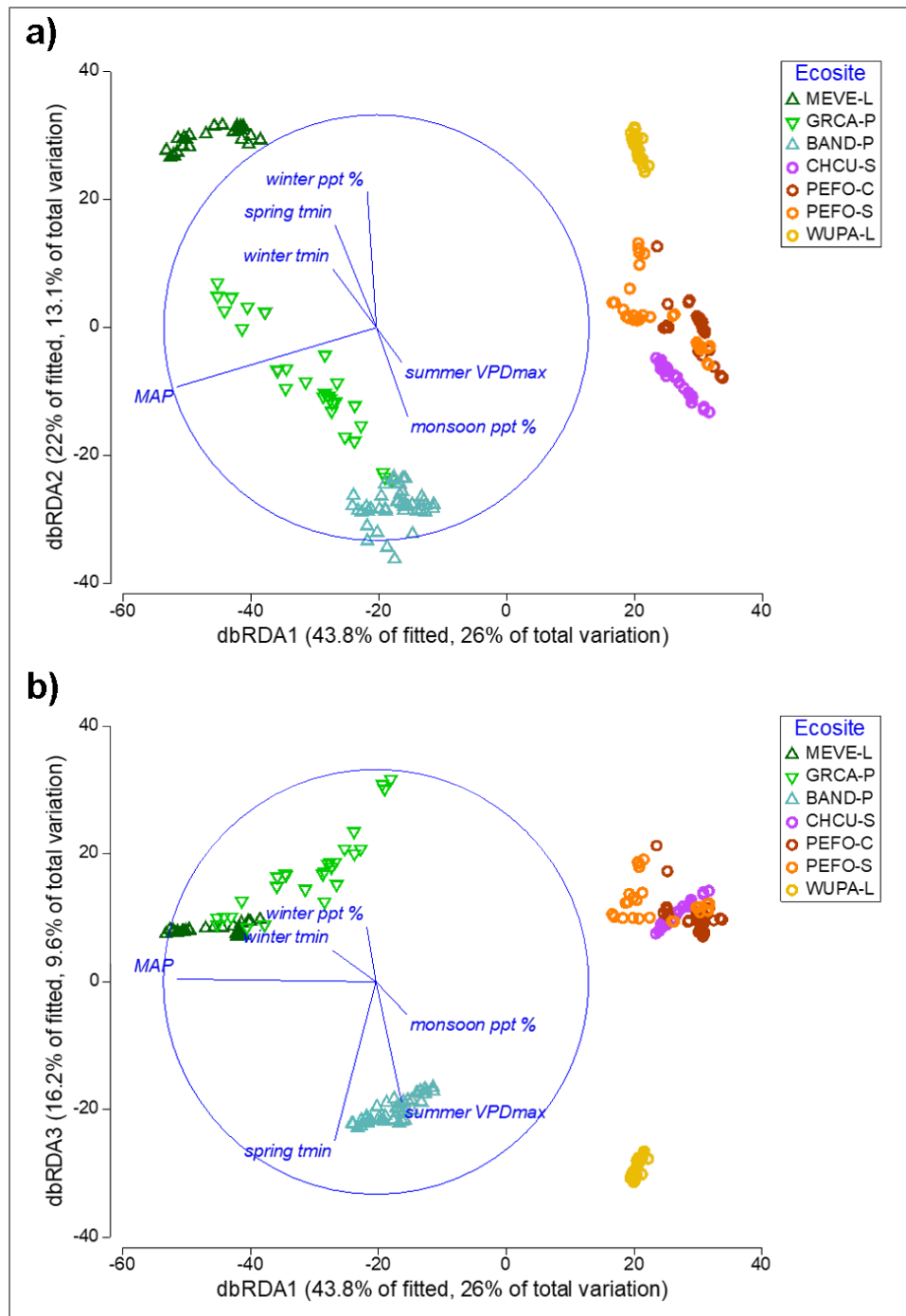


Figure 5. Results of distance-based redundancy analysis (dbRDA) to model relationship between the combined 7-ecosite species matrix (211 plots) and PRISM 30-year normal climate data (1981–2010). The analysis was based on Bray-Curtis dissimilarity of square-root transformed abundance data. Species accounting for 0.1% relative abundance or greater in their respective ecosites were included. Figure 5a shows ordination axes 1 and 2; Figure 5b shows ordination axes 1 and 3. The climate variables are mean annual precipitation (MAP), the percentage of annual precipitation falling during the monsoon season (monsoon ppt %), the precipitation percentage falling in the winter months (winter ppt%), winter temperature minima (winter tmin), spring temperature minima (spring tmin) and summer Vapor Pressure Deficit maxima (summer VPDmax). NPS / LISA THOMAS

Table 7. Marginal tests of the relationship of each climate variable to the combined 7-ecosite species matrix from dbRDA modeling. The climate variables were derived from PRISM 30-year normal climate data (1981–2010).

Variable	SS(trace)	Pseudo-F	P-value	Proportion
MAP	1.61E+05	66.59	0.0001	0.242
monsoon ppt %	1.23E+05	47.37	0.0001	0.185
summer VPD _{max}	1.07E+05	39.77	0.0001	0.160
winter ppt %	94241	34.35	0.0001	0.141
spring t _{min}	69908	24.44	0.0001	0.105
winter t _{min}	51816	17.58	0.0001	0.078

Table 8. Results table from dbRDA to model the relationship between the combined 7-ecosite species matrix and PRISM 30-year normal climate data (1981–2010). The percentage of variation explained by each of the first three dbRDA axes is shown.

dbRDA axis	% Explained Variation out of Fitted Model		% Explained Variation out of Total Variation	
	Individual	Cumulative	Individual	Cumulative
1	43.83	43.83	26.01	26.01
2	22.04	65.87	13.08	39.09
3	16.16	82.03	9.59	48.69

Part 2: Within-Ecosite Composition Gradients in Relation to Environmental Factors

Differences in Environmental Factors Across Ecosites

Figure 6 shows differences among ecosites and variability within ecosites for elevation, soil factors and the overstory. The study areas occur along an elevational gradient extending from 1,373 m at the lowest WUPA-L plot to 2,212 m at the highest MEVE-L plot. The BAND-P study area includes the widest range of elevations (227 m span from 1,864 to 2,091 m). Slope is also higher and more variable for BAND-P than for the other study areas. Soils are relatively shallow for GRCA-P and WUPA-L whereas the BAND-P soils exhibit a wide range of depths. Soils for BAND-P and WUPA-L contain the highest proportion of rock fragments (means of 37.4% and 35.8%, respectively), while those for GRCA-P are moderately rocky (20.6% mean).

There are also differences in soil texture across study areas (not shown), with fine-textured clay loams most common for the MEVE-L and GRCA-P ecosites and moderately fine to medium-textured loams more prevalent for PEFO-C and PEFO-S. CHCU-S includes a few plots with moderately fine soils, but most have moderately coarse sandy loam soils. BAND-P includes a broad range of soils from clay loams to loamy sands. The soils for WUPA-L are coarse, ranging from sandy loam to sand.

Overstory tree basal area is highest for MEVE-L, moderate for GRCA-P, and lowest for BAND-P (means of 33.0, 21.5 and 10.2 m²/ha, respectively; Figure 6). Canopy cover is similar for MEVE-L and GRCA-P (means of 35.6% and 38.6%, respectively), and lower for BAND-P (mean of 12.8%).

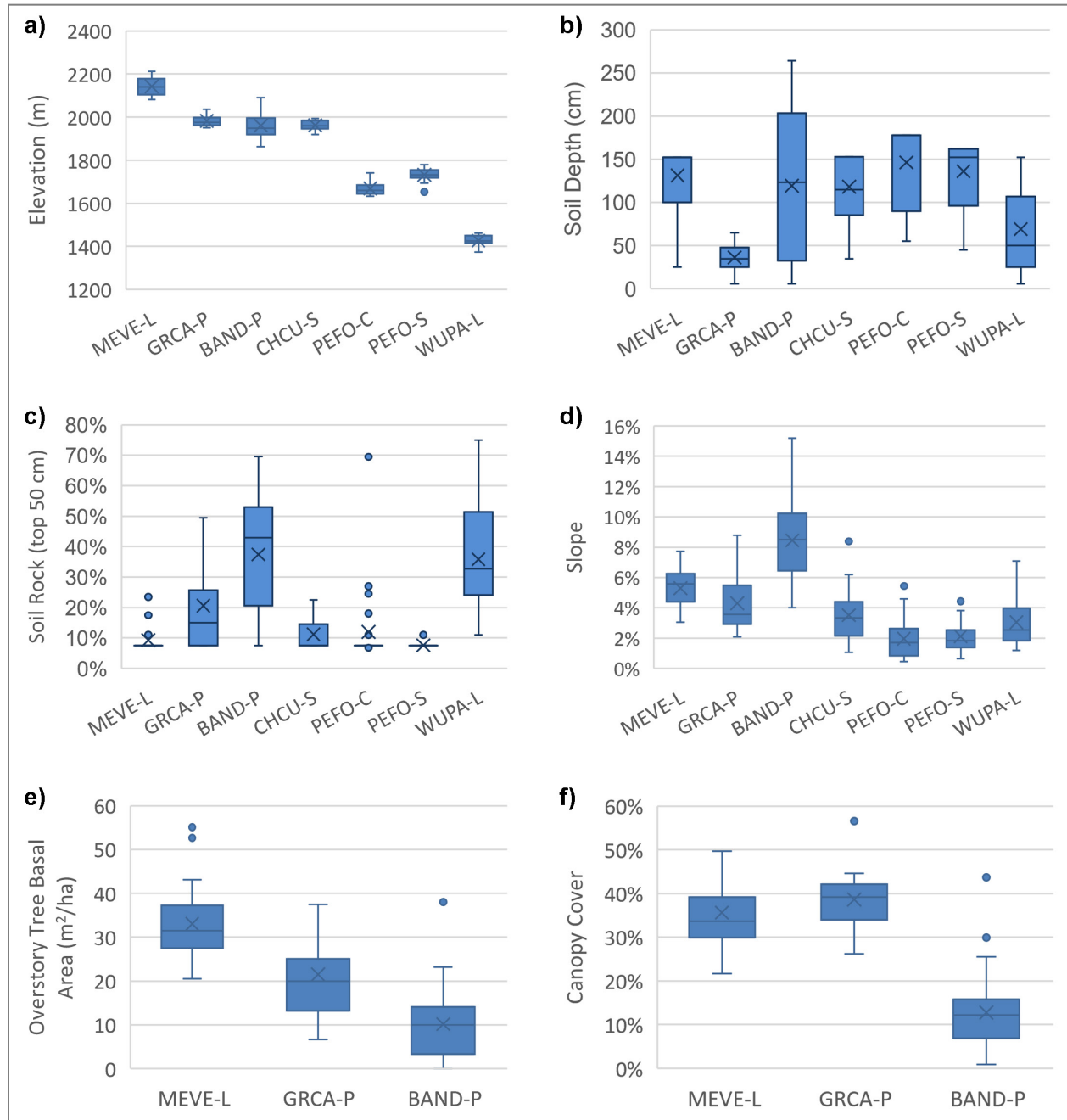


Figure 6. Box plots of topographic factors across all ecosites and overstory variables across woodland ecosites. Blue boxes are drawn from the first quartile to the third quartile with a horizontal line at the median. Values within 1.5 times the interquartile range are shown as whiskers, outliers as blue dots, and means as an X. NPS / LISA THOMAS

Within-Ecosite Compositional Gradients in Relation to Environmental Variables

The results of dbRDA to model the relationship between the species abundance matrix for each ecosite and its measured topographic and overstory variables are summarized in Table 9 and shown in Figures 28 and 29 in Appendix E. The dbRDA analysis identified significant relationships between within-ecosite compositional gradients and from one to five environmental variables per ecosite. Elevation was a significant model component for all study areas. Among grassland/shrubland ecosites, models based solely on elevation provided the best model fit for CHCU-S and PEFO-S, whereas a two-variable model adding soil texture was chosen for PEFO-C. A three-variable model adding soil depth and fine gravel cover was selected for WUPA-L. Among woodland ecosites, selected models included a two-variable model adding canopy cover for GRCA-P, and a three-variable model adding slope and surface cyanobacteria cover for MEVE-L. A five-variable model provided the best fit for BAND-P. The percentage of total variation explained by environmental factors ranged from lows of 9.9% and 12.7% for CHCU-S and GRCA-P respectively, to a high of 48.1% for MEVE-L.

Several patterns emerge from the dbRDA analysis. First, elevation had a significant association with compositional gradients within every ecosite, regardless of elevational range. Elevation was highly correlated with summer VPD_{max} across the seven study sites ($R^2 = 0.961$). Secondly, in two of the three woodland ecosites, canopy cover or tree basal area was aligned with understory composition gradients. Thirdly, soil depth was aligned with compositional gradients in the WUPA-L shrubland & grassland ecosite, and in the BAND-P woodland ecosite. Finally, adding ground surface cover variables significantly improved dbRDA models for WUPA-L, BAND-P and MEVE-L, with the largest improvements observed by adding fine gravel cover to the WUPA-L and BAND-P models.

Table 9. Distance-based redundancy analysis (dbRDA) results for each ecosite, modeling the relationship between composition gradients and local environmental factors. Sequential tests of environmental variables are shown, reporting how each added variable contributes to the explained variation. The Akaike information criterion (AIC) estimates the relative quality of the models.

Ecosite	Environmental Variable	AIC	R ²	Pseudo-F	P-value	Proportion Explained	Cumulative Proportion	Residual df
MEVE-L	Elevation	181.87	0.292	10.329	0.0001	0.292	0.292	25
	Slope	177.71	0.437	6.153	0.0001	0.144	0.437	24
	Surface Cyanobacteria	177.48	0.481	1.976	0.0214	0.045	0.481 ^A	23
GRCA-P	Canopy Cover	202.37	0.067	1.882	0.0315	0.067	0.067	26
	Elevation	202.54	0.127	1.695	0.0568	0.059	0.127 ^A	25
BAND-P	Elevation	307.78	0.111	4.969	0.0001	0.111	0.111	40
	Surface Fine Gravel	304.51	0.215	5.208	0.0001	0.105	0.215	39
	Tree Basal Area	303.68	0.266	2.650	0.0003	0.051	0.266	38
	Soil Depth	303.68	0.301	1.811	0.025	0.034	0.301	37
	Heat Load	303.7	0.333	1.731	0.0344	0.032	0.333 ^A	36
CHCU-S	Elevation	194.18	0.099	2.967	0.0021	0.099	0.099 ^A	27
PEFO-C	Elevation	201.64	0.125	3.859	0.0018	0.125	0.125	27
	Soil Texture	201.3	0.193	2.185	0.0327	0.068	0.193 ^A	26
PEFO-S	Elevation	188.67	0.161	4.992	0.0001	0.161	0.161 ^A	26
WUPA-L	Soil Depth	212.51	0.091	2.612	0.0237	0.091	0.091	26
	Elevation	212.23	0.162	2.123	0.0544	0.071	0.162	25
	Surface Fine Gravel	209.44	0.294	4.473	0.0009	0.132	0.294 ^A	24

^A Cumulative proportion of variation explained for each ecosite dbRDA model shown in **bold font**.

Clustering Results in Relation to NVC Associations and Environmental Variables

Hierarchical clustering combined with SIMPROF tests (5% significance level) indicate significant clustering in every assemblage except the GRCA-P ecosite. Detailed cluster dendrograms and shade plots resulting from cluster analysis, along with graphs of functional group cover, are shown in Figures 30 through 36 in Appendix E. Generally, hierarchical clustering results from this study were consistent with the vegetation associations described in each park's Vegetation Mapping Report. Consequently, I named clusters according to the matching NVC association. The full list of identified NVC associations and their U.S. distribution are provided in Table 14 in Appendix E.

Characterizing compositional gradients or clustering in relation to significant environmental factors provides local context for understanding how particular species and functional groups are responding to local environmental conditions. Non-metric MDS bubble plots provide an adequate representation of the relationship between compositional gradients and significant environmental factors for the ecosites with relatively simple compositional gradients, such as MEVE-L and three of the grassland/shrubland ecosites.

MEVE-L Pinyon–Juniper Woodland

Simple composition gradients are evident in the MEVE-L woodland assemblage (Figure 7) which also exhibited moderately low beta diversity. The dbRDA analysis found elevation, slope and cyanobacteria cover to be aligned with gradients in composition, with elevation accounting for most of the explained variation (29% out of 48% explained). *Poa fendleriana* and *Purshia tridentata* are co-dominants in mid and higher elevation plots (Figure 7; Figure 30 in Appendix E). *Yucca baccata* and *Opuntia* spp. dominate in lower elevation plots—with sparse shrub/herbaceous cover (5% or lower) and higher cyanobacteria cover of the ground surface. The plots in the latter group have relatively low slopes and are located on Chapin Mesa.

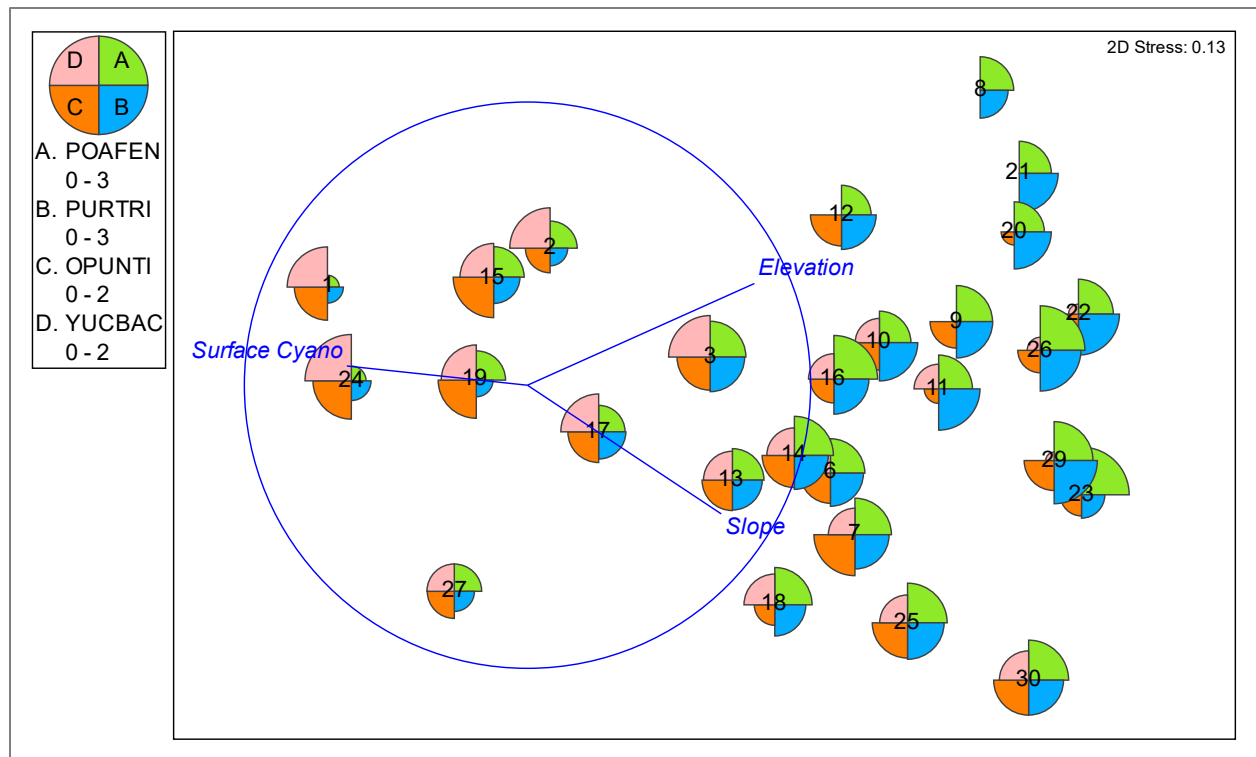


Figure 7. Non-metric multidimensional scaling (NMDS) bubble plot for the MEVE-L woodland assemblage, depicting the abundance of the dominant species: *Poa fendleriana* (POAFEN), *Purshia tridentata* (PURTRI), *Opuntia* spp. (OPUNTI) and *Yucca baccata* (YUCBAC). The focus of a NMDS plots is on the ordering of data points relative to one another, thus axis labels are typically omitted. Bubble size is scaled to square-root abundance for each species (see legend). Plot ID numbers are indicated. Blue lines show significant topoedaphic vectors from distance-based redundancy analysis (dbRDA). Surface cyanobacterial crust cover is abbreviated as Surface Cyano. NPS / LISA THOMAS

Three Grassland/Shrubland Ecosites

- CHCU-S. A gradient in grass dominance is observed with *Hilaria jamesii* dominance or *H. jamesii* - *Bouteloua gracilis* co-dominance in low elevation plots, and *B. gracilis* dominance at higher elevations (Figure 8a; Figure 33 in Appendix E).
- PEFO-C. Greater abundance of *B. gracilis* and *H. jamesii* is observed in higher elevation/medium soil-texture plots, with *Sporobolus* spp. as dominant at lower elevation/fine soil-texture plots. The halophytic shrub, *Atriplex obovata*, is more abundant in lower elevation/fine soil-texture plots, as are the annual grasses, *Bouteloua barbata* and *Sporobolus coromandelianus* (Figure 8b; Figure 34 in Appendix E).
- PEFO-S. There are no clear gradients in abundance for the three co-dominant grasses. Species turnover in sub-dominant shrub species is evident, with *Artemisia filifolia* more abundant at low elevations, *Krascheninnikovia lanata* and *Ephedra torreyana* more abundant at intermediate elevations, and *Chrysothamnus Greenei* more abundant at high elevations (Figures 8c and 8d; Figure 35 in Appendix E). Within the lowest elevation plots, the perennial grass, *Bouteloua eriopoda*, occurs as a subdominant.

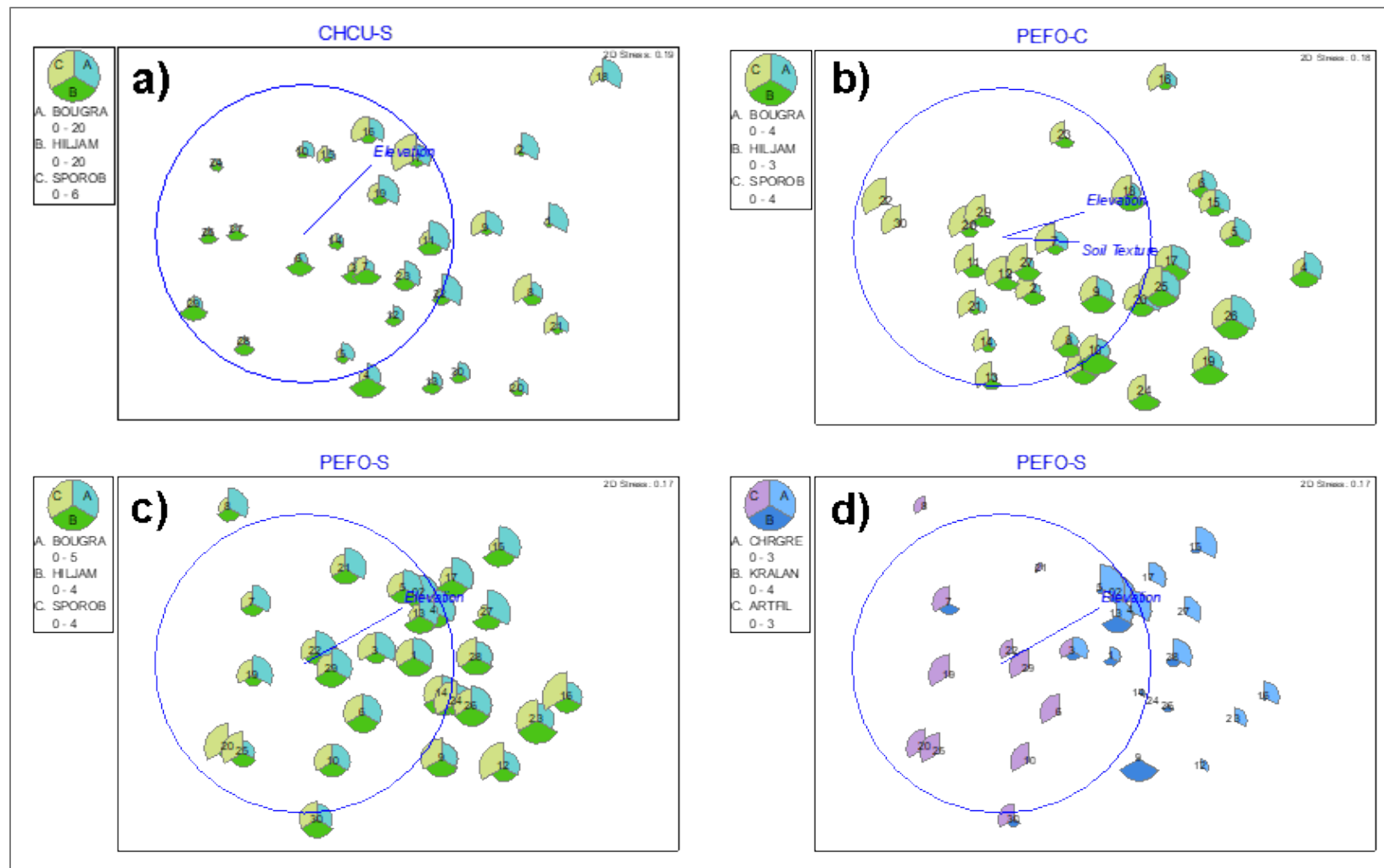


Figure 8. Non-metric multidimensional scaling (NMDS) bubble plots for CHCU-S, PEFO-C and PEFO-S study areas. The plots depict abundance of the dominant perennial grass species, *Bouteloua gracilis* (BOUGRA), *Hilaria jamesii* (HILJAM), and *Sporobolus* spp. (SPOROB) within three grassland/shrubland ecosites (plots a–c). Plot d shows abundance of several moderately abundant shrub species, *Chrysothamnus Greenei* (CHRGRE), *Krascheninnikovia lanata* (KRALAN), and *Artemisia filifolia* (ARTFIL), for PEFO-S. Ordinations are based on Bray-Curtis similarity of square-root transformed abundance data. Bubble size is scaled to square-root abundance for each species (see legend). Plot ID numbers are shown. Blue lines indicate significant topoedaphic vectors from distance-based redundancy analysis (dbRDA). NPS / LISA THOMAS

PEFO-C Study Area Note

Though similar in overall species composition, the PEFO-C (Clayey Fan) ecological site is distinct from the upland CHCU-S and PEFO-S ecosites. Occurring below exposures of the Chinle Formation, these clayey fans are formed through fluvio-alluvial processes, as fine-textured clays from the Chinle Formation are carried by water and deposited on soils derived from coarser parent materials (Bowker et al. 2013).

To summarize, beta diversity was relatively low for these three grassland/shrubland assemblages. Simple compositional gradients among dominant perennial grass species or subdominant shrub species were apparent. As reported above, dbRDA identified significant relationships between compositional gradients and elevation (CHCU-S, PEFO-S) or elevation and soil texture (PEFO-C). By contrast, beta diversity was significantly higher in the BAND-P and WUPA-L study areas. This greater compositional heterogeneity translates into more complex composition patterns. PCO plots are used to depict major plot clusters in these two study areas.

WUPA-L Shrubland/Grassland

Study Area Note

The Wupatki landscape experienced relatively recent volcanic activity, with the ca. 1085 CE eruption of the Sunset Crater Volcano which blanketed the area with a 5–10 cm layer of cinder or tephra (Baril et al. 2018). The dark, easily eroded cinder was then reworked into a patchy cover of variable thickness. The tephra layer acted as a mulch to increase crop yields for prehistoric Sinagua and Anasazi farmers and today the mulching effect improves soil water retention for native plant communities (Lightfoot 1996; Harrigan unpublished). Through time, the highly erodible tephra layer is being transported downwind and downslope towards the northeast (Baril et al. 2018). The Loamy Upland Ecological Site includes a mixed parent materials phase (igneous tephra rock, sandstone, and limestone) and a cinder dunes phase (USDA-NRCS and DOI-NPS 2015).

Hierarchical cluster analysis identified three major clusters for the WUPA-L plots (Figure 9). *Hilaria jamesii* was the dominant species across WUPA-L plots, with abundance gradients in sub-dominant species differentiating the three plot clusters (Figure 36 in Appendix E). Table 15 in Appendix E provides a summary of the three plot clusters, along with my interpretation of the closest NVC Association (Hansen et al. 2004) and the corresponding NRCS Ecological Sites and soils for each cluster (USDA-NRCS and USDOI-NPS 2015). Plot photos of the three associations are shown in Figure 10. As reported above, dbRDA for the WUPA-L ecosite found elevation, soil depth and surficial gravel cover to be aligned with compositional gradients.

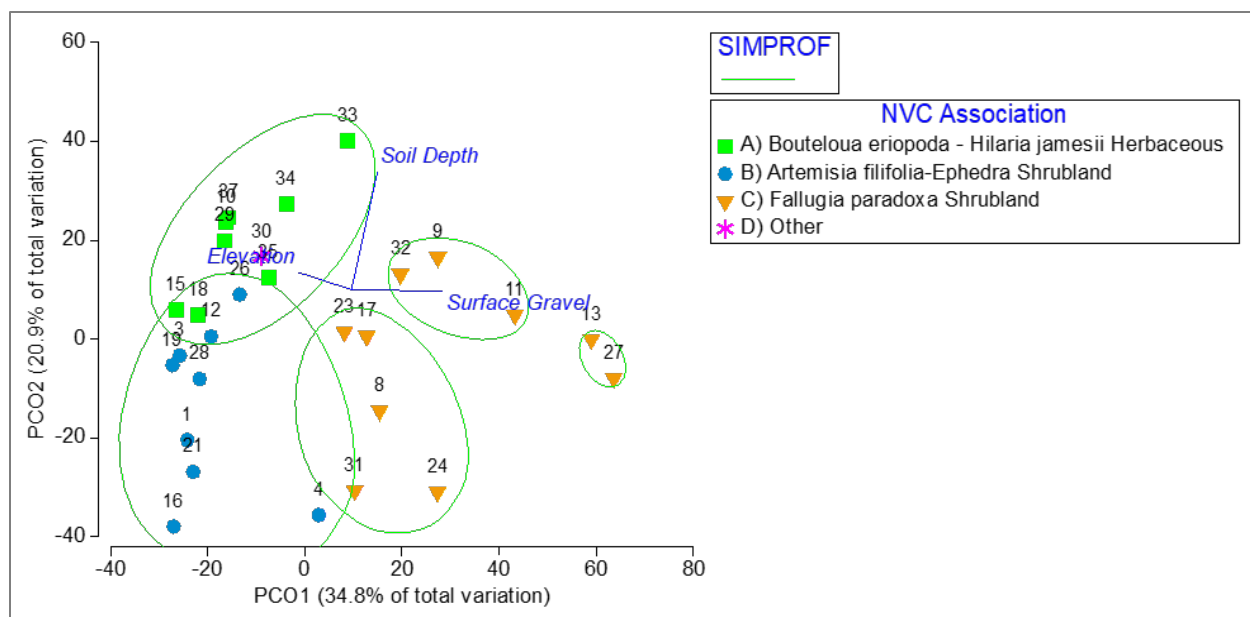


Figure 9. Principal coordinates analysis (PCO) plot for WUPA-L shrubland/grassland assemblage, based on Bray-Curtis similarity of square-root transformed abundance data. Light green ovals indicate significant plot clusters from SIMPROF test (5% significance level). Higher-order plot clusters (see legend) named according to closest National Vegetation Classification (NVC) association from vegetation mapping report (Hansen et al. 2004). Plot ID numbers are shown. Blue lines indicate significant environmental vectors from distance-based redundancy analysis (dbRDA). NPS / LISA THOMAS

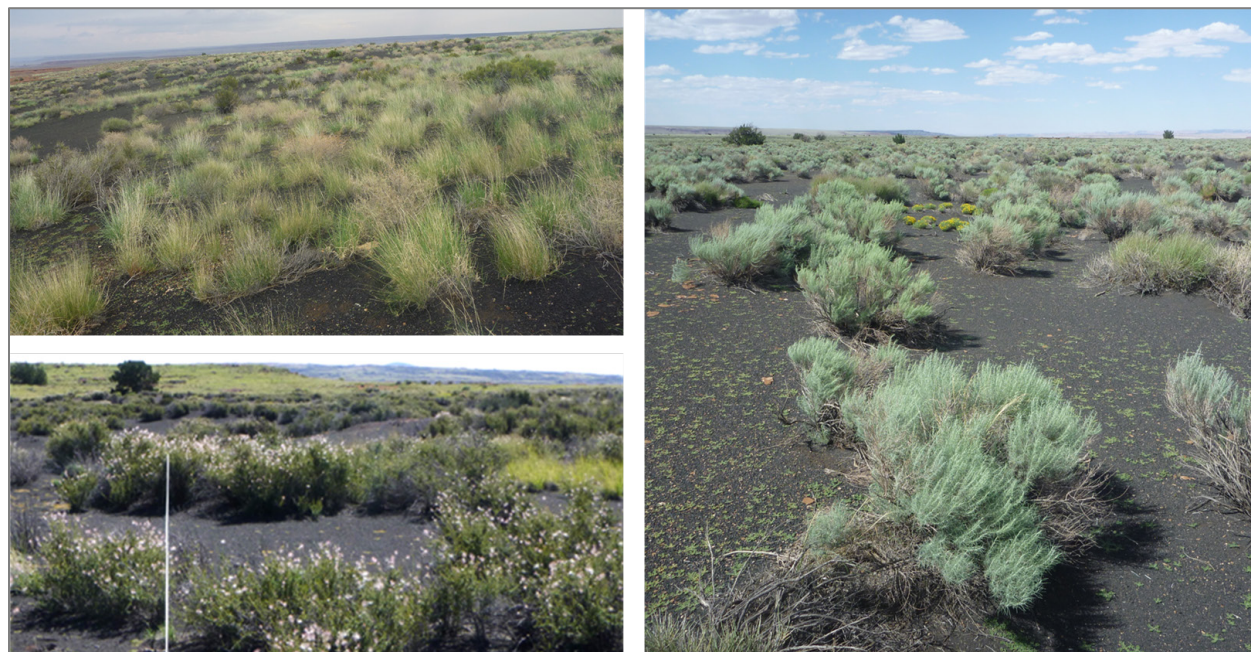


Figure 10. Plot photos of three associations observed in the WUPA-L study area. They include the *Bouteloua eriopoda* – *Hilaria jamesii* herbaceous (top left), *Artemisia filifolia* – *Ephedra* shrubland (right), and *Fallugia paradoxa* – (*Atriplex canescens* – *E. torreyana*) cinder shrubland (bottom left). NPS

Cluster A corresponds to the *Bouteloua eriopoda* – *Hilaria jamesii* herbaceous association (Figure 9). The plots in this cluster occur at higher elevations and generally on moderately deep to deep sandy loam soils. Hansen and colleagues (2004) note that the presence of *B. eriopoda* and *Muhlenbergia porteri* in the *B. eriopoda* – *H. jamesii* association suggests that this grassland is transitional to Chihuahuan Desert grasslands that begin 100 miles to the south. **Cluster B** aligns with the *Artemisia filifolia* – *Ephedra (torreyana, viridis)* shrubland association. These Cluster B plots also occur at higher elevations, but on shallow, loamy sand to sandy soils. **Cluster C** corresponds to the *Fallugia paradoxa* – (*Atriplex canescens* – *E. torreyana*) cinder shrubland. These plots are mostly located at lower elevations with greater fine gravel cover. The plots in Cluster C include several soil types with soil depths ranging from shallow to moderately deep, and textures from sandy loams to sand. Hansen and colleagues (2004) describe the *F. paradoxa* – (*A. canescens* – *E. torreyana*) cinder shrubland as occurring in areas with deep cinder deposits.

To summarize, the WUPA-L assemblage exhibits the highest beta diversity observed in this study. Both dominant and moderately abundant species occur at high abundance in distinct subsets of plots, and are absent or occur at low abundance in other plots (Figure 36 in Appendix E). Soil depth, elevation, and surficial fine gravel cover account for a moderate portion (29.4%) of compositional variation. From a functional group perspective, perennial grasses dominate in plots occurring on moderately deep soils at higher elevations. One set of shrub species dominate on shallow soils at higher elevation soils and another set dominate in low elevation plots with variable soil depth and high cinder cover.

BAND-P Juniper Woodland

Study Area Notes

1. Bandelier NM lies at the intersection of the Jemez lineament and the Rio Grande rift, the site of a series of volcanic events which began 13 million years ago and ended in two massive explosions (Muldavine et al. 2011). The Toledo and Valles eruptions (1.61 and 1.23 million years ago) cumulatively deposited 300 m of rock and ash on the Bandelier landscape. Through time the Bandelier Tuff deposits were eroded and reworked, leaving pumice patches predominately on east-facing slopes and deep alluvial deposits on lower slopes (Goff et al. 1995).
2. As described above, we purposefully included a diverse group of six soil map units for the Bandelier woodland study area. They include moderately developed soils (haplustalfs) of plateau tops (Canuela, Hackroy, and Nyjack series), weakly developed shoulder and backslope soils (ustorthents and ustipsaments), and rock outcrops (Hibner 2009; Muldavine 2011). By contrast, this group also includes Armenta and Adornado soils derived from rhyolitic El Cajete pumice, which overlays the Bandelier Tuff. The Armenta and Adornado soils are deeper (haplustolls), and have better developed, but coarser surface horizons (sandy and gravelly loams) (Hibner 2009; Muldavine 2011).
3. Two events affected the BAND-P study area just prior to and during the initial monitoring period. A multi-year drought (2000–2003) and associated bark beetle outbreak resulted in

greater than 90% mortality of mature overstory pinyon trees (Jacobs et al. 2015). A juniper-thinning restoration treatment (2007–2010), designed to improve the eco-hydrologic condition of degraded transitional woodlands, affected approximately two-thirds of the BAND-P monitoring plots (Jacobs 2015; Jacobs et al. 2015). The majority of plots in Clusters B, C, and D were thinned during the 2007–2010 restoration treatments.

Hierarchical Cluster Analysis identified four major clusters of plots within the BAND-P ecosite (Figure 11; Figure 32 in Appendix E). The composition of three of the four clusters is comparable to NVC Woodland Associations described in the Bandelier NM Vegetation Mapping Report. The last cluster represents a degraded state of one these associations. Table 16 in Appendix E provides a summary of the four plot clusters, along with my interpretation of their closest NVC Association (Muldavin 2011) and the corresponding Soil Map Units for each cluster (Hibner 2009). Plot photos of the four associations are shown in Figure 12.

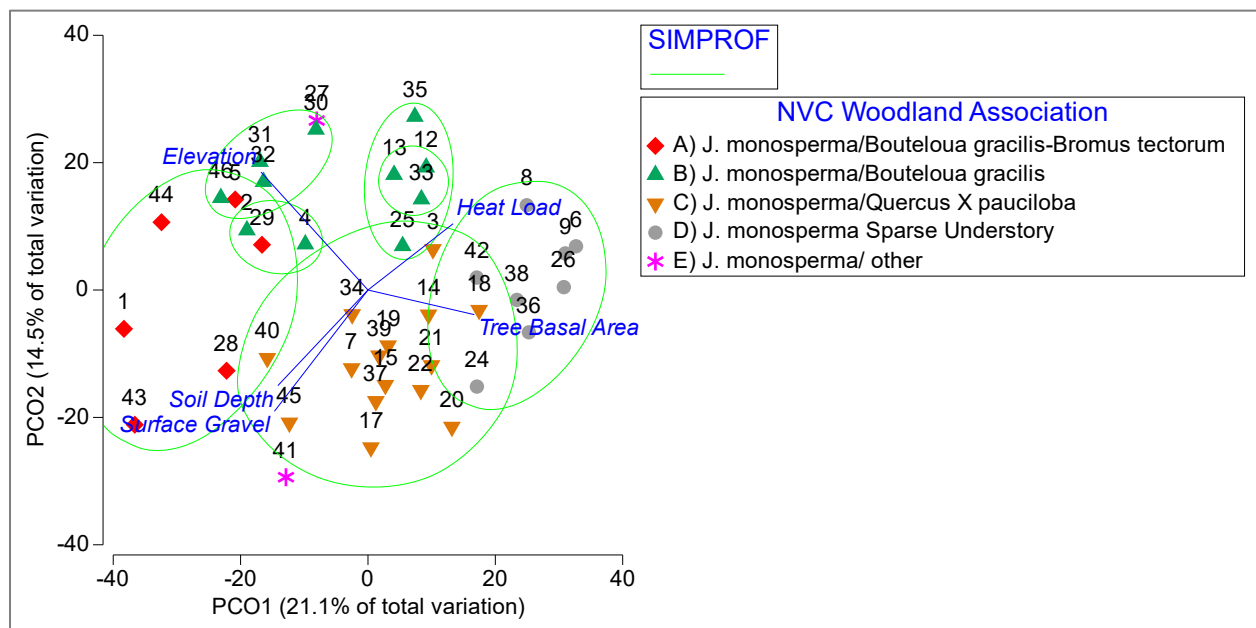


Figure 11. Principal coordinates analysis (PCO) plot for BAND-P *Juniperus monosperma* woodland assemblage, based on Bray-Curtis similarity of square-root transformed abundance data. Light green ovals indicate significant plot clusters from SIMPROF test (5% significance level). Higher-order plot clusters (see legend) are named according to closest National Vegetation Classification (NVC) association from vegetation mapping report (Muldavin et al. 2011). The association name for Cluster A was modified to indicate *Bromus tectorum* invasion. Plot ID numbers are shown. Blue lines indicate significant environmental vectors from distance-based redundancy analysis (dbRDA). NPS / LISA THOMAS



Figure 12. Plot photos of the four associations observed in the BAND-P study area. They include the *Juniperus monosperma/Bouteloua gracilis* woodland – *Bromus tectorum* invaded (upper left), *J. monosperma/B. gracilis* woodland (upper right), *J. monosperma* sparse understory woodland (lower right), and *J. monosperma/Quercus x pauciloba* woodland (lower left). NPS

Cluster B (*Juniperus monosperma/Bouteloua gracilis* woodland association) and **Cluster C** (*J. monosperma/Quercus x pauciloba* woodland association) represent high and low elevation versions of a similar mosaic of soils (Figure 11; Table 16 in Appendix E). In terms of composition, Cluster B plots display greater relative abundance of perennial grass species, while the lower elevation Cluster C plots exhibit greater relative abundance of shrubs (*Quercus*, *Rhus*, *Cercocarpus*, and *Fallugia*). **Cluster A** represents a degraded state of the *J. monosperma/B. gracilis* woodland association, with the non-native winter annual grass, *Bromus tectorum* achieving co-dominance with *B. gracilis*. The plots in this cluster generally occur at high elevations on deep, sandy loam soils (Adornado, Armenta) with high fine gravel cover of the soil surface. Tree basal area and heat load were somewhat lower in Cluster A plots compared to the other clusters. See Text Note E1 at the end of Appendix E for additional comments about *B. tectorum* invasion. **Cluster D** plots are comparable to the *J. monosperma* sparse understory woodland association, occurring at lower elevations on very shallow to shallow sandy loam soils (Palatka-Canuela-Rock Outcrop complex). Shrub/herbaceous cover is sparse (mean of 11.2%).

The dominant understory species, *B. gracilis* and *Gutierrezia sarothrae*, showed moderate to high abundance across most plots (Figure 32 in Appendix E). Otherwise, the BAND-P understory assemblage displays compositional variation in several ways. Total shrub/herbaceous cover varies both within and between the four major plot clusters, suggesting differences in productivity (Figure

32 in Appendix E). High turnover in subdominant species and shifts in functional group dominance were also observed. Compared to the other ecosites, more forb species were moderately abundant in this study area.

To summarize, the BAND-P assemblage exhibits the second highest beta diversity observed in this study. Elevation, fine gravel cover, tree basal area, soil depth and heat load account for a moderate portion (33%) of the strong compositional variation observed within the BAND-P study area. The plots with an understory dominated by perennial grass species generally occur at higher elevations (Cluster B), while those with shrub dominance occur at lower elevations (Cluster C).

Part 3: Community Metrics and Species Identities

Total Shrub and Herbaceous Cover

Mean foliar cover for shrub and herbaceous species ranged from 7.8% to 20.8% across the seven ecosites (Figure 13). Foliar cover was lowest for the GRCA-P and MEVE-L woodland understories and highest for the PEFO-S grassland/shrubland.

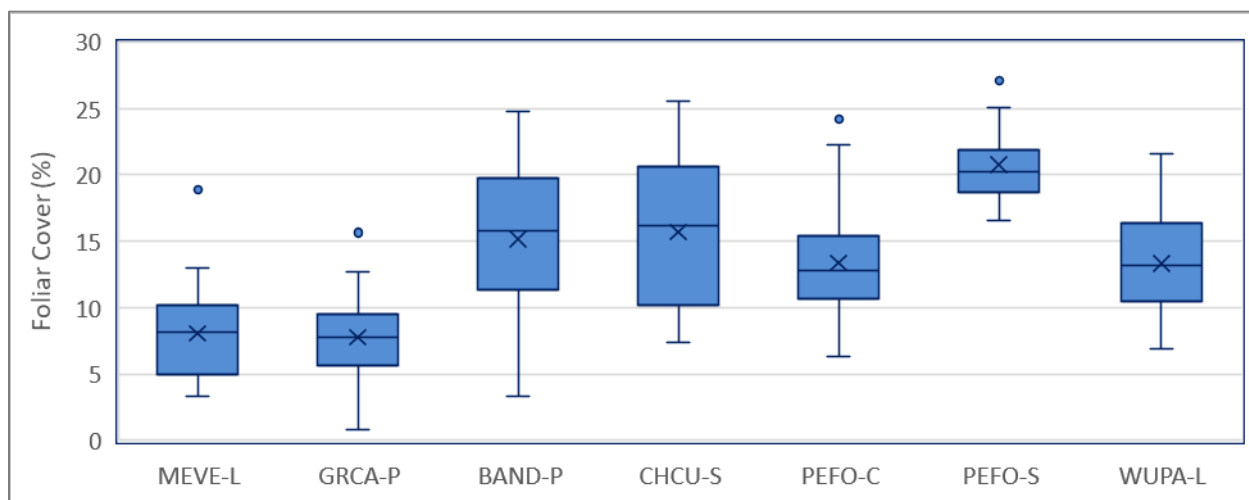


Figure 13. Box plots of shrub/herbaceous foliar cover across the seven ecosites. Blue boxes are drawn from the first quartile to the third quartile with a horizontal line at the median. Values within 1.5 times the interquartile range are shown as whiskers, outliers as blue dots, and means as an X. NPS / LISA THOMAS

Dominance and Diversity Patterns

Simpson Concentration (or dominance) and Shannon Diversity, two distinct but related metrics, are used to summarize diversity across the seven ecosites (Figure 14). They are provided, along with their associated Hill Numbers, in Table 10. Dominance is relatively high for the PEFO-C and MEVE-L ecosites, moderate for CHCU-S, GRCA-P, PEFO-S and WUPA-L, and lowest for BAND-P. Shannon diversity is relatively low for the PEFO-C and MEVE-L ecosites, moderate for CHCU-S, GRCA-P, PEFO-S and WUPA-L, and highest for BAND-P. The effective number of common (N1) and dominant (N2) species is highest for BAND-P.

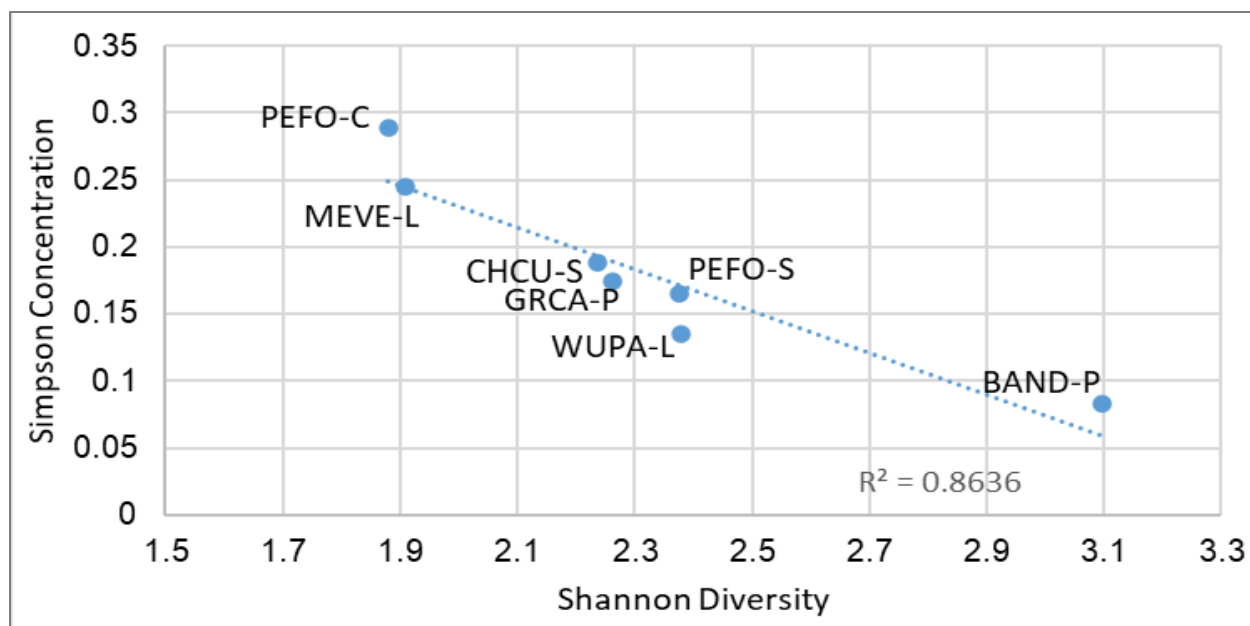


Figure 14. Simpson Concentration (or dominance) and Shannon Diversity across the seven ecosystems.
NPS / LISA THOMAS

Table 10. Shannon Diversity, Simpson Concentration, and respective Hill Numbers for the seven ecosystems.

Ecosite	Shannon Diversity (H')	Hill Number N1 = exp(H') ^A	Simpson Concentration (D)	Hill Number N2 = (1/D) ^B
MEVE-L	1.91	6.74	0.245	4.08
GRCA-P	2.26	9.60	0.175	5.72
BAND-P	3.10	22.12	0.083	12.03
CHCU-S	2.24	9.36	0.188	5.32
PEFO-C	1.88	6.56	0.289	3.46
PEFO-S	2.37	10.75	0.165	6.06
WUPA-L	2.38	10.78	0.135	7.40

^A Effective number of species with an emphasis on common species.

^B Effective number of species with an emphasis on dominant species.

Rank Abundance Curves

Partial dominance curves (Figures 15 and 16) add graphical detail to the Simpson and Shannon index values reported above. The strongest dominance patterns were observed for the PEFO-C and MEVE-L ecosystems. *Sporobolus* spp. accounted for 49% of relative abundance for PEFO-C. In the MEVE-L ecosystem, *Poa fendleriana* dominated (40% relative abundance) with *Purshia tridentata* as sub-dominant (26% relative abundance). Four ecosystems displayed moderate dominance patterns. *Bouteloua gracilis* dominated the CHCU-S and PEFO-S ecosystems (33% relative abundance in each) with *Hilaria jamesii* and *Sporobolus* spp. as sub-dominants. For the GRCA-P ecosystem the shrub,

Purshia stansburiana, and two perennial grass species, *B. gracilis* and *P. fendleriana*, were co-dominant (24%, 23% and 22% relative abundance, respectively). In the WUPA-L ecosite *H. jamesii* was dominant (24% relative abundance) with three shrub and one forb species as sub-dominant (each representing from 10% to 14% relative abundance). The BAND-P ecosite displayed the weakest dominance structure (Figure 15). *B. gracilis* and the shrub *Gutierrezia sarothrae* co-dominated (18% and 17% relative abundance, respectively) with sixteen species (including shrubs, grasses and forbs) occurring at moderate abundance (ranging from 1% to 8% relative abundance). BAND-P was the only ecosite to include an invasive non-native species, *Bromus tectorum*, among the dominant species observed in some plots.

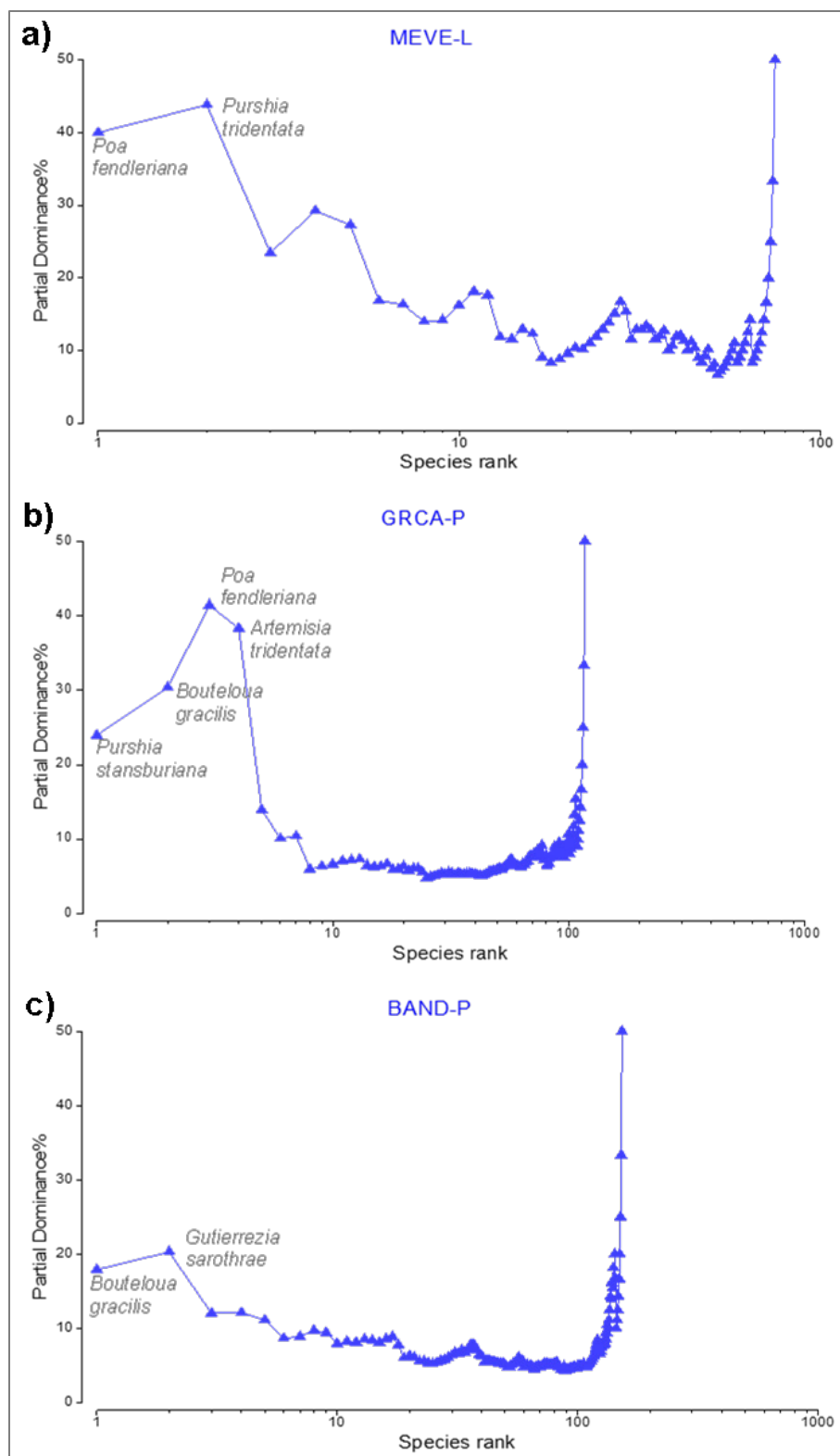


Figure 15. Partial dominance curves for MEVE-L, GRCA-P and BAND-P ecosystems. Partial dominance curves plot the abundance of each species relative to the total of its own abundance plus that of all other less-abundant species against species rank (log-scale). Dominant species in each ecosystem are labeled.

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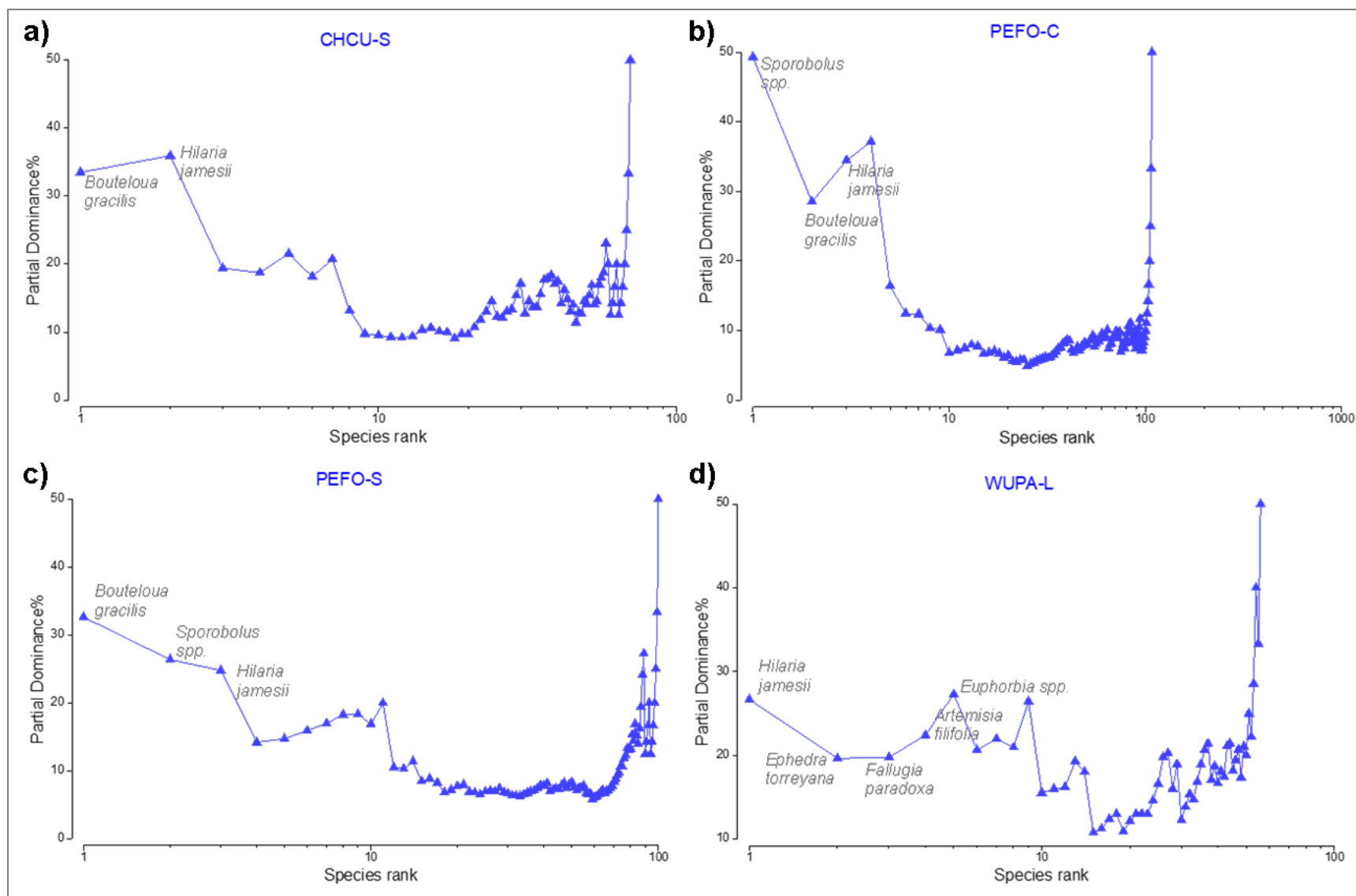


Figure 16. Partial dominance curves for the CHCU-S, PEFO-C, PEFO-S and WUPA-L ecosites. Partial dominance curves plot the abundance of each species relative to the total of its own abundance plus that of all other less-abundant species against species rank (log-scale). Dominant species in each ecosite are labeled. NPS / LISA THOMAS

Species Identities of Dominant and Moderately Abundant Species

Figures 17 and 18 give species identities to the dominance patterns and compositional similarities described above. Taken together, these figures underscore the relatedness of the seven ecosite assemblages. Most of the dominant species in a particular ecosite are also present at lower relative abundance in other ecosites.

Functional Group	Species	MEVE-L	GRCA-P	BAND-P	CHCU-S	PEFO-C	PEFO-S	WUPA-L
Perennial Grasses	<i>Poa fendleriana</i> (C ₃)							
	<i>Bouteloua gracilis</i>							
	<i>Hilaria jamesii</i>							
	<i>Sporobolus</i> spp.							
Shrubs	<i>Artemisia filifolia</i>							
	<i>Artemisia tridentata</i>							
	<i>Ephedra torreyana</i>							
	<i>Fallugia paradoxa</i>							
	<i>Gutierrezia sarothrae</i>							
	<i>Purshia stansburiana</i>							
	<i>Purshia tridentata</i>							
Forbs	<i>Euphorbia</i> spp.							

Dominant		>35 to 50%
		>25 to 35%
		>15 to 25%
		>10 to 15%
Moderate Abundance		>1 to 10%
Low Abundance		>0.1 to 1%

Figure 17. Dominant species across the seven ecosites. Species with relative abundance > 10% in one or more ecosites are included, with green shading showing abundance level. Species with lower relative abundance in other ecosites indicated by gray shading. C₃ grass species are indicated. [Tabular data shown in this figure are presented in Appendix F, Table 17.](#) NPS / LISA THOMAS

Functional Group	Species	MEVE-L	GRCA-P	BAND-P	CHCU-S	PEFO-C	PEFO-S	WUPA-L
Perennial Grasses	<i>Achnatherum hymenoides</i> (C ₃)							
	<i>Bouteloua eriopoda</i>							
	<i>Elymus elymoides</i> (C ₃)							
	<i>Hesperostipa comata</i> (C ₃)							
	<i>Muhlenbergia porteri</i>							
	<i>Poa fendleriana</i> (C ₃)							
	<i>Sporobolus</i> spp.							
Shrubs	<i>Amelanchier utahensis</i>							
	<i>Artemisia filifolia</i>							
	<i>Atriplex canescens</i>							
	<i>Atriplex obovata</i>							
	<i>Cercocarpus montanus</i>							
	<i>Chrysothamnus Greenei</i>							
	<i>Ephedra torreyana</i>							
	<i>Ephedra viridis</i>							
	<i>Ericameria nauseosa</i>							
	<i>Fallugia paradoxa</i>							
	<i>Gutierrezia microcephala</i>							
	<i>Gutierrezia sarothrae</i>							
	<i>Krascheninnikovia lanata</i>							
	<i>Quercus</i> spp.							
	<i>Rhus aromatica</i>							
Cacti and Succulents	<i>Opuntia</i> spp.							
	<i>Yucca baccata</i>							
Forbs	<i>Amauriopsis dissecta</i>							
	<i>Artemisia campestris</i>							
	<i>Artemisia carruthii</i>							
	<i>Artemisia dracunculoides</i>							
	<i>Astragalus</i> spp.							
	<i>Chenopodium</i> spp.							
	<i>Croton texensis</i>							
	<i>Mentzelia</i> spp.							
	<i>Penstemon linarioides</i>							
	<i>Petrorhiza pumila</i>							
	<i>Phlox hoodii</i>							
	<i>Sphaeralcea</i> spp.							
	<i>Verbascum thapsus</i> ^e							
Annual Grasses	<i>Bromus tectorum</i> ^e							
	<i>Sporobolus coromandelianus</i>							

Dominant
Moderate Abundance
Low Abundance

>10%

>5 to 10%

>2 to 5%

>1 to 2%

>0.1 to 1%

Figure 18. Moderately abundant species across the seven ecosites. Species with relative abundance >1% and ≤ 10% in one or more ecosite are included, with orange shading showing abundance level. Higher or lower relative abundance for those species in other ecosites indicated by gray shading. C₃ grass species are indicated. Non-native species are indicated by a superscript e. [Tabular data shown in this figure are presented in Appendix F, Table 18.](#) NPS / LISA THOMAS

Understory dominance is shared between perennial grass and shrub species for the woodland ecosites and WUPA-L (Figure 17). By contrast, in the CHCU-S, PEFO-C and PEFO-S ecosites no shrub species appear as dominants, but several shrub species are moderately abundant (Figure 18). Dominance patterns also vary by the species composing each functional group (Figures 17 and 18). Four perennial grass species occur as dominants, with the warm-season (C₄) species, *Bouteloua gracilis* and *Hilaria jamesii*, dominating across five and four ecosites, respectively. The cool-season (C₃) grass species, *Poa fendleriana*, occurs as a dominant species in the MEVE-L and GRCA-P ecosites. It and several other C₃ grass species are moderately abundant in four of the other five ecosites, with lower C₃ grass abundance observed for WUPA-L. Seven shrub species occur as dominants, with each species dominating in a single ecosite. However, among the 13 moderately abundant shrub species, about one third are moderately abundant in two or more ecosites, with *Atriplex canescens* occurring at intermediate abundance in four ecosites. Cacti and succulents (specifically *Opuntia* spp. and *Yucca baccata*) occur at moderate abundance in the woodland ecosites. MEVE-L and BAND-P also include more forb species among the moderately abundant species.

Discussion

In this study I have described the similarity of seven Colorado Plateau assemblages within a regional climate context, modeled the relationship between individual assemblages and local environmental factors, and explored difference in diversity and dominance. Below I consider the results for each study area, along with previous Soil Water Potential (SWP) modeling of their exposure to climate change, in order to pose hypotheses and comparisons for future analysis.

But first, from a regional perspective, it is important to reiterate that these NPS study areas represent high quality examples of their respective ecosystem types. These landscapes share a long history of human use but have experienced low levels of anthropogenic impact over recent decades. Most notably these NPS units are currently protected from livestock grazing, which is pervasive over much of the Colorado Plateau (Copeland et al. 2017). Only one study area shows evidence of serious non-native species invasion. Park managers involved in planning SCPN monitoring emphasized the importance of these lands as reference sites for more degraded Colorado Plateau ecosystems.

Climate Context, Ecosite Similarity and Beta Diversity

The results of across-ecosite analysis of compositional gradients in relation to climate variables are consistent with the conclusion by others that seasonal moisture availability on the Colorado Plateau is driven by the strength of winter versus summer precipitation patterns and by evaporative demand (Comstock and Ehleringer 1992; Gremer et al. 2015; Hoover et al. 2021). The first dbDRA axis, aligning with a gradient in annual precipitation, separates woodland plots from grassland/shrubland plots, in keeping with Merriam's (1890) "life-zone" concept for shifts in dominant life-form with elevation. The second axis aligns with precipitation seasonality, reflecting greater perennial C₄ grass dominance in plots with a stronger North American Monsoon System (NAMS) signal. The third axis differentiates ecosites within the woodland and grassland/shrubland groups based on seasonal temperature and Vapor Pressure Deficit (VPD) extremes, separating out the warmest study area within each group.

In comparing the seven shrub/herbaceous assemblages, Permanova results suggest that each assemblage has a unique composition, with a range in Bray-Curtis similarity observed between ecosite pairs (Tables 5 and 6). These results confirm several expectations but also provide new insight regarding the relatedness of the seven shrub/herbaceous assemblages. As expected, the two assemblages at elevational endpoints (MEVE-L and WUPA-L) share the least similarity with the other assemblages, three of the four grassland/shrubland assemblages are similar to each other, and the similarity between the MEVE-L and GRCA-P understory is comparable to that between GRCA-P and BAND-P. However, I did not anticipate that the similarity of the understory assemblages for BAND-P and GRCA-P would be the same as that between BAND-P and CHCU-S (Bray-Curtis similarity of 19.3 for both), or close to that between BAND-P and PEFO-S (18.2). Nor did I expect to see such low similarity between the BAND-P and MEVE-L understories (9.3). This highlights the current savanna character of the BAND-P woodland and the compositional similarity of its understory to Colorado Plateau grassland/shrubland.

Beta diversity values were relatively low for five study areas, reflecting the homogenous species abundance patterns we expected (Figure 4). Yet even in these relatively homogenous assemblages, subtle abundance gradients are evident among dominant or subdominant species. In contrast, the BAND-P and WUPA-L assemblages display significantly higher beta diversity. For the BAND-P study area, given the relatively wide elevational range and broad definition (i.e., inclusion of six soil map units), we anticipated a more heterogenous assemblage. In contrast, for the WUPA-L study area with two soil map units included, we did not expect the high beta diversity that was observed. Potential explanations relating to topoedaphic factors are discussed below.

Local Compositional Gradients in Relation to Topoedaphic and Overstory Factors

Moving down in scale to individual study areas, dbRDA analysis showed significant relationships between within-ecosite compositional gradients and from one to five environmental variables per study area (Table 9). The prevalence of elevation as a significant model component suggests the influence of summer VPD_{max} and other temperature-related microclimatic conditions on species abundance patterns at the local spatial scale. Summer VPD_{max} was highly correlated with elevation across ecosites ($R^2 = 0.96$).

With a focus on dominant shrub/herbaceous species and functional groups, this study demonstrates several compositional patterns that are consistent with sorting along elevation gradients including:

- Perennial C₄ grasses dominate at higher elevations and shrub species dominate at lower elevations (BAND-P, WUPA-L).
- Species turnover among dominant C₄ grasses with *Bouteloua gracilis* more abundant at higher elevation (CHCU-S, PEFO-C).
- Species turnover among moderately abundant shrub species with elevation (PEFO-S).
- Cactus/succulents more abundant in low-elevation, sparsely vegetated woodland plots (BAND-P, MEVE-L).

However, while elevation is the sole factor with a significant relationship to compositional gradients for CHCU-S and PEFO-S, other topoedaphic factors are significant dbRDA model components in four study areas. Soil depth is aligned with compositional gradients for BAND-P and WUPA-L, consistent with similar results from other Colorado Plateau studies (Duniway et al. 2022). Slope is a significant model component for MEVE-L. Heat load is a significant model component for BAND-P, the study area with greater and more variable slope conditions. Soil texture is a significant model component for the PEFO-C ecosite. Compositional gradients are strongly aligned with surficial gravel cover in the BAND-P and WUPA-L ecosites. For WUPA-L, with relatively recent volcanic activity, surface gravel cover is likely serving as a proxy for cinder depth. This is supported by Hansen and colleagues' (2004) description of the *F. paradoxa* – (*A. canescens* – *E. torreyana*) cinder shrubland as occurring in areas with deep cinder deposits, and the inclusion of a cinder dunes phase in the ecological site description (USDA-NRCS and DOI-NPS 2015). In contrast, for the BAND-P study area with over a million years of weathering and erosion since the last eruptions, surficial

gravel cover varies by soil type with the deep, well-developed haplustolls (Adornado, Armenta) characterized by high pumiceous gravel cover (Hibner 2009).

Variation in topoeidaphic conditions, as seen in these study areas, may influence compositional patterns directly, as well as indirectly through their mediation of soil moisture availability (Comstock and Ehleringer 1992; Miller 2005; Duniway et al. 2022). In ecosystems characterized by high spatial heterogeneity in topoeidaphic conditions, the task of quantifying future ecological drought is more complex than in ecosystems with more homogenous conditions (Bradford et al. 2020).

Tree overstory factors are aligned with compositional gradients in two of the three woodland ecosites. Canopy cover is a significant dbRDA model component for GRCA-P and tree basal area is a significant model component for BAND-P. See below for further discussion.

In three grassland/shrubland assemblages (CHCU-S, PEFO-C and PEFO-S) and for GRCA-P, topoeidaphic variables are significantly aligned with compositional gradients but accounted for less than 20% of compositional variation. Future dbRDA modeling may be improved by considering additional factors. For the SCPN vegetation monitoring project, field collection of environmental data has been limited, partly due to logistic and access constraints, but also because most SCPN study areas are also important cultural/archeological landscapes, where any proposed disturbance of the ground surface must go through a clearance process. Variables describing depositional environment and geomorphic setting (e.g., topographic wetness index) have been linked to plant composition patterns on the Colorado Plateau (Duniway et al. 2022) and may be useful, depending upon observed variability at the spatial scale of a study area. Soil chemistry analysis may also improve model fit for some ecosites. Specific suggestions include: 1) for PEFO-C, as part of a state-and-transition modeling effort for Colorado Plateau parks, Bowker and colleagues (2013) identified salinity and distance from a wash, as two abiotic factors that may influence compositional patterns in the clay fan ecological site, 2) for GRCA-P, the canyon's depth and related topography influence thermal stratification and wind patterns (Whiteman et al. 1999), so perhaps proximity to the canyon rim is a relevant variable, and 3) for the WUPA-L ecosite, measuring cinder depth (perhaps through remote sensing), rather than surface gravel cover, might improve modeling results. WUPA-L also includes both sandstone and limestone parent materials, which may influence composition patterns.

Within-ecosite hierarchical clustering identified groups of plots that share distinct species abundance patterns for all study areas except GRCA-P. In the most typical clustering pattern observed, a few perennial grass and shrub species are abundant across most plots in a study area, with subtle compositional gradients observed for some of the dominant or moderately abundant species. Shrub species may dominate in one cluster of plots, and perennial grass species dominate in another. Within state-and-transition models, this pattern of reference states including a range of functional group dominance is often characterized as alternative stable states (Collins et al. 2014). It is common across arid and semi-arid landscapes (Collins et al. 2014), and is included in many NRCS Ecological Site Descriptions for the Colorado Plateau (Duniway et al. 2016). Transitions between states are influenced by many factors, including edaphic conditions and changes in the amount or variability of

precipitation (Collins et al. 2014). Recognizing the inherent spatial variability in functional group dominance within these ecosite study areas may be important to interpreting future trends.

Five of the seven ecosite study areas display similar levels of measured topoeconomic variability and are represented by relatively homogenous assemblages, as indicated by low to moderate beta diversity and subtle clustering patterns. In my opinion, these study areas fit within the original intent behind the SCPN's use of the ecological site concept; that is, to identify and monitor study areas with fairly homogenous edaphic conditions and vegetation patterns.

In contrast, the BAND-P and WUPA-L study areas display stronger topoeconomic variability, with assemblages that show greater beta diversity and more pronounced clustering patterns. We expected a more varied composition for the BAND-P study area because of the broader inclusion of six soil map units, but did not anticipate greater compositional variation for WUPA-L. In retrospect, with greater knowledge of variable cinder cover, a range of soil depths, and mixed soil parent materials included in the two WUPA-L soil map units, high beta diversity for this assemblage is not surprising. In fact, reference conditions for this Ecological Site are described to include several phases, with perennial grass or shrub dominance (USDA-NRCS and DOI-NPS 2015).

Long-term monitoring of these more complex assemblages could ultimately yield a more in-depth ecological understanding than what could be gained from more homogenous study areas. But it also poses unique challenges and questions. If distinct plot clusters within a study area are likely to respond differently to changing climate conditions, then following the compositional trajectories of each cluster may provide more insight into their relative stability than analysis of averaged patterns. Can we maintain the flexibility to track the full suite of plots as a single assemblage, and also track significant plot clusters with potentially divergent temporal trajectories? Are current samples sizes sufficient to divide a study area into subsets? Do we have the relevant environmental data (and is it collected at the right scale) to adequately interpret more complex monitoring results? However, if we can devote the necessary resources to provide sufficient interpretation, these more heterogeneous assemblages are likely to yield valuable insights into community dynamics.

Comparing Clustering Results to Associations from Vegetation Mapping Reports

Hierarchical clustering results from this study generally fit well with described National Vegetation Classification (NVC) associations from each park's Vegetation Mapping Report. The close agreement with NVC associations was probably due to the temporal proximity between vegetation mapping field work and the initial phase of long-term monitoring (approximately within a decade). If cluster analysis is repeated through time, I would expect the specific compositional groupings to be somewhat fluid, gradually diverging from associations described in the early 2000s.

Because the Vegetation Mapping Reports included both local and global descriptions for each association, they lend a broader geographic context to interpretation (Table 14 in Appendix E). For example, the *Pinus edulis* – *Juniperus osteosperma*/*Purshia stansburiana* association which aligns with GRCA-P plots is known only from the Colorado Plateau (Kearsley et al. 2015), while the *Juniperus monosperma*/*Bouteloua gracilis* association, which aligns with some BAND-P plots, is

more widespread, occurring in the southern Rockies, southeast Colorado Plateau, southwest Great Plains, and Chihuahuan Desert mountains and mesas (Muldavin et al. 2011).

Within the three lowest elevation ecosites (PEFO-C, PEFO-S and WUPA-L), several of the plot clusters align most closely with NVC associations described as occurring on the Colorado Plateau as well as in the Chihuahuan Desert (Table 14 in Appendix E). The landform settings of these associations in the Chihuahuan Desert were described as basins or depressions and swales of alluvial plains, rather than the upland settings of this study. This suggests that the difference in soil water availability between depressional settings in the northern Chihuahuan Desert and low-elevation upland settings in the southern Colorado Plateau may be relatively small. It also reminds us to look to compositional trajectories for similar associations in neighboring ecoregions in order to anticipate how species and communities will respond to a warmer and dryer climate.

Pairing Multivariate Analysis with Distribution-based Approaches

Thus far, discussion has focused on the results of multivariate analysis to first compare the seven assemblages, and then to model the relationship of each assemblage to its local environment. Once a sufficient temporal record has been compiled, these methods will be equally appropriate for detecting compositional shifts through time and relating them to temporally variable conditions (Collins et al. 2020; Jones et al. 2017). A limitation of multivariate analysis, however, is that it does not fully describe the nature of the observed spatial variability or temporal change (Collins et al. 2008). One way of improving the explanatory capacity of temporal analysis is to pair multivariate methods with distribution-based approaches. In this section, differences between assemblages based upon a few univariate community metrics are discussed, followed by a comparison of dominance patterns and the species identities of dominant and moderately abundant species.

Shrub/Herbaceous Cover, Dominance, and Diversity

A comparison of total shrub and herbaceous cover across ecosites underscores the generally sparse nature of these semi-arid Colorado Plateau systems (averaging from 7.8% to 20.8% cover).

Shrub/herbaceous cover was lowest for GRCA-P and MEVE-L (7.8% and 8.1%, respectively), the two pinyon-juniper woodlands with highest tree canopy cover. In these ecosites, and for BAND-P, shrub and herbaceous cover fell below 5% in some plots (Figure 13). Because soil erosion has been identified as a potential degradational pathway in some ecosites (e.g., PEFO-C, BAND-P), tracking long-term trends in total live cover will continue to be relevant to ecosystem stability. See the next section for further discussion of shrub/herbaceous cover in the woodland study areas.

Using Simpson Concentration (i.e., dominance) and Shannon Diversity to summarize diversity, we see a range of shrub/herbaceous patterns across the seven study areas. Dominance was strongest for PEFO-C and MEVE-L (with the two dominant species accounting for 64% and 66% of total abundance, respectively) and weakest for BAND-P and WUPA-P (with the two dominant species accounting for 35% and 40% of total abundance, respectively). Of course, weaker dominance patterns would be expected in assemblages exhibiting the high beta diversity observed for these study areas. But Shannon Diversity further clarifies the differences between WUPA-L and BAND-P. The moderate Shannon Diversity values for WUPA-L, similar to those for three other assemblages,

denote a medium effective number of common species. However, for BAND-P, both beta diversity and Shannon diversity are relatively high, indicating more turnover in abundant species across plots, as well as a greater effective number of common species. This pattern is shown by the relatively high number of moderately abundant species (16) observed for BAND-P (Figure 18).

When dominance is concentrated in one or two species, as observed for the PEFO-C and MEVE-L ecosites (Figures 15 and 16), the stability of the assemblage may hinge on the population stability of the dominant species (Doak et al. 1998; Hillebrand et al. 2008; Hallett et al. 2014). Thus, if the dominant species is tolerant of disturbance or changing conditions, stability is enhanced; if it is more sensitive, the assemblage will have lower resistance than communities with more even species distributions.

By considering both the strength of current dominance patterns and the identities of dominant species against the backdrop of projected climate impacts, one can develop hypotheses concerning future assemblage stability. For example, in the GRCA-P and MEVE-L ecosites, the dominant C₃ grass, *Poa fendleriana*, stands out as a species that is vulnerable to projected spring drying (Hoover et al. 2021). Both ecosites are characterized by sparse understory cover and are dominated by *Poa fendleriana* and a *Purshia* shrub species. The MEVE-L ecosite displays the stronger dominance pattern, with *Poa fendleriana* dominating (40% relative abundance) and *Purshia tridentata* as sub-dominant (26% relative abundance) (Figure 15). By contrast, in the GRCA-P ecosite, dominance is shared, with similar relative abundance for *Poa fendleriana*, *Purshia stansburiana* and *Bouteloua gracilis* (22%, 24% and 23%, respectively). According to USGS/NPS soil water modeling, both areas are projected to experience reduced spring SWP, with impacts projected by mid-century for GRCA-P, and by late-century for MEVE-L. Thus, if *Poa fendleriana* is intolerant to reduced spring SWP, dominance shifts are likely to occur first in the GRCA-P ecosite. However, the overall impact may eventually be more pronounced for MEVE-L, given the current strong dominance by *Poa fendleriana*. In addition, the presence of a perennial C₄ grass as a current co-dominant species in GRCA-P might contribute to potential resilience for that assemblage.

Reordering among dominant species may be a key mechanism of community change at intermediate timescales (Avolio et al. 2019; Collins et al. 2020). Tracking species identities and their rank abundance is well-suited to detecting such compositional shifts. More specifically, Rank Abundance Curves (RACs) and their derived measures such as RAC Change or RAC Difference may provide a useful complement to multivariate analysis of community change through time (Collins et al. 2008; Jones et al. 2017; Avolio et al. 2019).

Species Identities of Dominant and Moderately Abundant Species

From the perspective of monitoring ecosystem stability, I have focused on dominant species, and also on moderately abundant species due to their potential importance as communities shift. Across the seven study areas, only 12 species are dominant, that is, achieving relative abundance of 10% or greater in their respective ecosites (Figure 17). An additional 34 species are moderately abundant, with relative abundance between 1% and 10% (Figure 18). Among these are seven perennial grass species and fifteen shrub species, potential candidates for recruitment into dominant positions should

rank shifts occur among the current dominants. In a study of 91 dryland communities from across the globe, Ulrich and colleagues conclude that dryland systems tend to accumulate a “middle class” of species with intermediate relative abundances (Ulrich et al. 2016). Many of these moderately abundant species may be functional equivalents of the dominant species, but with different environmental requirements and tolerances (Walker et al. 1999). Hillebrand and colleagues (2008) propose that resistance to disturbance may be more connected to dominance, while resilience relies upon the response diversity of the assemblage. Examining the identities of moderately abundant species might also provide warning of increasing instability, such as an increase in the relative abundance of short-lived (annual, biennial), ruderal, or non-native species.

Influence of Pinyon–juniper Overstory on Shrub/Herbaceous Composition

For status and trends reporting on woodland study areas, tree health, the size structure of overstory and sapling layers, and regeneration are important components to include. In this study, however, I have focused on the shrub and herbaceous layers of woodlands in order to make community comparisons across a broader range of semi-arid systems. We know that overstory pinyon and juniper trees influence shrub and herbaceous vegetation by competing for resources and modifying their local environment. The most obvious compositional difference I observed between woodland and grassland/shrubland ecosites is reduced shrub/herbaceous cover in the two moderately dense woodland ecosites (MEVE-L and GRCA-P; Figure 13). In contrast, for the more open BAND-P woodland, mean shrub/herbaceous cover is similar to that for the grassland/shrubland ecosites, but with a high standard deviation (Figure 13).

This is consistent with the results of experimental tree thinning in Colorado Plateau pinyon-juniper woodlands. In trials preceding the juniper thinning treatments in Bandelier NM, forb and grass biomass in treated areas was twice that of control plots five years post-treatment, while shrub cover was unresponsive to treatment (Jacobs 2015). Another thinning experiment in north-central New Mexico found the standing crop of grasses to be two to three times greater in treatment areas compared to controls five and ten years following treatment (Almalki et al. 2023). The authors conclude that the increase likely resulted from reduced competition from trees for soil water and soil nutrient resources (Almalki et al. 2023). Similar restoration treatments in northwestern Arizona pinyon-juniper woodland also reported increases in grass cover in treatment plots compared to controls (Stoddard et al. 2008; Huffman et al. 2019). Most thinning studies followed the understory response for relatively short timeframes. Longer term studies are needed to confirm whether increases in cover are confined to herbaceous species, or also observed for shrub species. A study documenting the response of understory vegetation to juniper mortality shows similar patterns. In a northern Arizona *Juniperus monosperma* woodland, Kane and colleagues (2011) found that areas under dead junipers contained nearly double the understory cover of areas under living trees.

Beyond this basic relationship between woodland tree density and shrub/herbaceous productivity, our current understanding of pinyon juniper overstory effects on shrub/herbaceous composition is limited. However, through their seminal work on patch dynamics and cross-scale interactions (conducted in northern New Mexico, in and around Bandelier NM) Allen (2007) and Breshears (2006), provide a framework for future inquiry. Canopy and intercanopy patches in a pinyon-juniper

woodland are connected through tree root systems that extend into intercanopy patches. Thus, the influence of tree density on intercanopy composition varies along the grassland-woodland continuum (Breshears 2006). Similarly, surface cover by shrub and herbaceous species also affects ecosystem processes (e.g., through moderating water runoff and erosion or by providing fine fuel connectivity) (Allen 2007). Both the relative proportion of canopy and intercanopy patches, and the connectivity between patches, influence ecosystem processes and disturbance dynamics (Breshears 2006). Allen demonstrates how changes in patch-scale patterns such as these can interact with disturbance processes to drive major ecosystem transitions (Allen 2007).

Recent modeling suggests that Arizona and New Mexico are likely to lose greater than 50% of suitable habitat for Colorado Plateau pinyon-juniper woodland (Harris et al. 2023). Widespread treeline shifts to higher elevations are also projected for Colorado Plateau pinyon-juniper woodlands (Urza et al. 2020). Given the likelihood that current pinyon-juniper vegetation may shift on the continuum toward wooded shrublands or savanna, understanding understory composition patterns may become increasingly important as we strive to strengthen the resilience of existing woodlands and manage those communities undergoing rapid compositional change. In the pinyon-juniper woodlands with greatest exposure to climate change, supporting the health of native shrub and perennial grass populations may be critical to maintaining ecosystem functioning and resisting non-native plant invasion (Redmond et al. 2023).

Questions and Considerations for Future Work

Are Environmentally Heterogeneous Study Areas More Resilient to Climate Change?

In terms of measured topographic factors, the BAND-P and WUPA-L study areas displayed rocky soils with high variability, a wide range of soil depths, and variable fine gravel cover of the ground surface. The BAND-P plots also extend across the broadest elevation range. These study areas were shaped by volcanic influences, with recent volcanic activity for WUPA-L. While it may seem self-evident to expect topographic heterogeneity in volcanic landscapes, it is also quite relevant, given the extensive Neogene (20–0 million years ago) volcanic fields that occur across the southern Colorado Plateau (Karlstrom et al. 2022), including in El Malpais and Petroglyph National Monuments.

Other than the relationship with volcanism, it is difficult to generalize from the inherent heterogeneity of these two study areas to broader ecosystem resilience. For the BAND-P study area, this difficulty stems in part from two events that occurred just prior to and during the first decade of SCPN monitoring. The 2003–2004 drought, which was described as “subcontinental drought accompanied by anomalously high temperatures” (Breshears et al. 2005, 2009), resulted in 90% pinyon overstory mortality across Bandelier NM (Jacobs et al. 2015). In addition, a juniper-thinning restoration treatment (2007–2010), designed to improve the eco-hydrologic condition of woodlands (Jacobs 2015; Jacobs et al. 2015) affected approximately two-thirds of the plots. As a consequence, the BAND-P shrub/herbaceous assemblage may have been in the midst of compositional change, just as baseline data were being collected. SCPN monitoring did capture an early phase of a subsequent invasion by *Bromus tectorum*. The invasion has worsened in recent years, with increasing *B. tectorum* frequency of occurrence and dominance in some plots (Swan 2020). Given this recent

history, it is doubtful that the relative roles of disturbance and edaphic heterogeneity in relation to current composition patterns can be untangled.

More generally, environmental heterogeneity is thought to enhance community resilience by providing a range of resources and microrefugia, and by increasing overall species richness and functional redundancy (Oliver et al. 2015). However, the effect of spatial heterogeneity on diversity and resilience may vary with environmental severity. Yang and colleagues (2015) proposed a model of heterogeneity-diversity relationships based on the trade-off between stress-tolerance and competitive ability (Grime 1973). Their model simulations show that environmental heterogeneity-diversity relationships may depend on the position of communities along gradients of environmental severity (Yang et al. 2015).

Factoring in environmental severity as one considers the role of topoeadaphic heterogeneity seems appropriate in these semi-arid Colorado Plateau study areas. Whether heterogeneity results in greater resistance to change may depend upon the details of the relationship between edaphic heterogeneity and environmental stressors such as drought. For example, the PEFO-S and PEFO-C study areas are quite similar in composition, but with subtly differing edaphic conditions. The soils are moderately fine to medium-textured loams for both ecosites, but the PEFO-C soils exhibit a fine-scaled soil texture mosaic with clayey soils intermixed with sandy loams. These clayey fans are formed through fluvio-alluvial processes, as fine-textured clays from the Chinle Formation are carried by water and deposited on soils derived from coarser parent materials (Bowker et al. 2013). The PEFO-C assemblage exhibits a much stronger dominance pattern and lower Shannon diversity compared to PEFO-S. Shrub/herbaceous cover is on average 36% lower in the PEFO-C plots compared to the PEFO-S plots, dropping below 10% foliar cover in some plots. Annual grasses are also more abundant in the PEFO-C plots. In their proposed state-and-transition models for this ecosite, Bowker and colleagues (2013) identify an annual-species dominated state and a severely eroded state as potential degradational outcomes from severe drought. As spring soil moisture stress becomes more severe, and with the potential for more extreme rainfall events, I hypothesize that the PEFO-C assemblage will be less resistant than the PEFO-S assemblage to non-native species invasion and increased soil erosion because of its inherent edaphic heterogeneity. In contrast, consider the WUPA-L ecosite in which variable cinder cover of the ground surface is partially responsible for observed edaphic heterogeneity. In this case, greater cinder depth in some plots may provide a moderating influence by reducing evaporative water loss from the ground surface.

Which Species and Functional Groups Are Most Vulnerable?

Current climate modeling projects increasing chronic drought, drier spring soil conditions, and drying earlier in the year for the southern Colorado Plateau (Bradford et al. 2020). A delayed onset to the monsoon is also projected, further lengthening the summer drought period, followed by increased precipitation in later summer and early fall (Cook and Seager 2013). However, a major uncertainty with projections of summer precipitation is that global climate models have systematic deficiencies in representing the NAMS in the Southwest U.S. (Geil et al. 2013). The ecological effects of early 21st century droughts in the Southwest have been worsened by anomalously warm summer temperatures (Cayan et al. 2010). As summer temperatures continue to rise in coming decades,

increased evapotranspiration will intensify the impact of summer soil moisture deficits (Gonzalez et al. 2018).

The perennial C₄ grass species that are dominant across these Colorado Plateau study areas exhibit drought tolerance strategies such as high root:shoot ratios (*Bouteloua gracilis* and *Hilaria jamesii*) and root structures well-adapted to using summer rainfall events of varying size (Hoover et al. 2019; Schwinning et al. 2002). For example, rhizomatous *H. jamesii* is characterized by high lateral root spread and relatively deep roots, and *Sporobolus* spp. exhibits shallow, densely fibrous roots (Hoover et al. 2019). However, long-term monitoring (Rondeau et al. 2018) and artificial drought experiments on the Colorado Plateau and in nearby short-grass steppe ecosystems have shown that while C₄ grasses are less vulnerable than C₃ grasses to drought, they are not impervious (Evans et al. 2011; Hoover et al. 2019, 2021; Wertin et al. 2015). These studies have demonstrated reductions in photosynthesis and biomass production, as well as shifts in green-up and senescence for both C₃ and C₄ grasses in response to prolonged drought. For the CHCU-S study area, spring precipitation has been found to have a strong positive effect on the cover of dominant C₄ grasses (Swan 2022). Most recently, Swan (2024) found small but significant declines in dominant C₄ grass cover for the 2007–2021 period in all four grassland/shrubland ecosites included in this study. She notes that extreme drought conditions at the end of the sampling interval likely had a strong influence on trend slopes.

Increased chronic drought and prolonged fore-summer drying are likely to impact C₃ grass populations more than C₄ grass populations (Hoover et al. 2021). In order to detect declines in C₃ grass abundance we should look to study sites that are 1) projected to experience mid-century decreases in spring SWP, and 2) include C₃ grasses among the dominant or moderately abundant species. The BAND-P and GRCA-P study areas meet these criteria, with *Poa fendleriana* co-dominant in the GRCA-P ecosite and moderately abundant in BAND-P. Another C₃ grass, *Elymus elymoides*, is also moderately abundant in the BAND-P study area. With late-century reduced spring SWP, compositional shifts may eventually be most pronounced in the two ecosites in which *Poa fendleriana* is currently co-dominant (GRCA-P and MEVE-L). While the WUPA-L ecosite will likely experience more extreme spring water deficits by mid-century, change detection may be difficult due to the currently low relative abundances (<1%) for the C₃ grass species that occur there. Swan (2024) observed significant decreases in cover of the moderately abundant C₃ grass species, *Achnatherum hymenoides*, in the CHCU-S, PEFO-C and PEFO-S study areas over the 2007–2021 time period and found spring and summer water deficits to have a negative effect on *Achnatherum hymenoides* cover.

In contrast to perennial grasses, shrub dominance in dryland systems is promoted by fall/winter precipitation, with shrubs favored over perennial grasses where moisture is available in deeper soil layers (Noy-Meir 1973; Comstock and Ehleringer 1992; Sala et al. 1997). Even in rocky and shallow soils, the multiple taproots of some shrub species find their way through joints and cracks to access deep soil water reserves (Comstock and Ehleringer 1992). In an experiment conducted near Bandelier NM, McDowell and colleagues (2019) documented resistance of *Pinus edulis* and *Juniperus monosperma* trees to severe heat and drought treatments, attributing resistance to taproot

access to water in bedrock fractures. Thus, contact with fractured bedrock may make soils “ecohydrologically deep” for tap-rooted species, regardless of soil depth to bedrock.

Soil water modeling for SCPN ecosites found shrub dominance to be most related to the availability of soil water during January–March (Gremer et al. 2018). Modeling of future conditions predicts extreme water scarcity in the fall/winter for the WUPA-L study area by mid-century, and for the PEFO-C and PEFO-S study areas by late-century. BAND-P and GRCA-P are also expected to experience reduced fall/winter SWP by late-century. Reduced fall/winter SWP is likely to negatively impact shrub species over other functional groups because of their reliance on deep soil water. Schwinning and colleagues (2002) posit that the amount of stored water from winter precipitation may be largely responsible for maintaining the Leaf Area Index of shrub populations through the year, which may in turn enhance or inhibit use of summer precipitation. This may ultimately result in declines for shrub populations, but with impacts delayed for most ecosites until the late 21st century.

Cactus and succulents are moderately abundant in the woodland ecosites, dominating in some low-elevation plots. Because of their unique CAM (Crassulacean Acid Metabolism) photosynthetic pathway, the stomata of these species only open at night, thus minimizing water loss. They have shallow roots and thrive under conditions of high daytime temperatures coupled with large diurnal temperature fluctuations (Comstock and Ehleringer 1992). However, high mortality of yucca and cactus were observed on the Colorado Plateau following the 2002 drought (Schwinning et al. 2008). It will be interesting to see how these species fare under projected hot, dry, early summer conditions.

Based on Climate Projections, Which Study Areas Will See the Greatest Exposure?

The low-elevation WUPA-L study area is projected to experience the greatest near-term exposure to climate change, with extreme water scarcity projected for the spring and fall-winter by mid-century (Table 4; Figure 26 in Appendix C). Declines in spring SWP for BAND-P and GRCA-P are also expected by mid-century (Table 4; Figures 21 and 22 in Appendix C). By late-century, six of the seven study sites will see extreme water scarcity in the spring, with high-elevation MEVE-L experiencing more moderate reductions in spring SWP. Extreme water scarcity in the fall/winter is projected for PEFO-C and PEFO-S by late-century.

Given the extreme water scarcity projected for the low elevation WUPA-L ecosite in the decades to come, we should be alert to potential dominance shifts for this assemblage, with particular attention to the Cluster A plots (*Bouteloua eriopoda* – *Hilaria jamesii* herbaceous association) (Figure 9; Table 15 in Appendix E). Strong directional change has been documented in a similar grassland association in central New Mexico (Sevilleta NWR), co-dominated by *B. eriopoda* and *Bouteloua gracilis*. In recent years, *B. eriopoda* has doubled in abundance in the Sevilleta grassland, with *B. gracilis* remaining stable (Collins & Xia 2015). This reordering is attributed to higher interannual climate variability under increasing aridity (Jones et al. 2017).

Declines in spring SWP potential are also projected for BAND-P and GRCA-P by mid-century. I offer two hypotheses for BAND-P, based on study results. First, under the mid-century forecast of reduced spring SWP, I expect the low-elevation Cluster C plots, with variable soil depths and

understory shrub dominance, to be the most resistant to compositional shifts (Figure 11; Table 16 in Appendix E). This is because many shrub species rely more on winter precipitation (Comstock and Ehleringer 1992) and because woody species with long tap-root systems may access water via contact with bedrock fractures (McDowell et al. 2019). By contrast, I expect Cluster B plots, with current dominance by perennial grass species, to be more vulnerable to reduced spring SWP in coming decades (Figure 11; Table 16 in Appendix E). In addition, if the high abundance of *Bromus tectorum* in Cluster A plots persists or if *B. tectorum* abundance continues to increase in Cluster B plots, this non-native species could further threaten the stability of these areas due to its disruptive role in usurping scarce spring soil water. Although this concern warrants close observation, the productive soils and high Shannon Diversity of these areas also suggest the potential, at least, for ecosystem resilience.

Proposed Cross-site Comparisons Based on Study Results

Cross-site comparisons of community change trajectories following a pulse disturbance (e.g., wildfire, hurricane) are common in the ecological literature, with comparisons of community response to climate-related ecological presses (e.g., increasing aridity) becoming more frequent (e.g., Hallett et al. 2014, Jones et al. 2017). A recent overview of the first forty years of dryland ecosystem research completed through the U.S. National Science Foundation's Long-term Ecological Research Network emphasized the importance of cross-site comparisons to expand understanding of the range of variability across a larger spatial extent, and to document divergent local responses to large-scale climate events or variability (Hudson et al. 2022).

In my view, the several lines of inquiry developed in this paper provide the basis for proposing cross-site comparisons for these semi-arid SCPN study areas. I use study results along with previous modeling of Soil Water Potential (SWP) to pose potential comparisons for future inquiry (Table 11). For example, one could compare study areas that are similar in current composition but differ in projected climatic conditions, or compare areas that share the same climate and similar compositions but differ in topo-edaphic conditions. Such comparisons may provide earlier warning of subtle changes in dominance strength or species rank shifts than would be apparent if one relied solely on comparing a single assemblage to itself through time.

Table 11. Proposed assemblage comparisons between and within ecosite study areas.

Comparison	Ecosites	Description
Compositionally similar ecosites with contrasting climate projections	PEFO-S vs. CHCU-S	The PEFO-S and CHCU-S ecosites receive similar MAP, but the CHCU-S plots occur at higher elevation with lower MAT values. These grassland ecosites share the greatest compositional similarity among the study areas with the same dominant C ₄ grass species. They also exhibit comparable relative abundance of shrubs in relation to perennial grasses. With projected warming temperatures and prolonged droughts, I anticipate dominance shifts in the lower elevation PEFO-S plots prior to compositional changes occurring in the CHCU-S plots.
	GRCA-P vs. MEVE-L	The MEVE-L and GRCA-P pinyon-juniper ecosites are characterized by sparse shrub/herbaceous cover. Tree basal area is higher for MEVE-L than for GRCA-P. Both ecosites are dominated by the C ₃ grass, <i>Poa fendleriana</i> , and <i>Purshia</i> shrub species. <i>Bouteloua gracilis</i> is a third co-dominant species for GRCA-P. Though similar climatically, the MEVE-L ecosite occurs at higher elevation and thus exhibits lower MAT and higher MAP than GRCA-P. Of the ecosites in this study, these two are the least affected by the North American Monsoon, with 33–35% of total precipitation coming in July–September. Soil water modeling projects no change for the MEVE-L ecosite in the near-term (2020–2059), but decreased near-term spring SWP for GRCA-P. With a C ₃ grass among the dominant species, both assemblages seem vulnerable to dominance shifts, with such shifts likely to be observed first for GRCA-P.
Ecosites similar in composition and climate projections, but with different edaphic conditions	PEFO-C vs. PEFO-S	The PEFO-C and PEFO-S ecosites share the same climate and are quite similar in composition, with the same perennial grass species dominating. They differ in terms of soils, with the PEFO-S plots occurring on moderately fine to medium textured loams, and the PEFO-C plots occurring on clayey fans with a fine-scaled patchiness of soils ranging from clay loams and sandy clay loams to fine sandy loams. Mean shrub/herbaceous cover is higher in the PEFO-S plots than in the PEFO-C plots. The species composition of PEFO-S plots is relatively homogenous, while PEFO-C plots fall into two distinct clusters, reflecting the underlying soil texture. <i>Atriplex obovata</i> and annual species are moderately abundant in the plots with greater clay content. The non-native species, <i>Bromus tectorum</i> and <i>Salsola tragus</i> , are also more common in PEFO-C plots. With increased drought frequency, I expect to see annual and non-native species abundance increase in PEFO-C. With an increase in extreme rainfall events, I expect increased soil erosion to exacerbate the loss of perennial herbaceous cover in PEFO-C.
Within ecosites with high beta diversity, compare compositional trajectories for distinct plot clusters	BAND-P: Cluster B to Cluster C	Cluster B (<i>J. monosperma/Bouteloua gracilis</i> association) and Cluster C (<i>J. monosperma/Quercus x pauciloba</i> association) represent high and low elevation versions of a similar mosaic of soils. Cluster B plots display greater relative abundance of perennial grass species, while the lower elevation Cluster C plots display greater relative abundance of shrub species. Tree basal area is similar in the two clusters. Soil water modeling projects decreased spring SWP for BAND-P in the near-term (2020–2059). I anticipate that the C ₃ grass, <i>Poa fendleriana</i> , may decline in abundance with lower spring SWP. I expect the low-elevation Cluster C plots, with variable soil depths and understory shrub dominance, to be most resistant to compositional shifts because of shrub reliance on winter precipitation, and because woody species with long tap-root systems may access water via contact with bedrock fractures. Cluster B plots are more vulnerable to reduced spring SWP because of greater susceptibility of forb and perennial grass species (particularly C ₃) to spring drought.

Conclusions

These seven southern Colorado Plateau communities share many characteristics in common, including a range of shrub to perennial grass dominance, and considerable overlap among the dominant and moderately abundant species composing each assemblage. For two woodland and three grassland study areas, current shrub/herbaceous composition is relatively homogenous and aligns with fairly simple topoedaphic gradients. In these study areas, I would expect the plots within a study area to respond similarly as climate conditions continue to change. In contrast, the WUPA-L and BAND-P study areas currently exhibit greater beta diversity and more complex relationships between composition patterns and topoedaphic conditions. In these study areas, I expect compositional patterns to further diverge as climate conditions become more extreme.

When a community changes, many aspects of community structure are affected. It makes sense to rely on a variety of community attributes and analytic tools to detect and describe the resulting shifts because it is the aggregate impact of these varied structural changes that ultimately determine ecosystem function (Bannar-Martin et al. 2018). Combining multivariate analysis with Rank Abundance Curves and related diversity measures helped to summarize and explain differences between assemblages in this study. Over the long term, global climate change will likely result in species turnover through local extinction and colonization. However, reordering among dominant species is likely to precede more dramatic changes, and so may be an effective leading indicator for long-term monitoring.

This study has focused on one topic—composition patterns of dominant and moderately abundant shrub and herbaceous species in semi-arid communities. But because long-term monitoring efforts such as the SCPN Upland Vegetation Project collect species-level abundance data for the full target assemblage, they are applicable to a broad array of ecological questions and resource management issues. This flexibility is important and should be sustained, given the large uncertainties regarding the future integrity of ecosystems and the unknown challenges that land managers may encounter.

In this era of accelerating ecological change, consistent long-term community data is essential, not only to address local land management issues, but also to support ecological research and regional assessments. In plant communities dominated by long-lived perennial species, the wait for a meaningful temporal record is long, but this interval can be used to understand the regional context, local environment, and disturbance history of individual study areas more fully. Comparing related assemblages that represent different environmental conditions will contribute to this understanding and may provide early indication of subtle changes in dominance or rank shifts among species. Such comparisons will complement ongoing longitudinal analyses and are particularly applicable in monitoring networks composed of an ecologically related collection of study areas, such as are found in many NPS-IMD networks, including the SCPN.

Literature Cited

- Albano, C. M. 2015. Identification of geophysically diverse locations that may facilitate species' persistence and adaptation to climate change in the southwestern United States. *Landscape Ecology* 30: 1023-1037.
- Allen, C. D. 2007. Interactions across spatial scales among forest dieback, fire, and erosion in northern New Mexico landscapes. *Ecosystems*: 797-808.
- Allen, C. D. and D. D. Breshears. 1998. Drought-induced shift of a forest–woodland ecotone: rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences* 95: 14839-14842.
- Almalki, Y.M., A.G. Fernald, C.G. Ochoa, A.F. Cibils, A.M. Faist, D.S. Cram, and R.L. Steiner. 2023. Understory vegetation response to thinning pinyon-juniper woodlands. *Rangeland Ecology & Management* 88:152-158.
- Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26:32–46.
- Anderson, M.J. 2006. Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* 62:245–253.
- Anderson, M.J., K.E. Ellingsen, and B.H. McArdle. 2006. Multivariate dispersion as a measure of beta diversity. *Ecology Letters* 9: 683–693.
- Anderson, M.J., R. N. Gorley, and K. R. Clarke. 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth, UK.
- Anderson, M. J., T.O. Crist, J.M. Chase, M. Vellend, B.D. Inouye, A.L. Freestone, and N.G. Swenson. 2011. Navigating the multiple meanings of β diversity: A roadmap for the practicing ecologist. *Ecology Letters* 14: 19–28.
- Anderson, M.J. and D.C.I. Walsh. 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? *Ecological Monographs* 83: 557-574.
- Avolio, M.L., K.J. La Pierre, G. Houseman, S.E. Koerner, E. Grman, F. Isbell, D.S. Johnson, and K.R. Wilcox. 2015. A framework for quantifying the magnitude and variability of community responses to global change drivers. *Ecosphere* 6:280.
- Avolio, M.L., E.J. Forrester, C.C. Chang, K.J. La Pierre, K.T. Burghardt, and M.D. Smith. 2019. Demystifying dominant species. *New Phytologist* 223: 1106–1126.

- Baer, S.G., J.M. Blair, and S.L. Collins. 2015. Environmental heterogeneity has a weak effect on diversity during community assembly in tallgrass prairie. *Ecological Monographs* 86: 94–106.
- Baker, W.L. and D.J. Shinneman. 2004. Fire and restoration of piñon–juniper woodlands in the western United States: a review. *Forest Ecology and Management* 189: 1–21.
- Bannar-Martin, K.H., C.T. Kremer, S.K. Morgan Ernest, M. A. Leibold, H. Auge, J. Chase, and S.R. Supp. 2018. Integrating community assembly and biodiversity to better understand ecosystem function: The Community Assembly and the Functioning of Ecosystems (CAFE) approach. *Ecology Letters* 21: 167–180.
- Baril, L., P.L. Valentine-Darby, K. Struthers, P. Whitefield, W. Romme, and K. Anderson. 2018. Wupatki National Monument: Natural resource condition assessment. Natural Resource Report NPS/SCPN/NRR—2018/1613. National Park Service, Fort Collins, Colorado.
- Bowker, M.A., M.E. Miller, R.T. Belote, and S.L. Garman. 2013. Ecological thresholds as a basis for defining management triggers for National Park Service vital signs—Case studies for dryland ecosystems: U.S. Geological Survey Open-File Report 2013–1244, 94 p.
- Bradford, J.B., D.R. Schlaepfer, W.K. Lauenroth, and K.A. Palmquist. 2020. Robust ecological drought projections for drylands in the 21st century. *Global Change Biology* 26: 3906–3919.
- Breshears, D.D. 2006. The grassland–forest continuum: trends in ecosystem properties for woody plant mosaics? *Frontiers in Ecology and the Environment* 4:96–104.
- Breshears, D.D., P.M. Rich, F.J. Barnes, and K. Campbell. 1997. Overstory-imposed heterogeneity in solar radiation and soil moisture in a semiarid woodland. *Ecological Applications* 7:1201–1215.
- Breshears, D.D., N.S. Cobb, P.M. Rich, K.P. Price, C.D. Allen, R.G. Balice, W.H. Romme, and J. J. Anderson. 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences* 102: 15144–15148.
- Breshears, D.D., O.B. Myers, C.W. Meyer, F.J. Barnes, C.B. Zou, C.D. Allen, N.G. McDowell, and W.T. Pockman. 2009. Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. *Frontiers in Ecology and the Environment* 7: 185–189.
- Bureau of Reclamation. 2016. West-Wide Climate Risk Assessment: Hydroclimate Projections. Technical Memorandum No. 86-68210-2016-01. U.S. Bureau of Reclamation, Technical Service Center, Denver, CO, 140 pp.
- Cayan, D.R., T. Das, D.W. Pierce, T.P. Barnett, M. Tyree, and A. Gershunov. 2010. Future dryness in the southwest US and the hydrology of the early 21st century drought. *Proceedings of the National Academy of Sciences* 107: 21271–21276.

- Chao, A., C.-H. Chiu, and T. C. Hsieh. 2012. Proposing a resolution to debates on diversity partitioning. *Ecology* 93: 2037–2051.
- Chao, A., C.-H. Chiu, and L. Jost. 2016. Unifying Species Diversity, Phylogenetic Diversity, Functional Diversity, and Related Similarity and Differentiation Measures Through Hill Numbers. *Annual Review of Ecology, Evolution and Systematics* 45:297–324.
- Chao, A. and C.-H. Chiu. 2016. Bridging the variance and diversity decomposition approaches to beta diversity via similarity and differentiation measures. *Methods in Ecology and Evolution* 7: 919–928.
- Chapin III, F.S., M.S. Bret-Harte, S.E. Hobbie, and H. Zhong. 1996. Plant functional types as predictors of transient responses of Arctic vegetation to global change. *Journal of Vegetation Science* 7: 347–358.
- Clarke, K.R. and R.N. Gorley. 2015. *PRIMER v7: User manual/Tutorial*. PRIMER-E Ltd, Plymouth.
- Clarke, K.R., R.N. Gorley, P.J. Somerfield, and R.M. Warwick. 2014. *Change in marine communities: an approach to statistical analysis and interpretation*. PRIMER-E Ltd, Plymouth.
- Collins, S.L. and Y. Xia. 2015. Long-term dynamics and hotspots of change in a desert grassland plant community. *American Naturalist*, 185: E30–E43.
- Collins, S.L., K.N. Suding, E.E. Cleland, M. Batty, S.C. Pennings, K.L. Gross, J.B. Grace, L. Gough, J.E. Fargione, and C.M. Clark. 2008. Rank clocks and community dynamics. *Ecology* 89:3534–3541.
- Collins S.L., J. Belnap, N.B. Grimm, J.A. Rudgers, C.N. Dahm, P. D'odorico, M. Litvak, D.O. Natvig, D.C. Peters, W.T. Pockman, and R.L. Sinsabaugh. 2014. A multiscale, hierarchical model of pulse dynamics in arid-land ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 45:397–419.
- Collins, S.L., M.L. Avolio, C. Gries, L.M. Hallett, S.E. Koerner, K.J. La Pierre, and M.B. Jones. 2018. Temporal heterogeneity increases with spatial heterogeneity in ecological communities. *Ecology* 99: 858–865.
- Collins, S.L., Y.A. Chung, L.E. Baur, A. Hallmark, T.J. Ohlert, and J.A. Rudgers. 2020. Press–pulse interactions and long-term community dynamics in a Chihuahuan Desert grassland. *Journal of Vegetation Science* 31: 722–732.
- Comstock, J.P. and J.R. Ehleringer. 1992. Plant adaptation in the Great Basin and Colorado Plateau. *The Great Basin Naturalist* 52: 195–215.
- Cook, B. I. and R. Seager. 2013. The response of the North American Monsoon to increased greenhouse gas forcing. *Journal of Geophysical Research: Atmospheres* 118: 1690–1699.

- Cook, B.I., T.R. Ault, and J.E. Smerdon. 2015. Unprecedented 21st century drought risk in the American Southwest and Central Plains. *Science Advances*, 1: e1400082.
- Copeland, S.M., J.B. Bradford, M.C. Duniway, and R.M. Schuster. 2017. Potential impacts of overlapping land-use and climate in a sensitive dryland: a case study of the Colorado Plateau, USA. *Ecosphere* 8: p.e01823.
- DeCoster, J.K., C.L. Lauver, M.E. Miller, J.R. Norris, A.E.C. Snyder, M.C. Swan, L.P. Thomas, and D.L. Witwicki. 2012. Integrated upland monitoring protocol for the Southern Colorado Plateau Network. Natural Resource Report NPS/SCPN/NRR–2012/577. National Park Service, Fort Collins, CO.
- Dettinger, M., B. Udall, and A. Georgakakos. 2015. Western water and climate change. *Ecological Applications* 25:2069-2093.
- Doak, D. F., D. Bigger, E. K. Harding, M. A. Marvier, R. E. O'Malley, and D. Thomson. 1998. The statistical inevitability of stability-diversity relationships in community ecology. *American Naturalist* 151:264–276.
- Dornelas, M., N.J. Gotelli, B. McGill, H. Shimadzu, F. Moyes, C. Sievers, and A.E. Magurran. 2014. Assemblage time series reveal biodiversity change but not systematic loss. *Science* 344: 296–299.
- Duniway, M.C., K.A. Snyder, and J.E. Herrick. 2010. Spatial and temporal patterns of water availability in a grass-shrub ecotone and implications for grassland recovery in arid environments. *Ecohydrology* 3:55–67.
- Duniway, M.C., T.W. Nauman, J.K. Johanson, S. Green, M.E. Miller, J.C. Williamson, and B.T. Bestelmeyer. 2016. Generalizing ecological site concepts of the Colorado Plateau for landscape-level applications. *Rangelands* 38: 342-349.
- Duniway, M.C., C. Benson, T.W. Nauman, A. Knight, J.B. Bradford, S.W. Munson, D. Witwicki, C. Livensperger, M. Van Scoyoc, T.T. Fisk, D. Thoma, and M.E. Miller. 2022. Geologic, geomorphic, and edaphic underpinnings of dryland ecosystems: Colorado Plateau landscapes in a changing world. *Ecosphere* 13, p.e4273.
- Evans, S.E., K.M. Byrne, K.M., W.K. Lauenroth, and I.C. Burke. 2011. Defining the limit to resistance in a drought-tolerant grassland: long-term severe drought significantly reduces the dominant species and increases ruderals. *Journal of Ecology* 99: 1500-1507.
- Floyd, M.L., D.D. Hanna, and W.H. Romme. 2004. Historical and recent fire regimes in Pinon-Juniper woodlands on Mesa Verde, Colorado, USA. *Forest Ecology and Management* 198: 269–289.

- Floyd M.L., M. Clifford, N.S. Cobb, D. Hanna, R. Delph, P. Ford, and D. Turner. 2009. Relationship of stand characteristics to drought-induced mortality in three Southwestern piñon–juniper woodlands. *Ecological Applications* 19:1223–30.
- Floyd, M.L., W.H. Romme, and D.D. Hanna. 2021. Effects of recent wildfires in piñon-juniper woodlands of Mesa Verde National Park, Colorado, USA. *Natural Areas Journal* 41:28–38.
- Gauch, H.G., Jr. 1982. *Multivariate Analysis in Community Ecology*. Cambridge University Press, New York.
- Geil, K. L., Y. L. Serra, and X. Zeng. 2013. Assessment of CMIP5 model simulations of the North American monsoon system. *Journal of Climate* 26:8787–8801.
- Goff, F., D. E. Broxton, and Eller, P.G. 1995. Geologic map of technical area 21. *Earth Science Investigations for Environmental Restoration—Los Alamos National Laboratory Technical Area 21*, p.7.
- Gonzalez, P., G.M. Garfin, D.D. Breshears, K.M. Brooks, H.E. Brown, E.H. Elias, and B.H. Udall. 2018. Southwest. In *Impacts, Risks, and Adaptation in the United States: Fourth National Climate Assessment, Volume II* [Reidmiller, D.R., C.W. Avery, D.R. Easterling, K.E. Kunkel, K.L.M. Lewis, T.K. Maycock, and B.C. Stewart (eds.)]. U.S. Global Change Research Program, Washington, DC, USA, pp. 1101–1184.
- Gremer, J.R., J.B. Bradford, S.M. Munson, and M.C. Duniway. 2015. Desert grassland responses to climate and soil moisture suggest divergent vulnerabilities across the southwestern United States. *Global Change Biology* 21:4049–4062.
- Gremer, J.R., C. Andrews, J.R. Norris, L.P. Thomas, S.M. Munson, M.C. Duniway, and J.B. Bradford. 2018. Increasing temperature seasonality may overwhelm shifts in soil moisture to favor shrub over grass dominance in Colorado Plateau drylands. *Oecologia* 188:1195–1207.
- Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242: 344–347.
- Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* 86: 902–910.
- Hallett, L.M., J.S. Hsu, E.E. Cleland, S.L. Collins, T.L. Dickson, E.C. Farrer, and K.N. Suding. 2014. Biotic mechanisms of community stability shift along a precipitation gradient. *Ecology* 95: 1693–1700.
- Hansen, M., J. Coles, K. A. Thomas, D. Cogan, M. Reid, J. Von Loh, and K. Schulz. 2004. USGS-NPS Vegetation Mapping Program: Wupatki National Monument, Arizona, vegetation classification and distribution. U.S. Geological Survey Technical Report. Southwest Biological Science Center, Flagstaff, AZ. 229 pp.

- Harrigan, J. unpublished. Why tephric epipedons for USDA taxonomy - a taxonomy amendment proposal for a diagnostic layer.
- Harris GM, S.E. Sesnie, and D.R. Stewart. 2023. Climate change and ecosystem shifts in the southwestern United States. *Scientific Reports* 13:19964.
- Hereford, R. and R.H. Webb. 1992. Historic variation of warm-season rainfall, southern Colorado Plateau, southwestern USA. *Climatic Change* 22:239-256.
- Hibner, C. D., C.A. Ferguson, and J.M. Puttner. 2009. Special Project Soil Survey of Bandelier National Monument [Interim report]. Final Review Copy, USDA, Natural Resources Conservation Service, Santa Fe, New Mexico.
- Hill, M.O. 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology* 54: 427–432.
- Hillebrand, H., D. M. Bennett, and M. W. Cadotte. 2008. Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology* 89:1510–1520.
- Hillebrand, H., B. Blasius, E.T. Borer, J.M. Chase, J.A. Downing B.K. Eriksson, and A.B. Ryabov. 2018. Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring. *Journal of Applied Ecology* 55:169–184.
- Holmgren, C.A., J. Norris, and J.L. Betancourt. 2007. Inferences about winter temperatures and summer rains from the late Quaternary record of C₄ perennial grasses and C₃ desert shrubs in the northern Chihuahuan Desert. *Journal of Quaternary Science* 22: 141-161.
- Hoover, D.L., M.C. Duniway, and J. Belnap. 2015. Pulse-drought atop press-drought: unexpected plant responses and implications for dryland ecosystems. *Oecologia* 179: 1211-1221.
- Hoover, D.L., M.C. Duniway, and J. Belnap. 2017. Testing the apparent resistance of three dominant plants to chronic drought on the Colorado Plateau. *Journal of Ecology* 105: 152-162.
- Hoover, D.L., K. Koriakin, J. Albrigtsen, and T. Ocheltree. 2019. Comparing water-related plant functional traits among dominant grasses of the Colorado Plateau: Implications for drought resistance. *Plant and Soil* 441: 207-218.
- Hoover, D.L., A.A. Pfennigwerth, and M.C. Duniway. 2021. Drought resistance and resilience: The role of soil moisture–plant interactions and legacies in a dryland ecosystem. *Journal of Ecology* 109:3280-3294.
- Hudson, A.R., D.P. Peters, J.M. Blair, D.L. Childers, P.T. Doran, K. Geil, M. Gooseff, K.L. Gross, N.M. Haddad, M.A. Pastore and J.A. Rudgers. 2022. Cross-site comparisons of dryland ecosystem response to climate change in the US Long-Term Ecological Research Network. *BioScience* 72: 889-907.

- Huffman, D.W., P.Z. Fulé, K.M. Pearson, and J.E. Crouse. 2008. Fire history of pinyon-juniper woodlands at upper ecotones with ponderosa pine forests in Arizona and New Mexico. *Canadian Journal of Forest Research* 38: 2097–2108.
- Huffman, D.W., J.E. Crouse, W.W. Chancellor, and P.Z. Fulé. 2012. Influence of time since fire on pinyon-juniper woodland structure. *Forest Ecology and Management* 274: 29–37.
- Huffman, D.W., M.T. Stoddard, J.D. Springer, J.E. Crouse, A.J.S. Meador, and S. Nepal. 2019. Stand dynamics of pinyon-juniper woodlands after hazardous fuels reduction treatments in Arizona. *Rangeland Ecology & Management* 72:757-767.
- Jackson, S., M. Hitchner, M. Ritchie, and J. Miotke. 2022. Grand Canyon Ecological Forecasting: Using NASA Earth Observations to Monitor and Model Juniper Woodland Mortality in Grand Canyon National Park.
- Jacobs, B.F. 2011. Spatial patterns and ecological drivers of historic piñon–juniper woodland expansion in the American southwest. *Ecography* 34: 1085-1095.
- Jacobs, B.F. 2015. Restoration of degraded transitional (piñon-juniper) woodland sites improves ecohydrologic condition and primes understory resilience to subsequent disturbance. *Ecohydrology* 8:1417–1428.
- Jacobs, B. F., W. H. Romme, and C.D. Allen. 2008. Mapping “old” vs. “young” piñon–juniper stands with a predictive topo-climatic model. *Ecological Applications* 18: 1627-1641.
- Jacobs, B., B. Judy, S. Fettig, C. Schwemm, J. Palumbo, and L. Thomas. 2015. Bandelier National Monument Natural Resource Condition Assessment, Natural Resource Report NPS/BAND/NRR—2015/1000. National Park Service, Fort Collins, CO.
- Jones, S.K, J. Ripplinger, and S.L. Collins. 2017. Species reordering, not changes in richness, drives long-term dynamics in grassland communities. *Ecology Letters* 20: 1556–1565.
- Jost, L. 2006. Entropy and diversity. *Oikos* 113:363–375.
- Kane, J.M., K.A. Meinhardt, T. Chang, B.L. Cardall, R. Michalet, and T.G. Whitham. 2011. Drought-induced mortality of a foundation species (*Juniperus monosperma*) promotes positive afterlife effects in understory vegetation. *Plant Ecology* 212:733-741.
- Kannenberg, S.A., A.W. Driscoll, D. Malesky, and W.R.L. Anderegg. 2021. Rapid and surprising dieback of Utah juniper in the southwestern USA due to acute drought stress. *Forest Ecology and Management* 480:118639.
- Karlstrom, K. E., J. Wilgus, J.O. Thacker, B. Schmandt, D. Coblentz, and M. Albonico. 2022. Tectonics of the Colorado Plateau and its margins. *Annual Review of Earth and Planetary Sciences* 50:295-322.

- Kearsley, M. J. C., K. Green, M. Tukman, M. Reid, M. Hall, T. J. Ayers, and K. Christie. 2015. Grand Canyon National Park-Grand Canyon/Parashant National Monument vegetation classification and mapping project. Natural Resource Report NPS/GRCA/NRR—2015/913. National Park Service, Fort Collins, Colorado.
- Keddy, P.A. 1992. Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science* 3: 157–164.
- Knapp, A. K., and M.D. Smith. 2001. Variation among biomes in temporal dynamics of aboveground primary production. *Science* 291: 481-484.
- Knapp, A. K., C.J. Carroll, E.M. Denton, K.J. La Pierre, S.L. Collins, and M.D. Smith. 2015. Differential sensitivity to regional-scale drought in six central US grasslands. *Oecologia* 177: 949-957.
- Legendre, P. and M.J. Anderson. 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs* 69: 1–24.
- Legendre, P. and E. D. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129: 271-280.
- Legendre, P. and O. Gauthier. 2014. Statistical methods for temporal and space-time analysis of community composition data. *Proceedings of the Royal Society B: Biological Sciences* 281: 20132728.
- Legendre, P. and L. Legendre. 2012. *Numerical Ecology*, 3rd English ed. Elsevier Science BV, Amsterdam.
- Lightfoot, D.R. 1996. The nature, history, and distribution of lithic mulch agriculture: An ancient technique of dryland agriculture. *Agricultural History Review* 44: 206-222.
- Lundholm, J.T. 2009. Plant species diversity and environmental heterogeneity: spatial scale and competing hypotheses. *Journal of Vegetation Science* 20: 377–391.
- Mariotte, P. 2014. Do subordinate species punch above their weight? Evidence from above-and below-ground. *New Phytologist* 203: 16-21.
- Matthews, T. J., and R.J. Whittaker. 2015. On the species abundance distribution in applied ecology and biodiversity management. *Journal of Applied Ecology* 52: 443–454.
- McArdle, B.H. and M.J. Anderson. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82: 290–297.
- McCune, B. and D. Keon. 2002. Equations for potential annual direct incident radiation and heat load. *Journal of Vegetation Science* 13: 603-606.

- McDowell, N.G., C. Grossiord, H.D. Adams, S. Pinzón-Navarro, D.S. Mackay, D.D. Breshears, C.D. Allen, I. Borrego, L.T. Dickman, A. Collin, and M. Gaylord. 2019. Mechanisms of a coniferous woodland persistence under drought and heat. *Environmental Research Letters*, 14, p.045014.
- McGill, B.J. 2011. Species abundance distributions. *Biological Diversity: Frontiers in Measurement and Assessment* (eds. A. Magurran & B.J. McGill), pp. 105–122. Oxford University Press, Oxford.
- Merriam, C. H., and L.H. Stejneger. 1890. Results of a Biological Survey of the San Francisco Mountain Region and Desert of the Little Colorado, Arizona. US Government Printing Office.
- Miller, M.E. 2005. The Structure and Functioning of Dryland Ecosystems—Conceptual Models to Inform Long-Term Ecological Monitoring: U.S. Geological Survey Scientific Investigations Report 2005-5197, 74 p.
- Moeys, J. 2018. The soil texture wizard: R functions for plotting, classifying, transforming and exploring soil texture data. [Cran.r-project.org](http://cran.r-project.org).
- Muldavin, E., A. Kennedy, C. Jackson, P. Neville, T. Neville, K. Schulz, and M. Reid. 2011. Vegetation classification and map: Bandelier National Monument. Natural Resource Technical Report NPS/SCPN/NRTR— 2011/438. National Park Service, Fort Collins, Colorado.
- Munson, S.M., R.H. Webb, D.C. Housman, K.E. Veblen, K.E. Nussear, E.A. Beever, and N.G. Tallent. 2015. Long-term plant responses to climate are moderated by biophysical attributes in a North American desert. *Journal of Ecology* 103:657–668.
- Noy-Meir, I., 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4: 25-51.
- Oliver, T.H, M.S. Heard, N.J.B. Isaac, D.B. Roy, D. Procter, F. Eigenbrod, and J.M. Bullock. 2015. Biodiversity and resilience of ecosystem functions. *Trends in Ecology and Evolution* 30: 673–684.
- Peters, D.P.C. and J. Yao. 2012. Long-term experimental loss of foundation species: consequences for dynamics at ecotones across heterogeneous landscapes. *Ecosphere* 3: 1-23.
- Peters, D.P.C, J.E. Herrick, H.C. Monger, and H.T. Huang. 2010. Soil-vegetation-climate interactions in arid landscapes: effects of the North American monsoon on grass recruitment. *Journal of Arid Environments* 74: 618–623.
- PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>. Accessed 05/06/2022.
- Redmond, M.D., A.K. Urza, and P.J. Weisberg. 2023. Managing for ecological resilience of pinyon–juniper ecosystems during an era of woodland contraction. *Ecosphere* 14: e4505.

- Romme, W.H., C.D. Allen, J.D. Bailey, W.L. Baker, B.T. Bestelmeyer, P.M. Brown, and P.J. Weisberg. 2009. Historical and modern disturbance regimes, stand structures, and landscape dynamics in piñon–juniper vegetation of the western United States. *Rangeland Ecology and Management* 62: 203-221.
- Rondeau, R.J., K.L. Decker, and G.A. Doyle. 2018. Potential consequences of repeated severe drought for shortgrass steppe species. *Rangeland Ecology and Management* 71: 91-97.
- Sala, O. E., W.K. Lauenroth, and R.A. Gollucio. 1997. Plant functional types in temperate, semi-arid regions. In T. M. Smith, H. H. Shugart, & F. I. Woodward (Eds.), *Plant functional types* (pp. 217–233). Cambridge, UK: Cambridge University Press.
- Salas, D., L. Floyd-Hanna, and D. Hanna. 2011. Vegetation classification and mapping project report: Chaco Culture National Historical Park. Natural Resource Technical Report NPS/SCPN/NRTR—2011/452. National Park Service, Fort Collins, Colorado.
- Sasaki, T. and W.K. Lauenroth. 2011. Dominant species, rather than diversity, regulates temporal stability of plant communities. *Oecologia* 166: 761-768.
- Schwinning, S., K. Davis, L. Richardson, and J.R. Ehleringer. 2002. Deuterium enriched irrigation indicates different forms of rain use in shrub/grass species of the Colorado Plateau. *Oecologia* 130: 345-355.
- Schwinning, S., J. Belnap, D.R. Bowling, and J.R. Ehleringer. 2008. Sensitivity of the Colorado Plateau to change: climate, ecosystems, and society. *Ecology and Society*, 13(2).
- Schwinning, S., M. E. Litvak, W. T. Pockman, R. E. Pangle, A. M. Fox, C-W. Huang, and C. D. McIntire. 2020. A 3-dimensional model of *Pinus edulis* and *Juniperus monosperma* root distributions in New Mexico: implications for soil water dynamics. *Plant and Soil* 450: 337-355.
- Smith, M.D., A.K. Knapp, and S.L. Collins. 2009. A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology* 90: 3279-3289.
- Soil Science Division Staff. 2017. Soil survey manual. C. Ditzler, K. Scheffe, & H. C. Monger (eds.), USDA Handbook 18. Government Printing Office. Washington, DC: Office.
- Stoddard, M.T., D.W. Huffman, T.M. Alcoze, and P.Z. Fulé, 2008. Effects of slash on herbaceous communities in pinyon–juniper woodlands of northern Arizona. *Rangeland ecology & management*, 61: 485-495.
- Swan, M. C. 2022. Status and trends in grassland vegetation at Chaco Culture National Historical Park: Upland vegetation and soils monitoring 2007–2018. Natural Resource Report NPS/SCPN/NRR—2022/2348. National Park Service, Fort Collins, Colorado.

- Swan, M.C. 2024. Site characterization and change over time in semi-arid grasslands and shrublands at three parks, Chaco Culture National Historical Park, Petrified Forest National Park, and Wupatki National Monument: Upland vegetation and soils monitoring 2007-2021. Natural Resource Report. NPS/SCPN/NRR--2024/2616.
- Swan, M., L. McCoy, and C. Veety. 2020. Bandelier National Monument mesa-top pinyon-juniper 2019 data summary: Southern Colorado Plateau Network integrated upland monitoring. Natural Resource Data Series NPS/SCPN/NRDS—2020/1287. National Park Service, Fort Collins, Colorado.
- Thomas, K. A., M. L. McTeague, A. Cully, K. Schulz, and J. M. S. Hutchinson. 2009. Vegetation classification and distribution mapping report: Petrified Forest National Park. National Resource Technical Report NPS/SCPN/NRTR—2009/273. National Park Service, Fort Collins, Colorado.
- Thomas, K. A., M. L. McTeague, L. Ogden, M. L. Floyd, K. Schulz, B. Friesen, T. Fancher, R. Waltermire, and A. Cully. 2009. Vegetation classification and distribution mapping report: Mesa Verde National Park. Natural Resource Report NPS/SCPN/NRR—2009/112. National Park Service, Fort Collins, Colorado.
- Thomas, L.P., M.N. Hendrie (editor), C.L. Lauver, S.A. Monroe, N.J. Tancreto, S.L. Garman, and M.E. Miller. 2006. Vital Signs Monitoring Plan for the Southern Colorado Plateau Network. Natural Resource Report NPS/SCPN/NRR-2006/002. National Park Service, Fort Collins, Colorado.
- Tillman, F.D., S. Gangopadhyay, and T. Pruitt. 2020. Recent and projected precipitation and temperature changes in the Grand Canyon area with implications for groundwater resources. *Scientific Reports* 10: 19740.
- Ulrich, W., M. Olrik, and K.I. Ugland. 2010. A meta-analysis of species-abundance distributions. *Oikos* 119: 1149–1155.
- Ulrich, W., S. Soliveres, A.D. Thomas, A.J. Dougill, and F.T. Maestre. 2016. Environmental correlates of species rank – abundance distributions in global drylands. *Perspectives in Plant Ecology, Evolution and Systematics* 20: 56-64.
- Urza, A.K., P.J. Weisberg, and T. Dilts. 2020. Evidence of widespread topoclimatic limitation for lower treelines of the Intermountain West, United States. *Ecological Applications* 30: e02158.
- USDA-NRCS. 2003. National range and pasture handbook. U.S. Department of Agriculture, Washington, D.C.
- USDA-NRCS and USDOI-NPS. 2015. Soil survey of Wupatki National Monument, Arizona.
- USNVC (United States National Vegetation Classification) Database, Version 2.02. 2023. Federal Geographic Data Committee, Vegetation Subcommittee. Washington D.C. Accessed 02/13/2023.

- Vankat, J.L. 2006. Montane and subalpine terrestrial ecosystems of the Southern Colorado Plateau—literature review and conceptual models. Supplement II to Vital Signs Monitoring Plan for the Southern Colorado Plateau Network. Natural Resource Report NPS/SCPN/NRR-2006/002. National Park Service, Fort Collins, Colorado.
- Vankat, J.L. 2017. Post-1935 changes in pinyon-juniper persistent woodland on the South Rim of Grand Canyon National Park, Arizona, USA. *Forest Ecology and Management* 394: 73-85.
- Walker, B., A. Kinzig, and J. Langridge. 1999. Plant attribute diversity, resilience, and ecosystem function: The nature and significance of dominant and minor species. *Ecosystems* 2: 95-113.
- Wehner, M.F., J.R. Arnold, T. Knutson, K.E. Kunkel, and A.N. LeGrande. 2017: Droughts, floods, and wildfires. In: *Climate Science Special Report: Fourth National Climate Assessment, Volume I* [Wuebbles, D.J., D.W. Fahey, K.A. Hibbard, D.J. Dokken, B.C. Stewart, and T.K. Maycock (eds.)]. U.S. Global Change Research Program, Washington, DC, USA, pp. 231-256.
- Wertin, T.M., S.C. Reed, and J. Belnap. 2015. C₃ and C₄ plant responses to increased temperatures and altered monsoonal precipitation in a cool desert on the Colorado Plateau, USA. *Oecologia* 177: 997-1013.
- Whiteman, CD, S. Zhong, and X Bian. 1999. Wintertime boundary layer structure in the Grand Canyon. *Journal of Applied Meteorology and Climatology* 38:1084-1102.
- Williams, A.P., C.D. Allen, A.K. Macalady, D. Griffin, C.A. Woodhouse, D.M. Meko, T.W. Swetnam, S.A. Rauscher, R. Seager, H.D. Grissino-Mayer, and J.S. Dean. 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change* 3(3): 292-297.
- Williams, A.P., E.R. Cook, J.E. Smerdon, B.I. Cook, J.T. Abatzoglou, K. Bolles, and Livneh, B. 2020. Large contribution from anthropogenic warming to an emerging North American megadrought. *Science* 368: 314-318.
- Yang, Z., X. Liu, M. Zhou, D. Ai, G. Wang, Y. Wang, and J.T. Lundholm. 2015. The effect of environmental heterogeneity on species richness depends on community position along the environmental gradient. *Nature Scientific Reports* 5: 15723.

Appendix A. Sampling Methods Detail

Table 12 shows the cover class scale and Table 13 shows soil texture by soil texture class observed during this study.

Table 12. Cover class scale for estimating foliar cover.

Cover Class	Cover Range	Midpoint
1	< 0.1%	0.05%
2	0.1 to 0.5%	0.30%
3	>0.5 to 1%	0.75%
4	>1 to 2%	1.5%
5	>2 to 5%	3.5%
6	>5 to 10%	7.5%
7	>10 to 15%	12.5%
8	>15 to 25%	20%
9	>25 to 35%	30%
10	>35 to 50%	42.5%
11	>50 to 75%	62.5%
12	>75 to 100%	87.5%

Table 13. Soil texture as assigned by texture class (Moeys 2018); with slight modification (re-ordering of Si and SaLo) to conform to current NRCS soil texture groups (Soil Science Division Staff 2017).

Texture Class	Abbreviation	Name	Soil Texture Group
1	Cl	clay	fine textured
2	SiCl	silty clay	fine textured
3	SaCl	sandy clay	fine textured
4	ClLo	clay loam	moderately fine textured
5	SiClLo	silty clay loam	moderately fine textured
6	SaClLo	sandy clay loam	moderately fine textured
7	Lo	loam	medium textured
8	SiLo	silty loam	medium textured
9	Si	silt	medium textured
10	SaLo	sandy loam	moderately coarse textured
11	LoSa	loamy sand	coarse textured
12	Sa	sand	coarse textured

Appendix B. Comparing Alternative Species Abundance Datasets for the BAND-P Ecosite

Figure 19 shows the Non-metric Multidimensional Scaling (NMDS) used for this study.

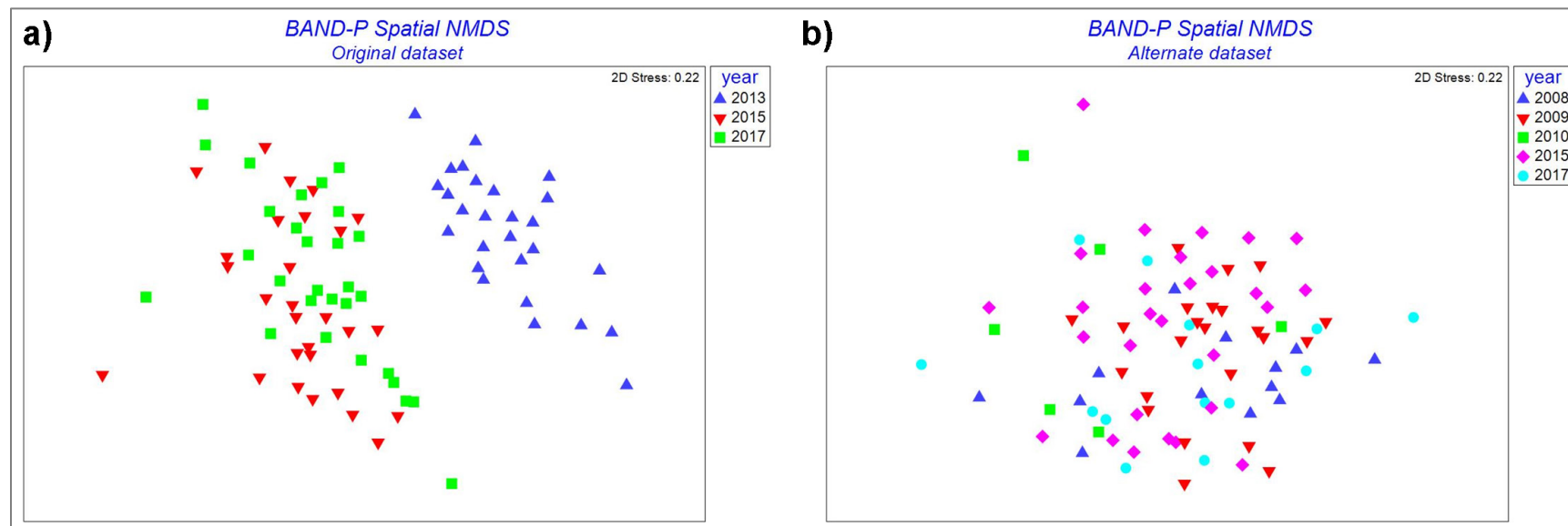


Figure 19. Non-metric Multidimensional Scaling (NMDS) plots for the BAND-P ecosite from the 2012–2017 time period and from an alternate temporal dataset. To describe spatial variability across the full complement of plots within an ecosite, I averaged species abundance data from the two initial years of sampling for each plot for the 2012–2017 time period. However, as seen in the NMDS plot on the left, 2013 was distinct from other years for the BAND-P ecosite. Consequently, I used an alternate dataset for this ecosite, substituting data from 2008–2010 for the 2013 data. The NMDS plot for the alternate dataset on the right shows no marked differences among years and was used for all analyses. NPS / LISA THOMAS

Appendix C. Historical and Projected Soil Water Potential across Seven Study Areas

Figures 20 through 26 depict historical conditions (A) and future projections (B) for soil water potential (SWP) at intermediate soil depths (20–50 cm) for three seasons: fall/winter (October–February), spring (March–June), and summer (July–September) for the seven ecosite study areas. Panel A shows historical annual variability (fine lines) and moving 10-year averages (thick lines) of drying and wetting from 1915–2010. Panel B compares variability amongst years for three time periods, current (C; 1970–2010), near future (N; 2020–2059), and long-term future (L; 2060–2099), grouped by season. Boxplot whiskers are 1.5 times the inter-quartile range of values, while dots are values outside this range. Dashed lines in both panels highlight plant-relevant SWP levels: traditional wilting point (-1.5 MPa) and a drylands wilting point (-3.0 MPa; Kolb and Sperry 1999a, 1999b). These graphs are reprinted from Andrews et al. 2019, 2020.

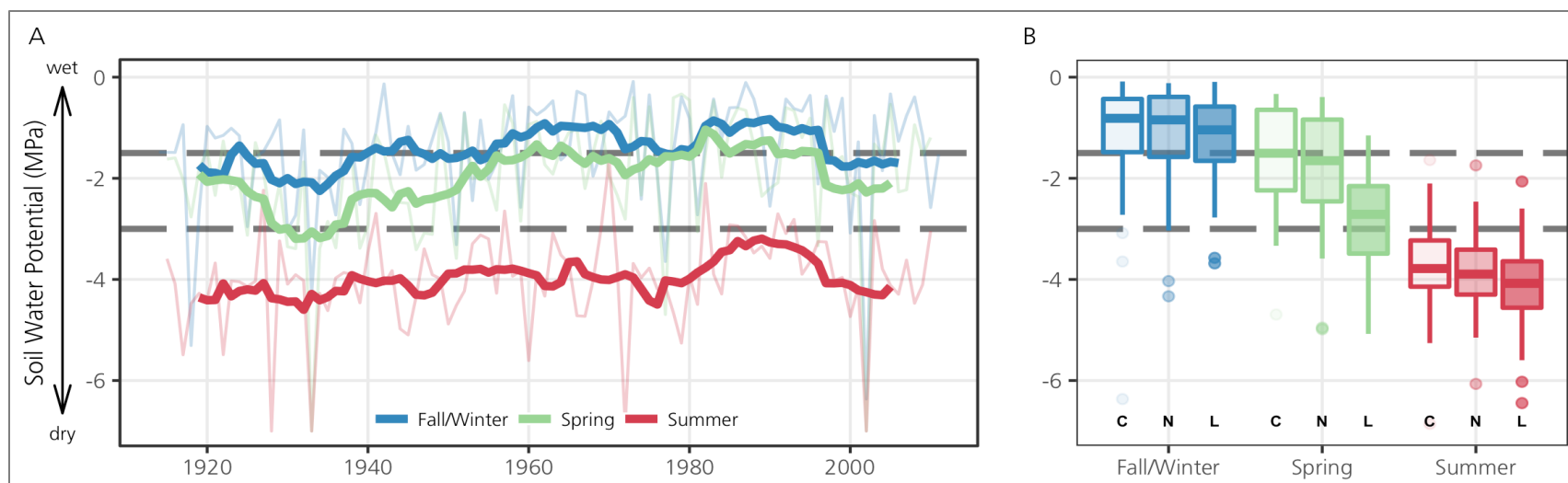


Figure 20. Historical (A) and projected (B) soil water potential for the MEVE-L ecosite. NPS / CAITLIN ANDREWS

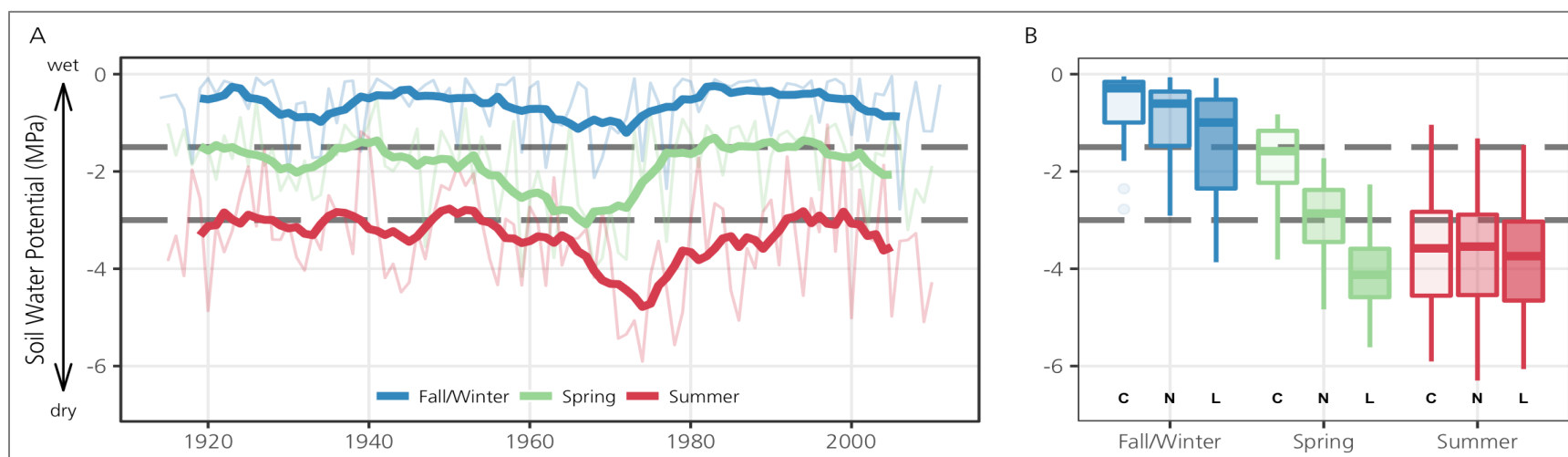


Figure 21: Historical (A) and projected (B) soil water potential for the GRCA-P ecosite. NPS / CAITLIN ANDREWS

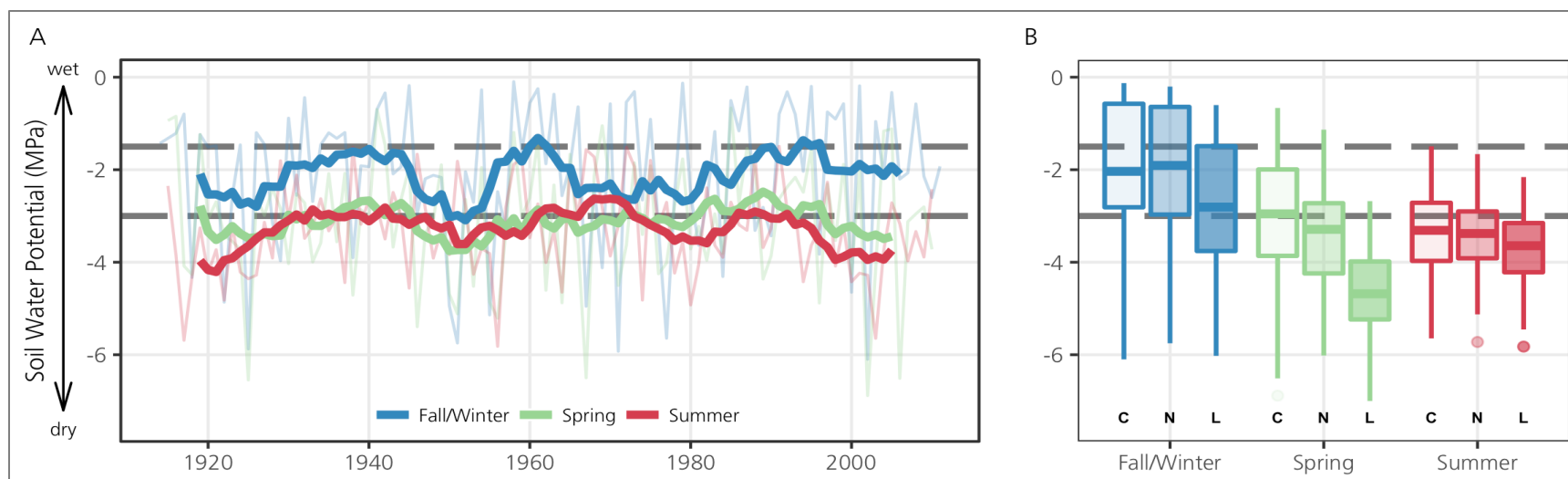


Figure 22: Historical (A) and projected (B) soil water potential for the BAND-P ecosite. NPS / CAITLIN ANDREWS

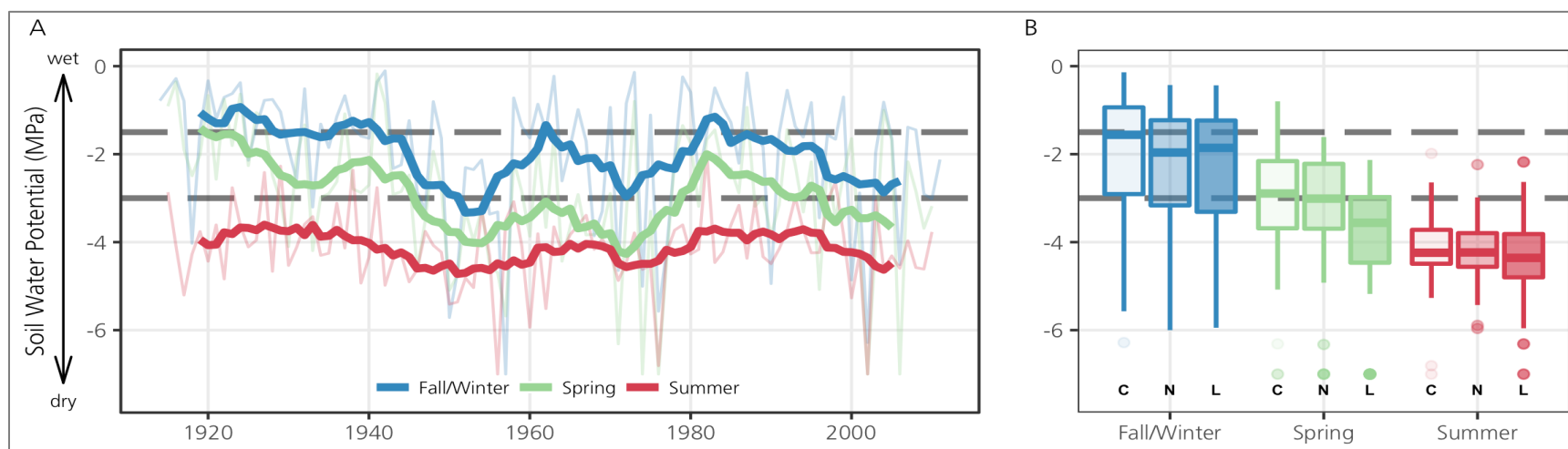


Figure 23: Historical (A) and projected (B) soil water potential for the CHCU-S ecosite. NPS / CAITLIN ANDREWS

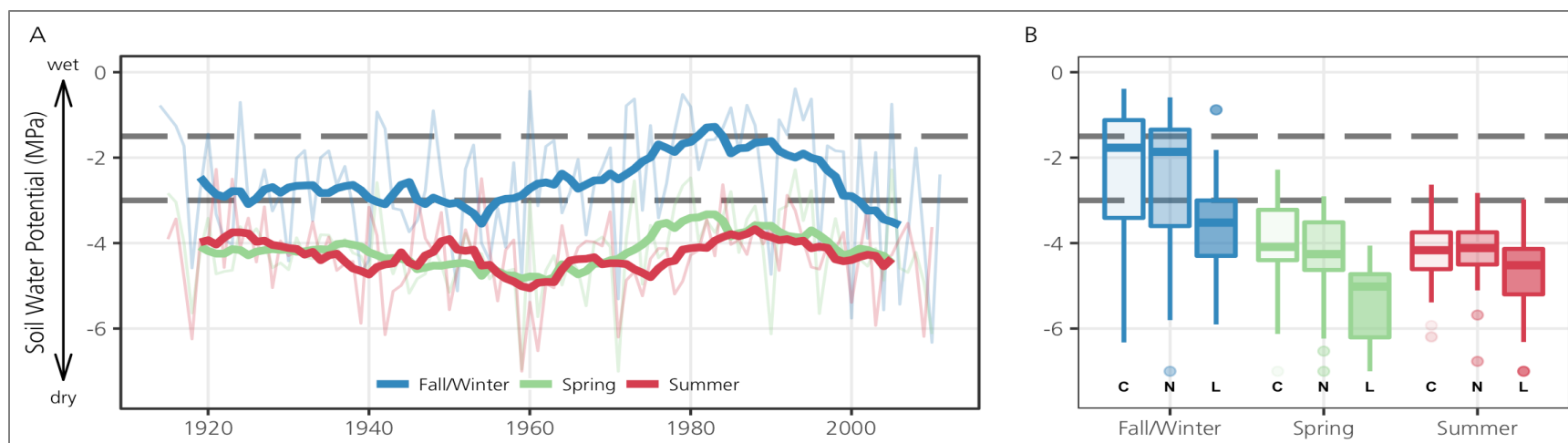


Figure 24: Historical (A) and projected (B) soil water potential for the PEFO-C ecosite. NPS / CAITLIN ANDREWS

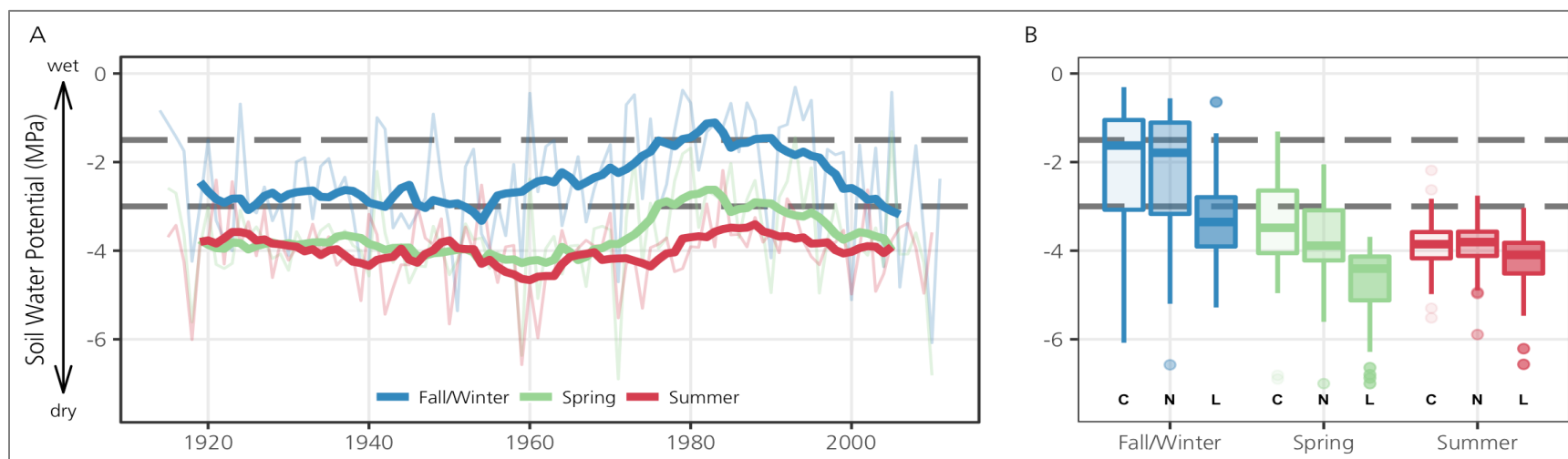


Figure 25: Historical (A) and projected (B) soil water potential for the PEFO-S ecosite. NPS / CAITLIN ANDREWS

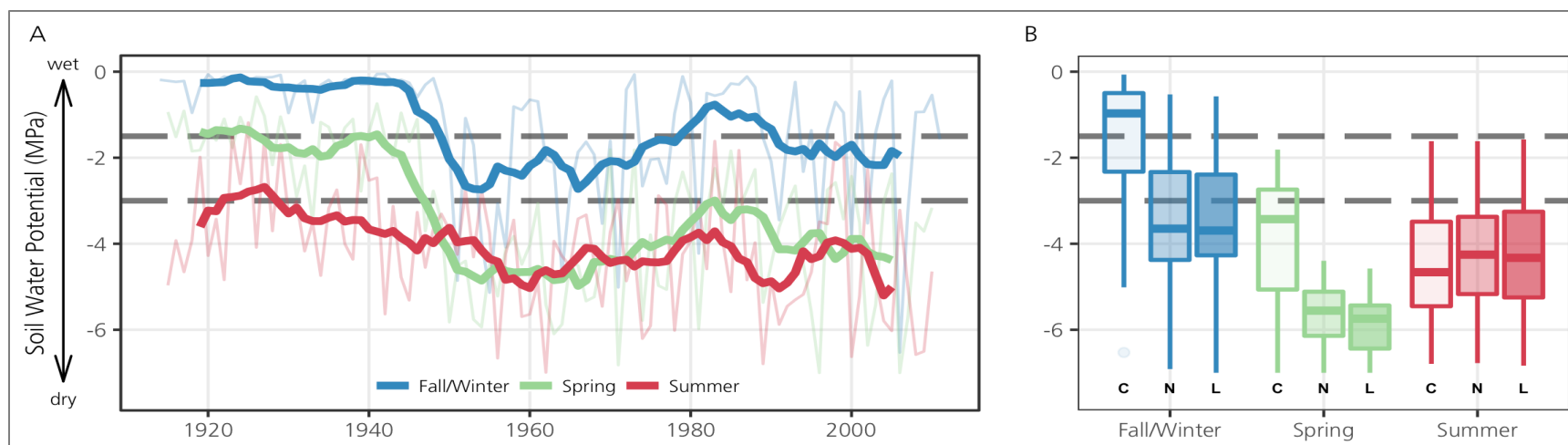


Figure 26: Historical (A) and projected (B) soil water potential for the WUPA-L ecosite. NPS / CAITLIN ANDREWS

Literature Cited

Note that Figures 20 to 26 were reprinted from the following publications:

Andrews, C., J. Bradford, J. Norris, J. Gremer, M. Duniway, S. Munson, L. Thomas, and M. Swan. 2020. Describing trends in past and future soil moisture in the loamy mesa-top pinyon-juniper woodland ecosystem in Mesa Verde National Park. Natural Resource Report NPS/MEVE/NRR—2020/2116. National Park Service, Fort Collins, Colorado.

Andrews, C., J. Bradford, J. Norris, J. Gremer, M. Duniway, S. Munson, L. Thomas, and M. Swan. 2020. Describing trends in past and future soil moisture in the pinyon-juniper woodland ecosystem in Grand Canyon National Park. Natural Resource Report NPS/GRCA/ NRR—2020/2115. National Park Service, Fort Collins, Colorado.

Andrews, C., J. Bradford, J. Norris, J. Gremer, M. Duniway, S. Munson, L. Thomas, and M. Swan. 2020. Describing trends in past and future soil moisture in the mesa-top pinyon-juniper woodland ecosystem in Bandelier National Monument. Natural Resource Report NPS/ BAND/NRR—2020/2114. National Park Service, Fort Collins, Colorado.

Andrews, C., J. Bradford, J. Norris, J. Gremer, M. Duniway, S. Munson, L. Thomas, and M. Swan. 2019. Describing trends in past and future soil moisture in the sandy loam upland grassland ecosystem in Chaco Culture National Historical Park. Natural Resource Report NPS/CHCU/NRR—2019/1998. National Park Service, Fort Collins, Colorado.

Andrews, C., J. Bradford, J. Norris, J. Gremer, M. Duniway, S. Munson, L. Thomas, and M. Swan. 2019. Describing trends in past and future soil moisture in the clayey fan grassland ecosystem in Petrified Forest National Park. Natural Resource Report NPS/PEFO/NRR— 2019/1993. National Park Service, Fort Collins, Colorado.

Andrews, C., J. Bradford, J. Norris, J. Gremer, M. Duniway, S. Munson, L. Thomas, and M. Swan. 2019. Describing trends in past and future soil moisture in the sandy loam upland grassland ecosystem in Petrified Forest National Park. Natural Resource Report NPS/PEFO/ NRR—2019/1992. National Park Service, Fort Collins, Colorado.

Andrews, C., J. Bradford, J. Norris, J. Gremer, M. Duniway, S. Munson, L. Thomas, and M. Swan. 2019. Describing trends in past and future soil moisture in the Loamy Upland Shrubland ecosystem in Wupatki National Monument. Natural Resource Report NPS/ WUPA/NRR—2019/1994. National Park Service, Fort Collins, Colorado.

Appendix D. Climate Variables Used in dbRDA Analysis to Model Relationships with Across-Ecosite Composition Gradients

Figure 27 shows box plots of the climate variables used in this study.

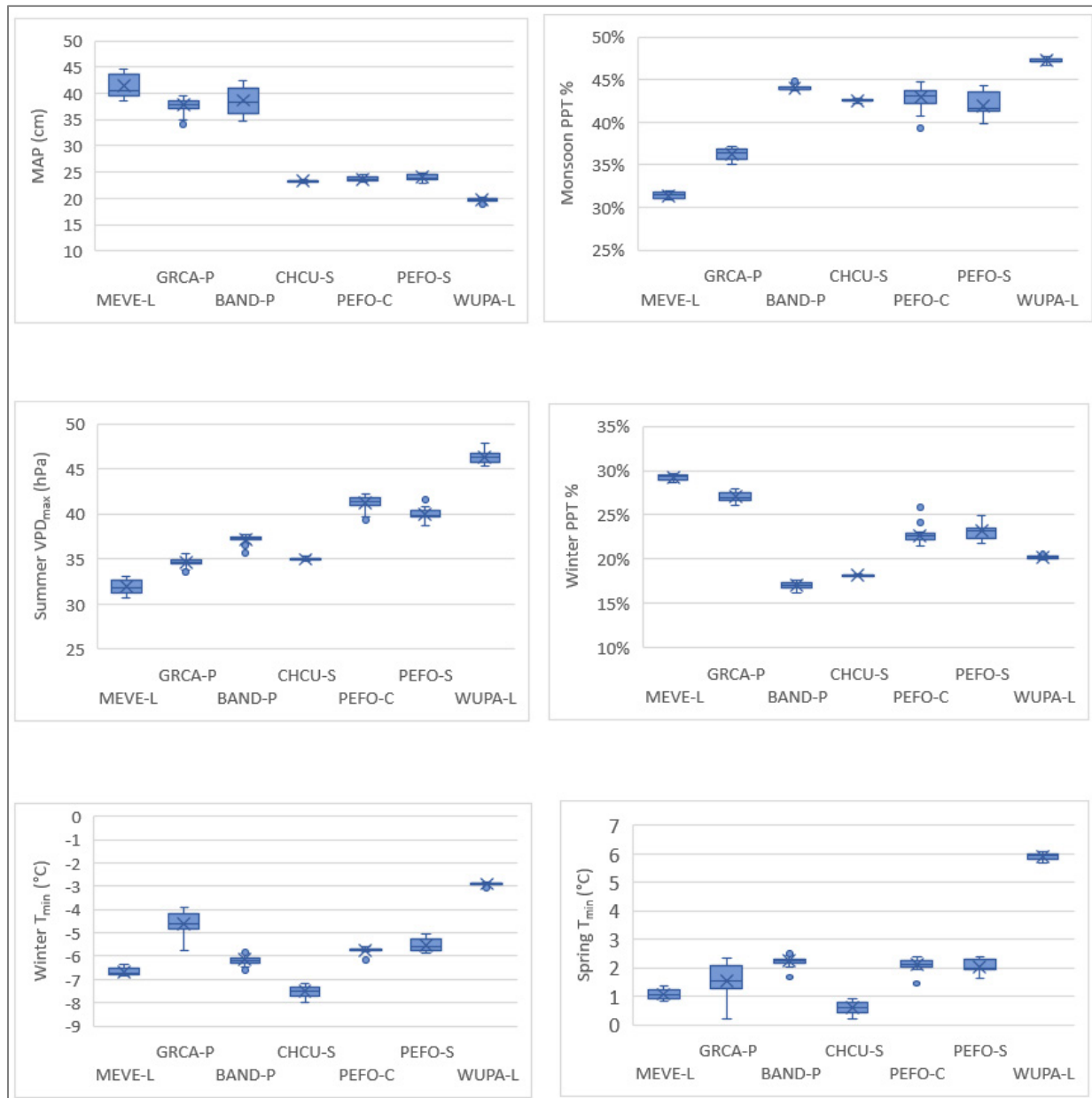


Figure 27. Box plots of climate variables across the seven ecosites. Climate data are derived from the PRISM 800-m 30-year normal dataset for 1981–2010 (PRISM Climate Group, OSU). Climate variables are mean annual precipitation (MAP), monsoon precipitation percentage (PPT %), summer vapor pressure deficit maximum (VPDmax), winter precipitation percentage (PPT %), winter temperature minimum (Tmin) and spring temperature minimum (Tmin). NPS / LISA THOMAS

Appendix E: Results Detail for Individual Study Areas— Figures, Tables and Notes

The details for individual study areas can be seen in Figures 28 through 36 and Tables 14 through 16.

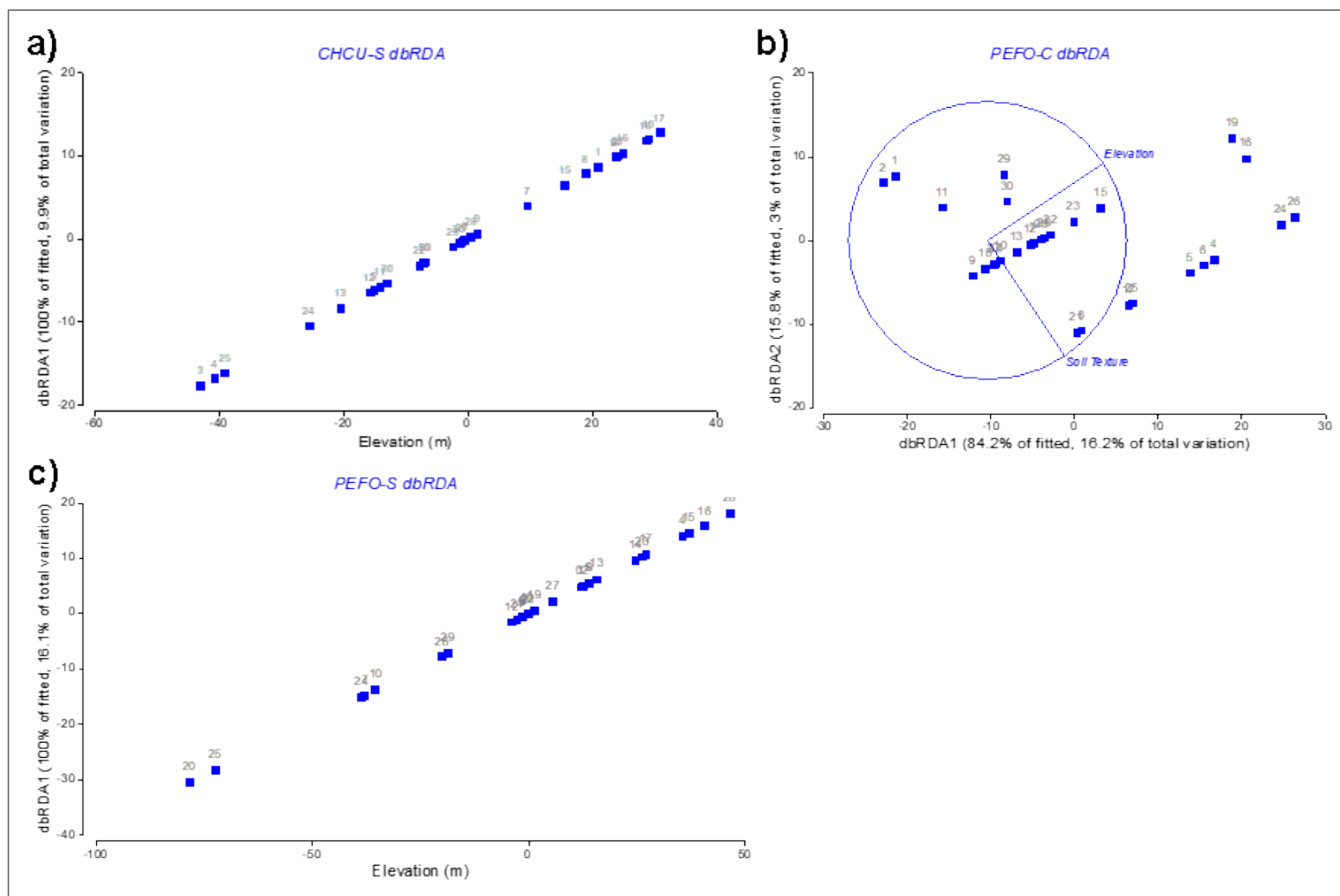


Figure 28. Results of distance-based Redundancy Analysis (dbRDA) to model relationship between species matrices and significant environmental variables for CHCU-S, PEFO-C, and PEFO-S. In figure b, blue lines indicate significant environmental vectors. NPS / LISA THOMAS

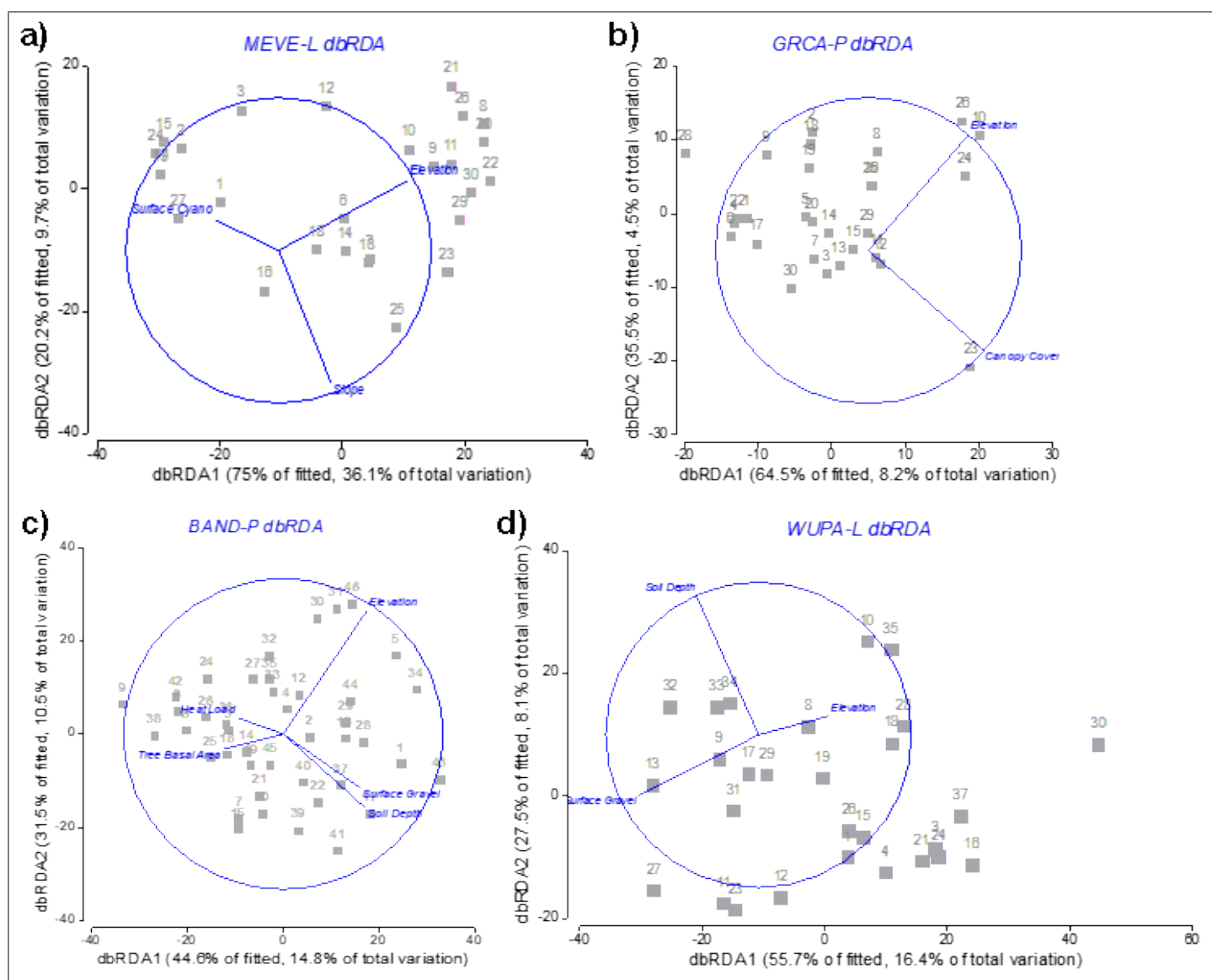


Figure 29. Results of distance-based Redundancy Analysis (dbRDA) to model relationship between species matrices and environmental variables for MEVE-L, GRCA-P, BAND-P and WUPA-L. Blue lines indicate significant environmental vectors. NPS / LISA THOMAS

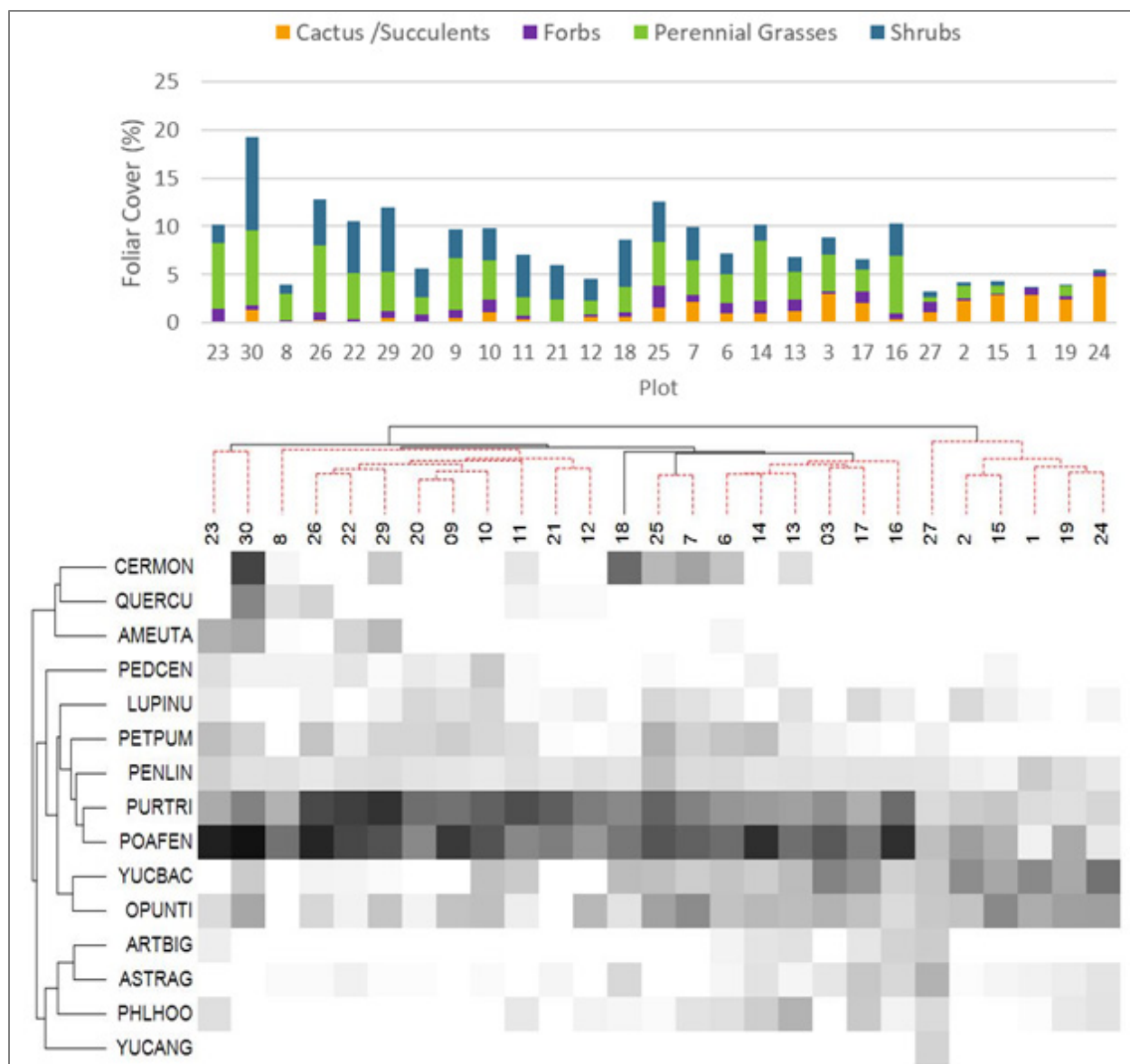


Figure 30. Functional Group Cover (top) and Clustered Shade Plots (bottom) for MEVE-L. Solid black lines in the plot dendrogram (bottom) indicate significant plot clusters (5% significance level). The species composition of significant plot clusters is compared to vegetation associations as described in the park's vegetation mapping report (Thomas et al. 2009). Several significant plot clusters are evident, all aligning with the *Pinus edulis* – (*Juniperus osteosperma*)/*Purshia tridentata* Woodland association (describing equal abundance of *Poa fendleriana* and *Purshia tridentata*). The large cluster on the left cluster (21 plots) exhibits turnover in forb/shrub occurrence as well as a gradient of *Purshia tridentata* and *Poa fendleriana* co-dominance. In the righthand cluster of six plots, understory cover is lower and is dominated by *Yucca baccata* and *Opuntia* spp. NPS / LISA THOMAS

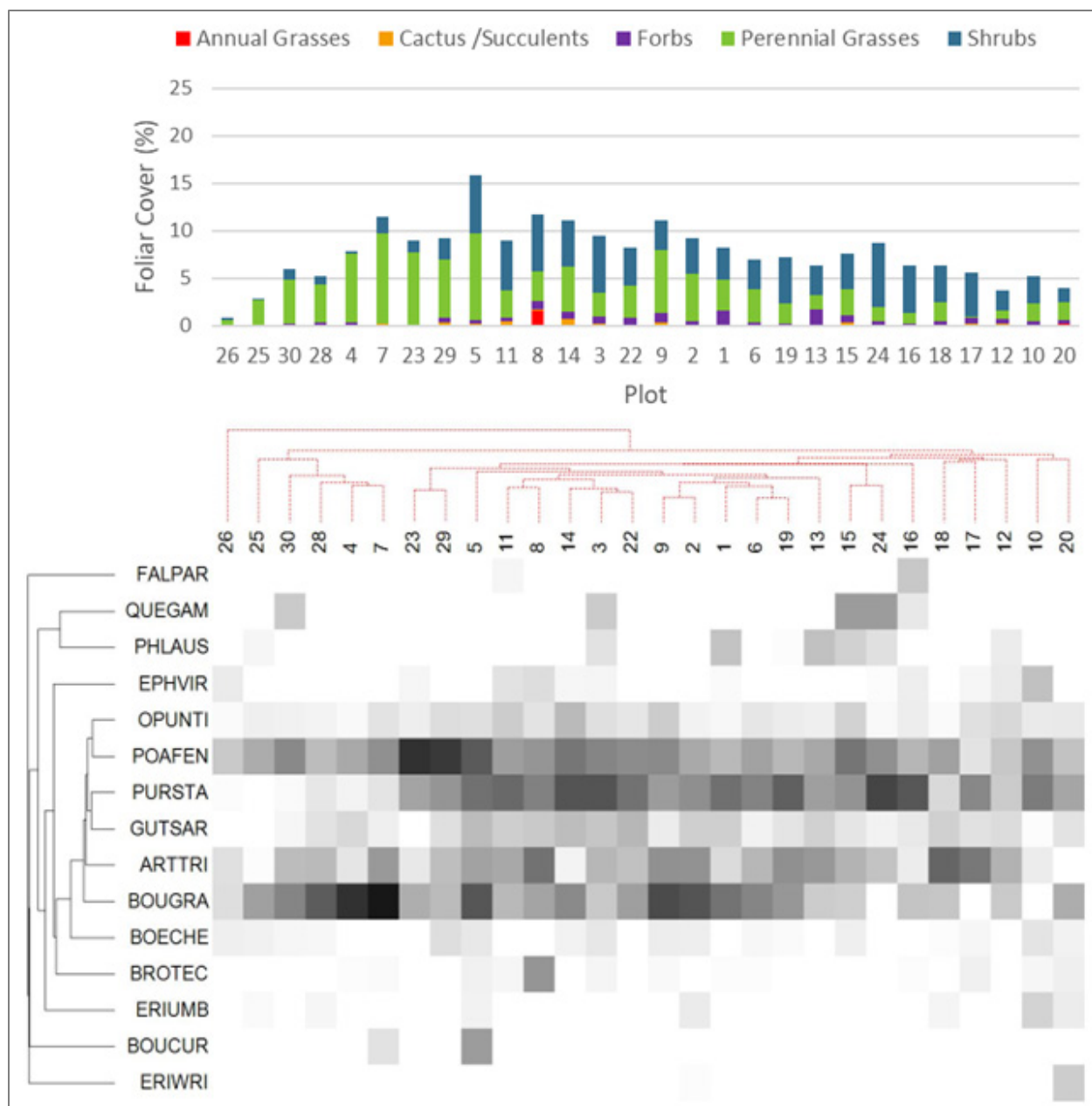


Figure 31. Functional Group Cover (top) and Clustered Shade Plot (bottom) for GRCA-P. The absence of solid black lines in the plot dendrogram (bottom) indicates no significant clustering (5% significance level). Subtle gradients in abundance among the co-dominant species (*Purshia stansburiana*, *Poa fendleriana* and *Bouteloua gracilis*) are evident. The species composition of significant plot clusters is compared to vegetation associations as described in the park's vegetation mapping report (Kearsley et al. 2015). All plots align with the *Pinus edulis* – *Juniperus osteosperma* / *Purshia stansburiana* Woodland association. NPS / LISA THOMAS

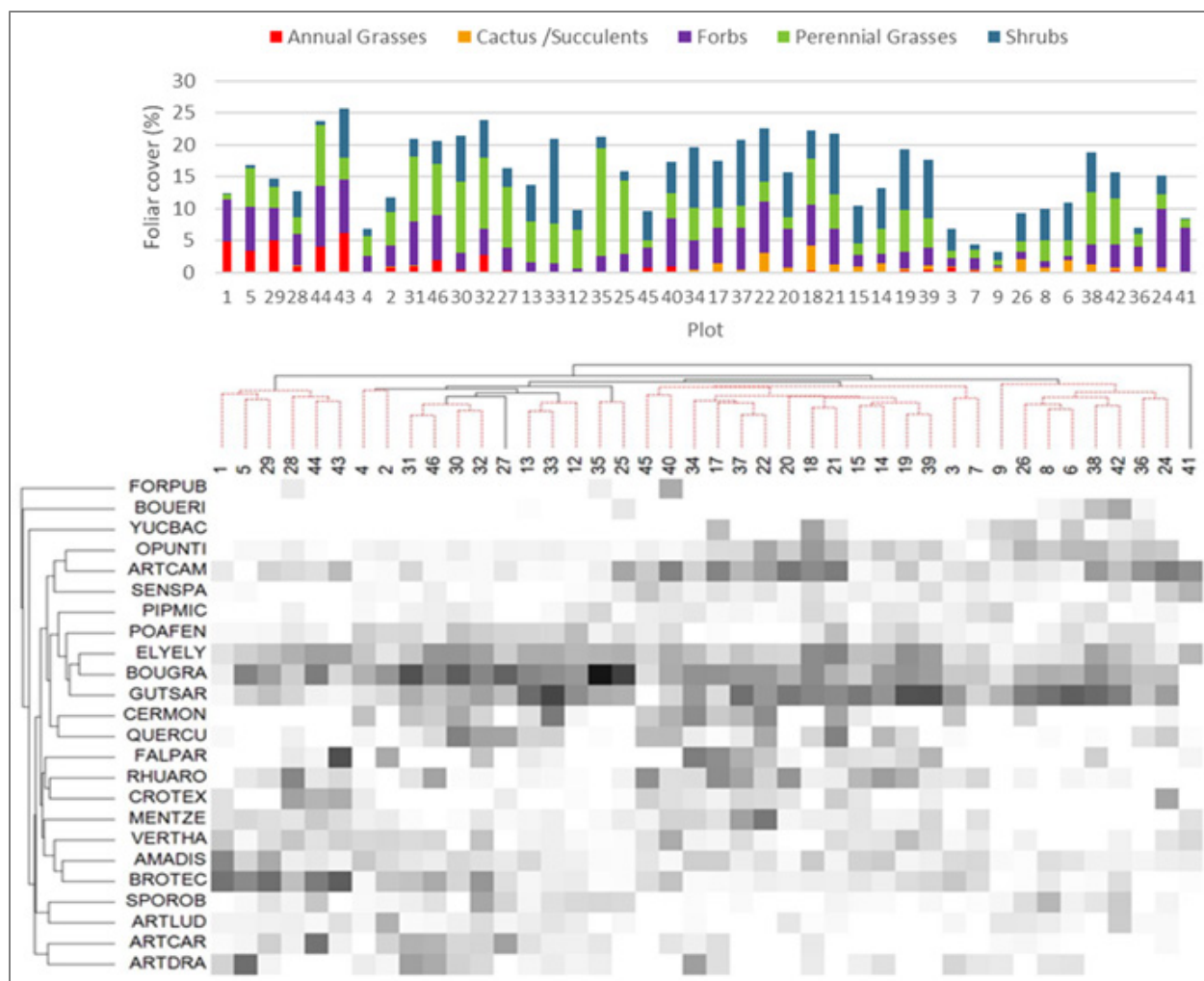


Figure 32. Functional Group Cover (top) and Clustered Shade Plots (bottom) for BAND-P. Solid black lines in the plot dendrogram indicate significant plot clusters (5% significance level). The species composition of significant plot clusters is compared to vegetation associations as described in the park's vegetation mapping report (Muldavin et al. 2011). Four main clusters are evident in the plot dendrogram. The left cluster of six plots correspond to *Juniperus monosperma*/*Bouteloua gracilis* Woodland, but with dominance by *Bromus tectorum*, an invasive exotic species. The second cluster of 12 plots also aligns with the *Juniperus monosperma*/*Bouteloua gracilis* Woodland. The third cluster of 15 plots corresponds to the *Juniperus monosperma*/*Quercus x pauciloba* Woodland, described by Muldavin as occurring on stony soils. Finally, the fourth cluster of eight plots aligns with the *Juniperus monosperma* Rockland/Woodland association, characterized by low understory cover and shallow soils. NPS / LISA THOMAS

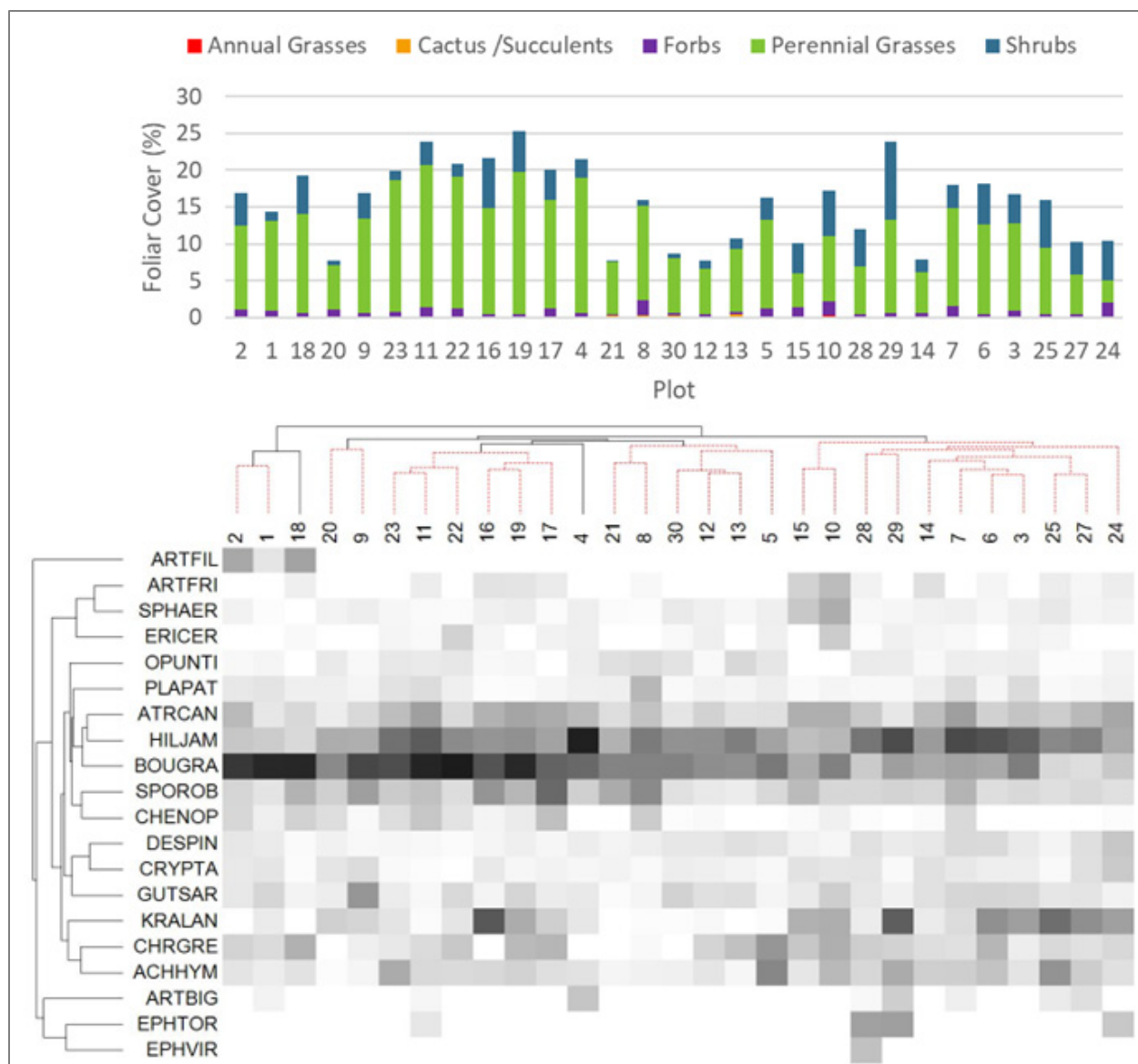


Figure 33. Functional Group Cover (top) and Clustered Shade Plots (bottom) for CHCU-S. Solid black lines in the plot dendrogram indicate significant plot clusters (5% significance level). The species composition of significant plot clusters is compared to vegetation associations as described in the park's vegetation mapping report (Salas et al. 2011). The dendrogram indicates five main plot clusters, with all aligning most closely to the *Atriplex canescens* – *Krascheninnikovia lanata* Shrubland association. A gradient of *Hilaria jamesii* / *Bouteloua gracilis* dominance is apparent, as well as turnover or abundance gradients in subdominant grass and shrub species. The CHCU-S ecosite exhibits a more subtle compositional gradient than most of the other ecosites. NPS / LISA THOMAS

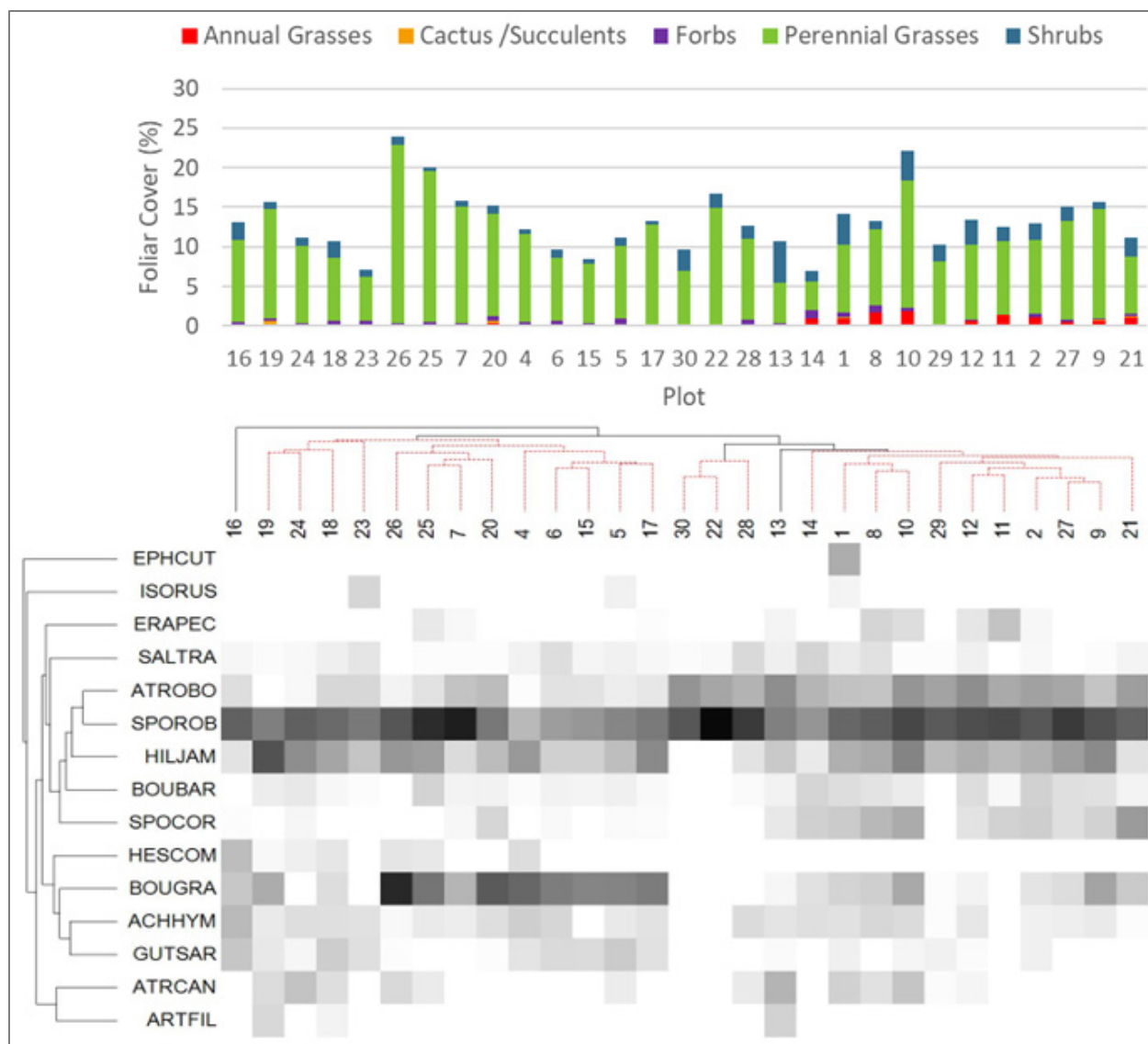


Figure 34. Functional Group Cover (top) and Clustered Shade Plots (bottom) for PEFO-C. Solid black lines in the plot dendrogram indicate significant plot clusters (5% significance level). The species composition of significant plot clusters is compared to vegetation associations as described in the park's vegetation mapping report (Thomas et al. 2009). The two main plot clusters translate to two described associations. The cluster of 13 plots on the left aligns most closely with the *Sporobolus airoides* – *Bouteloua gracilis* Herbaceous association. The cluster of 15 plots on the right corresponds to the *Atriplex obovata*/*Sporobolus airoides* – *Hilaria jamesii* Shrub Herbaceous association. Thomas (2009) cites this association as also occurring in Chihuahuan Desert swales or depressions. NPS / LISA THOMAS

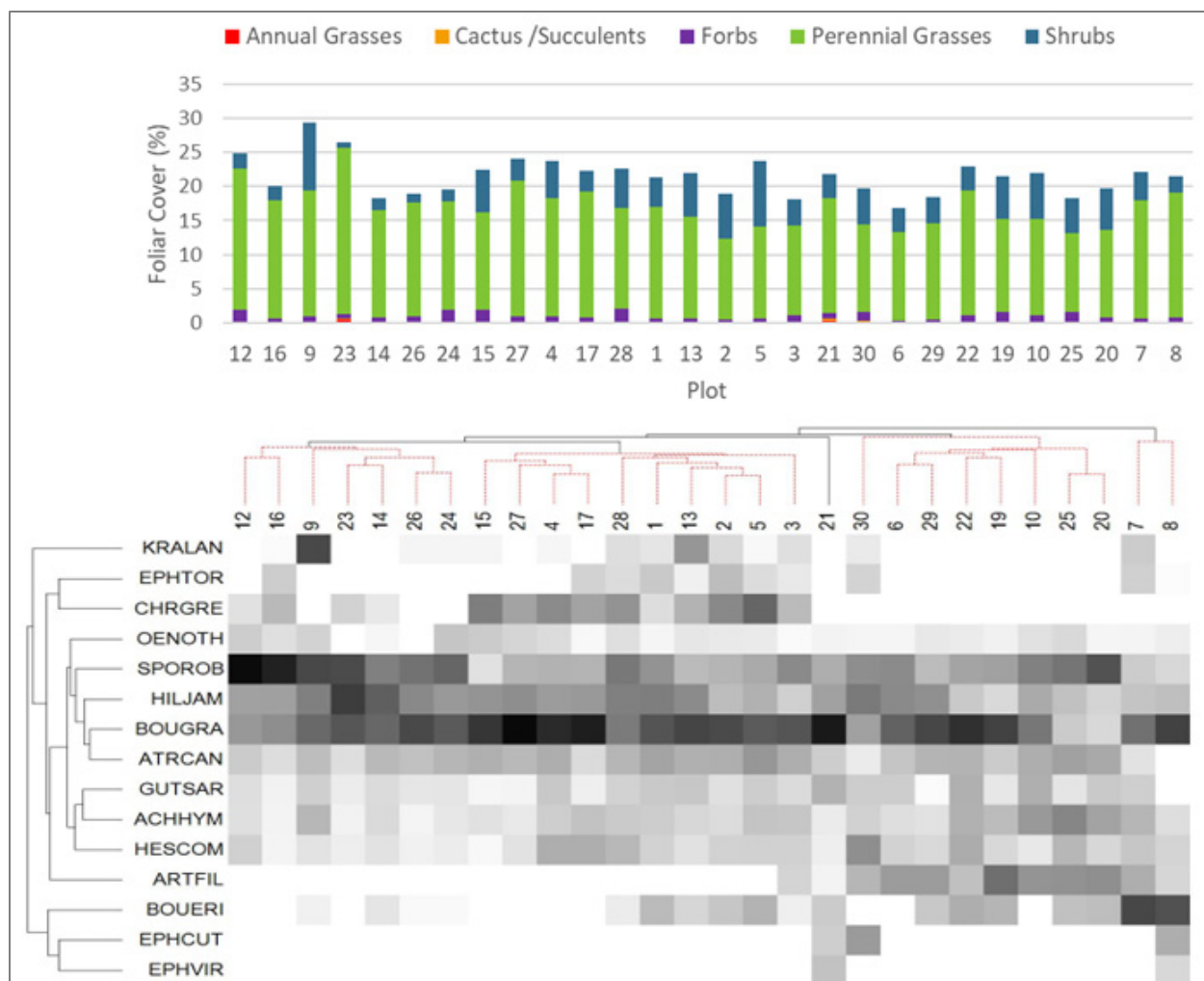


Figure 35. Functional Group Cover (top) and Clustered Shade Plots (bottom) for PEFO-S. Solid black lines in the plot dendrogram indicate significant plot clusters (1% significance level). The species composition of significant plot clusters is compared to vegetation associations as described in the park's vegetation mapping report (Thomas et al. 2009). The four main clusters translate to three named associations. The seven plots on the left correspond most closely to the *Sporobolus airoides* – *Bouteloua gracilis* Herbaceous association. The middle cluster of 10 plots aligns with the *Bouteloua gracilis* Herbaceous association (showing a strong *Chrysothamnus Greenei* component). The two clusters on the right (10 plots) align with the *Artemisia filifolia/Bouteloua eriopoda* Shrub Herbaceous association which can include *Bouteloua gracilis* as a co-dominant. The PEFO-S ecosite exhibits a more subtle compositional gradient than most of the other ecosites. Two of the three associations (*A. filifolia/B. eriopoda* and *S. airoides* – *B. gracilis*) are cited by Thomas (2009) as also occurring in Chihuahuan Desert basins or swales. NPS / LISA THOMAS

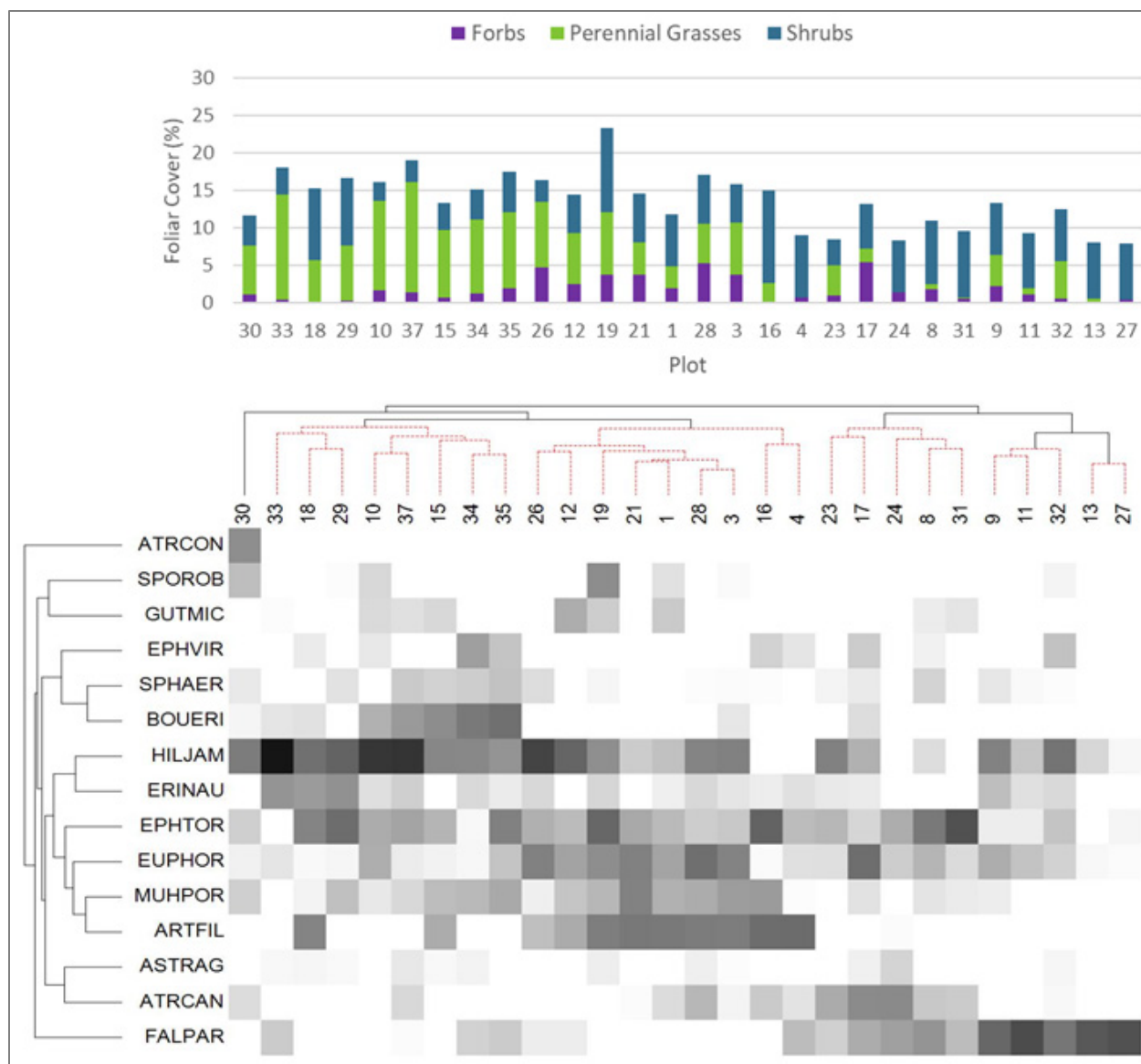


Figure 36. Functional Group Cover (top) and Clustered Shade Plots (bottom) for WUPA-L. Solid black lines in the plot dendrogram indicate significant plot clusters (5% significance level). The species composition of significant plot clusters is compared to vegetation associations as described in the park's vegetation mapping report (Hansen et al. 2004). Four main clusters can be seen in the shade plot which translates to three described associations. The left cluster of eight plots corresponds to the *Bouteloua eriopoda* – *Hilaria jamesii* Herbaceous association. The middle cluster of nine plots aligns with the *Artemisia filifolia* – *Ephedra (torreyana, viridis)* Shrubland association. The cluster of 10 plots on the right corresponds to the *Fallugia paradoxa* – (*Atriplex canescens* – *Ephedra torreyana*) Shrubland association. Hansen (2004) notes that the presence of *B. eriopoda* and *Muhlenbergia porteri* in the *B. eriopoda* – *H. jamesii* association suggests this grassland is transitional to Chihuahuan Desert grasslands. NPS / LISA THOMAS

Table 14. National Vegetation Classification (NVC) associations identified in seven study areas, and their U.S. distributions. The species composition of significant plot clusters was compared to vegetation associations described in each park’s vegetation mapping report, using the map, map class keys, and association descriptions to determine a match. Distribution descriptions and association codes were drawn from the USNVC database (USNVC 2023).

Study Area	NVCS Vegetation Association	U.S. Distribution
MEVE-L	<i>Pinus edulis</i> – (<i>Juniperus osteosperma</i>)/ <i>Purshia tridentata</i> Woodland (CEGL000789)	Sandia & Jemez ranges in New Mexico, Mesa Verde NP, the high plateaus of southern Utah & Dinosaur NM
GRCA-P	<i>Pinus edulis</i> – <i>Juniperus osteosperma</i> /Purshia stansburiana Woodland (CEGL000782)	on the Colorado Plateau of central Arizona, western New Mexico, southwestern Colorado and southern Utah
BAND-P	<i>Juniperus monosperma</i> /Bouteloua gracilis Woodland (CEGL000710)	Rocky Mountains woodland occurring in foothills of south-central Colorado & northern New Mexico, extending into southwestern Great Plains, extending westward into southeast portion of Colorado Plateau and southward into south central New Mexico
	<i>Juniperus monosperma</i> /Quercus x pauciloba Woodland (CEGL000721)	in Rocky Mountains in central New Mexico, and locally in northern New Mexico and southeastern Colorado
	<i>Juniperus monosperma</i> Rockland Woodland (CEGL005369)	only described for Bandelier NM
CHCU-S	<i>Atriplex canescens</i> – <i>Krascheninnikovia lanata</i> Shrubland (CEGL001285)	Colorado and New Mexico; Nevada and California
PEFO-C	<i>Atriplex obovata</i> /Sporobolus airoides – <i>Hilaria jamesii</i> Shrub Herbaceous (CEGL001775)	alluvial flats in the southern Colorado Plateau in northwestern New Mexico and adjacent Arizona
	<i>Sporobolus airoides</i> – <i>Bouteloua gracilis</i> Herbaceous (CEGL001686)	northern Chihuahuan Desert in south-central New Mexico and in the southern Colorado Plateau in northwestern New Mexico and northern Arizona
PEFO-S	<i>Artemisia filifolia</i> /Bouteloua eriopoda Shrub Herbaceous (CEGL001077)	northern Chihuahuan Desert in south-central New Mexico and at Petrified Forest NP in the southern Colorado Plateau
	<i>Bouteloua gracilis</i> Herbaceous (CEGL001760)	Arizona, Colorado, New Mexico, Utah and Wyoming
	<i>Sporobolus airoides</i> – <i>Bouteloua gracilis</i> Herbaceous (CEGL001686)	northern Chihuahuan Desert in south-central New Mexico and on the southern Colorado Plateau in northwestern New Mexico and northern Arizona
WUPA-L	<i>Bouteloua eriopoda</i> – <i>Hilaria jamesii</i> Herbaceous (CEGL001751)	on the Colorado Plateau from northern Arizona and northwestern New Mexico and locally in Capitol Reef NP; extending south to central New Mexico (transition zone with northern Chihuahuan Desert) & west into eastern Mojave Desert of California and Nevada; may also be found in Mexico

Table 14 (continued). National Vegetation Classification (NVC) associations identified in seven study areas, and their U.S. distributions. The species composition of significant plot clusters was compared to vegetation associations described in each park's vegetation mapping report, using the map, map class keys, and association descriptions to determine a match. Distribution descriptions and association codes were drawn from the USNVC database (USNVC 2023).

Study Area	NVCS Vegetation Association	U.S. Distribution
WUPA-L (continued)	<i>Artemisia filifolia</i> – <i>Ephedra (torreyana, viridis)</i> Shrubland (CEGL002786)	on the Colorado Plateau from southeastern Utah and northern Arizona
	<i>Fallugia paradoxa</i> – (<i>Atriplex canescens</i> – <i>Ephedra torreyana</i>) Shrubland (CEGL005806)	only described for Wupatki and Sunset Crater Volcano NMs in Arizona

Table 15. Major plot cluster for WUPA-L ecosite in relation to closest matching NVC association from the Vegetation Mapping Report (Hansen et al. 2004). Plot-based soil measures and the Wupatki NM Soil Survey (USDA-NRCS and DOI-NPS 2015) were used to estimate the Ecological Site and Predominant Soil Series for each cluster.

Cluster	Number of Plots	Closest NVC Association	Predominant Elevation (m)	Predominant Soil Characteristics	Ecological Site
a	8	<i>Bouteloua eriopoda</i> – <i>Hilaria jamesii</i> Herbaceous ^A	1410–1460	moderately deep to deep, sandy loam, surface very dark gray to dark grayish brown	Loamy Upland (mixed parent materials phase), parent material is igneous tephra rock, Moenkopi Formation sandstone, and Kaibab Formation limestone (Miburn Tephra, Typic Haplocambids)
b	9	<i>Artemisia filifolia</i> – <i>Ephedra (torreyana, viridis)</i> Shrubland	1400–1460	very shallow to shallow, loamy sands or sandy loam, surface very dark gray coarse sand (some plots moderately channery)	Loamy Upland (Cambidic Haplodurids), Sandstone/Shale Upland (Moenkopic)
c	10	<i>Fallugia paradoxa</i> – (<i>Atriplex canescens</i> – <i>Ephedra torreyana</i>) cinder Shrubland ^B	1370–1430	shallow to moderately deep, sandy loam to sand, surface very dark gray, occurs in areas with deep cinder deposits	Loamy Upland (dunes phase), influenced by eolian processes

^A Perennial grasses predominate with shrubs present. *Bouteloua eriopoda* is subdominant

^B Sparse vegetation, shrub dominance

Table 16. Major plot clusters for BAND-P ecosite in relation to closest matching NVC association from the Vegetation Mapping Report (Muldavin et al. 2011). Plot-based soil measures and Bandelier NM Soil Survey (Hibner 2009) were used to estimate predominant Soil Map Units/Family associated with each cluster. My modification to NVC association name for Cluster A is indicated by *.

Cluster	Number of Plots	Closest NVC Woodland Association	Predominant Elevation (m)	Predominant Soil Map Units (soil characteristics)	Soil Family
a	6	<i>J. monosperma/Bouteloua gracilis (Bromus tectorum invaded)</i> * high abundance of ruderal forbs & non-native <i>B. tectorum</i>	1950 – 2100	● 408 Adornado (very deep, very paragravelly, ashy coarse sandy loam) ● 413 Armenta (very deep, very paragravelly, ashy coarse sand)	● Deep (haplustolls) with well-developed but coarse surface horizons; derived from rhyolitic El Cajate pumice
b	12	<i>J. monosperma/Bouteloua gracilis</i> high abundance of perennial grass species, with <i>B. gracilis</i> dominating	1950 – 2100	● 408 Adornado (very deep, very paragravelly, ashy coarse sandy loam) ● 409 Hackroy-Nyjack Complex (shallow to moderately deep, clayey or fine loamy) ● 400 Palatka-Canuela-Rock Outcrop Complex (very shallow to shallow, paragravelly sandy loam or cobbly ashy coarse sandy loam)	● Deep (haplustolls) with well-developed but coarse surface horizons; derived from rhyolitic El Cajate pumice ● Hackroy and Nyjack Series - shallow to moderately deep, moderately developed (haplustalfs) of plateau tops ● Palatka Series - weakly developed shoulder and backslope soils (ustorthents and ustipsaments); Canuela Series - shallow, moderately developed (haplustalfs) of plateau tops
c	15	<i>J. monosperma/Quercus x pauciloba</i> high shrub abundance (<i>Quercus</i> , <i>Rhus</i> , <i>Cercocarpus</i> , <i>Fallugia</i>) and forbs; lower perennial grass abundance; moderate <i>Opuntia</i> abundance	1860 – 1950	● 413 Armenta (very deep, very paragravelly, ashy coarse sand) ● 412 Canuela-Hackroy Complex (shallow, loamy or clayey) ● 410 Palatka-Canuela-Rock Outcrop Complex (very shallow to shallow, paragravelly, ashy sandy loam to sandy loam)	● Deep (haplustolls) with well-developed but coarse surface horizons; derived from rhyolitic El Cajate pumice ● Canuela Series - shallow, moderately developed; Hackroy Series – shallow to moderately deep, moderately developed; both (haplustalfs) of plateau tops ● Palatka Series - weakly developed shoulder and backslope soils (ustorthents and ustipsammments); Canuela Series - shallow, moderately developed (haplustalfs) of plateau tops

Table 16 (continued). Major plot clusters for BAND-P ecosite in relation to closest matching NVC association from the Vegetation Mapping Report (Muldavin et al. 2011). Plot-based soil measures and Bandelier NM Soil Survey (Hibner 2009) were used to estimate predominant Soil Map Units/Family associated with each cluster. My modification to NVC association name for Cluster A is indicated by *.

Cluster	Number of Plots	Closest NVC Woodland Association	Predominant Elevation (m)	Predominant Soil Map Units (soil characteristics)	Soil Family
d	8	<i>J. monosperma</i> sparse understory reduced shrub, perennial grass and forb cover; moderate <i>Opuntia</i> abundance	1860 – 1950	● 410 Palatka-Canuela-Rock Outcrop Complex (very shallow to shallow, paragravelly, ashy sandy loam to sandy loam)	● Palatka Series - weakly developed shoulder and backslope soils (ustorthents and ustipsamments); Canuela Series - shallow, moderately developed (haplustalfs) of plateau tops

Text Note E1: Observations regarding BAND-P Cluster A plots

(6 plots within *Juniperus monosperma*/*Bouteloua gracilis* association with high *Bromus tectorum* abundance)

The BAND-P species abundance data capture an early phase of *Bromus tectorum* invasion in the BAND-P study area. In recent years *B. tectorum* has become pervasive, dominating in some plots (Swan 2020). Although the sample size is quite small, several observations regarding the six Cluster A plots in which high *B. tectorum* cover was first observed may be relevant. First, the increase in *B. tectorum* abundance seems to fall approximately in the same timeframe as the juniper-thinning restoration treatments, yet only one of the six Cluster A plots was thinned, while over the entire study area 30 of the 42 plots were thinned. Thus, *B. tectorum* dominance in these plots does not seem to be a direct response to the thinning treatment, although perhaps increased human traffic resulted in more widespread seed dispersal. Secondly, the Bandelier NM Vegetation Map indicates that these six plots are adjacent to a ruderal grassland association with evidence of fire within the last 50 years and probable postfire seeding (Muldavin et al. 2011). This adjacent association was characterized by reduced perennial grass cover and relatively high abundance of ruderal forb species. Perhaps this more disturbed area served as a seed source for *B. tectorum*. Finally, the soils of the plots where *B. tectorum* initially dominated are very deep with coarse sandy loam surface horizons and relatively high gravel cover, most likely belonging to the well-developed haplustoll series (Adornado and Armenta) (Hibner et al. 2009). As part of a pinyon-juniper tree-thinning trial at Bandelier NM in the late 1990s, Julius (1999) found that in pumiceous, non-argillic soils such as these, 90% of herbaceous biomass was produced by forbs and only 10% by perennial grasses following tree-thinning. In contrast, he found that on soils that were both pumiceous and had an argillic layer (such as Hackroy-Nyjack Complex soils), 62% of the herbaceous biomass was produced by perennial grass species and 38% by forbs. One hypothesis to consider is that the deep, coarse haplustoll soils associated with the Cluster A plots can be productive under optimal conditions, but are less resistant to invasion, perhaps due to lower cover of perennial grasses, the interaction of soil properties with hot, dry conditions, or both. Tree basal area and heat load were also somewhat lower in Cluster A plots. It will be interesting to follow these plots through time to see if *B. tectorum* and ruderal forb abundance remains high, or if this cluster represents a transient response to disturbance with perennial grass or shrub species gradually becoming more prevalent.

Literature Cited

- Hibner, C. D., C.A. Ferguson, J.M. Putterli. 2009. Special Project Soil Survey of Bandelier National Monument [Interim report]. Final Review Copy, USDA, Natural Resources Conservation Service, Santa Fe, New Mexico.
- Julius, C. 1999. A comparison of vegetation structure on three different soils at Bandelier National Monument, New Mexico. Thesis. Rheinischen Friedrich-Wilhelms University, Bonn, Germany.
- Muldavin, E., A. Kennedy, C. Jackson, P. Neville, T. Neville, K. Schulz, and M. Reid. 2011. Vegetation classification and map: Bandelier National Monument. Natural Resource Technical Report NPS/SCPN/NRTR— 2011/438. National Park Service, Fort Collins, Colorado.

Swan, M., L. McCoy, and C. Veety. 2020. Bandelier National Monument mesa-top pinyon-juniper 2019 data summary: Southern Colorado Plateau Network integrated upland monitoring. Natural Resource Data Series NPS/SCPN/NRDS—2020/1287. National Park Service, Fort Collins, Colorado.

Appendix F. Fully Accessible Versions of Figures 17 and 18.

Tables 17 and 18 are fully accessible versions of Figures 17 and 18.

Table 17. [Data from Figure 17](#). Dominant species across the seven ecosites. Species with relative abundance greater than 10% in one or more ecosites are included. The relative abundance of a species at an ecosite is indicated by lettering: L = low abundance (>0.1 to 1%); M = moderate abundance (>1 to 10%); D-1 = dominant (>10 to 15%); D-2 = dominant (>15 to 25%); D-3 = dominant (>25 to 35%); D-4 = dominant (>35 to 50%); a dash (–) indicates that the species was not observed in that ecosite or occurred with a relative abundance of 0.1% or less. C₃ grass species are identified following their species name.

Functional Group	Species	MEVE-L	GRCA-P	BAND-P	CHCU-S	PEFO-C	PEFO-S	WUPA-L
Perennial Grasses	<i>Poa fendleriana</i> (C ₃)	D-4	D-2	M	–	–	–	–
Perennial Grasses	<i>Bouteloua gracilis</i>	–	D-2	D-2	D-3	D-1	D-3	–
Perennial Grasses	<i>Hilaria jamesii</i>	–	–	L	D-2	D-1	D-1	D-3
Perennial Grasses	<i>Sporobolus</i> spp.	–	–	M	M	D-4	D-2	M
Shrubs	<i>Artemisia filifolia</i>	–	–	–	L	L	M	D-1
Shrubs	<i>Artemisia tridentata</i>	–	D-1	–	L	–	–	–
Shrubs	<i>Ephedra torreyana</i>	–	–	–	M	L	L	D-1
Shrubs	<i>Fallugia paradoxa</i>	–	L	M	–	–	–	D-1
Shrubs	<i>Gutierrezia sarothrae</i>	–	M	D-2	M	L	M	–
Shrubs	<i>Purshia stansburiana</i>	–	D-2	–	–	–	–	–
Shrubs	<i>Purshia tridentata</i>	D-3	–	–	–	–	–	–
Forbs	<i>Euphorbia</i> spp.	–	L	L	–	L	L	D-1

Table 18. [Data from Figure 18](#). Moderately abundant species across the seven ecosites. Species with relative abundance greater than 1% and less than 10% in one or more ecosites are included. The relative abundance of a species at an ecosite is indicated by lettering: L = low abundance (>0.1 to 1%); M-1 = moderate abundance (>1 to 2%); M-2 = moderate abundance (>2 to 5%); M-3 = moderate abundance (>5 to 10%); D = dominant (>10%); a dash (–) indicates that the species was not observed in that ecosite or occurred with a relative abundance of 0.1% or less. Names of cool season grass species are followed by (C₃), and non-native species are followed by an asterisk (*).

Functional Group	Species	MEVE-L	GRCA-P	BAND-P	CHCU-S	PEFO-C	PEFO-S	WUPA-L
Perennial Grasses	<i>Achnatherum hymenoides</i> (C ₃)	L	–	–	M-2	M-1	M-2	L
Perennial Grasses	<i>Bouteloua eriopoda</i>	–	–	L	–	L	M-2	M-2
Perennial Grasses	<i>Elymus elymoides</i> (C ₃)	L	L	M-3	L	–	–	–
Perennial Grasses	<i>Hesperostipa comata</i> (C ₃)	–	L	–	L	L	M-2	–
Perennial Grasses	<i>Muhlenbergia porteri</i>	–	–	–	–	–	–	M-3
Perennial Grasses	<i>Poa fendleriana</i> (C ₃)	D	D	M-1	–	–	–	–
Perennial Grasses	<i>Sporobolus</i> spp.	–	–	M-1	M-3	D	D	M-1
Shrubs	<i>Amelanchier utahensis</i>	M-1	–	–	–	–	–	–
Shrubs	<i>Artemisia filifolia</i>	–	–	–	L	L	M-2	D
Shrubs	<i>Atriplex canescens</i>	–	–	L	M-3	M-1	M-3	M-2
Shrubs	<i>Atriplex obovate</i>	–	–	–	–	M-3	–	–
Shrubs	<i>Cercocarpus montanus</i>	M-2	–	M-2	–	–	–	–
Shrubs	<i>Chrysothamnus Greenei</i>	–	–	–	M-2	–	M-2	–
Shrubs	<i>Ephedra torreyana</i>	–	–	–	M-1	–	–	–
Shrubs	<i>Ephedra viridis</i>	–	L	–	L	–	L	M-1
Shrubs	<i>Ericameria nauseosa</i>	–	–	L	L	L	–	M-2
Shrubs	<i>Fallugia paradoxa</i>	–	L	M-2	–	–	–	D
Shrubs	<i>Gutierrezia microcephala</i>	–	–	–	–	–	–	M-1
Shrubs	<i>Gutierrezia sarothrae</i>	–	M-2	D	M-1	L	M-2	–
Shrubs	<i>Krascheninnikovia lanata</i>	–	–	–	M-3	L	M-2	–
Shrubs	<i>Quercus</i> spp.	M-1	M-1	M-2	–	–	–	–
Shrubs	<i>Rhus aromatica</i>	–	–	M-2	–	–	–	–

Table 18 (continued). [Data from Figure 18](#). Moderately abundant species across the seven ecosites. Species with relative abundance greater than 1% and less than 10% in one or more ecosites are included. The relative abundance of a species at an ecosite is indicated by lettering: L = low abundance (>0.1 to 1%); M-1 = moderate abundance (>1 to 2%); M-2 = moderate abundance (>2 to 5%); M-3 = moderate abundance (>5 to 10%); D = dominant (>10%); a dash (–) indicates that the species was not observed in that ecosite or occurred with a relative abundance of 0.1% or less. Names of cool season grass species are followed by (C₃), and non-native species are followed by an asterisk (*).

Functional Group	Species	MEVE-L	GRCA-P	BAND-P	CHCU-S	PEFO-C	PEFO-S	WUPA-L
Cacti and Succulents	<i>Opuntia</i> spp.	M-3	M-1	M-2	L	L	L	–
Cacti and Succulents	<i>Yucca baccata</i>	M-3	L	L	–	–	–	–
Forbs	<i>Amauriopsis dissecta</i>	–	–	M-2	–	–	–	–
Forbs	<i>Artemisia campestre</i>	–	–	M-3	–	–	–	–
Forbs	<i>Artemisia carruthii</i>	–	–	M-2	–	–	–	–
Forbs	<i>Artemisia dracunculus</i>	–	–	M-2	–	–	–	–
Forbs	<i>Astragalus</i> spp.	M-1	L	–	–	L	–	L
Forbs	<i>Chenopodium</i> spp.	–	–	L	M-1	–	L	–
Forbs	<i>Croton texensis</i>	–	–	M-1	–	–	–	–
Forbs	<i>Mentzelia</i> spp.	–	–	M-1	–	–	–	–
Forbs	<i>Penstemon linarioides</i>	M-1	–	–	–	–	–	–
Forbs	<i>Petradoria pumila</i>	M-2	–	–	–	–	–	–
Forbs	<i>Phlox hoodii</i>	M-1	–	–	–	–	–	–
Forbs	<i>Sphaeralcea</i> spp.	–	–	–	L	L	L	M-1
Forbs	<i>Verbascum thapsus</i> *	–	–	M-1	–	–	–	–
Annual Grasses	<i>Bromus tectorum</i> *	–	L	M-3	–	–	–	–
Annual Grasses	<i>Sporobolus coromandelianus</i>	–	–	–	–	M-2	–	–

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