SPATIAL AND TEMPORAL DYNAMICS OF CONIFER EXPANSION IN SOUTHWEST MONTANA

by

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Abstract

Since the mid-19th century, pinyon-juniper woodlands in western North America have experienced an expansion in range and density and a corresponding degradation in the provision of ecological goods and services including forage production, watershed function, biological diversity, and habitat values. While this is well-documented in other systems, there is little information characterizing shifts in tree range and abundance within the northern extent of these juniper and pine woodlands. The purpose of this research project was twofold: 1) identify and improve understanding of Rocky Mountain juniper and limber pine age distribution and compare these data to other systems, and 2) evaluate understory dynamics along the gradient of woodland development to assess impacts to understory species composition and abundance, as tree densities and range increase. We aged 278 trees across 38 plots in southwest Montana. We recorded soil moisture throughout the growing season (May-July), aspect, elevation, soil texture, herbaceous production and diversity, and tree density and canopy cover from 2019-2021.

Greater than 95% of all trees were under 100 years old and the oldest tree (juniper) was 247 years old. Across the study site, limber pine was younger than Rocky Mountain juniper and appeared to prefer different sites. Maximum and mean juniper age was higher on dry sites with high sand content and lower on moist sites with low sand content in the top 15cm of the soil profile. Understory shrub and cool-season perennial grass cover was negatively influenced by heavy tree canopy cover on southwest to southeast aspects.

The results from this study indicate 1) limber pine and Rocky Mountain juniper generally occupy different sites, 2) juniper and pine stand age is lower on north facing aspects with coarse soils and higher soil moisture content in late spring and early summer. Currently, increasing conifer dominance on north facing aspects appears to minimally impact cool-season perennial grass cover and production. Comparatively, increasing conifer dominance on south facing slopes may reduce cool-season perennial grass and shrub cover and production. We recommend the inclusion of these findings, as land managers seek to sustain delivery of necessary ecological goods and services.

CHAPTER ONE

GENERAL INTRODUCTION

Woody plant expansion is a global phenomenon across multiple continents including Africa, Australia, North America and the Arctic (Vegten 1984; Miller et al. 2000; Robinson et al. 2008; Naito and Cairns 2011; Archer et al. 2011; Archer et al. 2017). Reduced wildfire frequency and extent in the late 19th century led to a global increase in woody plant density and extent (Miller and Rose 1999; Bates et al. 2000; Miller et al. 2005; Briske et al. 2011).

In northern California and eastern Oregon, western juniper (*Juniperus occidentalis* Hook.) density has increased dramatically in the last 140 years (Miller et al. 2005). Eastern red cedar (*Juniperus virginiana* L.) has rapidly expanded into grassland communities in the eastern mid-west (Engle et al. 1996). In New Mexico, research suggests that black grama (*Bouteloua eriopoda* Torr.) grasslands have been replaced with mesquite in the last 100 years (*Prosopis glandulosa* Torr.); (Connin et al. 1997). In the Florida Everglades, an absence of fire led to an increase in invasive woody species in native marshes and pine savannahs (Beckage and Platt 2003).

Rocky Mountain juniper *(Juniperus scopulorum* Sarg.) and limber pine (*Pinus flexilis* James) occur throughout much of southwest Montana and a knowledge of the impacts of increasing conifer density and range on ecosystem goods and services should be considered by public and private land managers. Presently, the knowledge regarding Rocky Mountain juniper and limber pine expansion in southwest Montana is limited. It must be asked if Rocky Mountain juniper and limber pine invasion causes a loss in forage production, alters wildlife habitat, or increases soil erosion rates as recorded in previous studies (Miller et al. 2005; Briske et al. 2011; Kitchen et al. 2016).

Research Justification

Currently, land managers are actively removing Rocky Mountain juniper with the intention of improving wildlife habitat, increasing forage production, or increasing groundwater and stream flows (Joe Sampson – personal communication). However, there are very little data available that explain ecosystem dynamics in Rocky Mountain juniper-limber pine vegetation types and even less regarding the efficacy and justification of various treatment options. Generally, juniper and pine expansion has been well documented throughout many systems in western North America (Archer 1995; Miller and Rose 1995; Heyerdahl et al. 2006). Even so, little is known about the potential expansion of Rocky Mountain juniper and limber pine and the expected environmental and understory impacts.

First, it is important to identify if Rocky Mountain juniper and limber pine are expanding into grass and shrub dominated communities. Since management goals vary across landscapes and administrative boundaries, an improved understanding of the impacts associated with juniper woodland expansion in southwest Montana will allow for a more appropriate and refined approach to site-specific management. In order to understand the impacts of Rocky Mountain juniper and limber pine expansion, land managers must understand the spatial and temporal variation of tree occurrence across heterogenous landscapes in southwest Montana. This not only allows for a robust understanding of drivers associated with increases in pine and juniper density and extent, but also variability in physical site characteristics and understory response to conifer encroachment.

CHAPTER TWO

LITERATURE REVIEW

Rocky Mountain Juniper

Rocky Mountain juniper is a native evergreen tree in western North America occurring throughout drier montane biomes from western Texas, New Mexico, Arizona, north through the Great Basin and Rocky Mountains to British Columbia and Saskatchewan in Southern Canada (Fig. 1, Fig. 2; Sudworth 1915; Scher 2002; Kartesz 2015). This species is long-lived (200-300+ years) and generally grows to 7-10 meters in height (Scher 2002). Morphological traits and subsequent descriptions vary widely across its native range as it hybridizes readily with other juniper species (Scher 2002).

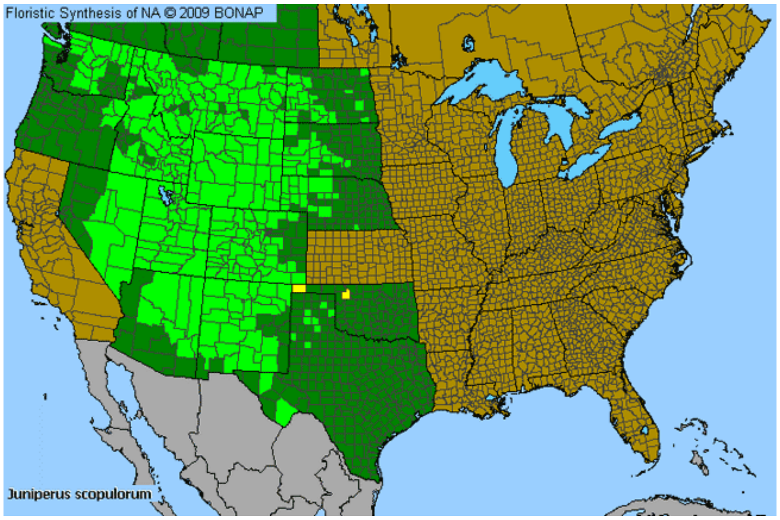
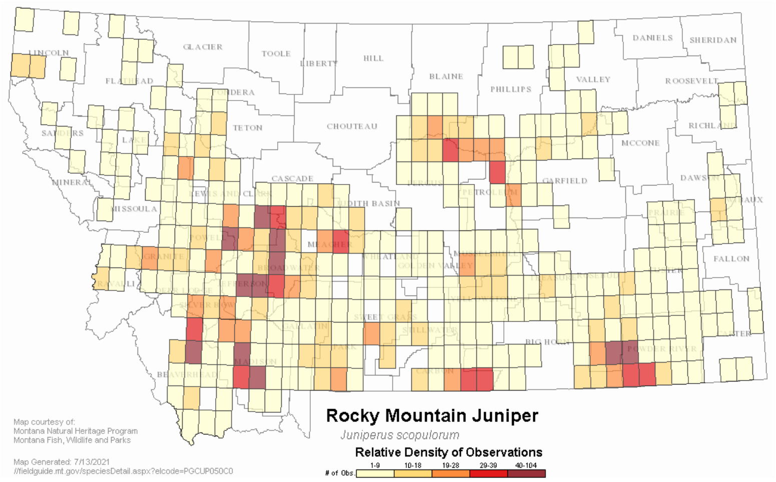


Figure 1: County based distribution map of Rocky Mountain juniper in the western United States (Kartesz 2015). Bright green represents counties in which Rocky Mountain juniper is present.



Map courtesy of:
Montana Natural Heritage Program
Montana Fish, Wildlife and Parks

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Figure 2: Relative density of observations map of Rocky Mountain juniper in Montana (MTNHP 2022). A plant observation is visual, audio, specimen, genetic, or other documentation of a species at a location with an assigned spatial precision during a given time period. "Observations" must be reported by a credible observer within appropriate time periods and within appropriate habitats or ecological settings in order to be included in the MTNHP plant database (MTNHP 2022).

Rocky Mountain juniper is most abundant on dry, rocky slopes, with very shallow to shallow soils that are sandy-skeletal over hard bedrock and often calcareous throughout (Scher 2002; T. Keck, personal communication, April 29, 2022). This species generally prefers calcareous and mildly alkaline soils; however, juniper can be found on soils derived from basalt, sandstone, and shale, including areas with no soil development (Noble 1990; Scher 2002). The lack of specificity in bedrock type potentially suggests that juniper distribution is less driven by soil chemistry or development (T. Keck, personal communication, April 29, 2022).

Rocky Mountain juniper is mostly dioecious and begins reproducing around 10 years of age (Scher 2002). Trees will bear seed nearly every year and bear heavier crops during years with above average precipitation (Herman 1958). Rocky Mountain juniper prolifically produce small seeds at 8000-19000 seeds/kilogram (Herman 1958). Seeds are usually dispersed by birds; whose digestive tracts have little to no effect on viability and germination capability (Scher

2002). Avian dispersers include turkeys (*Meleagris* spp.), robins (*Turdus* spp.), waxwings (*Bombycilla* spp.), solitaires (*Myadestes* spp.) and other upland bird species (Scher 2002). While avian species primarily disperse seeds, it is also common for small mammals and large ungulates to browse and disperse as well. Runoff and heavy rain events also help disperse seed. The degree of juniper seed dormancy greatly varies by seed source, age, crop and within and among individual trees (Young et al. 1988; Rietveld 1989).

Rocky Mountain juniper readily establishes in rocky crevices and broken terrain. This may be due to increased trapped water in these locations (Scher 2002). While seeds require moist conditions to germinate, Rocky Mountain juniper grows well in drier areas with little to no soil development (Sudworth 1915). This species is certainly not limited to drier conditions and readily occupies well-developed soils (Noble 1990). Due to its ability to tolerate a wide range of ecological conditions, Rocky Mountain juniper grows in areas near sea level and up to 9000 feet in elevation (Noble 1990).

Limber Pine

Limber Pine is a native five needled pine occurring throughout southern Canada, Montana, Wyoming, Colorado, California, Utah and as far south as New Mexico and Arizona (Fig. 1, Fig. 2; Johnson 2001). This species of pine is very long-lived and mature adults can exceed 1000 years in age. On sites with adequate moisture, limber pine may be abundant, while on harsher, water limited sites limber pine are often widely spaced individuals (Johnson 2001).

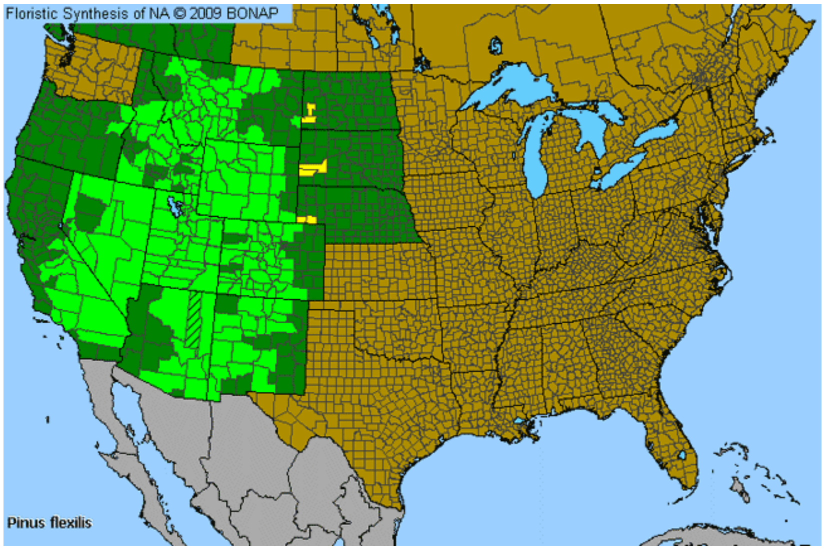

Figure 3: County based distribution map of limber pine in the western United States (Kartesz 2015). Bright green represents counties in which limber pine is present.

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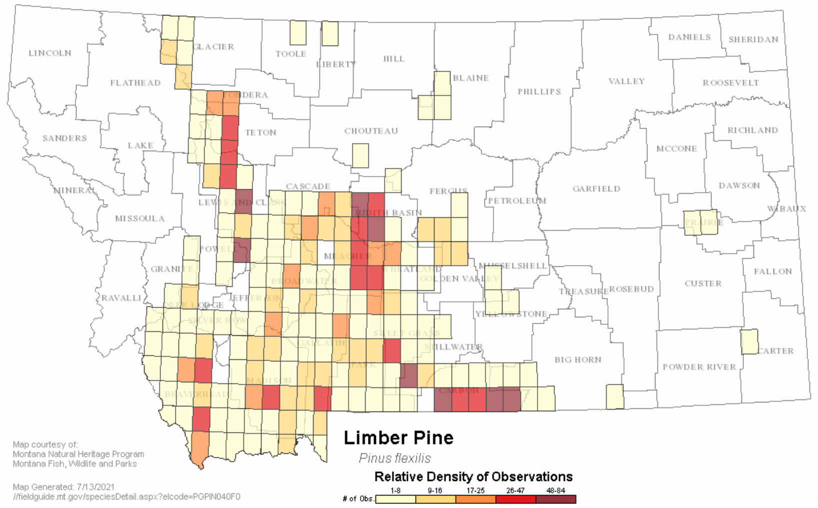

Figure 4: Relative density of observations map of limber pine in Montana (MTNHP 2022). A plant observation is a visual, audio, specimen, genetic, or other documentation of a species at a location with an assigned spatial precision during a given time period. "Observations" must be reported by a credible observer within appropriate time periods and within appropriate habitats or ecological settings in order to be included in the MTNHP plant database (MTNHP 2022).

Limber pine only reproduces from seed. Clark's nutcracker (*Nucifraga columbiana*) caches large amounts of limber pine seeds and is the primary disperser, thereby influencing distribution and spacing of limber pine in much of its distribution throughout the west (Lanner and Vander Wall 1980). Thus, limber pine often establishes in patches where cached seeds have been left by nutcrackers. These patches thin over time, due to competition for resources between conifer saplings. Limber pine generally inhabits rocky, nutrient poor and well drained sites and has the greatest elevational range of any tree species in the Rocky Mountains (Schoettle and Rochelle 2000). This pine often grows on rock outcroppings and high elevation ridgelines but it also found in the transition zone of forest and grassland. Due to its ability to colonize harsh sites, limber pine may act as a pioneer species that facilitates establishment of other species by providing wind protection and shade; however, successional status may differ according to site productivity (Johnson 2001). Limber pine is capable of inhabiting some of the driest sites that support trees and reportedly grows well in soils derived from many varieties of parent material (Steele 1990; Johnson 2001). Limber pine is considered a very slow growing species; however, this may be more related to the productivity of the harsh sites on which it is usually found and not the capability of the tree to adequately utilize available water and resources.

Wildfire Refugia

Historically, wildfire played a major role in woody plant distribution across the west (Miller and Tausch 2000; Heyerdahl et al. 2006; Romme et al. 2009; Kolden et al. 2017). Wildfire refugia are locations where trees are minimally impacted by wildfire due to a lack of ladder fuels capable of carrying the fire to the trees. These areas provide security for fire sensitive species and seed sources for post-fire regeneration (Kolden et al. 2017). In the Pine Bluffs, Wyoming area, fire return intervals in open shrub communities with scattered limber pine were estimated at 2-30 years, before human induced fire suppression (Wright and Bailey 1982). However, broken terrain in the non-riparian woodlands and escarpments in this area provided refugia for limber pine and most likely only burned in the larger stand replacing fires (Schuster et al. 1995). In the Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) – Idaho fescue (*Festuca idahoensis* Elmer) habitat type in Montana, conifer were primarily confined to talus slopes, rock outcrops, and other less productive microsites that had little herbaceous vegetation and more exposed rock (Arno and Gruell 1983). In the Great Basin, old growth western juniper communities typically occupy shallow, rocky soils, rock outcrop, and sites with low production potential (Miller et al. 2005). Furthermore, presettlement fire return intervals in mountain big sagebrush steppe in this area historically ranged from 10 – 25 years (Burkhardt and Tisdale 1976; Miller et al. 1999). This would have limited western juniper persistence in sagebrush communities, since this species generally requires 40-50 years to attain a height that limits movement of fire into the tree canopy (Miller and Rose 1995). Currently, prolonged fire return intervals allow fire sensitive juniper species to expand from refugia areas into more productive areas as well as infill in areas where they were historically maintained at low densities (Davies et al. 2019). These refugia serve as seed sources and assist in woody plant recovery and propagation, especially in regard to species that sexually reproduce.

Factors Contributing to Woody Plant Expansion

Wildfire suppression allowed woody plants to move from refugia into sagebrush-steppe and grassland ecosystems (Miller et al. 2005; Romme et al. 2009). Without relatively frequent, low-intensity wildfire, many woody plant species are able to establish and grow to a more fire-resistant age. This allows cohorts of woody plants to better survive when fire returns (Miller and Rose 1995). Woody plant invasion to into grassland habitats has altered ecosystem characteristics and function across north America (Krannitz 2007). Extended fire return intervals, along with land use and altered climate, potentially accelerate large-scale transformations of grassland to forest ecosystems (Coop et al. 2019). In California, 84% of western juniper established between 1890 and 1920 (Young and Evans 1981). In Utah, as Utah juniper (*Juniperus osteosperma* (Torr.) Little) and single leaf pinyon (*Pinus monophyla* Torr. and Frem) dominate a site (60-80 years post-fire), understory plant growth was sharply reduced (Barney and Frischknecht 1974). In 1985, a Soil Conservation Service survey indicated that eastern red cedar (*Juniperus virginiana* L.) and ashe juniper (*Juniperus ashei* J. Buchholz) in Oklahoma had invaded nearly 1.5 million acres by 1950 and 3.5 million acres by 1985 (Engle et al. 1996). Heyerdahl et al. (2006) state that in the continued absence of wildfire, grasslands and mountain big sagebrush systems in southwestern Montana are likely to become less diverse as Douglas fir trees encroach.

Reduced wildfire frequency and extent is only one factor contributing to woody plant expansion. Other major factors attributed to the increase in range and density of woody plants are the introduction of livestock, shifts in climate, and industrial increases in atmospheric CO_2 (Miller et al. 2005; Briske et al. 2011).

Cooler, wetter periods in the late 19th and early 20th century promoted vigorous growth in western juniper stands (Holmes et al. 1986; Miller et al. 2005). Tree ring growth in western juniper is also highly influenced by local climate conditions (Miller et al. 2005; Soule et al. 2004). Increased precipitation allows juniper saplings to survive at greater rates compared to droughty years. In western juniper stands, juveniles have higher leaf conductance, transpiration, and greater total CO_2 assimilation per unit of leaf weight during the growing season than saplings or mature stems (Miller et al. 1992). The change from juvenile to mature foliage reduces the amount of carbon assimilated per unit leaf area and the amount of water transpired by 40 percent; furthering the claim that woody plants would undoubtedly have benefitted from the cool, wet period during the 19th and 20th centuries (Miller et al. 1993). Bates et al. (2000) and Miller et al. (2005) predicted a moderately stocked (30 stems/ac) stand of western juniper could potentially extract 2 inches of soil water in dry years and 5.6 inches in wet years, without accounting for rain that is intercepted by juniper canopy. Bates et al. (2000) further reported that, due to differences in available water, the understory growing season was six weeks shorter in uncut western juniper stands compared to adjacent cut stands. Since the process of photosynthesis requires H_2 molecules from water and CO_2, reduced water availability leads to reduced carbon assimilation by plants.

Relative to woody plant expansion, increasing atmospheric CO_2 is a widely studied and debated topic. Under atmospheric CO_2 levels of 350 ppm, C4 species still had quantum yields, photosynthetic rates and water use efficiencies comparable to those of coexisting C3 plants (Ehleringer and Monson 1993; Archer et al. 1995). There is considerable evidence that factors other than CO_2 enrichment have been the causal mechanisms leading to woody plant expansion into arid grasslands and savannahs (Archer et al. 1995). While increasing CO_2 concentrations are thought to contribute to increased woody plant density and range, this was already substantially increasing in the late 18th century, before atmospheric CO_2 concentrations dramatically increased (Neftel et al. 1985). These exceptions limit the viability of atmospheric CO_2 concentrations as a direct cause of increased woody plant abundance in the previous 200 YBP (Archer et al. 1995). Nevertheless, some evidence suggests, particularly during drought years, that atmospheric CO_2 fertilization has positively affected juniper growth rates in the 20th century (Knapp et al. 2001). This appears to be a function of increases in intrinsic water use efficiency by juniper, as CO_2 concentrations increase (Knapp et al. 2001).

The introduction of livestock and continuous heavy grazing in the 19th and early 20th century mirrors woody plant expansion in the western United States (Burkhardt and Tisdale 1976; Eddleman 1987; Miller and Rose 1999). Grazing reduces fine fuels and herbaceous competition with woody plant seedlings, likely contributing to this expansion (Miller and Rose 1995; Briske et al. 2011). Heavy livestock grazing also contributes to woody plant expansion by reducing the fine fuel biomass and continuity that would otherwise fuel more frequent and intense fires (Burkhardt and Tisdale 1976; Miller and Rose 1999; Miller et al. 2005; Briske et al. 2011; Davies et al. 2017). Even light to moderately grazed pastures often reduce fire frequency and intensity (Davies et al. 2017).

Many herbaceous species do not recover as well from prolonged, heavy grazing compared to light or moderate defoliation. I define heavy grazing as the allowance of animals to graze to the point of damaging vegetation, such that plants in a given area do not have the ability to regrow before the next grazing event. Currently, heavy livestock grazing is a leading cause of woody plant encroachment and declining ecosystem structure and function in shrublands (Eldridge et al. 2013). Heavy grazing weakens the herbaceous vegetation’s ability to compete while also reducing fuels, leading to reduced fire range and intensity (Miller and Rose 1995). Under heavy grazing, shrub density, biomass, and soil infiltration diminished in Australian shrublands (Eldridge and Soliveres 2013). Conversely, on sites with a history of heavy grazing, livestock removal may further promote rather than deter woody plant encroachment (Browning and Archer 2011; Briske et al. 2011). Browning and Archer (2011) suggest that thresholds for grassland resistance to woody plant encroachment may be crossed, resulting in increased abundance in woody plants after livestock are removed. While the exact point at which a threshold is crossed is not well understood, fire management rather than grazing management may be the key to maintaining grassland physiognomy (Browning and Archer 2011). Fire can efficiently remove woody plants before saplings mature and become more fire resistant while changes in grazing management generally do not alter system trajectory in favor of woody plants (Heyerdahl 2006; Browning and Archer 2011). Furthermore, it is not always realistic to expect brush management to enhance herbaceous production, especially on extensively eroded sites (Briske et al. 2011).

The interaction of grazing and fire suppression must be considered in unison and not as separate disturbance events (Browning and Archer 2011). In the southwestern United States, mesquite invasion increased dramatically after livestock were introduced and currently, grazed savannahs have higher woody plant densities, compared to ungrazed savannahs (Madany and West 1983; Brown and Archer 1989). White fir (*Abies concolor* (Gord. & Glend.) Lindl. Ex Hildebr.) readily invaded southeastern slopes in California after heavy sheep grazing (Vale 1975). Heavily grazed plateaus in Zion National Park, Utah, had much higher densities of pine, juniper and oak, compared to other relict mesas (Madany and West 1983). In eastern Oregon, historic grazing and fire suppression combined with favorable conditions for seed germination and establishment led to unprecedented changes to the vegetation structure and the fire regime of ponderosa pine (*Pinus ponderosa* Lawson and C. Lawson) forests (Carr and Kreuger 2011).

Management of shrub-grassland ecosystems in the Northern Rocky Mountains is directed towards sustained delivery of desired ecological goods and services. These goods and services, such as water, forage, and wildlife habitat, are sustained when ecological processes are functioning within a normal range of variation for a specific ecological site. Ecological processes including site hydrology, nutrient cycling, and energy flow are altered as community structure changes from grass and shrub dominated vegetation to trees. Thus, increasing tree density and abundance is a potential threat to shrub-grasslands in the Northern Rocky Mountains and the goods and services they provide.

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CHAPTER THREE

ROCKY MOUNTAIN JUNIPER AND LIMBER PINE AGE DISTRIBUTION IN SOUTHWEST MONTANA

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Chapter Three Manuscript

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Contributions: Collected samples and analyzed data. Wrote first draft of the manuscript.

Co-Author: Craig A. Carr

Contributions: Created and implemented study design. Advised and collaborated on sampling and data analysis. Offered direction and feedback on manuscript drafts.

Co-Author: Clayton B. Marlow

Contributions: Advised and collaborated on sampling and data analysis. Provided feedback on manuscript drafts.

Co-Author: Thomas J. Keck

Contributions: Collaborated on sampling and data analysis. Supplied feedback on manuscript drafts.

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ROCKY MOUNTAIN JUNIPER AND LIMBER PINE AGE DISTRIBUTION IN SOUTHWEST MONTANA

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Abstract

Woody plant expansion is a dominant concern in rangeland management. This expansion alters forage productivity, watershed function, and habitat values. Woody plant expansion also jeopardizes the long-term sustainability of the infrastructure that is foundational to the western range livestock industry. Historically, wildfires were frequent enough to limit woody plant expansion into productive vegetation types by reducing densities before many could reach a more fire-resistant age. Presently, there is little knowledge regarding Rocky Mountain juniper (*Juniperus scopulorum*-Sarg) and limber pine (*Pinus flexilis*-James) stand age in southwest Montana. We initiated this study to quantitatively support our hypothesis that juniper and pine are expanding into sagebrush and grassland dominated areas. We substituted space for time by sampling stand age in juniper and pine woodlands along a developmental gradient, in order to capture the variation in conifer age across different ecological sites. We used a generalized linear model assuming a Poisson distribution to determine site level influences on tree age and constructed histograms to assist in visualizing variation in stand age. Maximum and mean juniper age was higher on droughty sites with high sand content and lower on moist sites with

low sand content in the top 15cm of the soil profile. Total mean stand age was 34 years of age. 95% of all limber pine were less than 40 years old and 76% of all juniper were less than 50 years old. This expansion timeline corresponds to data from other systems, wherein increased woody plant dominance reduces forage production and soil moisture, increases sediment movement and soil loss, and alters species abundances and diversity.

Introduction

Woody plant expansion is a significant contemporary issue in rangeland management across the western United States (Archer et al. 2017). Observations from pinyon-juniper systems in the Great Basin have shown that this expansion negatively impacts forage production, watershed values, biological diversity, and wildlife habitat (Miller et al. 2005; Briske et al. 2011). This expansion might be explained by fire suppression in the 19th and 20th centuries leading to west-wide increases in the density and abundance of woody plants. At present, the range management paradigm suggests similar patterns exist in the limber pine and Rocky Mountain juniper woodlands of southwestern Montana. However, few data exist that characterize post European settlement vegetation dynamics within this open woodland type. To address this information gap, we evaluated the age distribution of limber pine and Rocky Mountain juniper in southwest Montana. Evaluating tree chronologies gives insight into timing and, in some cases, potential causes of tree establishment.

To illustrate this argument, in the pinyon-juniper systems of the interior north and southwestern U.S. and Great Basin, juniper and pine expansion into sagebrush steppe and grasslands coincides with Euro-American settlement and organized fire suppression (Burkhardt and Tisdale 1976; Miller and Rose 1999). In both of these systems, forage production, wildlife habitat, and watershed function are altered as tree density and dominance increases, leading to reduced ecosystem goods and services (Burkhardt and Tisdale 1976; Engle et al. 1996; Miller and Rose 1999). The primary method of evaluating tree age distribution is sampling a stand through the use of an increment borer. Capturing the gradient of age, from youngest to oldest, allows for a robust estimation of woodland establishment dates (Miller and Rose 1999; Heyerdahl et al. 2006). This method is vetted and has been previously used to construct tree establishment dates (Miller et al. 2005; Heyerdahl et al. 2006). Furthermore, sampling age also allows for clarity in patterns of age distribution and its relationship to physical site characteristics (e.g., ecological sites, soil texture, soil moisture). We hypothesize that Rocky Mountain juniper and limber pine are actively expanding into sagebrush and grassland dominated systems, leading to an altered vegetation community that favors woody plants in this area. We further expect age distribution to vary based on the physical site and that mean tree age is relatively young (<50 years).

Methods

Study Site

This study took place during the summers of 2019-2021. The four study sites are located in northern Rocky Mountains near the towns of Norris (45°34’06.43”N - 111°42’36.31”W) and Red Bluff (45°34’12.12”N - 111°36’54.44”W), Montana (Fig. 5, Google Earth Pro 2020). Soils and topography are a mixture of the Rocky Mountains northern extension of plains and isolated mountain masses (Mueggler and Stewart 1980). Soils in and around the Red Bluff study site range from cool Yetull loamy sands, Varney clay loams and Crago gravelly loams on 2 to 8% slopes to Sebud-Hapgood, Rochester and Shurley-Rock outcrop complexes on 25 to 60% slopes. These soils are shallow to deep loamy sands and sandy loams formed from schist, gneiss, and granite parent materials (Web Soil Survey 2022). Soils in the Norris site are dominated by Blaine loams and Tiban stony clay loams on 5-75% slopes. These are very deep, well drained mollisols that formed in colluvium, alluvium, or till and slide deposits (Web Soil Survey 2022). These soils are derived from mixed sources of parent material; however, basalt is the dominant rock outcrop on these lands.

The study sites see a mean annual temperature of 7°C with a range of -4 to 19°C (PRISM Climate Group 2022 - 30-year average). Average annual precipitation is 42cm and mostly comes as rain between April and July (PRISM Climate Group 2022 - 30-year average).

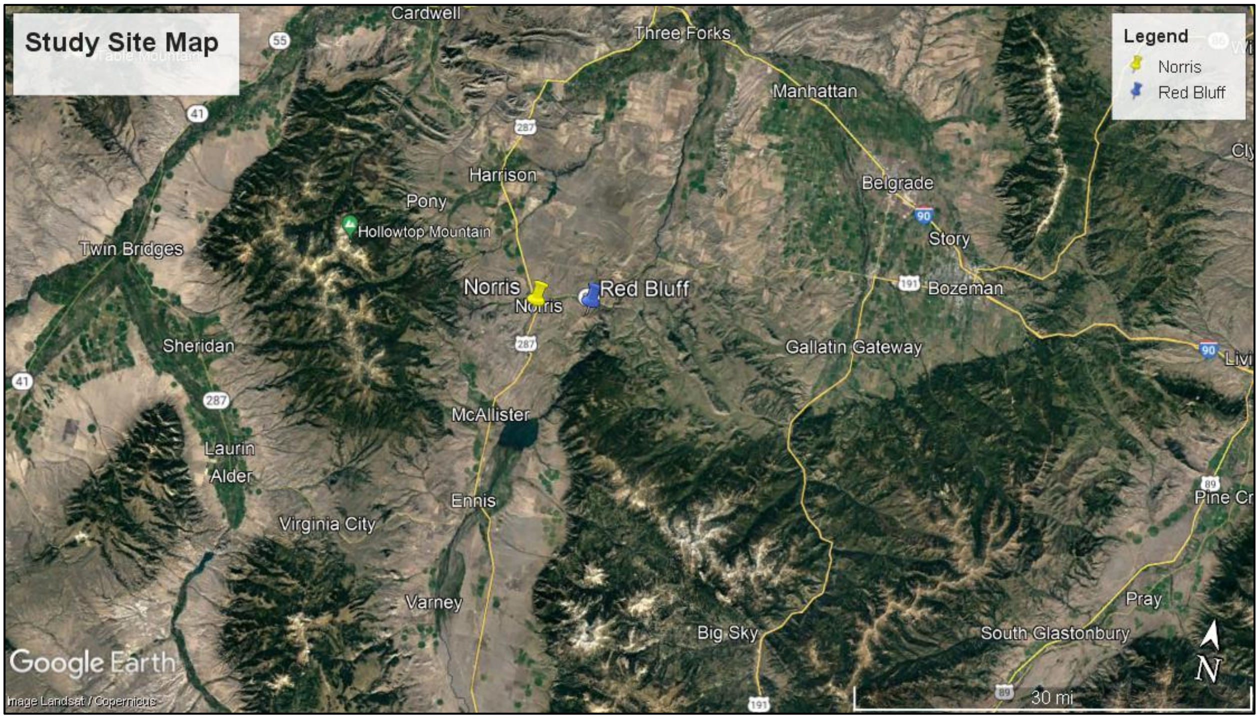

Figure 5: Map of the study sites near Norris, Montana.

Associated Vegetation

The most common grass species present at each of the four study sites were bluebunch wheatgrass (*Pseudoroegneria spicata* Pursh), Idaho fescue (*Festuca idahoensis* Elmer), Sandberg's bluegrass (*Poa secunda* J. Presl), threadleaf sedge (*Carex filifolia* Nutt.), prairie junegrass (*Koeleria macrantha* (Ledeb.) Schult.) and needle and thread (*Hesperostipa comata* (Trin. & Rupr.) Barkworth). Of these native grass species, Idaho fescue and bluebunch wheatgrass were most abundant. Cheatgrass (*Bromus tectorum* L.) was the most abundant non-native grass at Red Bluff. The Norris study site contained very little non-native grass. Common forbs included yellow salsify (*Tragopogon dubius* Scop.), dandelion (*Taraxacum officinale* Wigg.), lupine (*Lupinus spp.*), western yarrow (*Achillea millefolium* L.), fringed sagewort (*Artemisia frigida* Willd.) and prickly pear cactus (*Opuntia spp*.). The most abundant forbs at Red Bluff were western yarrow and prickly pear cactus while the most abundant forb at Norris was scarlet gilia (*Ipomopsis aggregata* Pursh).

Common shrubs were mountain big sagebrush (*Artemisia tridentata ssp. vaseyana (*Rydb.) Beetle), rubber rabbitbrush (*Ericameria nauseosa* (Pall. Ex Pursh) G.L. Nesom & Baird), green rabbitbrush (*Chrysothamnus viscidiflorus* (Hook.) Nutt.), skunkbrush sumac (*Rhus aromatica* Aiton) and black currant (*Ribes cereum* Douglas). Mountain big sagebrush was the most abundant shrub at both Norris and Red Bluff.

Sampling Procedures

In order to describe spatial and temporal attributes of conifer expansion, we substituted space for time by sampling the gradient of woodland density and development. This allowed us to evaluate differences in conifer age as woodland development varied across ecological sites. We randomly selected 38, 25x25m plots across four sites that were representative of surrounding plant associations in southwest Montana. Within these study sites, plots were selected to represent the range in tree abundance and variability of ecological sites.

To categorize and evaluate age distribution, we separated trees into three size classes; dominant (≥3m height), co-dominant (1-3m height), and sub-dominant (≤1m height); (Miller and Rose 1999; Miller et al. 2000). Tree age was sampled by taking a single tree core at a height of 15cm above the ground surface from a maximum of three trees from each species in each size class, allowing for a maximum of 18 sampled trees per plot (Heyerdahl et al. 2006). During the summer of 2021, we used a Haglof standard increment borer to age trees at a height of 15cm above the ground surface. If a tree was too small to be cored, we used a chainsaw to remove a wedge at 15cm above the ground surface. In some cases, we sampled multiple stems from a single tree to ensure the oldest age was captured. All cores and wedges were sanded, oiled and aged by counting tree rings and the date of establishment was estimated as the tree's pith date (Heyerdahl et al. 2006).

Soil moisture was estimated by sampling the top 15cm of soil depth at three random locations in each plot across the growing season. The top 15cm of soil was mixed with a shovel before each sample was taken. We sampled soil moisture in the first two weeks of May, June, and July for all plots in 2021. All samples were dried at 105°C for 24-48 hours to determine soil water content via the gravimetric method (Black 1965). In the first field season (2019), aspect and elevation were recorded for each plot. Heat load was calculated using a continuous scale from 0 to 1, where southwest aspects are weighted at a value of 1 (225°) and northeast aspects are weighted at a value of 0 (45°), based on solar radiation received (McCune and Grace 2002). The top 15cm of soil surface was hand textured as a component of evaluating ecological site descriptions at each plot (NRCS 2022). Percentages of sand, silt, and clay were based on hand texture and assigned as the midpoint of each relevant category in the soil texture triangle (NRCS 2022).

Data Analysis

We constructed histograms for both Rocky Mountain juniper and limber pine to summarize conifer age among plots. Juniper and pine were segregated into individual histograms, allowing for tree ages to be averaged by species. We analyzed relationship of tree age to physical site characteristics through use of a generalized linear model assuming a Poisson distribution in the program R, via R studio (R Development Core Team 2020; R Studio Team 2019). Tree age values used as dependent variables were separated by maximum and mean age in each tree size class (dominant, co-dominant, and sub-dominant). Juniper and pine were analyzed separately in each regression analysis. Relationship of maximum tree age values for each size class as explained by soil texture, soil moisture, heat load, and elevation were analyzed to gain insight into preferred sites for conifer of varying ages. Maximum and mean tree ages were selected to account for the range of tree ages across each size class and across plots.

Results

We aged a total of 278 (94 pine and 184 juniper) trees across 39 plots. Greater than 95% (265 trees) of all trees were under 100 years old, with the oldest tree (juniper) aged at 247 years. All limber pine were less than 80 years old and 93% (87 trees) of all limber pine were less than 40 years old (Fig. 6). Ninety-three percent (171 trees) of all juniper were less than 100 years old and 76% (140 trees) of all juniper were less than 50 years old (Fig. 7). No fire scars were observed or recorded across the entire study area.

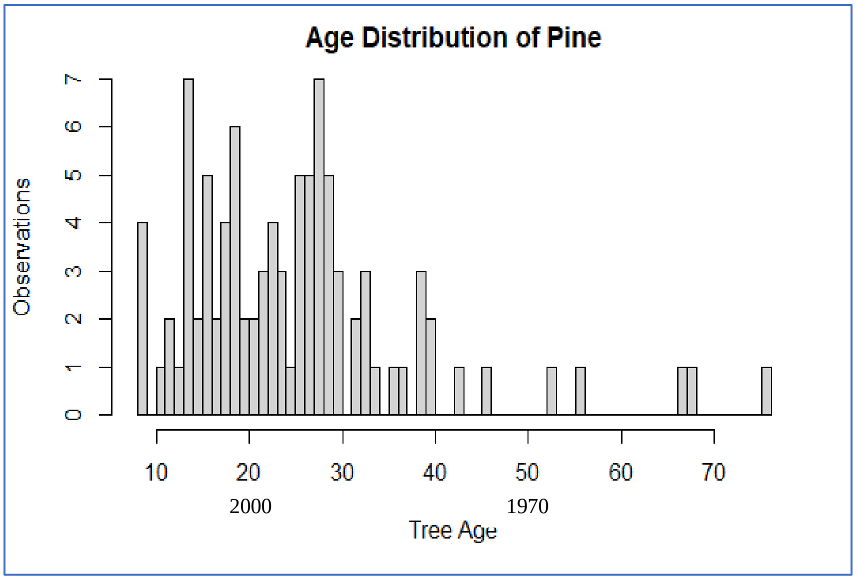

Figure 6: Histogram of limber pine age distribution across all plots.

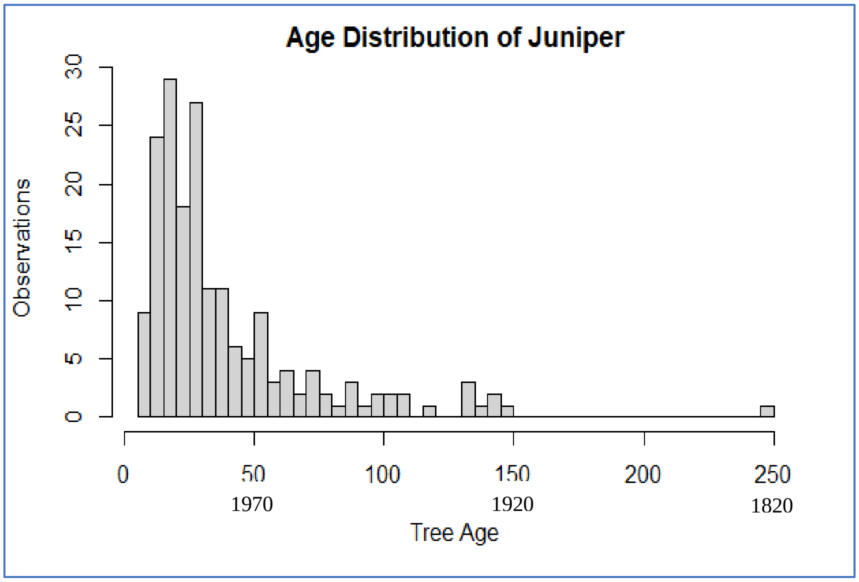

Figure 7: Histogram of Rocky Mountain juniper age distribution across all plots.

Across all samples, the mean age of Rocky Mountain juniper was 38.21 years and the mean age of limber pine was 25.88 years. Less than 5% of all sampled trees were over 100 years of age and all of these were juniper. Maximum (p = <.001) and mean (p = <.001) juniper age was higher on drier sites with high sand content and lower on moist sites with low sand content in the top 15cm of the soil profile (Fig 8; Fig 9). Maximum and Mean juniper ages for each plot were selected to represent the gradient of tree age across size classes and plots.

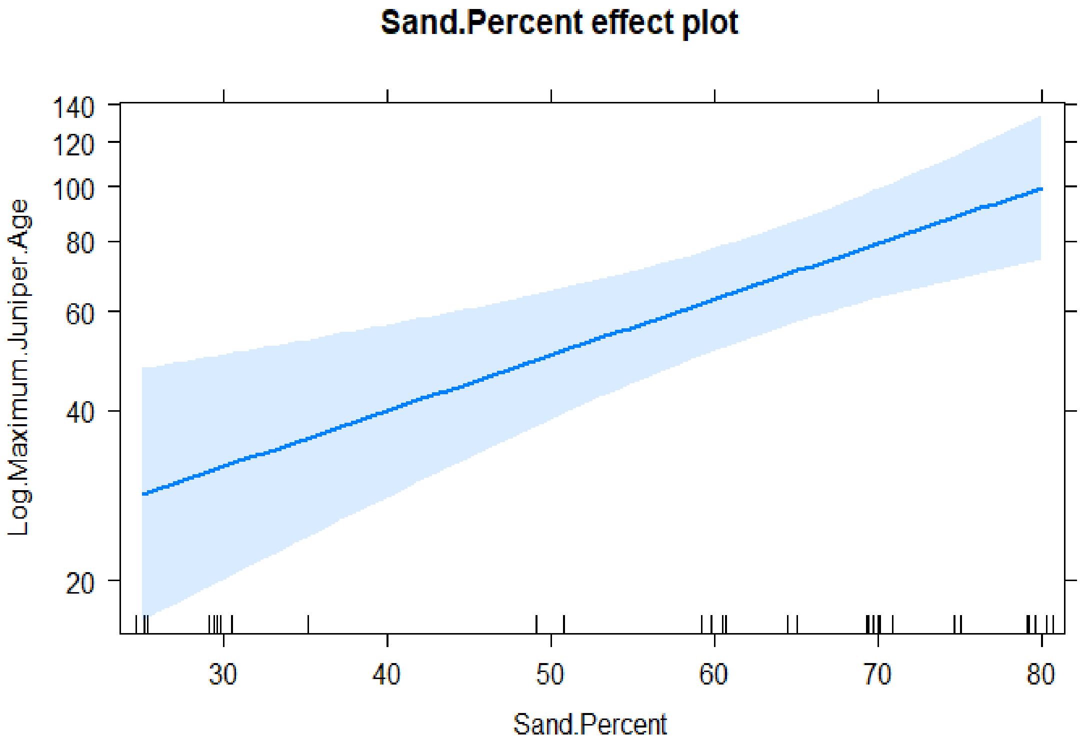

Figure 8: Poisson regression effect plot displaying the relationship of percent sand in the top 15 cm of soil to log maximum juniper age in each plot.

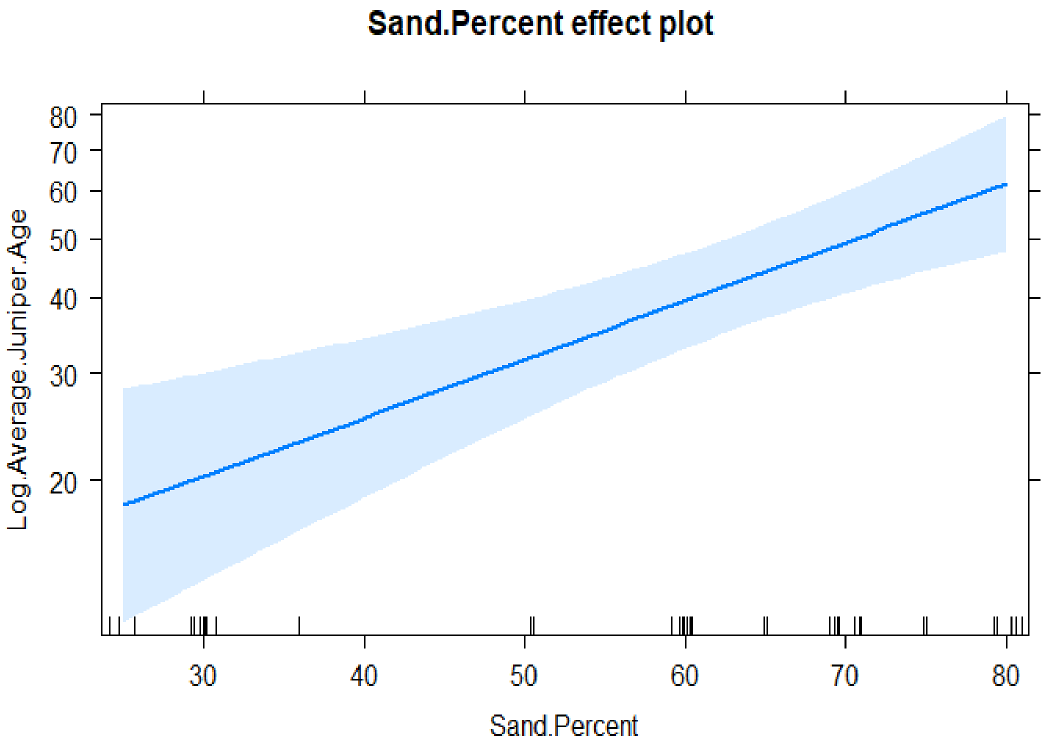

Figure 9: Poisson regression effect plot displaying the relationship of percent sand in the top 15cm of soil to log average juniper age in each plot.

Trees over 70 years of age were most often present on drier, coarse textured (>70% sand) sites while younger trees were generally more abundant on moist, fine textured (<50% sand, >20% clay) sites. Mean tree age on coarse textured sites was 40.21 years, and mean tree age on finer textured sites was 24.49 years of age. Aspect (heat load) and elevation were included as independent variables that may influence tree age in regression analysis but were not statistically important in explaining which sites conifer of varying ages preferred.

Discussion

In this area of southwest Montana, Rocky Mountain juniper establishment began to increase during the 20th century. This increase in conifer density coincides with other documented cases of woody plant expansion throughout North America and also coincides with historical increases in domestic livestock, reduced wildfire intensity, range and frequency, and favorable climate for germination and establishment (Miller et al. 2005; Heyerdahl et al. 2006; Briske et al. 2011). The chronology of establishment in southwest Montana is more recent than documented chronologies of other species in the United States, such as western juniper in the Great Basin, mesquite in the southwest, and eastern red cedar in the midwestern United States (Young and Evans 1981; Brown and Archer 1989; Engle et al. 1996; Miller and Rose 1999; Miller et al. 2005). These studies found that in the last 125 years, western juniper, mesquite, and eastern red cedar rapidly expanded into areas previously dominated by grass and shrubs.

Red Bluff, Montana was originally settled in 1864 as a mining town. Mining was active in this area through the turn of the 20th century and many pine stumps still remain from early harvest. Pine stumps are numerous at Red Bluff while juniper stumps rare. While some juniper stumps are present, pine appears to have been selected first as a fuel source (Dennis Rowe, personal communication, November, 2020). This may be why the range of limber pine age is considerably lower than juniper. If pine stumps were averaged at an age of 222 years old (established around 1800), mean age of limber pine would be 42 instead of 28 years of age. This establishment date would have been 64 years before Red Bluff was settled as a mining town. Even considering pine stumps, limber pine mean age at Red Bluff is young compared to previously reported age data (Brown and Schoettle 2008). White pine blister rust (*Cronartium ribbicola*) is another factor that may affect limber pine density on these sites. Limber pine, either alive and infected with blister rust or dead with blister rust scars, were observed within all Red Bluff sites. In some areas within our study sites, nearly all pine had been infected and killed by blister rust. Furthermore, black currant was routinely found growing under juniper and pine canopy and several currant (*Ribes spp.*) species are secondary hosts for white pine blister rust

(Geils et al. 2010). Thus, we expect that the overall age of limber pine is younger than expected due to timber harvest and white pine blister rust infections.

Between 1900 and 1930, precipitation averages were far greater than the current 50-year average for southwest Montana (Fig. 9, NIDIS-NOAA 2022). This time period coincides with early fire suppression and could have increased establishment and growth rates in woody plants (Eddleman 1987; Miller and Rose 1999). Another abnormally wet period in the 1940's and 1950's may have further contributed to increased woody plant establishment in southwest Montana. Altered fire severity, timing, and extent coupled with extended cool, wet periods offered favorable conditions for woody plant germination and establishment.

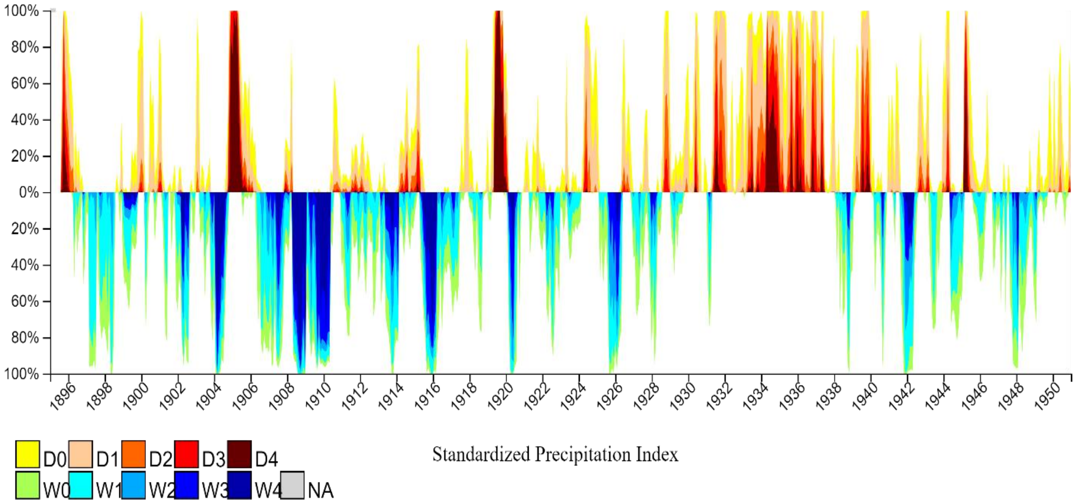

Figure 10: Standardized precipitation index for Madison County, Montana; where the top portion represents drought (D0-D4) and the bottom portion represents precipitation (W0-W4). Precipitation conditions were wetter than average from the years 1906 - 1918 and 1938 - 1949 (NIDIS-NOAA 2022).

Relict Rocky Mountain juniper stands on south facing aspects were characterized by coarse textured soils and, compared to north facing aspects, lower soil moisture percentages in the herbaceous rooting zone. Our findings are compatible with the idea of wildfire refugia, in which the oldest trees are expected to occupy sites with lower fuel loads and drier conditions (Kolden et al. 2017). Our findings also suggest that more recent stands (<50 years old) of juniper and pine are characterized by higher levels of soil moisture in the herbaceous rooting zone. Across the study site, mean Rocky Mountain juniper and limber pine age was low. In a previous study, mean age for western juniper was 68 years of age across all samples (Miller and Rose 1999). In our study, combined mean age of Rocky Mountain juniper and limber pine was 34 years of age. Over 95% of all juniper and pine on our study sites established after the beginning of the 20th century, which coincides with data from other species in Montana, such as Douglas fir (*Pseudotsuga menziesii*) and ponderosa pine (*pinus ponderosa*) ;(Arno and Gruell 1986; Metlen and Fiedler 2006). Arno and Gruell (1986) found that Douglas fir range and density increased dramatically in the 1940's due to fire suppression and seed crops experiencing unusually favorable moisture conditions.

In conclusion, we found that the majority of juniper (76%) on our study sites are young (<50 years old) and expect that juniper may be aggressively colonizing moist sites that were likely dominated by herbaceous plants and shrubs. The majority of pine are also recently established; however, this appears to primarily be a result of early timber harvest and white pine blister rust infections. We expect that this expansion is linked to the reduced presence of fire, historic livestock grazing, and favorable climate conditions. In the pinyon-juniper systems of the great Basin and southwest, ecosystem function and provision of services are altered as tree dominance increases, leading to changes in understory species abundance and production (Archer et al. 2017). Therefore, impacts to herbaceous and shrub species diversity, production, and distribution are of concern in this system.

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CHAPTER FOUR

UNDERSTORY IMPACTS OF ROCKY MOUNTAIN JUNIPER AND LIMBER PINE EXPANSION IN SOUTHWEST MONTANA

Contribution of Authors and Co-Authors

Chapter Three Manuscript

Author: Nathaniel Paul Haygood

Contributions: Collected samples and analyzed data. Wrote first draft of the manuscript.

Co-Author: Craig A. Carr

Contributions: Created and implemented study design. Advised and collaborated on sampling and data analysis. Offered direction and feedback on manuscript drafts.

Co-Author: Clayton B. Marlow

Contributions: Advised and collaborated on sampling and data analysis. Provided feedback on manuscript drafts.

Co-Author: Thomas J. Keck

Contributions: Collaborated on sampling and data analysis. Supplied feedback on manuscript drafts.

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UNDERSTORY IMPACTS OF ROCKY MOUNTAIN JUNIPER AND LIMBER PINE EXPANSION IN SOUTHWEST MONTANA

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Abstract

Pinyon-juniper woodlands in western North America have increased in range and density in the previous 150 years. This documented increase in woody plants has altered the provision of ecological goods and services such as forage production, habitat values, and watershed function. Data from other ecosystems suggest impacts from woody plant expansion include reduced forage production, altered community composition, structure, and wildlife habitat, and accelerated erosion rates. Comparatively, few data exist that characterize changes in tree range and abundance within the northern extent of these pine and juniper woodland types including the limber pine and Rocky Mountain juniper type in Montana. We investigated the effect of increased tree density and range on understory species diversity and abundance. In 38 plots across four sites, we evaluated stem density, tree age, tree canopy cover, and sampled understory vegetation production and cover. Multivariate cluster, principal component analysis, and non-metric multidimensional scaling analyses were used to evaluate relationships of tree attributes to understory and site characteristics. Cluster analysis showed understory species were different on north facing slopes with higher soil moisture than south facing slopes with lower soil moisture.

Ordination analyses showed shrub cover and cool-season perennial grass cover and production were positively correlated to an axis while tree canopy cover and density were negatively correlated to the same axis. This indicates that understory composition on tree dominated sites differs from sites with limited tree densities and canopy cover. While tree dominance did not appear to negatively impact cool-season perennial grass cover and production on north facing slopes, both cool-season perennial grass cover and production, as well as shrub cover were lower on tree dominated south facing slopes. Understory appeared to differ in pine dominated sites compared to juniper dominated sites. The results of this study show that cool season perennial grass cover and production and shrub cover are lower on south facing sites with heavy juniper canopy.

Introduction

Since the mid-19th century, pinyon-juniper woodlands in western North America have experienced an expansion in range and density and a corresponding degradation in the provision of ecosystem goods and services including forage production, watershed function, biological diversity and habitat values (Burkhardt and Tisdale 1976; Miller and Rose 1999; Miller et al. 2005; Briske et al. 2011; Archer et al. 2017). This is well documented in systems such as the central Great Plains and the Great Basin, where various impacts include accelerated soil erosion, reduced forage production, altered wildlife habitat, changes in plant community composition, structure, and biodiversity, and the replacement of mesic and semi-arid plant communities with woodlands (Arno and Gruell 1983; Engle et al. 1996; Miller et al. 2005).

In comparison, few data exist that characterize shifts in tree range and abundance within the northern extent of these juniper and pine woodlands including the Rocky Mountain juniper (*Juniperus scopulorum*-Sarg) and limber pine (*Pinus flexilis*-James) type in southwest Montana.

Thus, we initiated a study to investigate if the presence and abundance of these tree species are related to change in understory species abundance and diversity in southwestern Montana. Based on previous literature, we hypothesize that understory species diversity, abundance, and production will differ in areas with high juniper and pine densities and cover compared to areas with limited tree presence. We further hypothesize that juniper and pine densities and cover and the subsequent impact to shrub and herbaceous diversity, abundance and production will vary based on physical site and climatic characteristics.

Methods

Study Area

This study took place during the summers of 2019-2021. The study areas are located in the northern extension of the Rocky Mountains near the towns of Norris (45°34’06.43”N - 111°42’36.31”W) and Red Bluff (45°34’12.12”N - 111°36’54.44”W), Montana (Fig. 10). Soils at the Red Bluff study site are described as cool Yetull loamy sands, Varney clay loams and Crago gravelly loams on 2 to 8% slopes to Sebud-Hapgood, Rochester and Shurley-Rock outcrop complexes on 25 to 60% slopes (Web Soil Survey 2022). Shurley-Rock outcrop complexes were the dominant series within the Red Bluff study plots and consist of shallow to deep, well drained sandy loams and loamy sands formed in material derived from gneiss, schist, and granite parent materials (Web Soil Survey 2022). Soils within the Norris site are dominated by Blaine loams and Tiban stony clay loams on 5-75% slopes. These are very deep, well drained mollisols that formed in colluvium, alluvium, or till and landslide deposits (Web Soil Survey 2022). These soils are derived from mixed sources of parent material; however, basalt is the dominant rock outcrop on these lands.

Table 1: Shurley and Tiban series information (Web Soil Survey 2022). Shurley-Rock outcrop complexes was the dominant series at Red Bluff and Tiban was the dominant series at Norris, MT.

Shurley Series	Tiban Series
Series Description The Shurley series consists of deep, well drained soils that formed in material derived from gneiss, schist, and granite rock. These soils are on hills, mountains, and alluvial fans. Slopes are 8 to 60 percent. Mean annual precipitation is about 12 inches, and mean annual temperature is about 40 degrees F	**Series Description** The Tiban series consists of very deep, well drained soils that formed in colluvium, alluvium, till or slide deposits derived from mixed rock sources. These soils are on escarpments, mountain slopes, hills, ridges, alluvial fans, stream terraces, fan remnants and moraines. Slopes are 0 to 75 percent. Mean annual precipitation is about 18 inches, and mean annual air temperature is about 42 degrees F
Taxonomy Sandy-skeletal, mixed, frigid Aridic Haplustepts	**Taxonomy** Loamy-skeletal, mixed, superactive Ustic Haplocryolls
Range in Characteristics Soil temperature averages 40 to 47 degrees F. Moisture control section - between 12 and 35 inches; dry in all parts between four-tenths and five-tenths of the cumulative days per year when the soil temperature at a depth of 20 inches is higher than 41 degrees F. Depth to Bk horizon - 10 to 24 inches	**Range in Characteristics** Mean annual soil temperature averages 35 to 45 degrees F. Mean annual summer soil temperature - 50 to 55 degrees F. Mollic epipedon thickness - 7 to 15 inches Depth to Bk horizon - 13 to 32 inches

The study sites see a mean annual temperature of 7°C (PRISM Climate Group 2022 - 30-year average). Average annual precipitation is 42cm and mostly comes as rain between April and July (PRISM Climate Group 2022 - 30-year average).

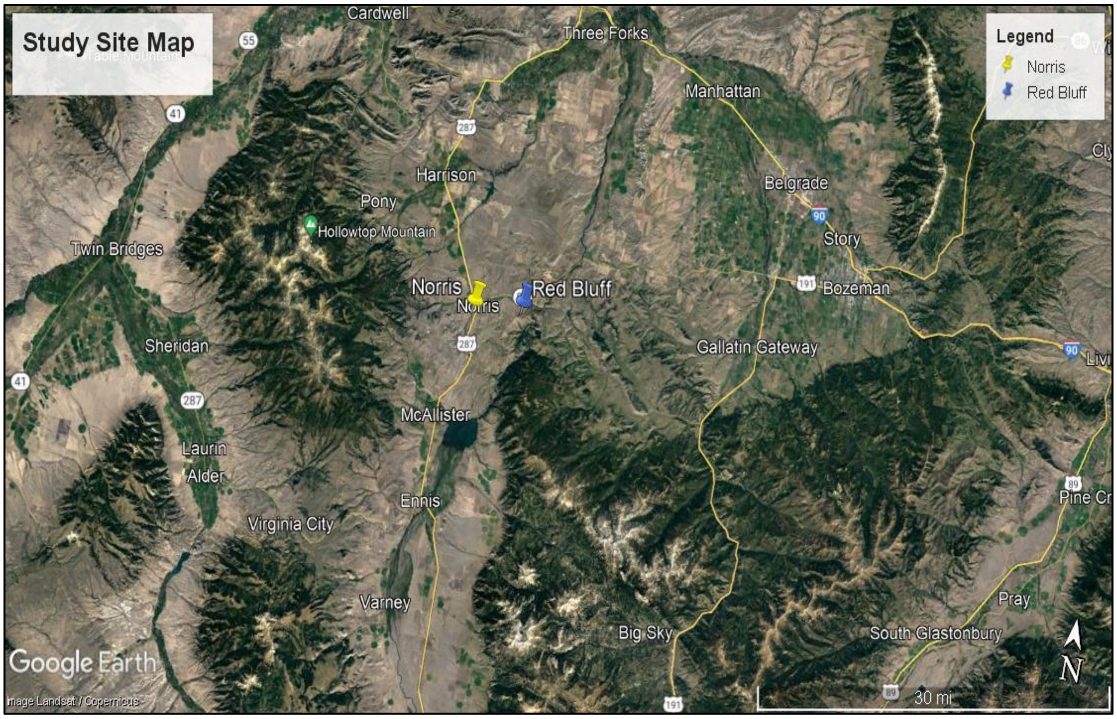

Figure 11: Map of the four study sites near Norris and Red Bluff, Montana.

Associated Vegetation

The most common grass species present at each of the four study sites were bluebunch wheatgrass (*Pseudoroegneria spicata* Pursh), Idaho fescue (*Festuca idahoensis* Elmer), Sandberg's bluegrass (*Poa secunda* J. Presl), threadleaf sedge (*Carex filifolia* Nutt.), prairie junegrass (*Koeleria macrantha* (Ledeb.) Schult.) and needle and thread (*Hesperostipa comata* (Trin. & Rupr.) Barkworth). Of these native grass species, Idaho fescue and bluebunch wheatgrass were most abundant. Cheatgrass (*Bromus tectorum* L.) was the most abundant non-native grass at Red Bluff. The Norris study site contained very little non-native grass. Common forbs included yellow salsify (*Tragopogon dubius* Scop.), dandelion (*Taraxacum officinale* Wigg.), lupine (*Lupinus spp.*), western yarrow (*Achillea millefolium* L.), fringed sagewort (*Artemisia frigida* Willd.) and prickly pear cactus (*Opuntia spp.*). The most abundant forbs at Red Bluff were western yarrow and prickly pear cactus while the most abundant forb at Norris was scarlet gilia (*Ipomopsis aggregata* Pursh).

Common shrubs were mountain big sagebrush (*Artemisia tridentata ssp. vaseyana (*Rydb.) Beetle), rubber rabbitbrush (*Ericameria nauseosa* (Pall. Ex Pursh) G.L. Nesom & Baird), green rabbitbrush (*Chrysothamnus viscidiflorus* (Hook.) Nutt.), skunkbrush sumac (*Rhus aromatica* Aiton) and black currant (*Ribes cereum* Douglas). Mountain big sagebrush was the most abundant shrub at both Norris and Red Bluff.

Sampling Procedures

We randomly selected 38, 25x25 m plots that ranged in tree abundance from 64 stems/hectare – 592 stems/hectare across four sites near Norris, Montana. In each plot we evaluated stem density, tree age, and tree canopy cover and sampled understory vegetation production and cover. Stem density was evaluated by counting total number of juniper and pine on each 25x25m plot. To sample the gradient of tree ages, trees were placed into three size classes; dominant (≥3m height), co-dominant (1-3m height), and sub-dominant (≤1m height). Tree age was sampled by taking a single tree core at a height of 15cm above the ground surface from a maximum of three trees from each species in each size class, allowing for a maximum of 18 sampled trees per plot, where present (Heyerdahl et al. 2006). If a tree was too small to be cored with an increment borer, we used a chainsaw to cut down and remove a wedge out of the tree. All cores and wedges were sanded, oiled, and tree rings were counted. We assumed the establishment date as the tree's pith date (Heyerdahl et al. 2006). Tree canopy cover was recorded in three random locations in each plot through use of a spherical convex densiometer.

Using one plot side, we randomly placed five, 25m transects with five 20x50cm quadrats per transect to evaluate understory vegetation cover using the Daubenmire cover class approach (Daubenmire 1959). Forage biomass was evaluated by clipping above ground herbaceous vegetation in two, randomly selected 20x50cm frames along each transect and separating material by functional group. Functional groups included cool-season perennial grass, warm-season perennial grass, cool-season annual grass, forbs, and shrubs. We oven-dried all clipped vegetation at 65°C for 48 hours to estimate biomass for each plot. Soil water content was estimated by sampling the top 15cm of soil depth at three random locations in each plot across the growing season. This depth was selected as it represents the general rooting depth of many understory species in rangeland systems (Carr and Krueger 2011). We sampled soil moisture during the first two weeks of May, June, and July in 2021 for all plots. All samples were dried at 105°C for 24-48 hours using the gravimetric method to determine soil water content (Black 1965). In the first field season (2019), aspect and elevation were recorded in each plot. Heat load was calculated from aspect, using a continuous scale from 0 to 1, where southwest aspects are weighted at a value of 1 (225°) and northeast aspects are weighted at a value of 0 (45°), based on solar radiation received (McCune and Grace 2002).

Data Analysis

Multivariate cluster and ordination analyses were used to evaluate relationships among tree attributes and understory characteristics. Understory species cover data were structured into a matrix consisting of 38 plots and 83 species. Species occurring in less than 3 plots were removed from the data to reduce noise (McCune and Grace 2002). We used hierarchical cluster analysis with Bray-Curtis distance (Sorenson) and flexible-beta linkage ($\beta = -0.25$) to group plots by understory species cover. We ran a cluster analysis for all plots and pruned the dendrogram at three groups. As groupings on the full data set appeared to follow site characteristics, we ran further cluster analyses on each of the three groups from the original cluster analysis for all plots. Each of these dendrograms were pruned at two groups.

Non-metric multidimensional scaling ordination (NMDS) for all plots in species space was implemented to view differences in understory species among groups partitioned via cluster analysis. NMDS is an iterative search for the best positions of *n* entities in *k* dimensions that minimizes stress in the *k*-dimensional configuration (McCune and Grace 2002). NMDS performs well even when diversity is high and as such, is the most generally effective ordination method for ecological community data (McCune and Grace 2002). We performed NMDS analysis using Bray-Curtis distance and 50 real data runs from a randomized start, a maximum of 250 iterations and an instability configuration of 0.00001. These ordinations were performed using the PC-ORD v. 5 application (McCune and Mefford 1999).

Groups identified through cluster analysis and their relationship to environmental variables in species space were visualized via joint-plots. Joints plots are a diagram of radiating lines used to show the relationship of environmental variables, such as soil moisture and heat load, to ordination scores, where the strength and direction of the relationship is judged by the line's angle and length. To increase interpretability, we rotated ordination solutions through the point cloud to maximize environmental criteria along one or two axes.

Principal component analysis (PCA) was used to create an artificial variable that represents the strongest tree attributes. These principal components can be used as environmental variables and overlayed across axes in species space to visualize relationships of tree attributes to plots based on understory species cover. As the most basic eigenvector method of ordination, PCA reduces a dataset with *n* objects and *p* variables to smaller number of artificial variables that represent the majority of information in the original dataset (McCune and Grace 2002). Principal components representing tree attributes were reduced from four tree attributes; canopy cover (plot level densiometer score), total stem density, juniper cover, and pine cover, to two tree attributes; pine cover and canopy cover. These two tree occupancy variables were included in NMDS analysis for groups identified through cluster analysis.

Results

NMDS Results from All Plots

Cluster analysis for all plots rendered three distinct groups based on similarity and dissimilarity of plot level understory species cover (38% of information remaining, Fig. 11). The three-dimensional solution to NMDS ordination for all plots was the most appropriate fit to the data (Fig. 12, final stress = 14.58). Cluster one (red triangles) was negatively associated with axis one and cluster two (teal squares) was positively correlated with axis two. Cluster three (blue circles) was positively associated with axis one. On the jointplot, cool-season annual grass production and warm-season perennial grass production were positively associated with axis one while cool-season perennial grass cover, juniper density, and soil moisture percentages for all months were negatively associated to axis one. Shrub cover and cool-season perennial grass production were positively associated to axis two and total tree canopy cover was negatively associated to axis two. Cluster one (red triangles) contained 15 plots and was characterized by high soil moisture values and cool-season perennial grass cover. Cluster two (teal squares) contained nine plots and was characterized by high shrub cover and low tree canopy. Cluster three (blue circles) contained 14 plots and was characterized by high warm-season perennial grass production, low soil moisture values, low cool-season perennial grass cover, and high cool-season annual grass production. In general, plots negatively associated with axis one have higher soil moisture and plots positively associated with axis one are droughty.

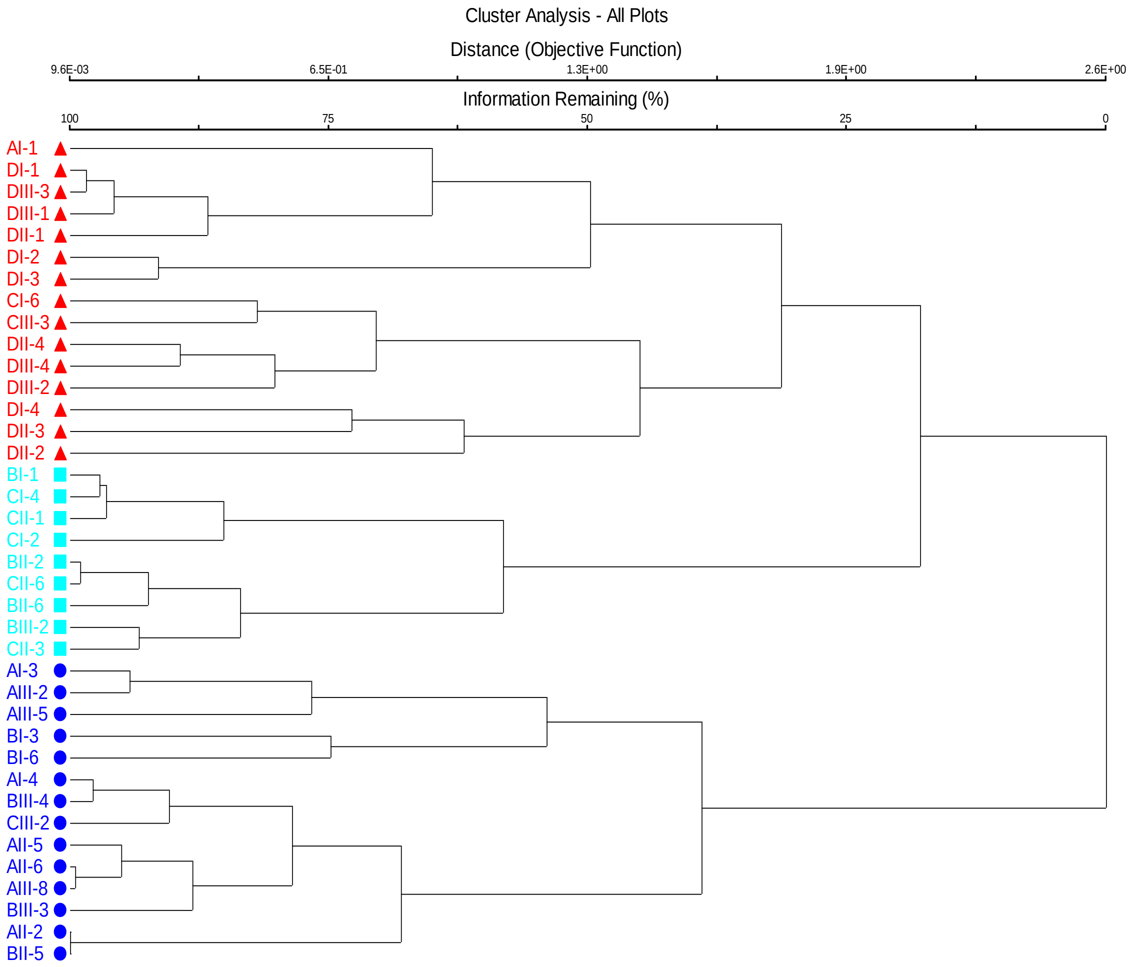

Figure 12: Cluster Dendrogram of all field plots (n = 38). Group one (red triangles) are associated with high soil moisture plots. Group two (teal squares) and three (blue circles) are associated with higher heat load and elevation values.

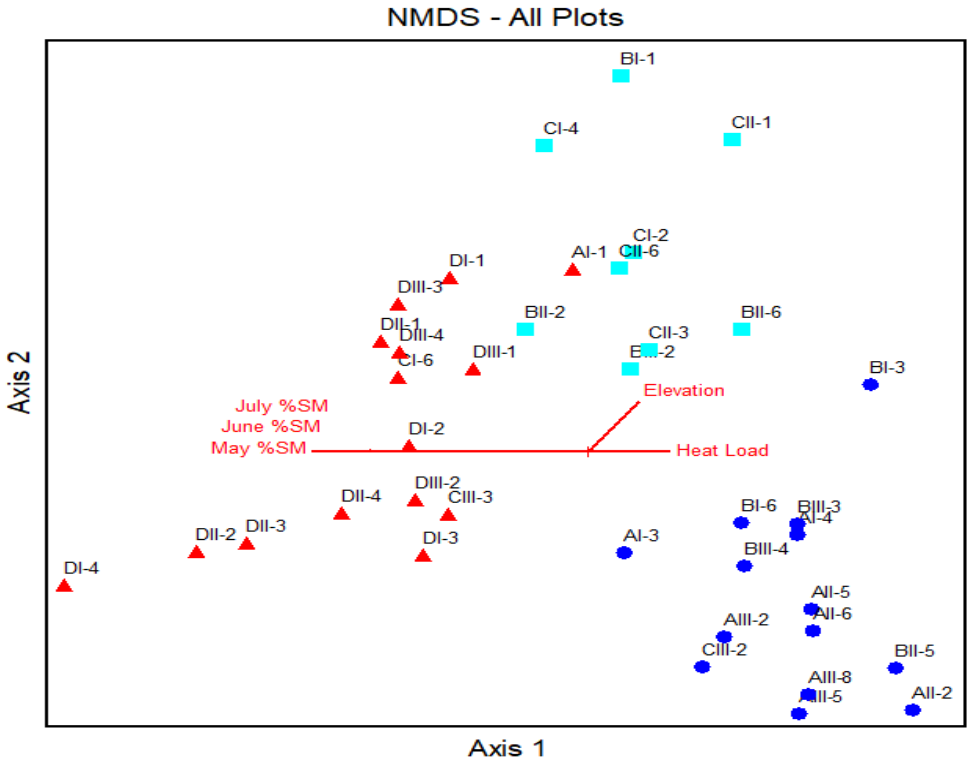

Figure 13: NMDS joint-plot with overlayed environmental variables.

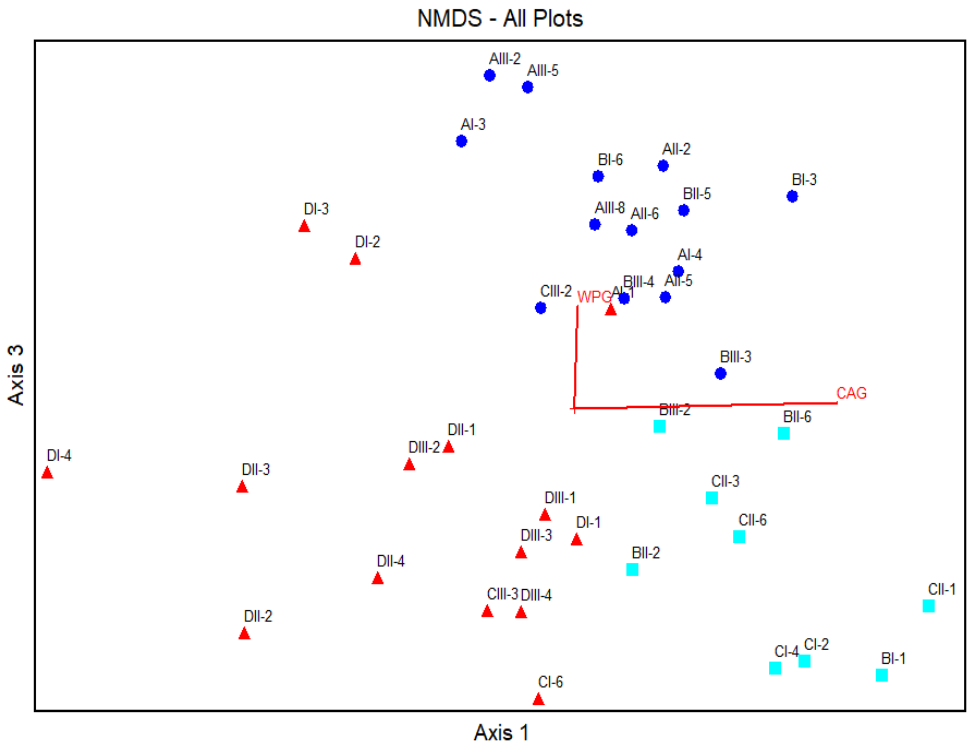

Figure 14: NMDS jointplot with overlayed understory variables.

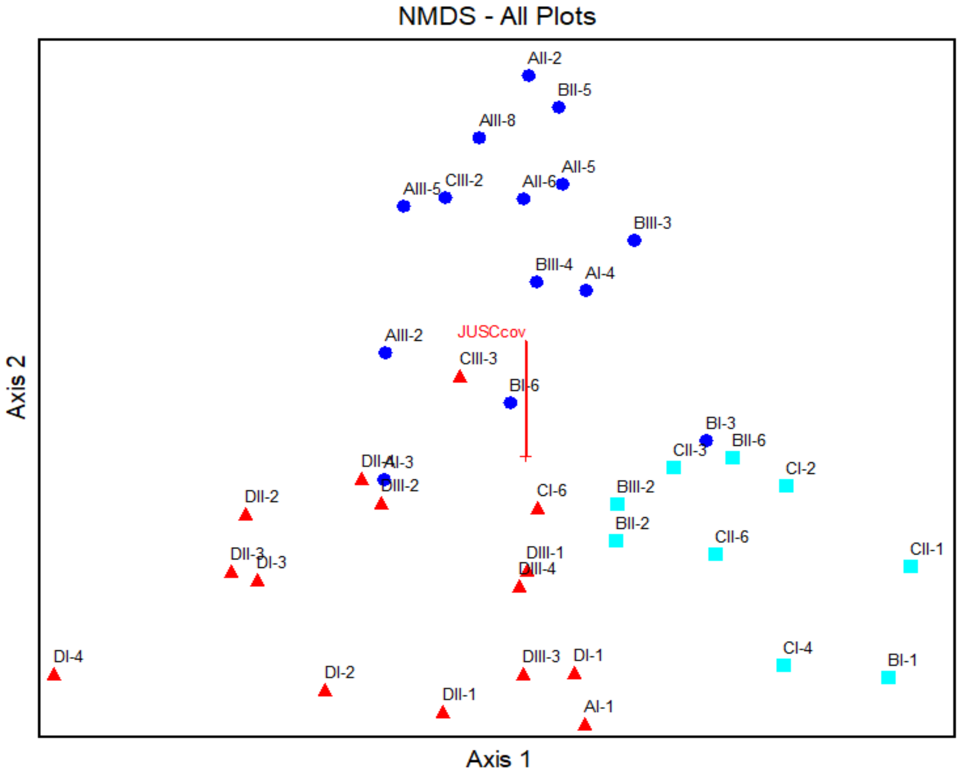

Figure 15: NMDS jointplot with overlayed tree variables.

NMDS Results from Group One

We performed another cluster analysis on group one (red triangles-high soil moisture, high cool-season perennial grass cover) which rendered two distinct sub-groups based on dissimilarity of plot level species cover (15 plots, 22% of information remaining, Fig. 15). The two-dimensional solution to NMDS ordination for these plots was the most appropriate fit to the data (Fig. 16-18, final stress = 10.07). These two axes represented 89.4% of total variance. We created three jointplots with environmental, tree, and understory variables overlayed across the distribution of plots in species space. For ease of interpretation, these will be referred to as understory, tree, and environmental jointplots. The understory jointplot showed cool-season perennial grass cover with a positive association to axis one (Fig. 18). Cool-season perennial grass production was also positively associated with axis one. Heat load was positively associated with axis two and May, June, and July soil moisture were negatively associated with the same axis on the environmental jointplot (Fig. 16). Plots in cluster one tended to have high cool-season perennial grass cover and production. Cluster two (blue) was characterized by high canopy cover and higher elevation sites.

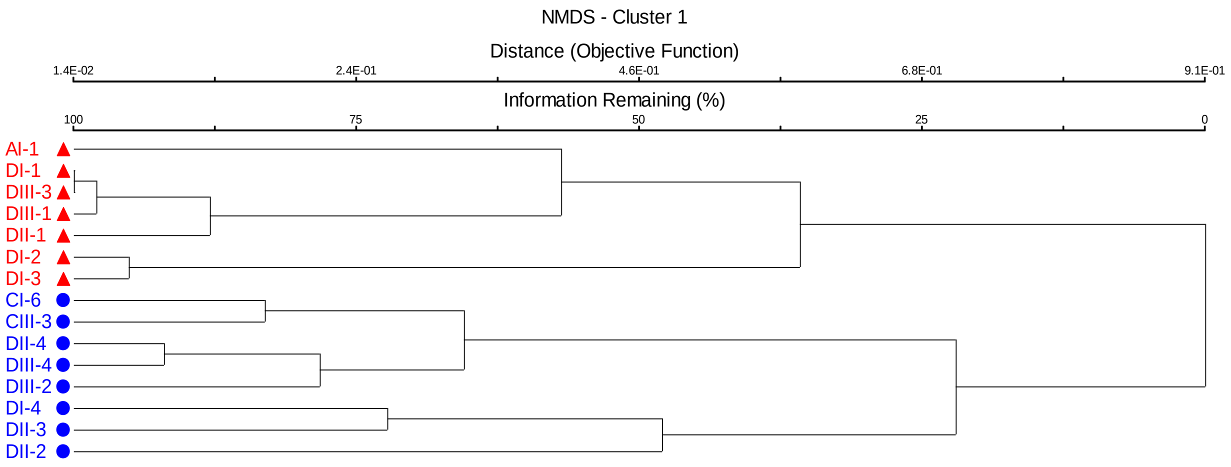

Figure 16: Dendrogram of group one.

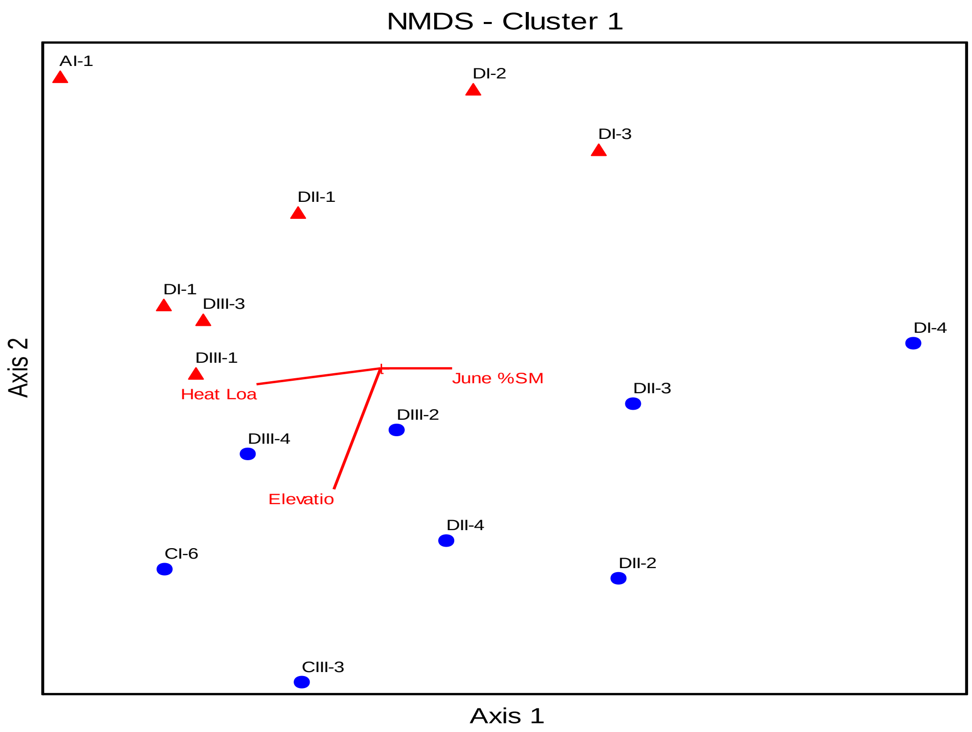

Figure 17: NMDS jointplot of group one with overlayed environmental variables.

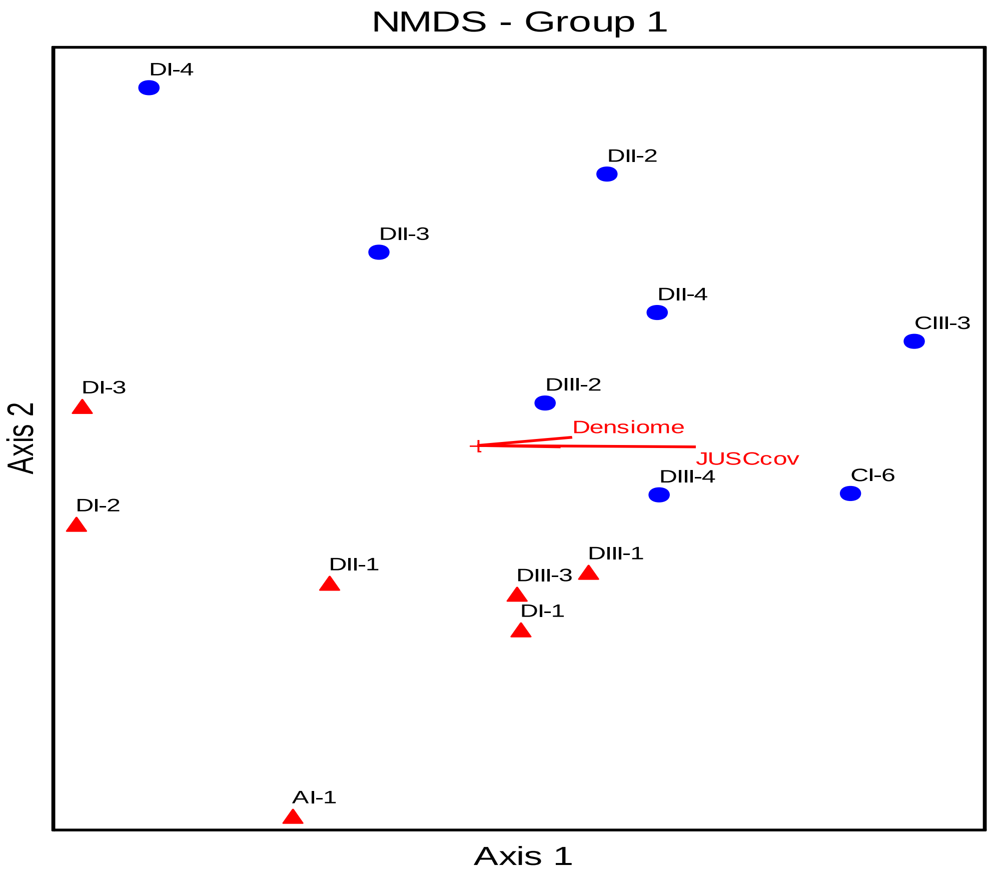

Figure 18: NMDS jointplot of group one with overlayed tree variables.

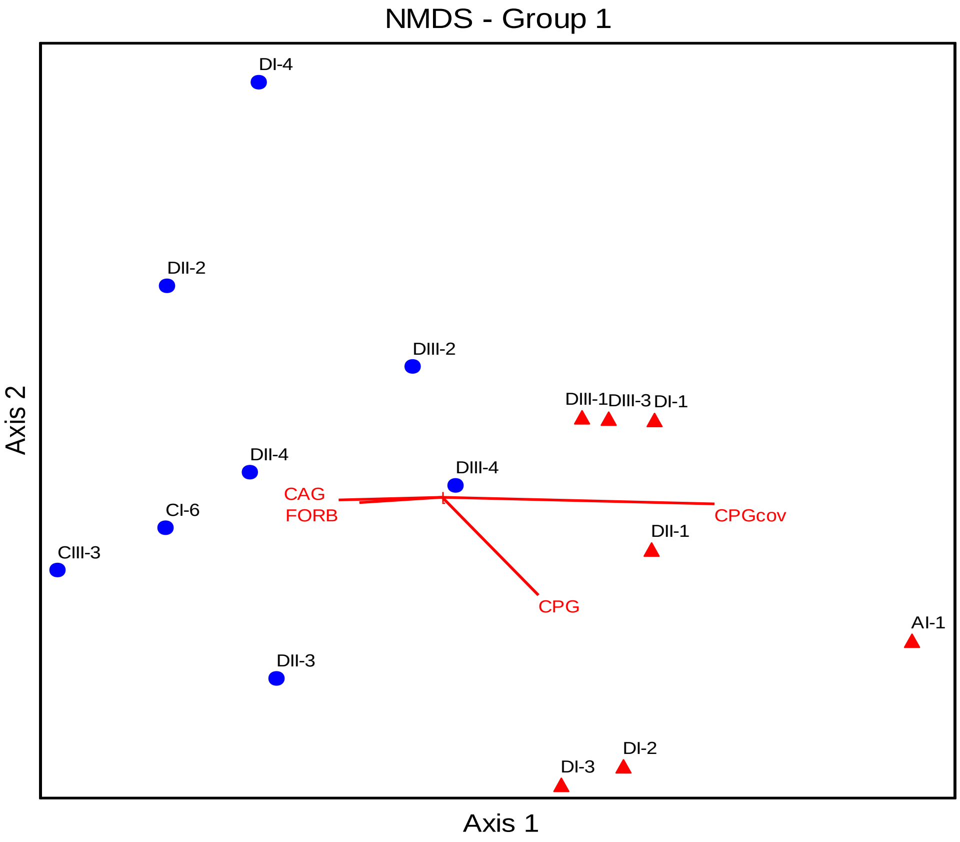

Figure 19: NMDS joint-plot of group one with overlayed understory variables.

NMDS Results from Group Two

Cluster analysis from group two (teal squares-high shrub abundance, low tree canopy cover) also produced two distinct groups (9 plots, 38% of information remaining, Fig. 19). The two-dimensional solution to NMDS ordination for these plots was once again the most appropriate fit to the data (Fig. 20-22, final stress = 6.37). These two axes represented 86.4% of total variance in the ordination. The understory jointplot displayed shrub cover with a very high negative association with axis one (Fig. 22). Total canopy (densiometer) had a very high positive association with axis one on the tree jointplot, as did pine cover, juniper cover, and stem density (Fig. 21). The environmental jointplot only showed heat load positively associated to axis two. Upon further investigation, this was primarily due to two plots with southwest facing aspects (BIII-2 and BII-6, Fig. 20).

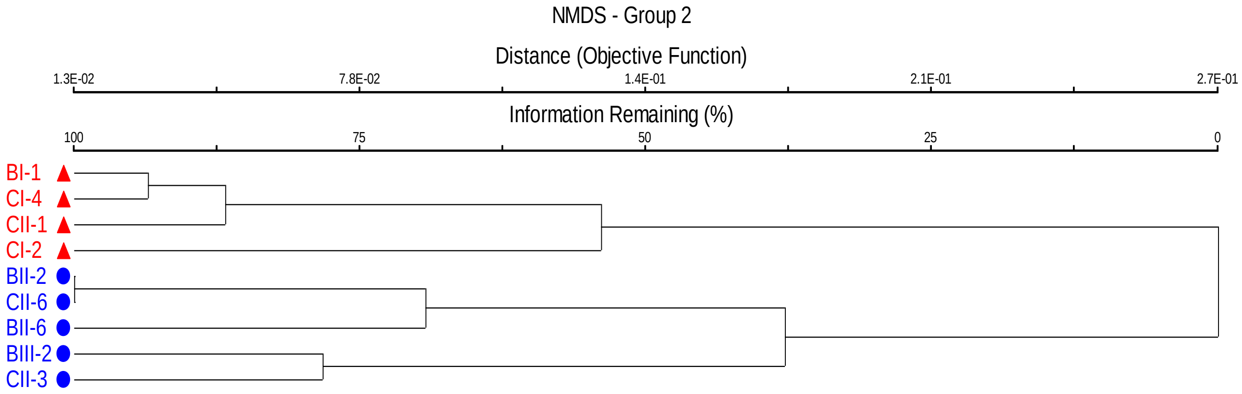

Figure 20: Dendrogram of group two.

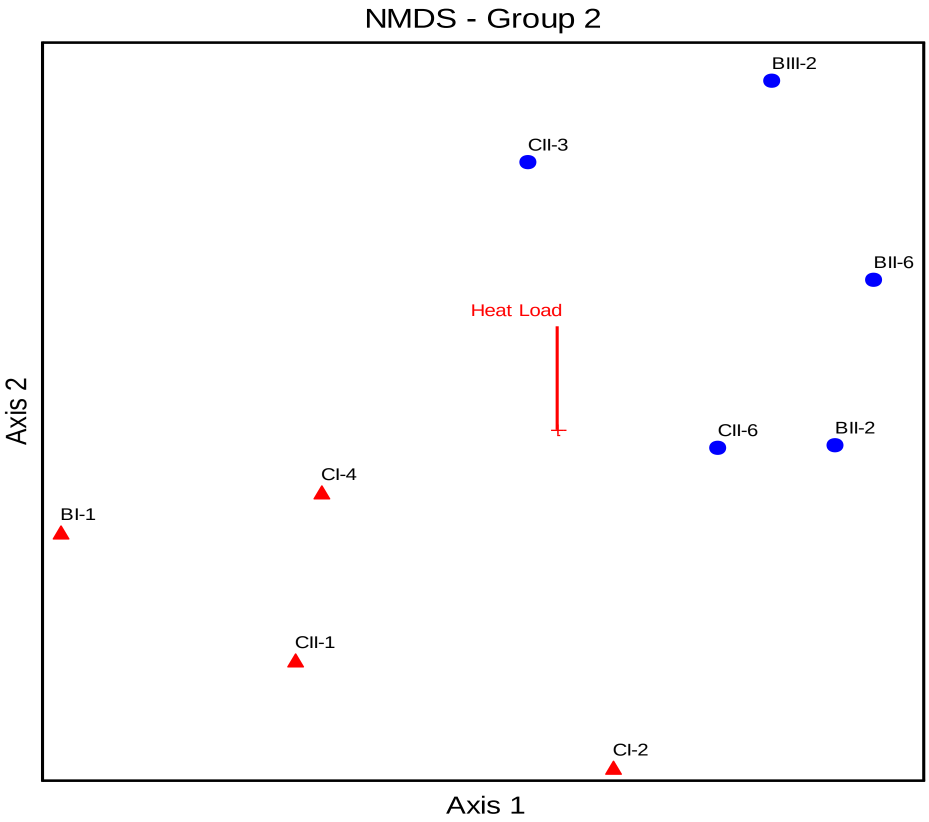

Figure 21: NMDS joint-plot of group two with overlayed environmental variables.

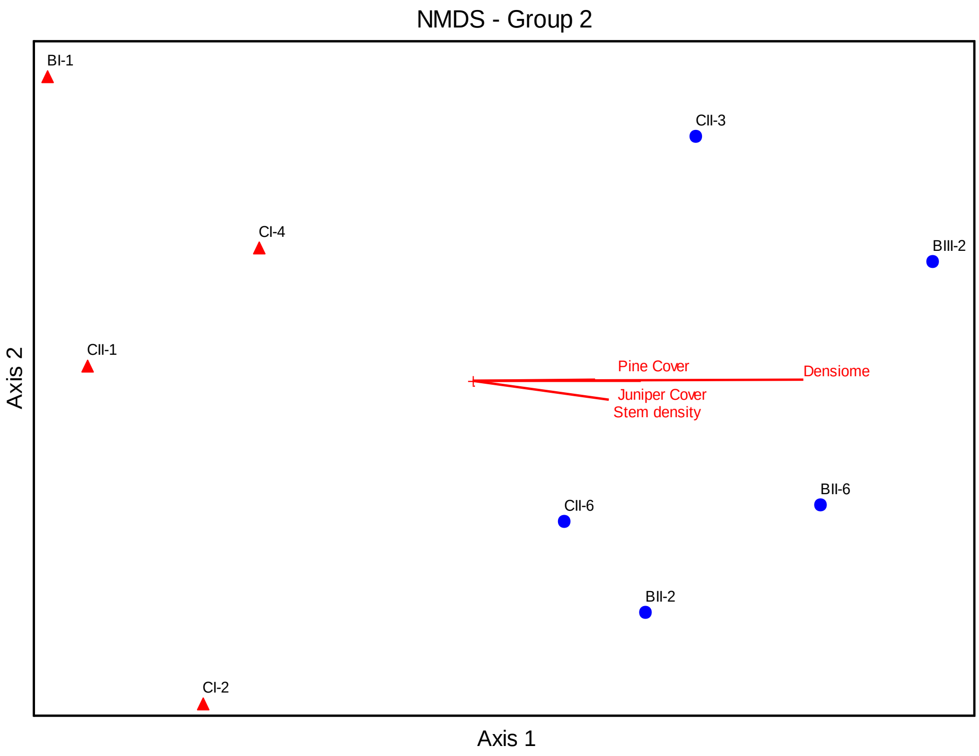

Figure 22: NMDS joint-plot of group two with overlayed tree variables.

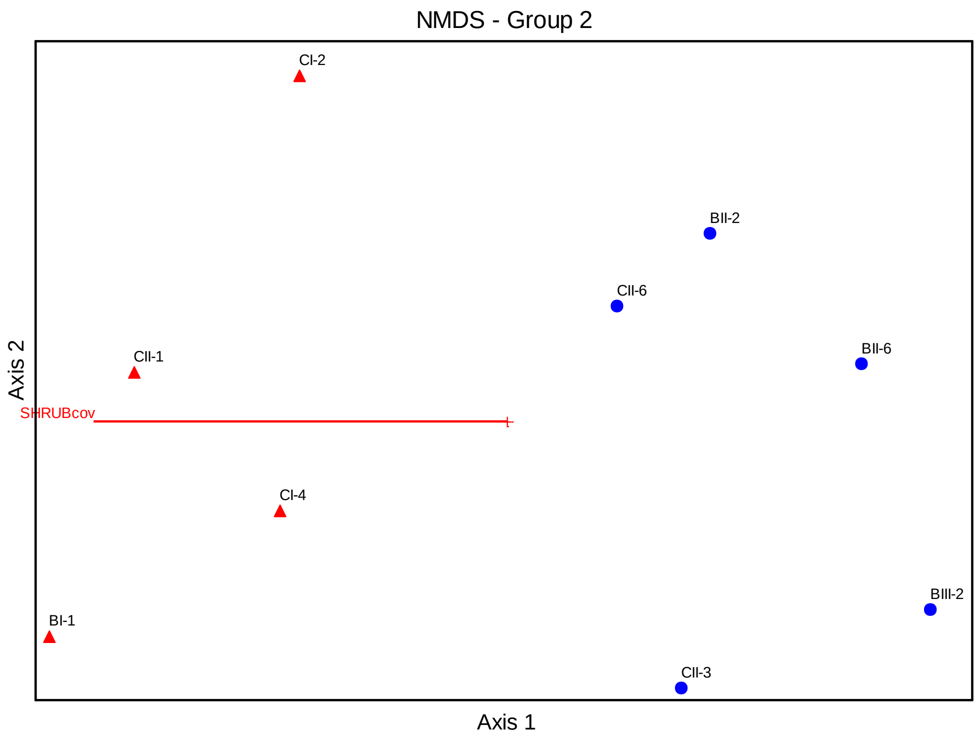

Figure 23: NMDS joint-plot of group two with overlayed understory variables.

NMDS Results from Group Three

Cluster analysis from group three (blue circles-high warm-season perennial grass production, low cool-season perennial grass cover, low soil moisture, high cool-season annual grass production) also produced two groups (14 plots, 27% of information remaining, Fig. 23). The two-dimensional solution to NMDS ordination for these plots was also the most appropriate fit to the data (final stress = 9.26, Fig. 24-26). These two axes represented 91.6% of total variance in this ordination. The understory jointplot showed cool-season perennial grass production strongly associated with axis one, as was cool-season perennial grass cover (Fig. 26). Tree density and total tree canopy cover were positively associated with axis one on the tree jointplot (Fig. 25). This suggests understory communities on plots with high tree density and cover differ from those with low tree density as observed in the general paucity of cool season perennial grasses associated with high tree abundance. Shrub cover was positively associated with axis two while May and June soil moisture were negatively associated with axis two (Fig. 25, 26). Principal components for pine cover were negatively associated with axis two, once more displaying that understory composition between pine and juniper dominated sites at least partially differ.

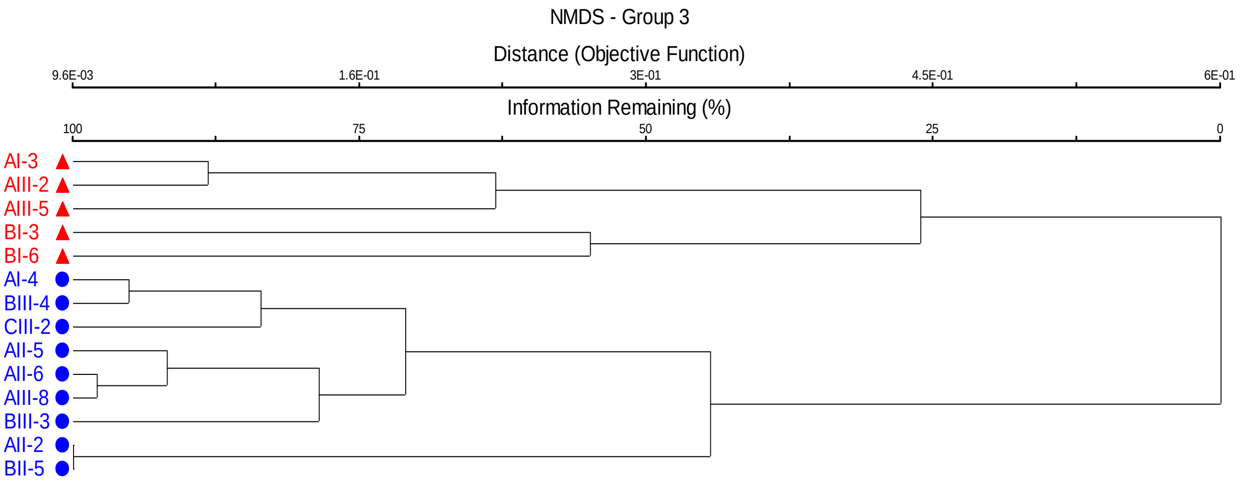

Figure 24: Dendrogram of group three.

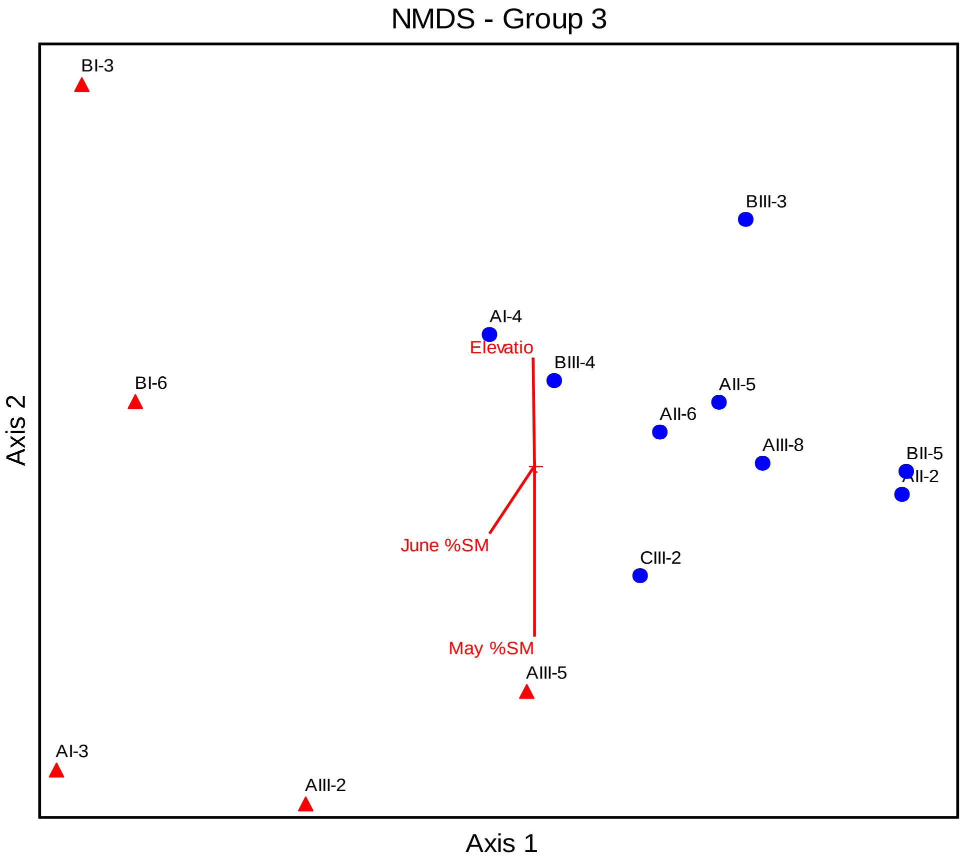

Figure 25: NMDS joint-plot of group three with overlayed environmental variables.

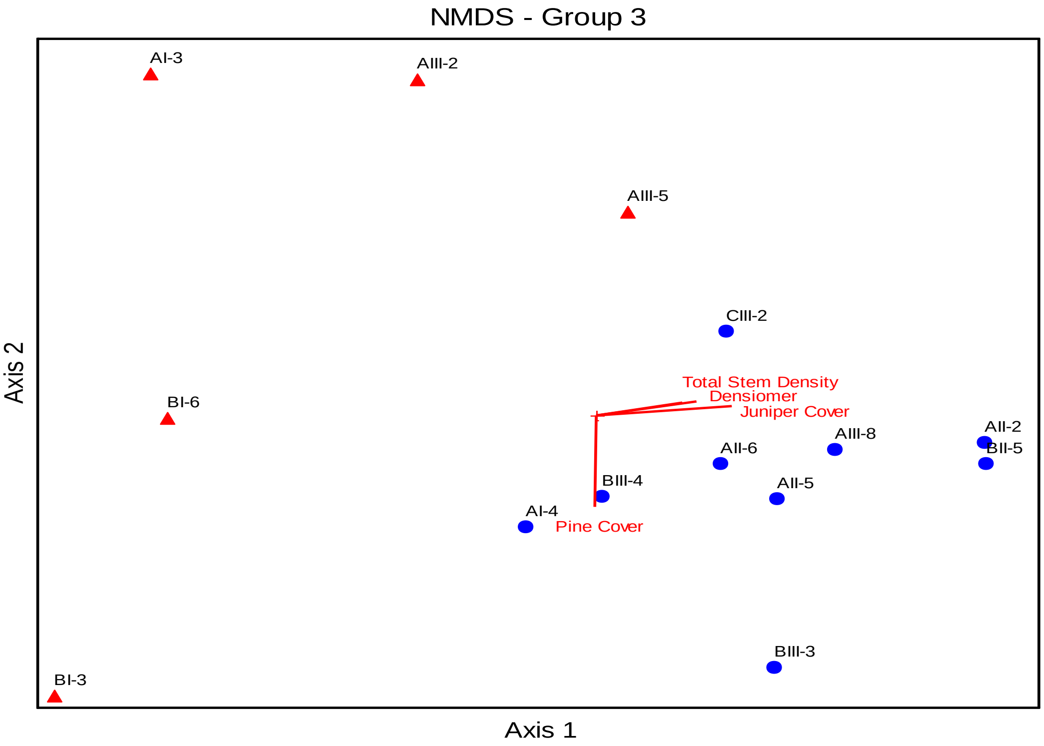

Figure 26: NMDS joint-plot of group three with overlayed tree variables.

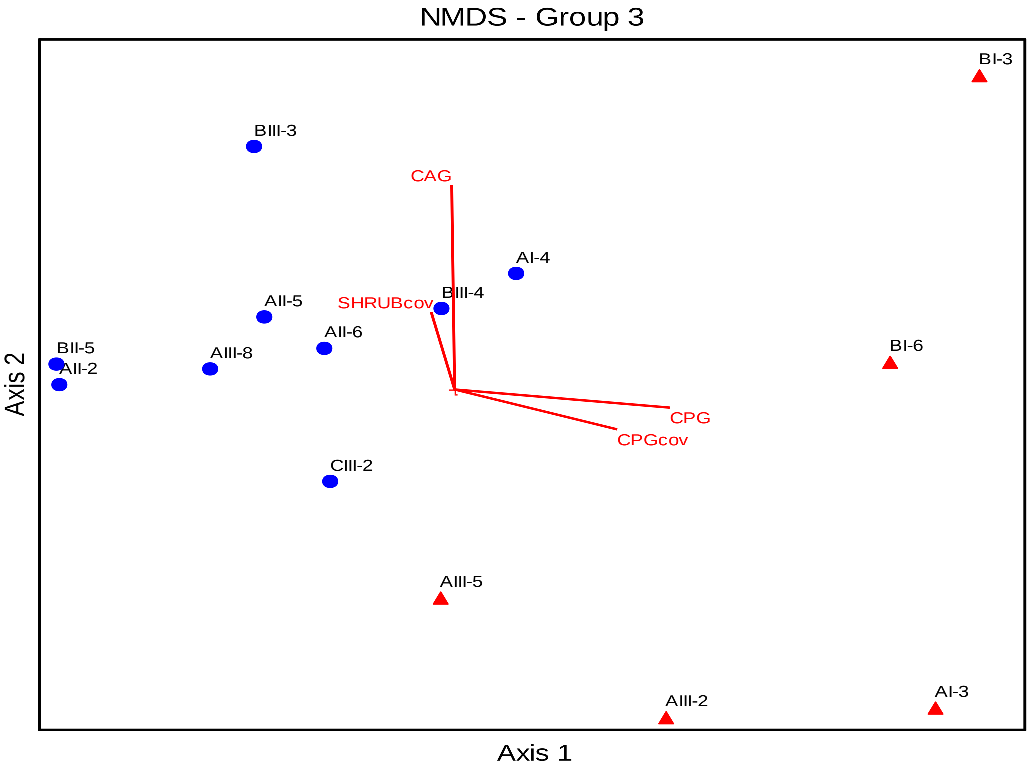

Figure 27: NMDS joint-plot of group three with overlayed environmental variables.

Across all Red Bluff plots (n = 26), cool-season perennial grass cover averaged 12.5% on sites with no conifer canopy and 4% on sites with 75% conifer canopy (Fig. 27). Shrub abundance averaged 19% on sites with no conifer canopy and were absent on sites with 70% conifer canopy (Fig. 28). Plots at Norris, Montana, were all on northeast to northwest facing aspects. These plots had the highest monthly soil moisture percentages (Table 2). There was no appreciable difference in cool-season perennial grass or shrub production or cover across these plots (n = 12), after accounting for the gradient in pine and juniper canopy cover and density.

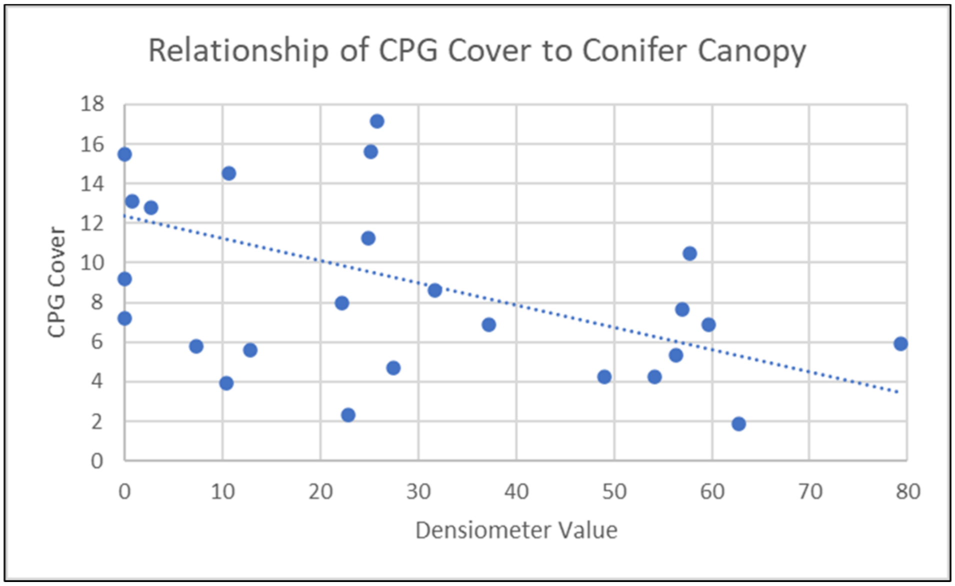

Figure 28: Relationship of cool-season perennial grass cover to pine and juniper canopy cover on Red Bluff plots.

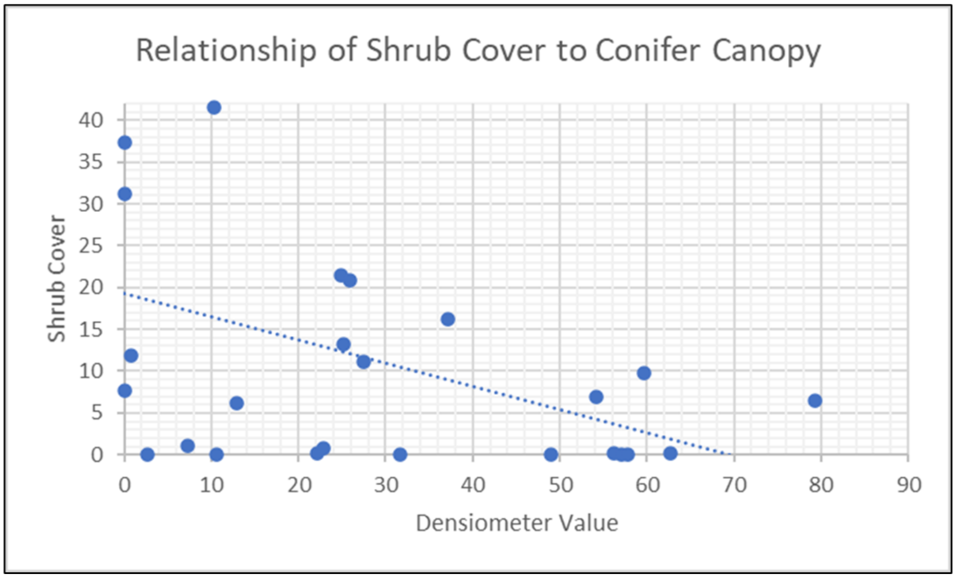

Figure 29: Relationship of shrub cover to pine and juniper canopy cover on Red Bluff plots.

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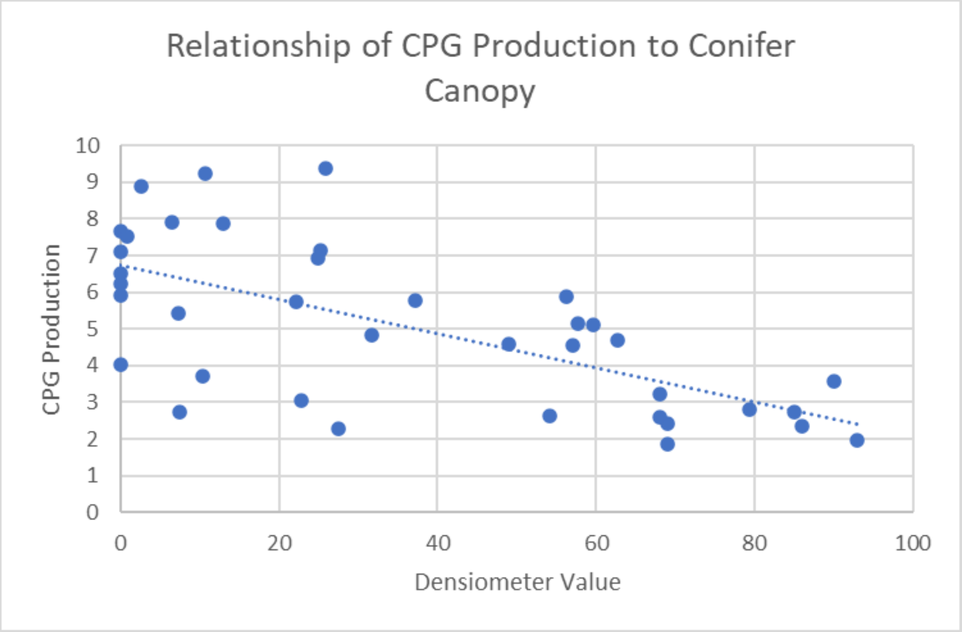

Figure 30: Relationship of cool-season perennial grass production to pine and juniper canopy cover on all plots.

Table 2: Mean soil moisture percentages in the top 15cm of the soil profile for all sites (May, June, and July). Plots at site D are on north facing aspects while plots at site A, B, and C contain no north facing aspects.

	Site A			**Site B**	
May % SM	June %SM	July %SM	May %SM	June %SM	July %SM
22.73	2.73	5	7.87	2.26	2.93
14.66	4.79	3.9	4.22	1.03	1.71
11.46	1.82	3.04	5.11	1.95	6.27
8.39	1.47	1.67	7.83	2.83	3.94
10.72	2.18	3.21	7.52	1.92	3.51
9.27	1.24	1.58	4.88	1.01	3.27
10.31	2.16	2.17	5.76	2.6	2.83
7.94	1.61	2.34	4.38	2.5	3.61
10.37	1.96	2.76	5.91	2.81	3.39
	Site C			**Site D**	
May % SM	June %SM	July %SM	May %SM	June %SM	July %SM
9.94	0.95	1.18	22.23	9.95	11.41
7	2.91	3.31	25.46	10.39	12.76
14.23	4.38	3.31	21.45	10.89	12.09
12.23	0.87	1.75	22.81	12.26	11.21
13.4	0.84	1.35	18.05	7.87	10.26
14.42	2.49	2.61	32.1	11.94	15.63
13.96	1.48	2.15	22.85	12.97	13.84
10.03	1.65	1.78	26.86	14.7	18.05
			27.5	12.27	22.42
			27.39	15.2	14.43
			24.5	14	19.32
			19.93	13.85	12.6

Discussion

NMDS for All Plots

Cluster analysis for all plots, when pruned at three groups and included in NMDS ordination, clearly separates into three distinct clusters in species space. When environmental variables are projected across plots in species space, several of these variables explain potential differences in species composition, as it pertains to physical site characteristics and tree occupancy parameters. The first cluster was characterized by high soil moisture values and cool-season perennial grass abundance. Since north facing aspects in the northern hemisphere receive less direct solar radiation than other aspects, soil moisture retention is generally higher than sites on other aspects (Warren 2008). This is especially prevalent on north facing aspects with heavy textured soils. Thus, all plots on northeast to northwest facing aspects (Norris plots) were included in this cluster. The second cluster was characterized by understory communities with high shrub abundances and low soil moisture. This high shrub association is opposite from total tree canopy cover along axis two. Cluster three was characterized by high warm-season perennial grass abundance and cool-season annual grass production and low soil moisture values as well as low cool-season perennial grass cover.

As evidenced by the influence of aspect and moisture on tree densities, climate plays a driving role in establishment and distribution of woody plants (Briske et al. 2011). On our study sites in Madison County, between 1900 and 1930 and again from 1940 to 1949, precipitation averages were far greater than the current 50-year average for southwest Montana (NIDIS-NOAA 2022, Fig. 30). This time period coincides with early fire suppression and likely would have increased establishment and growth rates in woody plants (Eddleman 1987; Miller and Rose 1999; Miller et al. 2005; Heyerdahl et al. 2006). Altered fire severity, timing, and extent coupled with extended cool, wet periods offered favorable conditions for woody plant germination and establishment (Miller et al. 2005, Archer et al. 2011).

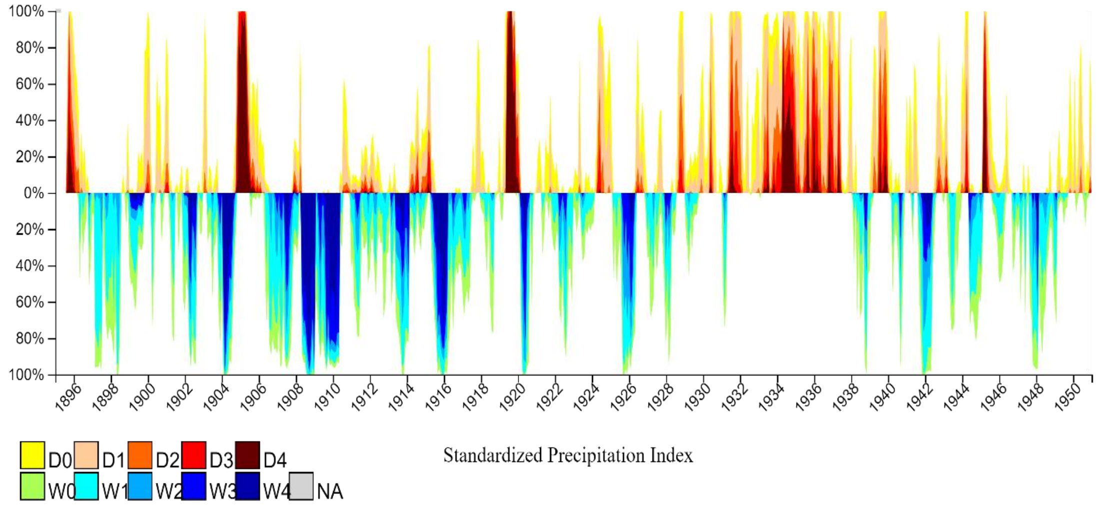

Figure 31: Standardized precipitation index for Madison County, Montana; where the top portion represents drought (D0-D4) and the bottom portion represents precipitation (W0-W4). Precipitation conditions were wetter than average from the years 1906 - 1918 and 1938 - 1949 (NIDIS-NOAA 2022).

Several relationships are noteworthy in the primary NMDS for all field plots. Specifically, understory communities with high shrub abundance differ from understory communities with high pine and juniper canopy cover, but not necessarily high juniper densities. This highlights findings (chapter two, this document) that older juniper have high canopy cover while younger juniper, even with high densities, do not necessarily have high canopy cover. This is also corroborated by data from Utah juniper and western juniper stands in the pinyon-juniper systems of the interior southwest (Barney and Frischknect 1974; Miller and Rose 1999). Barney and Frischknect (1974) found the oldest Utah juniper stands had the highest canopy cover values while tree densities had the highest values at age 86. This is in part a function of how we measured tree canopy cover. The densiometer is held one meter above the ground surface, leading to low canopy estimates for sites with juvenile trees.

Shrubs at Red Bluff and Norris primarily consisted of mountain big sagebrush, which persists best in full-sun environments (West et al. 1978). On droughty sites, high tree canopy cover is related to lower cool-season perennial grass cover and production. On north-facing slopes characterized by heavier textures and higher soil moisture, there appears to be little difference in cool-season perennial grass abundance and production as conifer cover increases. This also coincides with data from other pinyon-juniper systems, where spatial and temporal components of woodland development rates and understory impacts varied by aspect (Johnson and Miller 2006; Miller et al. 2000). Miller et al. (2000) observed reduced mountain big sagebrush and herbaceous cover in understory communities on drier sites with shallow soils. They further observed no decrease in herbaceous cover in understory communities on deeper soils, as juniper dominance increased (Miller et al. 2000).

NMDS for Cluster 1

Three out of the 15 plots in cluster one are positioned on southeast to southwest facing slopes while other 12 plots are located on north-facing slopes. Thus, understory composition for this cluster is described by a herbaceous community that persists on sites with high or prolonged moisture (north facing slopes). Much like the jointplot of the NMDS for all field plots, species composition and perennial grass production appear to differ for understory communities with high canopy cover, compared to communities with low canopy cover. Forb production appears to be greater on moist sites with less direct solar radiation (Coble et al. 2001). Principal components representing pine cover suggest communities with higher pine cover often have higher cool-season perennial grass production and abundance compared to communities with high juniper cover, cool-season annual grass production, and higher heat loads. Lastly, understory communities at higher elevations tend to have increased juniper canopy cover and cool-season annual grass production and, in some plots, more shrub cover than lower elevation communities. Ozeran (2016) found that higher elevation sites at Red Bluff had higher cheatgrass cover than lower elevation sites.

NMDS for Cluster 2

The NMDS jointplot for cluster two further supports previous inferences. Again, shrub abundance has a very high positive association while juniper density and total juniper and pine canopy cover has a very high negative association with axis one. From these relationships, we infer that shrub cover, primarily mountain big sagebrush, is lower on sites with high juniper canopy (Fig. 28; Davies et al. 2014). Shrub cover for these sites is almost entirely mountain big sagebrush (24% cover) with some rabbitbrush (0.01% cover) and black currant (0.1% cover). Of these species, black currant is the only shrub that can persist in shaded environments (Wolske et al. 2021). When initially looking at this jointplot, it seemed strange that principal components representing pine cover would be positively associated to axis one because plots that were also positively associated to axis one had high juniper cover and limited pine cover. However, the four plots negatively associated with axis one are dominated by young pine while the plots positively associated with axis one had limited, but mature pine. This reinforces our expectations that high tree densities do not necessarily equate to high cover values. At both Red Bluff and Norris, limber pine densities were only high on sites with little to no juniper presence. Limber pine often acts as a pioneer following disturbance and shows minimal evidence of maintaining its population densities in the presence of other, competing trees (Noble 1990).

NMDS for Cluster 3

The jointplots for cluster three contain few environmental variables that are strongly associated with either axis. Understory communities with higher pine and shrub cover tend to be found on droughty sites, perhaps suggesting that juniper moves into moist sites at a higher rate and pine struggles to compete on these sites (Chapter two - this document; Miller et al. 2000). Cool-season annual grass production was highest on drier, high elevations sites. We expect that these grasses, primarily cheatgrass, are able to respond to early season moisture due to snowmelt when most perennial grasses on these sites are not yet actively photosynthesizing and tillering in late winter (Ozeran et al. 2016). This may be why cheatgrass is more tolerant and productive on coarse-textured, droughty, high elevation hilltops (Harris and Wilson 1970; Ozeran 2016). Shrubs, such as mountain big sagebrush and rabbitbrush, are less abundant on sites with higher spring and early summer moisture. However, it is unclear why this relationship with drier, higher elevation sites exists.

In summary, cool-season perennial grass production and cover on south facing aspects is higher in areas with low tree canopy. As tree dominance increases on these sites, cool-season perennial grass production and cover declines, which is comparable to understory reductions in other pinyon-juniper systems (Miller et al. 2000, 2005; Davies et al. 2019). Heavy conifer canopy on north facing aspects does not appear to reduce cool-season perennial grass cover or production. Shrub cover is also influenced as trees exert dominance on south facing aspects. While these data suggest this influence is less apparent on north facing aspects, we observed numerous sagebrush skeletons under mature juniper on these sites. Furthermore, simply because we did not observe a loss in shrub cover does not negate the potential for future impacts to shrub cover on north facing slopes, as tree dominance continues to increase.

Cool season annual grass production was most prominent on high elevation hilltops and ridges. This may be a function of cheatgrass’s ability to respond to late winter and early spring moisture, before perennial species are actively photosynthesizing. Cool season annual grass production was also was much higher on south facing aspects and non-existent on north facing aspects. The heavier textured, north facing sites at Norris retain moisture longer than the coarse textured Red Bluff sites. Therefore, we infer that cool season perennial grasses on north facing aspects may be better able to compete with cool season annual grasses on sites with prolonged soil moisture retention. Forb production was highest on sites with north facing aspects and differed for north versus south facing aspects.

Rocky Mountain juniper and limber pine were both present, but never co-dominant throughout the entire study area. Interestingly, pine was present but minimal on juniper dominated sites while juniper was often present, if not abundant on pine dominated sites. The overstory in only one Red Bluff plot completely consisted of pine; however, young juniper was abundant in nearby pine dominated stands. Limber pine seems to be intolerant of competing conifer species, which would partially explain the sub-dominant, if not suppressed stature of pine on juniper dominated sites. The sites that are dominated by pine are most often droughty, south facing hillsides and ridgetops. Whether due to the harsh site characteristics or pine growth form and physiology, densiometer values and stem densities for pine dominated sites are less than juniper dominated sites. Thus, sagebrush cover appears to be higher on pine sites compared to juniper sites. Mountain big sagebrush may persist in these harsh environments either due to higher light availability or decreased competition for soil moisture, compared to juniper dominated sites. The pattern and development of juniper and pine woodlands parallels favorable climatic conditions, the introduction of domestic livestock, and the reduced role of fire in the 20th century. The co-occurrence of these factors likely contributed to conifer expansion in this area.

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CHAPTER FIVE

GENERAL CONCLUSIONS AND IMPLICATIONS

Nathaniel Paul Haygood

The purpose of this research project was twofold: 1) identify and improve understanding of Rocky Mountain juniper and limber pine age distribution in southwest Montana and compare these data to other systems where juniper and pine expansion is well documented, and 2) evaluate understory dynamics along the gradient of juniper and pine ages to assess potential impacts to understory species composition and abundance, as tree densities and range increase. Given these two primary study objectives, we analyzed the data separately with the goal of improving our understanding regarding spatial and temporal dynamics of conifer expansion in heterogeneous landscapes.

The age distribution of juniper and pine primarily varied by soil texture, soil moisture and aspect. Based on age distribution at Norris and Red Bluff, we speculate that Rocky Mountain juniper densities increased during the 20th century. Limber pine ages (mean age – 26) are younger than juniper (mean age – 38) and appear to be influenced by white pine blister rust infections, competition with juniper, and targeted removal by humans. Limber pine acts as a pioneer on recently disturbed or harsh sites and has difficulty maintaining population densities as other tree species colonize a site (Noble 1990).

This apparent reduction in conifer age coincides with other documented cases of woody plant expansion throughout North America and also coincides with historical increases in domestic livestock, reduced wildfire intensity, range and frequency, and favorable climate for germination and establishment (Miller and Rose 1999, Miller et al. 2005, Heyerdahl et al. 2006, Briske et al. 2011). The chronology of establishment in southwest Montana mirrors documented chronologies of other species in the United States, such as western juniper in the Great Basin, mesquite in the southwest, and eastern red cedar in the midwestern United States (Young and Evans 1981, Brown and Archer 1989, Engle et al. 1996, Miller and Rose 1999, Miller et al. 2005). These studies found that in the last 125 years, western juniper, mesquite, and eastern red cedar rapidly expanded into areas previously dominated by grass and shrubs, thereby reducing understory production and diversity. These authors reconstructed fire return intervals by aging fire scarred trees and examined historical imagery as evidence to support these findings.

Understory species composition and production differed along the gradient of juniper and pine abundance at Red Bluff sites. Specifically, perennial bunchgrass and shrub cover and production were reduced on droughty sites with high juniper canopy, which is comparable to previous data (Miller et al. 2000). This was evident on dry, south facing sites with juniper over the age of 70 and was less apparent on moist, north facing sites with juniper less than 50 years old. Droughty, south facing, high elevation sites often had higher annual grass production and mature juniper cover; however, these sites generally had lower canopy cover values. North facing aspects were lower in annual grass production, higher in cool-season perennial grass cover and production and had higher soil moisture percentages from May through July. Juniper on north facing aspects were higher in total stem density and lower in mean age but not necessarily lower in canopy cover across plots.

We infer that juniper and pine age distributions are younger on north facing aspects compared to south facing aspects and that pine is displaced as juniper dominates a site. Higher soil moisture retention due to heavier textured soils and north facing aspects may lead to more rapid increases in juniper range and density, but not necessarily reductions in cool-season perennial grass and shrub abundance. As conifer canopy increases, shrubs may be water limited on droughty sites, leading to a reduction in shrub cover and production. These findings also suggest that perennial grass cover and production may be lower on sites with high canopy cover.

Timely and appropriate resource management that provides ecological goods and services is predicated on a robust knowledge of potential threats to these goods and services. The results from this study indicate 1) limber pine and Rocky Mountain juniper often occupy different sites, 2) juniper and pine stand age is lower on north facing aspects with deeper soils and higher soil moisture content in late spring and early summer, 3) the understory impacts associated with increasing juniper and pine dominance differ for north and south facing aspects. Increasing conifer dominance on north facing aspects appears to minimally impact cool-season perennial grass cover and production; however, shrub cover may be impacted. Comparatively, increasing conifer dominance on south facing slopes may reduce cool-season perennial grass and shrub cover and production. We recommend the inclusion of these findings, as land managers seek to sustain delivery of necessary ecological goods and services such as forage production, wildlife habitat values, and biological diversity in southwest Montana.

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