

Fire Effects Following the Egley Fire Complex (OR, USA) in a Dry Ponderosa Pine Forest

A Thesis

Presented in Partial Fulfillment of the Requirements for the

Degree of Master of Science

with a

Major in Natural Resources

in the

College of Graduate Studies

University of Idaho

by

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May 2019

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ABSTRACT

Background

Wildfire has played an important role in ponderosa pine (*Pinus ponderosa*) forests in the western United States. However, after Euro-American settlement, fire suppression efforts and change in land use led to a decrease in low severity surface fires only to be replaced with large, high severity fires across much of the range of dry ponderosa pine. Land managers have been using mechanical treatments to alter fuels in ponderosa pine (*Pinus ponderosa*) forests to mitigate fire behavior and high severity fire effects. Before the 2007 Egley Fire Complex, mechanical thinning, slash and pile burns, and understory burns were implemented as fuel reduction treatments in the dry ponderosa pine-dominated Malheur National Forest in eastern Oregon. To compare post-fire vegetation recovery between mechanical treatments and untreated control areas, 35 treated and untreated paired plots were sampled in 2016. Post-fire vegetation recovery was assessed at the 35 paired field sites by measuring tree density, seedling regeneration, understory plant response by functional group, and fuel loads. Functional groups included shrub, graminoid, forb, invasive species of interest (cheatgrass, and Canadian and bull thistle), and moss/lichen/fungi. To evaluate the long-term effects of wildfire on bee abundance and diversity, Japanese beetle traps were placed in seven unburned and seven high severity burned sites ten years (2017) after the wildfire. Post-fire flowering plant community (i.e. diversity and abundance for each species) was assessed and compared to the bee community to determine if there was a correlation between them. Sites were stratified by elevation, aspect, and the remotely sensed burn severity gradient represented by the delta Normalized Burn Ratio (dNBR). The intent of this study was to document to what extent tree density, seedling regeneration, understory plant community composition, understory bee community composition, and fuels change across the burn severity gradient and to quantify to what extent pre-fire fuel treatments affect burn severity and long-term vegetation recovery.

Results

Burn severity (dNBR) was lower in treated than untreated sites across the Egley Complex. Annual NBR trends showed that treated sites nearly recovered to pre-fire values by

approximately three years post-fire, while untreated sites had a much slower recovery rate. Time since treatment and dNBR significantly affected tree canopy cover in 2008 and surface fuel loads in 2016. This suggests an increase in live tree canopy cover in areas that were treated recently pre-fire, likely due to reduced burn severity effects with decreased time since treatment, and an increase in fuels as burn severity and time since treatment increased. Live tree density was more affected by severity than by pre-fire treatment in either year, as was dead tree density one-year post-fire. None of the understory functional groups were affected by treatment or severity in 2008; in 2016 shrub, graminoid, forb, and invasive species cover were higher in high severity sites than low severity sites. Total fuel loads, dominated by 1000-hour fuels, nine years post-fire were highest in untreated, high severity sites. Tree canopy cover and density of mature trees, saplings, and seedlings were reduced nine years post-fire compared to one-year post-fire across treatments and severity, whereas live and dead tree basal area, understory surface cover, and fuel loads increased over time. Bee, flowering plant, and flower abundance and diversity decreased over summer months, but tended to be higher in burned sites than unburned sites. Bee, plant, and flower community compositions significantly differed between summer months and burn severity. Bee abundance correlated strongly with plant and flower abundance, suggesting generalist pollinator species that could potentially be used to pollinate agricultural lands.

Conclusions

Pre-fire fuel treatments effectively lowered the occurrence of high severity wildfire, likely due to successful reduction of pre-fire tree and sapling density, which supports the implementation of fuel treatments to reduce fire effects in ponderosa pine forests. Further, this study suggests low severity wildfire can lower surface fuel accumulations while not overly increasing overstory tree mortality. The higher abundance and diversity of bee, plant, and flower species found within high burn severity sites compared to unburned sites also suggest the importance of fire in increasing abundance and diversity of ponderosa pine understory vegetation and demonstrates ecosystem resilience to wildfire.

ACKNOWLEDGMENTS

This project was funded through three Joint Venture Agreements from the US Forest Service Rocky Mountain Research Station: 03-JV-111222065-279, #14-JV-11221633-112 (funded by JFSP project 14-1-02-27), and #17-JV-11221637-132. I want to thank the employees of the Forest Service Rocky Mountain Research Station, as well as students at the University of Idaho, who helped gather and enter 2008 field data (Christine Craig, Maike Holthuijzen and Joe Hulbert), 2016 (John Byrne, Sean McNeal, Eli Berman, Deborah Blanscet, and Maritza Hernandez), and 2017 field data (Justin Trujillo, Emily Mangini, and Caleb Ponczoch). Janet Braymen, Brian Austin, and Mike Bobbitt analyzed the initial burn severity, fuel treatment, and other GIS data. I also want to thank Beth Newingham, Christopher Bowman-Prideaux, Benjamin Spei, Samuel Wozniak, and Martha Schmidt for their friendly reviews and Benjamin Bright for his GIS and remote sensing help. I also want to give a special thanks to Dr. Penelope Morgan for her assistance in project development, 2008 field data collection, and her friendly review. Last, but not least, I especially want to thank Dr. Eva Strand, Dr. Andrew Hudak, Dr. Stephen Cook, and Darcy Hammond for helping me through every step in this project including data collection, data analyses, revisions, and stress management.

DEDICATION

Mom, I want to thank you for teaching me the beauty and importance of nature. Your passion for the outdoors has taught me the importance of exploration, preservation, and conservation.

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List of Abbreviations

ANOVA – Analysis of variance

BARC – Burned area reflectance classification

cm – centimeters

CWD – Coarse woody debris

DBH – Diameter at breast height

dNBR – differenced Normalized Burn Ratio

FWD – Fine woody debris

GEE – Google Earth Engine

ha – hectares

hr- hour

ISA – Indicator Species Analysis

Landtrendr - Landsat-based Detection of Trends in Disturbance and Recovery

M – Meters

Mg – Megagrams

MRBP –Blocked Multi-Response Permutation Procedure

MRPP – Multi-Response Permutation Procedure

MTBS – Monitoring Trends in Burn Severity

NBR- Normalized Burn Ratio

NPV- Non-Photosynthetic Vegetation

perMANOVA – permutation ANOVA

T – Treated

U – Untreated

CHAPTER 1: Introduction to Wildfire in Ponderosa Pine Forests

Wildfire has played an important role in ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) forests in the western United States. Prior to Euro-American settlement, the historic fire regime of ponderosa pine forests mostly consisted of high-frequency, low-severity fires (Cooper 1960; Allen *et al.* 2002; Agee and Skinner 2005), occasionally experiencing mixed- and high-severity fires (Weaver 1943; Swetnam and Baisan 1996). Severity here is defined as the amount of ecological change in vegetation and soil caused by fire (Morgan *et al.* 2001; Lentile *et al.* 2006; Keeley 2009). This historic fire regime would selectively kill established seedlings and saplings (Bradley *et al.* 1992), but rarely penetrated the thick bark enough to kill older ponderosa pine trees (Cooper 1960; McCune 1988). Ponderosa pine's thick bark and ability to self-prune their lower branches also makes it harder for fire to carry into the canopy (Bradley *et al.* 1992).

The historical habitat of a ponderosa pine forests is thought to have consisted of continuous mats of bunchgrasses that would sustain low-severity surface fires (Cooper 1960). The low-severity surface fire would create a negative feedback loop for shrubs and grasses (Fulé *et al.* 1997). Bunchgrasses like Sandberg bluegrass (*Poa secunda*), generally re-sprout after being top-killed (Pausas and Keeley 2014) by low-intensity fires (Ellsworth and Kauffman 2010). However, high fire intensity can decrease the percent cover of graminoids (Ellsworth and Kauffman 2010). After high-severity fires, shrubs can outcompete ponderosa pine seedlings and grasses after a fire, causing a vegetation shift from forest to shrub land (Savage and Mast 2005).

After Euro-American settlement, fire suppression efforts and change in land use, including grazing, logging, and building roads, led to a decrease in low severity surface fires in many dry ponderosa pine forests (Covington and Moore 1994; Allen *et al.* 2002). Without the frequent, low severity fires, many dry ponderosa pine forests have become over-crowded (Cooper 1960) with accumulating ladder fuels, which can carry flames into the crown (Allen *et al.* 2002), leading to more severe wildfires (Morgan *et al.* 2001; Lentile *et al.* 2006; Keeley 2009). The increase in high severity wildfires has decreased many dry ponderosa pine forests fire resilience, in other words, their ability to recover to the same state afterwards (Holling 1973; Groffman *et al.* 2006)

CHAPTER 2: Short- and Long-Term Effects of Ponderosa Pine Fuel Treatments Intersected by the Egley Fire Complex (OR, USA)

Forthcoming in *Fire Ecology*

Introduction

Many dry ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) forests in the western United States frequently experienced natural thinning due to low-severity surface fires prior to Euro-American settlement (Cooper 1960; Allen *et al.* 2002; Agee and Skinner 2005). Established seedlings and saplings were often selectively killed by low-severity surface fires, reducing fuel buildups (Bradley *et al.* 1992), but heat from the low-intensity flames rarely penetrated the thick bark enough to kill older ponderosa pine trees (Cooper 1960; McCune 1988). Ponderosa pines ability to self-prune lower branches resists fire from reaching the tree bole, and their open, loosely arranged crowns aid in reducing crown (Bradley *et al.* 1992).

After Euro-American settlement, fire suppression efforts and change in land use, including grazing, logging, and road development led to a decrease in low severity surface fires across much of the range of dry ponderosa pine (Covington and Moore 1994; Allen *et al.* 2002; Hessburg *et al.* 2005). The absence of frequent, low-severity surface fires has led to an accumulation of ladder fuels that carry flames into the crown (Allen *et al.* 2002) causing higher severity fires, or more ecological change in vegetation and soil, than low severity fires (Morgan *et al.* 2001; Lentile *et al.* 2006; Keeley 2009). Thus, many dry ponderosa pine forests have experienced a decrease in fire resilience, defined as an ecosystem's ability to recover to the same state after a disturbance (Holling 1973; Groffman *et al.* 2006).

To reduce the size and severity of wildfires and restore fire resilience in ponderosa pine forests, many land managers have implemented fuel treatments, such as thinning and prescribed fire (Covington and Moore 1994; Fulé *et al.* 1997; Agee and Skinner 2005). When precommercial thinning, land managers focus on removing small diameter trees to reduce stand density and to increase canopy base heights to exceed the flame length of surface fires. For commercial thinning, land managers will harvest larger trees to generate income and break up horizontal tree canopy continuity. Prescribed surface fires are used to reduce surface

fuels, small trees, and shrubs, much like the historical, low severity fire regimes of most ponderosa pine forests (Agee and Skinner 2005; Finney *et al.* 2005).

Thinning has been shown to effectively reduce burn severity in ponderosa pine ecosystems (Agee and Skinner 2005; Stephens *et al.* 2009; Hudak *et al.* 2011). Thinning of dense stands allows more sunlight to access the forest understory, generally increasing understory vegetation cover and diversity (Bartuszevige and Kennedy 2009a; Schwilk *et al.* 2009; Stephens *et al.* 2012c). However, tree removal reduces available nutrients that fires would recycle into the soil (Graham *et al.* 1999; Kaye *et al.* 2005). Thinning treatments tend to leave piles of slash that contribute to surface fuel loads and can increase burn severity in the event of a wildfire unless treated in a slash and pile burn (Graham *et al.* 1999; Hudak *et al.* 2011). Burning of these slash piles in wildland or prescribed fires can cause localized severe effects on soil patches, thereby altering soil characteristics, reducing soil microbiota and soil seed bank viability (Graham *et al.* 1999; Korb *et al.* 2004). Soil disturbances caused by thinning may also increase invasive species cover (Korb *et al.* 2004; Dodson and Fiedler 2006; Stephens *et al.* 2012c).

Prescribed fires are generally less costly than mechanical thinning and have been shown to be more effective at reducing surface fuels than mechanical treatments in multiple ecosystems (Schwilk *et al.* 2009; Bernau *et al.* 2018). The burning of surface fuels allows nutrients to be recycled into the soil and cueing recruitment of fire-resilient species (Stephens *et al.* 2012c). However, smoke hazards to urban populations and air quality (Ottmar *et al.* 2001), and liability concerns with fire escape into neighboring properties (Yoder *et al.* 2004) present significant barriers to prescribed fires in many areas (Stephens and Ruth 2005), making thinning treatments often preferred in the wildland urban interface (Kane *et al.* 2010).

Prescribed fires in combination with mechanical thinning have been shown to be most effective at reducing burn severity of subsequent wildfires (Agee and Skinner 2005; Finney *et al.* 2005; Stephens *et al.* 2009; Prichard *et al.* 2010; Hudak *et al.* 2011; Kalies and Yocom Kent 2016). However, treatment longevity and effectiveness vary by location. Stephens *et al.* (2012a) found that thinning followed by prescribed fire in a mixed conifer forest in Sierra Nevada was the most effective at reducing fire hazards (flame length and torching probability) for at least seven years post treatments, though they suggest timing prescribed fire treatments

ten-years post-thinning treatments to potentially increase treatment effectiveness by 15-20 years. Prichard *et al.* (2010) found that thinning treatments in combination with prescribed burning in a mixed conifer forests was the most effective at reducing tree mortality during the Tripod Complex fires compared to no treatment and thinning alone whereas Fulé *et al.* (2005) found that thinning and burning treatments in a ponderosa pine-Gable oak (*Quercus gambelii* Nutt.) forest had minor effects on fuel loads five years post treatments. Thus, each ecosystem and site may have varied treatment longevity and effectiveness (Fulé *et al.* 2005; Fulé *et al.* 2007; Battaglia *et al.* 2008; Vaillant *et al.* 2009; Stephens *et al.* 2012a; Tinkham *et al.* 2016).

A common way to assess effectiveness of fuel treatments aimed at reducing fire severity across landscapes is using the Normalized Burn Ratio (NBR), a remotely-sensed index sensitive to vegetation, soil, and char reflectance (Key and Benson 2006; Hudak *et al.* 2007). Subtracting the NBR value of a post-fire satellite image from a pre-fire satellite image provides the differenced NBR (dNBR), widely regarded as a useful indicator of burn severity (van Wagendonk *et al.* 2004; Key and Benson 2006). Prior studies have found dNBR is more influenced by the tree canopy (where present) than by ground conditions, typically defining high burn severity as overstory consumption by fire (Hudak *et al.* 2007; Lentile *et al.* 2009).

The increase in large wildfire frequency and area burned at high severity (Westerling *et al.* 2006; Littell *et al.* 2009; Abatzoglou and Williams 2016), as well as the cost invested in mechanical thinning (Gorte 2013), has prompted examination into the effectiveness of thinning (Graham *et al.* 1999; Fulé *et al.* 2007; Bartuszevige and Kennedy 2009a; Prichard *et al.* 2010; Tinkham *et al.* 2016). However, relatively few studies have investigated both short- and long-term ecological effects of pre-wildfire treatments on burn severity, understory vegetation recover, and fuel accumulation after wildfires (Fulé *et al.* 2005; Hudak *et al.* 2011; Stephens *et al.* 2012a). Understanding vegetation responses and fuel accumulations in response to burn severity post-wildfire on a long-term trajectory will assist land managers in prioritizing long-term fuel and fire management objectives. Therefore, our objectives were to 1) determine if pre-wildfire treatments lower burn severity (one-year post-fire dNBR); 2) evaluate relationships between one-year post-fire dNBR, years since treatment, and field-measured biophysical attributes one and nine years post-fire; 3) compare treated and untreated site pairs to better understand interactions between treatment and severity; and 4) assess

changes over time by comparing biophysical attributes measured in year one and re-measured in year nine post-fire across the Egley Complex.

Methods

Study Area

The study area was within the Malheur National Forest, approximately 55 km northwest of Burns, OR (43° 52' 50" N, 119° 38' 24" W). The Malheur National Forest occupies 688,000 hectares (ha) in the Blue Mountains of eastern Oregon and includes high desert grasslands, sagebrush (*Artemisia* spp.L.) steppe and juniper (*Juniperus occidentalis* Hook.) woodlands, ponderosa pine forests, and mixed conifer forests. Our study focused on the southern ponderosa pine forests of the Malheur National Forest. Mean monthly high temperature in the growing season (May through August) is 26°C and the mean monthly low temperature in winter (November through February) is -8°C. Mean annual rainfall precipitation is 279 mm (US Climate Data 2019) and mean annual snowfall precipitation is 889 mm, with the majority of precipitation accumulated between November and May and with less than 19 mm of precipitation accumulated between June and October. Elevation of study sites ranges from 1506 m to 1755 m above sea level. Common grass species included needlegrass (*Achnatherum* spp. P. Beauv.), squirreltail (*Elymus elymoides* (Raf.) Swezey), and Sandberg bluegrass (*Poa secunda* J. Presl). Forb species included common yarrow (*Achillea millefolium* L.), blue eyed Mary (*Collinsia* spp. Nutt.), and willowherb (*Epilobium* spp. L.). Invasives species included cheatgrass (*Bromus tectorum* L.), Canadian thistle (*Cirsium arvense* (L.) Scop.), and bull thistle (*C. vulgare* (Savi) Ten.). Snowbrush ceanothus (*Ceanothus velutinus* Douglas ex Hook.), creeping barberry (*Mahonia repens* (Lindl.) G. Don), and antelope bitterbrush (*Purshia tridentata* (Pursh) DC.) were the most common shrubs within the study area.

The Egley Complex, comprised of three lightning-ignited fires, burned approximately 56,802 ha (Figure 2.1) from 7 to 21 July 2007 under abnormally low precipitation and high temperatures for the area; total precipitation was 0.25 mm (usually around 10 mm of precipitation), the average high temperature was 34 °C (usual high temperature around 30 °C), and the average low temperature was 11 °C (usual low temperature around 8°C) in July 2007 (US Climate Data 2019). Prior to the Egley Complex, the Malheur National Forest

implemented fuel treatments for vegetation management and wildfire protection objectives beginning in 1985, with treatment units recorded as polygons in a Geographic Information System (GIS). Pre-fire silvicultural or fuel reduction treatments within the Egley Fire Complex perimeter included commercial harvests (7,280 ha), pre-commercial thinning (6,855 ha), slash and pile burns (6,853 ha), and understory prescribed burns (1,566 ha). Of the 42,459 ha of Malheur National Forest lands that burned in the Egley Complex, 19,233 ha (45.3%) had received some form of harvest, pre-commercial thinning, fuel, and/or fire treatment over the preceding 22 years dating back to 1985 (Figure 2.1A). Treatment units often had multiple entries; for instance, 668 of the 1041 treatment units intersected by the Egley Complex had been commercially harvested, thinned, and had slash piles burned, with the driving motivation being to achieve silvicultural objectives. Given the complexity imposed by multiple and interacting entries over a long range of years, we did not attempt to quantify separate effects of treatment types, but simply lumped together all lands within treatment units as “treated” to compare with untreated lands in our analysis. Three prior wildfires were also categorized as fuel treatments; the 1990 Squaw Flat Fire (540 ha), the 1990 Buck Springs Fire (8,485 ha), and the 1990 Pine Springs Basin Fire (28,790 ha, Figure 2.1A) that had previously burned on Malheur National Forest lands.

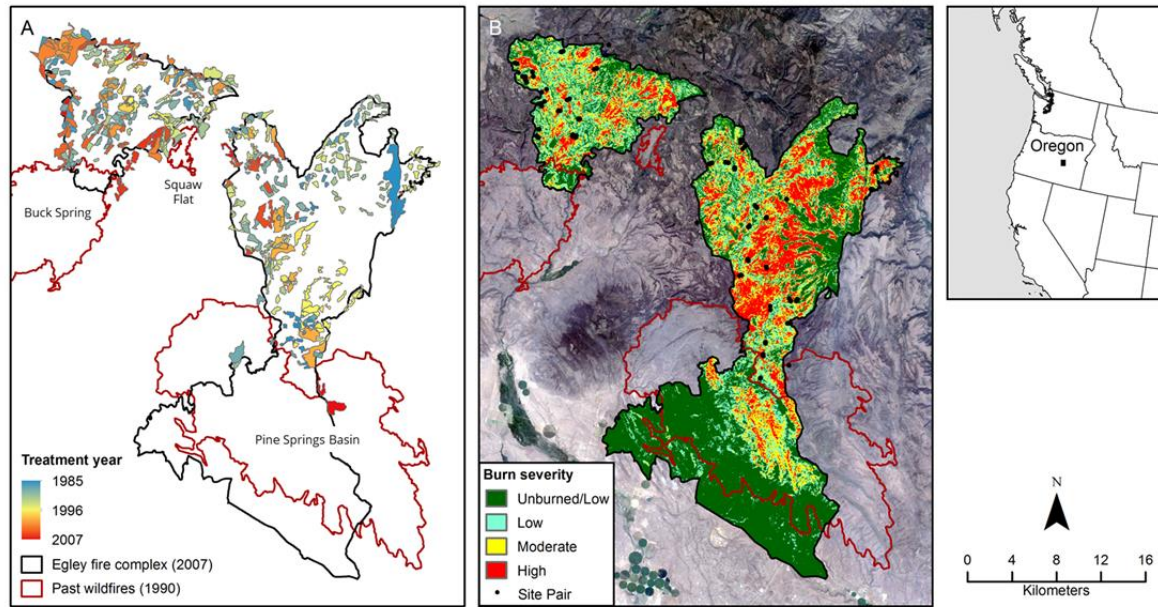


Figure 2.1. Egley Complex located in eastern Oregon, showing A) areas that had been treated pre-fire and B) distribution of 35 paired field sites overlaid on the classified delta Normalized Burn Ratio (dNBR) burn severity map (Finco *et al.* 2012).

Field Methods

Field sites were monumented and first characterized in the summer of 2008 (one-year post-fire) and then re-measured in 2016 (nine years post-fire). Field procedures are similar to those described by Hudak *et al.* (2011). Each site consisted of a central plot and four additional quadrats situated orthogonally 30 m from the center plot and oriented to the prevailing slope (Figure 2). Field sites were established from May to July 2008 prior to the availability of the MTBS classification of burn severity. Therefore, a rapid response, Burn Area Remote Classification (BARC) map based on immediate post-fire dNBR values (Parsons and Orlemann 2002) was used as a guide to distribute field sites along the burn severity gradient. In the immediate post-fire BARC map, low burn severity corresponds to predominantly green (live) tree crowns, moderate burn severity corresponds to predominantly brown (scorched) tree crowns, and high burn severity corresponds to predominantly black (charred) tree crowns (Hudak *et al.* 2011). Paired treated/untreated sites ($n=35$ each) were distributed across the burn severity gradient at locations constrained by four criteria: 1) field assessment of burn severity; 2) year of final treatment to distribute sites across the range of time since treatment;

3) adjacency of treatment units to untreated sites having similar topographic slope, aspect, and older tree (pre-treatment) age structure (between 90 and 500 m apart); and 4) proximity to a navigable road. (Figure 2.2).

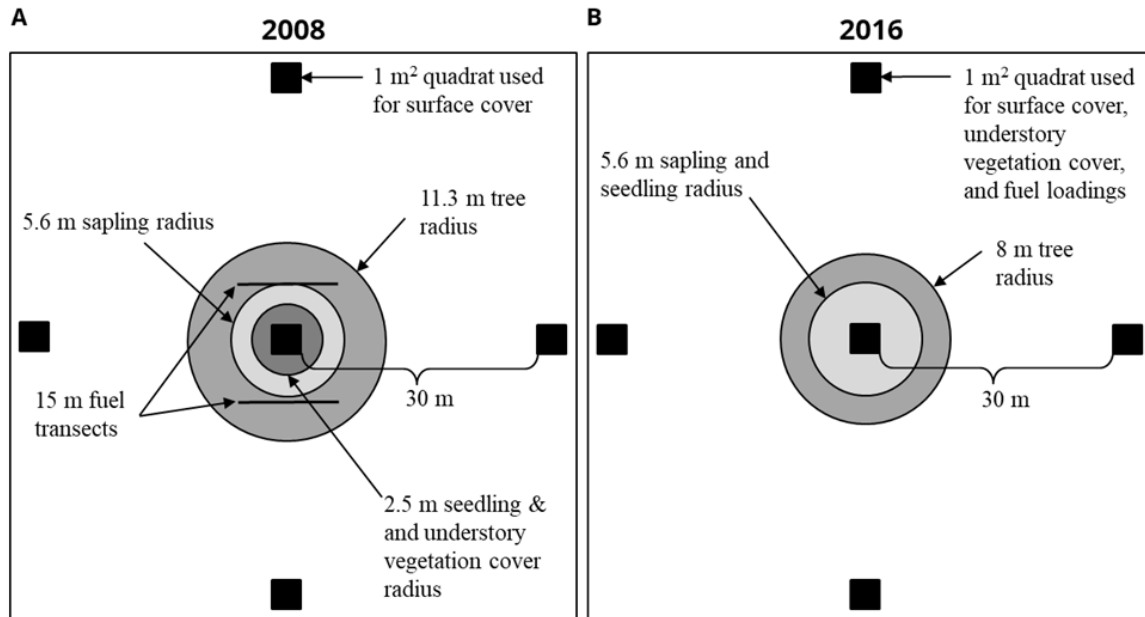


Figure 2.2. Field site layout (not drawn to scale) used at field sampling sites in A) 2008 and B) 2016 (Hudak *et al.* 2011).

At each site, overstory components (tree canopy cover, tree DBH, and tree density) and understory components (sapling and seedling density, surface cover, functional group understory species cover, and woody fuel loads) were measured. Tree canopy cover was estimated using a convex spherical densiometer facing the four cardinal directions around each plot. Tree density and basal area were measured at the center of the field site within a fixed radius of 11.3 m (1/25 ha) in 2008 or 8 m (1/50 ha) in 2016. Diameter at breast height (DBH, 1.37 m), status (live or dead), and species were recorded for each tree greater than 10 cm DBH.

Seedlings and sapling density (stems ha⁻¹) were used to estimate tree regeneration. All conifer saplings and seedlings taller than 5 cm were tallied by species and status (live and dead) recorded in circular plots. Saplings were tallied within a 5.6 m radius (1/100 ha) for both sample years; seedlings in 2008 were tallied within a 2.5 m radius (1/500 ha), whereas seedlings in 2016 were tallied within a 5.6 m radius. Saplings were defined as taller than

breast height and DBH less than 10 cm, whereas conifers less than breast height were considered seedlings.

Percent cover of understory components was estimated within five 1-m² quadrat at each site (Figure 2.2). Surface cover components included percent green vegetation, organic non-photosynthetic (dead or dormant) vegetation (NPV), mineral soil, rock, and the proportion of surface covers that had residual blackened carbon (char). Examples of NPV include woody debris, senesced grass, tree bark, litter, and duff. Due to low vegetation surface cover in 2008, understory vegetation cover was identified to functional groups and percent cover was estimated only within the 2.5 m radius understory center plot (Figure 2.2). Functional groups included shrub, graminoid, forb, invasive species of interest (cheatgrass, and Canadian and bull thistle), and moss/lichen/fungi.

Fuel loads in 2008 were estimated using Brown's transects (Brown 1974). Coarse woody debris (CWD; 1000-hr fuels) were measured in two 15 m transects laid along the slope on the upslope or downslope sides of the 5.6 m radius plot to prevent directional bias (Figure 2.2). Fine woody debris (FWD) were measured for each size class (1-hr, 10-hr, and 100-hr fuels) within the central 2 m section of each 15 m transect in 2008 and were converted to fuel loads (Mg ha⁻¹) per Woodall and Monleon (2006) for ponderosa pine. In 2016, the photoload fuel sampling technique was used to estimate CWD and each FWD size class fractions, opposed to Brown's transects to speed field sampling (Keane and Dickinson 2007). Fine woody debris size class fractions were estimated within the 1 m² quadrats at each plot, while CWD was estimated within a 5.6 m radius around the center plot. Litter and duff depths were measured with a ruler to the nearest 1 mm at each 1 m² plot in both 2008 and 2016 and then used to calculate litter and duff fuel load (Mg ha⁻¹; Stephens *et al.* 2004).

Remote Sensing Data

One-year post-fire dNBR values (burn severity) were obtained from the Monitoring Trends in Burn Severity (MTBS) program (Eidenshink *et al.* 2007). For the Egley Fire Complex, MTBS used Landsat 5 TM image from July 18, 2006 for the pre-fire image and an image from July 7, 2008 for the post-fire image to calculate dNBR. The MTBS thematic burn severity product binned the dNBR image into five thresholds: no data (-970), increased greenness (-150), low severity (100), moderate severity (215) and high severity (385; Eidenshink *et al.* 2007).

In addition to dNBR, LandTrendr (Landsat-based Detection of Trends in Disturbance and Recovery, Kennedy *et al.* 2010) implemented in Google Earth Engine (GEE, (Gorelick *et al.* 2017; Kennedy *et al.* 2018) was used to observe vegetation change after the Egley Fire Complex. Landsat image composites (30 m spatial resolution) of summer NBR from 1984 through 2016 were created across the Egley Fire extent. NBR image composites were then input into the LandTrendr algorithm, which modeled pixel-wise trends and trajectories while eliminating noise, resulting in an annual times series of Landsat NBR images fitted to LandTrendr segments. GEE was used to create NBR composites and implement the LandTrendr algorithm (Kennedy *et al.* 2018). NBR time series at site locations were extracted for vegetation recovery analysis. To determine when NBR recovered to unburned/low levels at plot locations, we tested whether NBR distributions varied by burn severity with Student's t-tests for each year post-fire.

Statistical Analysis

Variables collected at all five quadrat locations per field site were aggregated to the site level. Due to non-normal distributions, a non-parametric blocked multi-response permutation procedure (MRBP) with Euclidean distance measure (PC-ORD v.7; McCune and Mefford 2016), blocked by treatment (treated or untreated), was used to determine differences in burn severity (one-year post-fire dNBR) between pre-fire fuel treatment sites and untreated sites post-fire (Objective 1) and for differences in biophysical attributes (i.e., tree canopy cover, understory green vegetation cover, total char cover, and total fuel loads) between 2008 and 2016 (Objective 4). An MRBP provides the chance-corrected within-group agreement (A), which is the likelihood of homogeneity within a group that occurs by chance. If $A=1$, all variables are homogenous within a group, whereas if $A < 0$, there is more heterogeneity within a group than expected by chance. If $A = 0$, then heterogeneity within a group equals what was expected by chance (McCune and Grace 2002).

To test for interacting effects of burn severity and time since treatment on biophysical attributes (Objective 2), linear regression models predicting select biophysical attributes were fit as a function of one-year post-fire dNBR, time since treatment (years), and their interaction (R Core Team 2013). Untreated sites were considered as having been treated in 1910, when widespread wildfires occurred, and thus as 97 years since treatment. Linear regression models

were fit using the Global Validation of linear models' assumptions (gvlma) package in R (Pena and Slate 2006). Data that failed normality and heteroscedasticity assumptions were modeled either using beta regression models if data were proportions (Cribari-Neto and Zeileis 2010) or generalized models if data were continuous.

Due to an insufficient number of treated sites that burned at high severity (n=3), we evaluated differences in overstory and understory components for the combined effects of treatment and burn severity (one-year post-fire dNBR) by grouping sites by treatment status (treated or untreated) and burn severity (unburned/low or moderate/high; Objective 3). The 4-class dNBR burn severity classification was simplified to two classes to differentiate sites with or without stand-replacing fire (dNBR values 61-250 for low burn severity and 251-753 for high burn severity). The classification resulted in four groups; treated sites that were unburned or burned at low severity (T-low, n=30), treated sites burned at moderate or high severity (T-high, n=5), untreated sites that were unburned or burned at low severity (U-low, n=11), and untreated sites burned at moderate or high severity (U-high, n=24). A permutation ANOVA with "Exact" permutations that generate all permutations of Y was used to test significant interactions of all variables between treatment and severity, which were non-normally distributed, and Tukey's multiple comparisons tests were used for post-hoc pairwise comparisons (R Core Team 2013).

Results

Landscape-level summary of treatment effects on burn severity

The MTBS-based dNBR classification of burn severity summarized across the entire Egley Complex showed that 26.7% (6,085 ha) of untreated lands (23,226 ha) burned with high severity, whereas only 12.9% (2,150 ha) of treated lands (19,233 ha) burned with high severity (Figure 2.3); thus, untreated lands were twice as likely as treated lands to have burned with high severity. The complete landscape analysis of the Egley Complex showed that the proportion of treated areas that burned at high severity increased with time since treatment (Figure 2.3B); i.e., treated areas >10 years old had a high burn severity proportion more similar to that of untreated areas, than did more recently treated areas <10 years old (Figure 2.3B). Zonal statistics in GIS were used to ensure minimal differences in elevation and slope

between untreated (elevation: 1558 ± 74.8 m; slope: $7 \pm 5.7^\circ$) and treated (elevation: 1591 ± 70.5 m; slope: $7 \pm 5.9^\circ$) polygons.

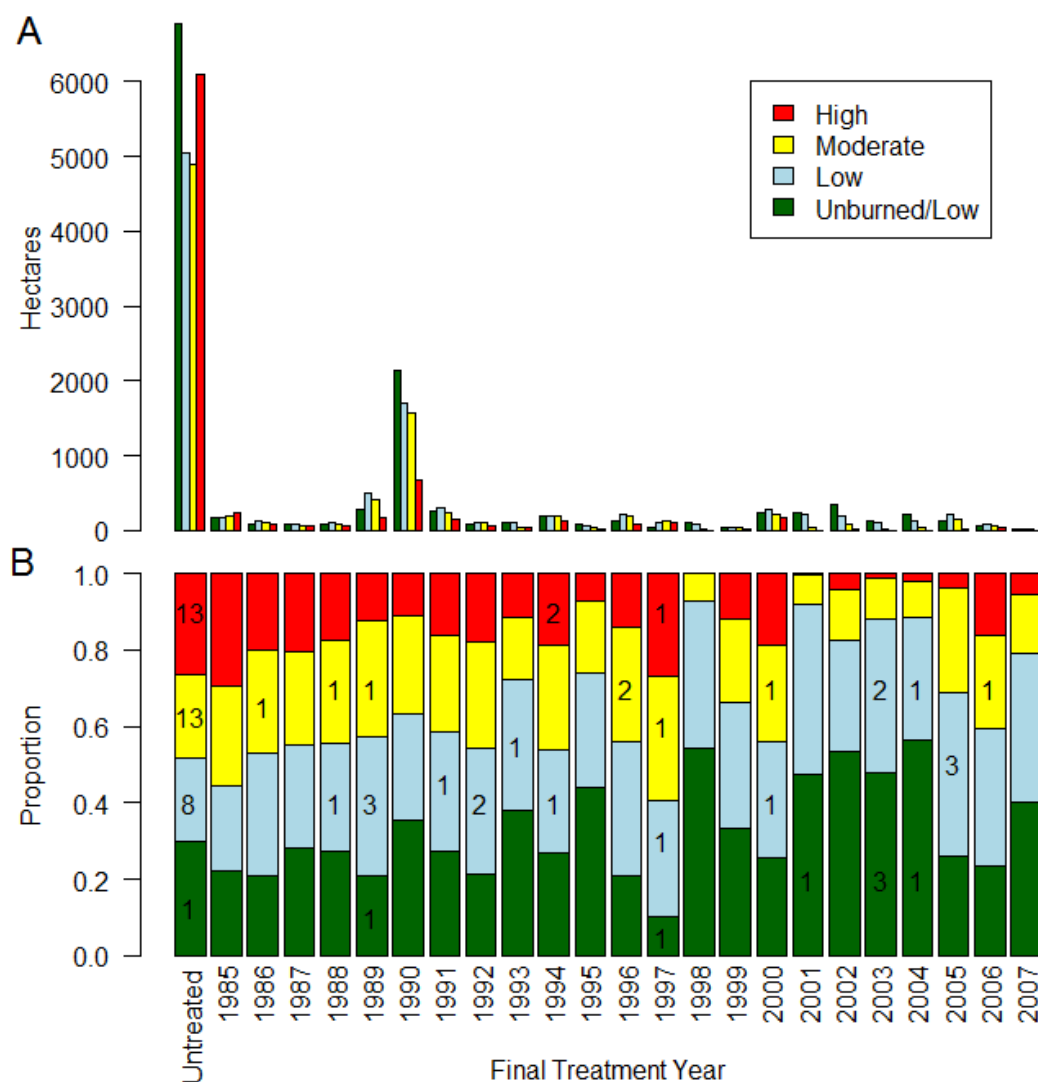


Figure 2.3. Burn severity class A) hectares and B) proportions summarized from delta Normalized Burn Ratio (dNBR) values mapped by Monitoring Trends in Burn Severity (MTBS) across the 2007 Egley Complex versus time since final fuels treatment. Numbers within columns in B) indicate number of field sites sampled in each treatment year across Monitoring Trends in Burn Severity (MTBS) burn severity classes, which were unavailable when the sites were installed in 2008 (Finco *et al.* 2012).

Site level analysis of remotely-sensed data

In accordance with the landscape analysis, student's t-test on the landscape variables elevation, slope, and distance to road between treated and untreated sites (all $P > 0.05$), per our paired site sampling design. However, one-year post-fire burn severity (dNBR) was significantly lower in treated sites than in their paired untreated sites (MRBP $P < 0.001$, $A = 0.27$). LandTrendr-derived trajectories of NBR decreased sharply following the fire and gradually increased over time as vegetation recovered. Treated sites that burned at high severity had recovered to unburned/low NBR levels within four years post-fire (Student's t-test, $P=0.052$ in 2010, $P=0.271$ in 2011), whereas untreated sites that burned at moderate or high severity had still not recovered to unburned/low NBR levels nine years post-fire (Student's t-test, $P=0.002$, Figure 2.4A and B).

Linear regression models showed that total (live and dead) tree canopy cover also increased with time since treatment in 2008 (Table 2.1). The interaction between one-year post-fire dNBR and time since treatment was also a significant predictor of 2008 tree canopy cover; as dNBR and time since treatment increased, tree canopy cover decreased (Table 2.1). Tree canopy cover measured in 2016 was lower at sites with higher one-year post-fire dNBR values; in other words, sites that burned at high severity still had lower tree canopy cover nine years post-fire. Understory green vegetation cover significantly decreased with dNBR in 2008 but significantly, though slightly, increased as dNBR and time since treatment increased. In 2016, understory green vegetation cover increased as one-year post-fire increased. Total char increased with one-year post-fire dNBR both in 2008 and 2016, expectedly. Total fuel loads were not significantly predicted by one-year post-fire dNBR, time since treatment, or the interaction between the two in 2008 or in 2016. It is important to note that, though most linear models were significant, they had relatively low coefficients of determination (R^2), therefore much of the variability is not being accounted for by the models (Table 2.1)

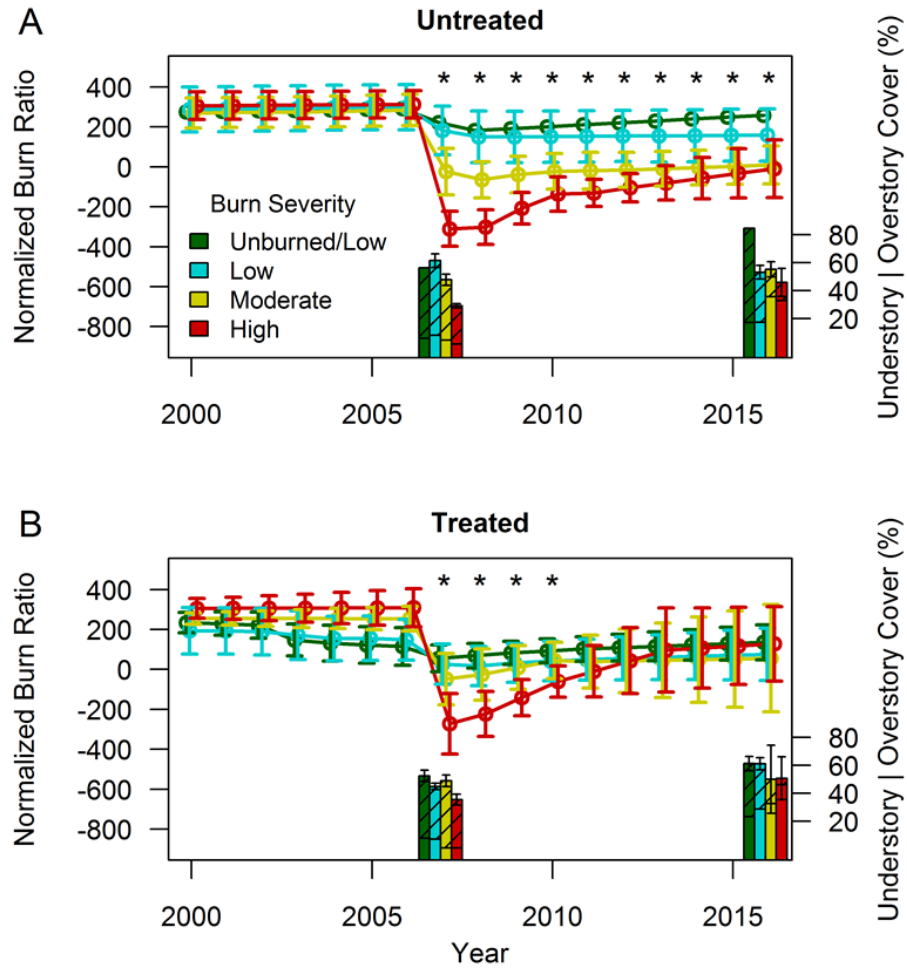


Figure 2.4. LandTrendr time series of the Normalized Burn Ratio (NBR) values for the Egley Fire Complex area from 2000 to 2016 for both A) untreated and B) treated sites. Column graphs demonstrate percent canopy cover including overstory tree cover (hatched columns) and surface green vegetation cover (unhatched columns). Standard error bars are additive for both cover components. Note, there was only 1 untreated-unburned/low site according to the Monitoring Trend in Burn Severity (MTBS) classification (Finco *et al.* 2012), hence there is no error bar. Significance of Student's t-tests between severity groups shown above each respective year; *, $P \leq 0.05$

Table 2.1. Regression models predicting percent tree canopy cover, understory green vegetation cover, total char cover, and total fuel loads (Mg/ha) measured in 2008 and 2016 as a function of one-year post-fire dNBR, time since treatment (years), and the interaction of one-year post-fire dNBR and time since treatment. Linear regression models were used for 2008 tree canopy cover, 2008 total char, and 2016 understory green vegetation cover and the degrees of freedom were 66 for all models. Beta regression models were used for 2008 understory green vegetation cover, 2016 tree canopy cover, and 2016 total char, number of iterations were 34 + 4 (Fisher scoring), 12 + 2, and 23 + 3 respectively. Generalized linear regressions with Gamma family were used for both 2008 and 2016 total fuel loads. Bold face denotes significance at the 95% confidence interval, and SE denotes standard error of the estimate.

		2008				2016			
Tree Canopy (%)	Predictor Variables	Estimate	SE	t	P	Estimate	SE	z	P
	Tree Canopy (%)	dNBR	0.008	0.016	0.491	0.625	-0.003	0.001	-2.623
Years		0.245	0.062	3.932	<0.001	0.003	0.005	0.649	0.516
dNBR* Years		-0.001	0.000	-2.944	0.004	-5.374E-08	0.000	-0.003	0.997
Model: F=8.6, P< 0.001 , R ² =0.281					Model: z = 6.1, P < 0.001 , pseudo R ² = 0.42				
Understory Green (%)	Predictor Variables	Estimate	SE	z	P	Estimate	SE	t	P
	dNBR	-0.005	0.001	-4.187	0.000	0.048	0.018	2.657	<0.001
	Years	-0.007	0.004	-1.731	0.084	-0.034	0.068	-0.491	0.625
	dNBR* Years	3.652E-05	0.000	2.376	0.018	-1.81E-04	0.000	-0.806	0.423
Model: z = 5.5, P < 0.001 , pseudo R ² = 0.44					Model: F=5.3, P = 0.003 , R ² =0.193				

		2008				2016			
Total Char (%)	Predictor Variables	Estimate	SE	t	P	Estimate	SE	z	P
	dNBR	0.083	0.023	3.635	< 0.001	0.003	0.001	2.849	0.004
	Years	0.11	0.087	1.265	0.210	0.004	0.004	0.977	0.328
	dNBR* Years	-3.65E-04	0.000	-1.271	0.208	-1.829E-06	0.000	-0.153	0.878
		Model: F=12.1, P < 0.001 , R ² =0.356				Model: z = 5.5, P < 0.001 , pseudo R ² = 0.26			
Total Fuel Loads (Mg/ha)	Predictor Variables	Estimate	SE	t	P	Estimate	SE	t	P
	dNBR	9.284E-05	0.000	0.618	0.539	3.786E-05	0.000	0.919	0.362
	Years	9.186E-06	0.000	0.022	0.982	1.243E-04	0.000	1.022	0.310
	dNBR* Years	-1.177E-06	0.000	-0.711	0.480	-8.221E-07	0.000	-1.824	0.073
		Null deviance: 82.234 on 68 degrees of freedom, Residual deviance: 79.626 on 65 degrees of freedom				Null deviance: 33.465 on 69 degrees of freedom, Residual deviance: 27.429 on 66 degrees of freedom			

Treatment and burn severity effects on biophysical attributes

All live trees, saplings, and seedlings sampled in both 2008 and 2016 were ponderosa pine, apart from two juniper saplings recorded in 2008. Tree canopy cover in 2008 was affected by severity and the interaction between treatment and severity (both $P \leq 0.034$, both $F \geq 4.7$), with untreated sites that burned at low severity ($53.2 \pm 4.3\%$ [mean \pm SE]) having significantly more canopy cover than treated sites that also burned at low severity ($38. \pm 1.9\%$) or untreated sites that burned at high severity ($36 \pm 2.6\%$; both $P \leq 0.005$). In 2016, tree canopy cover was only affected by severity ($P < 0.001$, $F = 17.3$), where sites that burned at low severity had higher canopy cover (treated: $33.1 \pm 3.0\%$, untreated: $38.6 \pm 4.9\%$), than sites that burned at high severity (treated: $9.8 \pm 6.0\%$, untreated: $16.7 \pm 4.3\%$), regardless of treatment (all $P \leq 0.045$). Live tree basal area in 2008 did not differ between treatments or severity, but it was affected by severity in 2016 ($P < 0.001$, $F = 13.7$); sites that burned at low severity had more live basal area (treated: $12.4 \pm 2.1 \text{ m}^2/\text{ha}$ untreated $20.6 \pm 1.1 \text{ m}^2/\text{ha}$) than untreated sites that burned at high severity (both $P \leq 0.005$, $1.6 \pm 5.3 \text{ m}^2/\text{ha}$). Dead tree basal area in 2008 was also influenced by severity ($P = 0.008$, $F = 7.4$): dead tree basal area was higher in untreated sites that burned at high severity ($2.2 \pm 0.1 \text{ m}^2/\text{ha}$) than in sites that burned at low severity (treated: $1.0 \pm 0.3 \text{ m}^2/\text{ha}$, untreated: $0.3 \pm 0.4 \text{ m}^2/\text{ha}$, both $P \leq 0.035$).

Live tree density in 2008 was affected by severity and the interaction between treatment and severity (both $P \leq 0.004$, both $F \geq 8.6$), and in 2016 live tree density was affected by severity, treatment, and their interaction (all $P \leq 0.008$, all $F \geq 8.8$); untreated sites that burned at low severity had higher live tree density than all other sites in both years (Figure 2.5). Dead tree density in 2008 was only affected by severity ($P < 0.001$, $F = 46.2$); being significantly higher in high severity burned sites than low severity burned sites, regardless of treatment ($P < 0.001$, Figure 2.5A). Live sapling density in 2008 did not vary between sites but in 2016 it was strongly influenced by treatment, severity, and the interaction between the two (all $P \leq 0.016$, all $F \geq 7.3$), being highest in untreated sites that burned at low severity (Figure 2.5). Dead sapling density in 2008 was only affected by treatment ($P < 0.001$, $F = 17.0$); being higher in untreated sites than treated, regardless of severity ($P = 0.002$, Figure 2.5A). In 2016, dead sapling density was influenced by treatment, severity, and their interaction (all $P \leq 0.02$, all $F \geq 5.6$), being highest in untreated sites that burned at low

severity (Figure 2.5B). Only dead seedling density in 2016 was influenced by severity ($P = 0.014$, $F = 6.4$) however, Tukey multiple comparisons tests showed no differences in live or dead seedling density by treatment or severity in 2008 or 2016 (Figure 2.5).

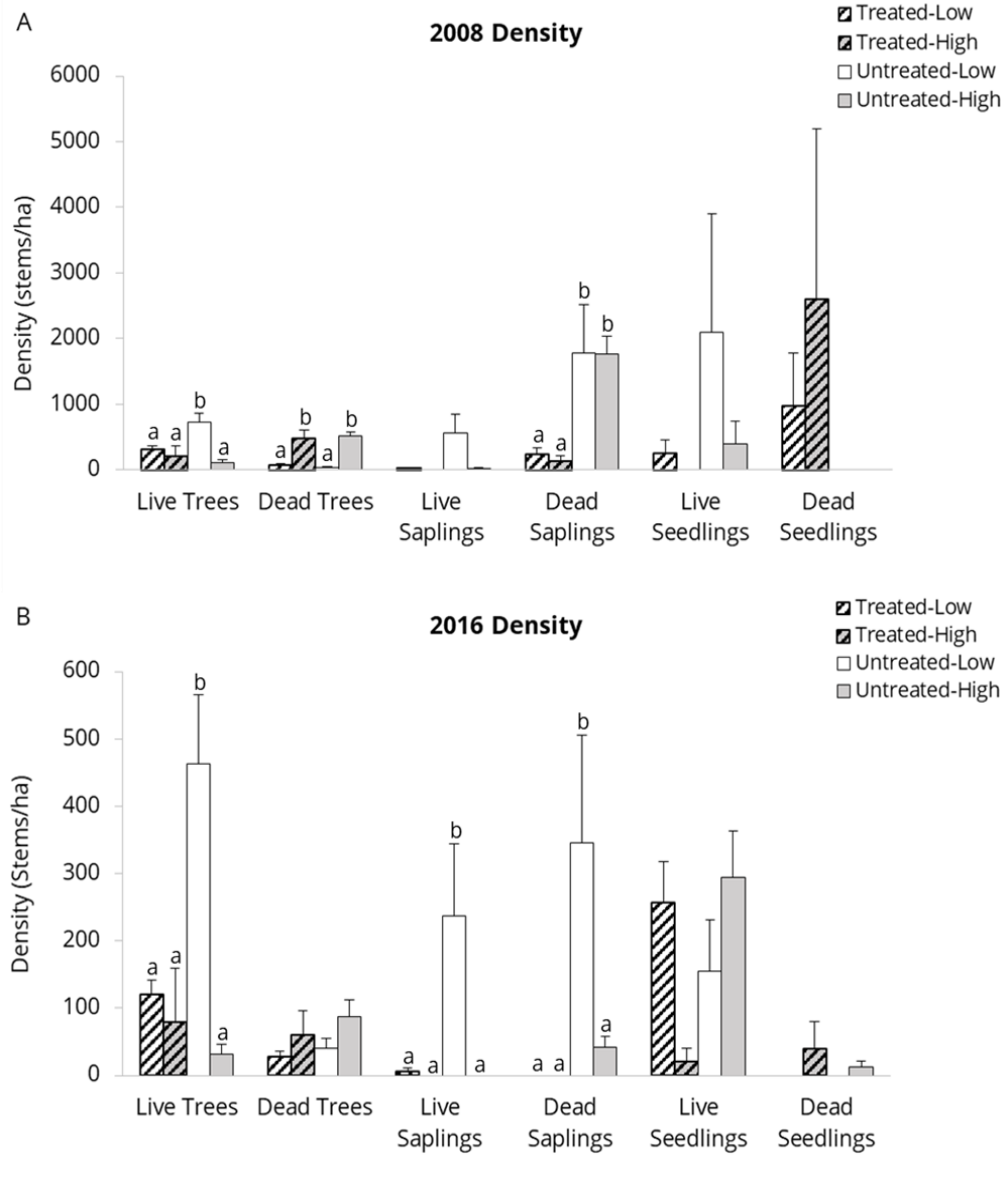


Figure 2.5. Density (stems/ha) of ponderosa pine trees, saplings, and seedlings for A) 2008 and B) 2016 contrasting treatment-severity groups. Letters shown above standard error bars denote significant Tukey multiple comparisons between treatment and severity groups, $P < 0.05$. Note that A) 2008 has a different scale than B) 2016.

Combined pre-fire treatment and severity effects on ground surface cover fractions varied between years. Understory green vegetation cover in 2008 was only affected by severity ($P < 0.001$, $F = 12.0$); being significantly higher in low severity sites than high severity sites, regardless of treatment (Figure 2.6A). In 2016, understory green vegetation cover was affected by treatment and severity (both $P \leq 0.025$, both $F \geq 5.2$), however, the trend was reversed from 2008; sites that burned with low severity had significantly lower green vegetation cover than treated that burned at high severity (Figure 2.6B). Non-photosynthetic vegetation (NPV) in 2008 and 2016 was affected by treatment and severity (in 2008, both $P \leq 0.001$, both $F \geq 11.6$; in 2016, both $P \leq 0.028$, both $F \geq 5.0$); being significantly reduced by treatment and high severity with untreated sites that burned at low severity have the highest NPV (Figure 2.6A). Both treatments and severity affected soil and rock cover in 2008 (both $P < 0.001$, both $F \geq 12.8$), with treatments and high severity causing more soil and rock exposure, though not detectable in 2016 (Figure 2.6). Total char cover in both sample years was only affected by severity (both $P < 0.001$, $F \geq 7.7$); being higher in sites that burned at high severity than low severity regardless of treatment in 2008 (Figure 2.6A) and untreated sites that burned at high severity than both treated and untreated sites that burned at low severity in 2016 (Figure 2.6B).

Cover of understory vegetation functional groups were not significantly affected by treatment or severity in 2008 (see Table 2.2 for statistics). However, in 2016, shrub and graminoid cover were affected by treatment and severity; treated sites that burned at high severity had higher shrub cover than sites that burned with low severity, whereas graminoid cover was higher in sites that were untreated and burned with high severity than sites that burned at low severity (Table 2.2). Forb and invasive cover in 2016 were both affected by burn severity; forbs were higher in untreated sites that burned with high severity than untreated sites that burned with low severity, and invasive species cover was higher in untreated sites that burned with high severity than sites that burned with low severity (Table 2.2). Moss/lichen/fungi cover significantly decreased as burn severity increased, though was unaffected by treatment (Table 2.2)

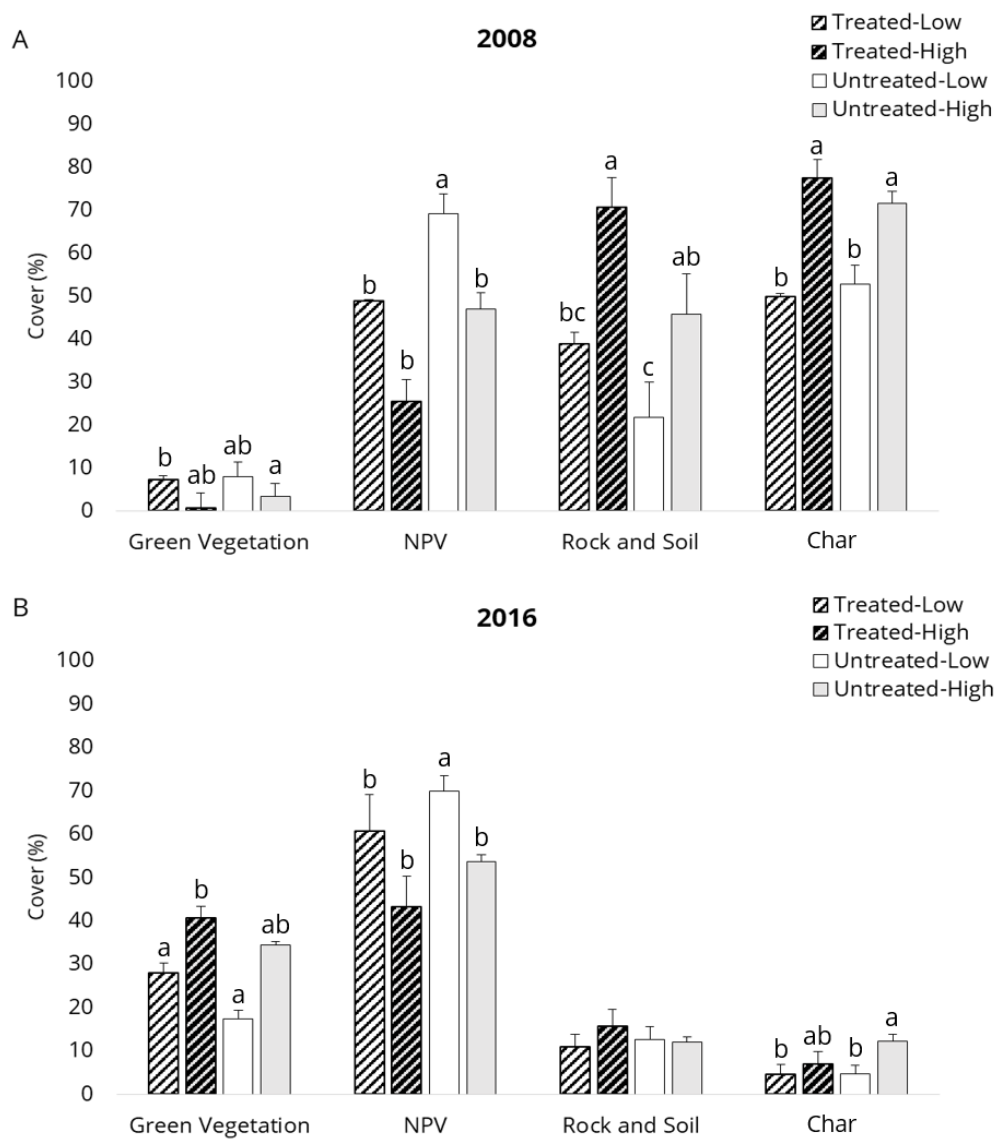


Figure 2.6. Mean percent surface cover by cover type for A) 2008 and B) 2016 contrasting treatment-severity groups, NPV= non-photosynthetic (dead or dormant) vegetation Letters shown above standard error bars denote significant Tukey multiple comparisons between treatment and severity groups.

Table 2.2. Permutation ANOVA and Tukey multiple comparison test results for treatment-severity interactions. Treat = treatment (two factors; treated or untreated), Sev = Severity (two factors; low or high), boldface denotes significance at the 95% confidence level, and dashes indicate no significant difference. Degrees of freedom for all permutation ANOVA tests were 1 for each predictor variable. Letters denote significant Tukey multiple comparisons (Tukey) between treatment and severity groups.

	Predictor Variables	Permutation ANOVA				Tukey Multiple Comparisons				
		2008		2016		Groups	2008		2016	
		F	P	F	P		Mean ± SE	Tukey	Mean ± SE	Tukey
Shrub Cover (%)	Treat	1.6	0.215	8	0.006	T-low	0.9 (0.4)	-	5.8 (1.6)	b
	Sev	3.3	0.074	10.9	0.002	T-high	0 (0)	-	19.1 (8.6)	a
	Treat:Sev	0.6	0.445	1.6	0.216	U-low	2.6 (1.8)	-	1.2 (0.5)	b
						U-high	0.4 (0.2)	-	7.2 (2.1)	ab
Graminoid Cover (%)	Treat	0.5	0.5	0.2	0.634	T-low	5.7 (1.3)	-	13.2 (1.2)	b
	Sev	3.1	0.085	4	0.049	T-high	0.2 (0.2)	-	12.2 (1.5)	b
	Treat:Sev	1.2	0.282	6.4	0.014	U-low	4.9 (1.8)	-	9.1 (1.3)	b
						U-high	3.6 (1.3)	-	18.1 (1.6)	a
Forb Cover (%)	Treat	0.2	0.624	1.5	0.223	T-low	8.7 (1.6)	-	11 (1.1)	ab
	Sev	2	0.161	4.3	0.043	T-high	2.2 (0.9)	-	12.4 (2.4)	ab
	Treat:Sev	1	0.313	1.5	0.23	U-low	7.3 (3.4)	-	6.8 (1.2)	a
						U-high	6.2 (1.7)	-	12.4 (1.2)	b
Invasive Cover (%)	Treat	0.4	0.51	0.2	0.672	T-low	0 (0)	-	1.2 (0.4)	a
	Sev	0.4	0.51	9.6	0.003	T-high	0 (0)	-	4.7 (2.5)	ab
	Treat:Sev	0.4	0.51	0	0.996	U-low	0 (0)	-	0.7 (0.5)	ab
						U-high	0.3 (0.3)	-	4.2 (1.1)	b
Moss/ Lichen/ Fungi Cover (%)	Treat	0	0.874	2.3	0.135	T-low	2.5 (1.7)	-	2.2 (0.3)	-
	Sev	1	0.315	4	0.049	T-high	0.2 (0.2)	-	1.7 (0.4)	-
	Treat:Sev	0	0.892	1.1	0.297	U-low	2.5 (1.8)	-	3.7 (1)	-
						U-high	0.8 (0.4)	-	1.9 (0.3)	-

Total fuel loads (1000-hr, 100-hr, 10-hr, 1-hr, litter and duff) were not affected by either treatment or severity in 2008 or 2016. However, CWD in 2016 was affected by severity and the interaction between treatment and severity (both $P \leq 0.038$, $F \geq 4.4$); being higher in untreated sites that burned with high severity than treated or untreated sites that burned with low severity (both $P \leq 0.007$, Figure 2.7B). Fine woody debris in 2008 were similarly influenced by severity ($P=0.001$, $F=11.6$), being higher in untreated sites that burned with low severity than sites that burned with high severity (both $P \leq 0.031$, Figure 2.7A). Fine woody debris in 2016 were affected by severity and treatment (all $P \leq 0.034$, all $F \geq 7.3$); untreated sites that burned with low severity had higher FWD loads than all other sites (all $P \leq 0.040$, Figure 2.7B).

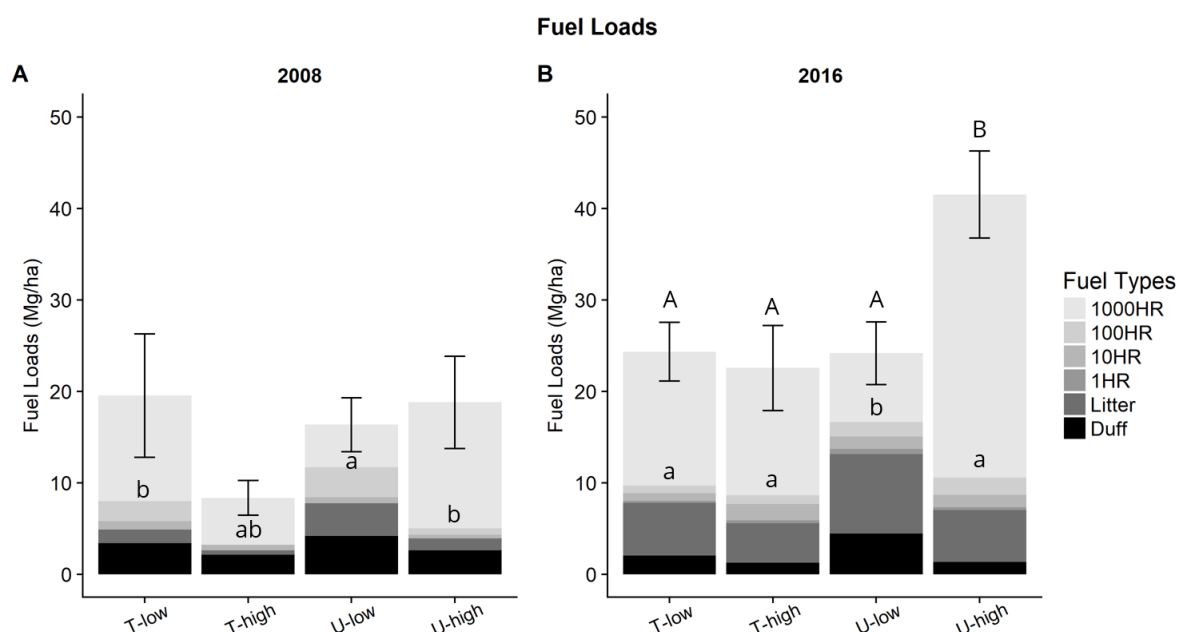


Figure 2.7. Fuel loads (Mg/ha) for A) 2008 and B) 2016 contrasting treatment-severity groups; T=treated, U=untreated. Standard error bars are for total surface fuels (all fuel components added together). Significance of Tukey multiple comparisons test between treatment-severity groups: *, $P < 0.05$.

Changes over time

All variables measured in 2008 significantly differed from variables measured in 2016 except for dead seedling density and duff (see Table 2.3 for statistics). Tree canopy cover and density were significantly reduced over time with fairly high within group agreement whereas tree

basal area significantly increased over time, though within group agreement was low (Table 2.3) Surface cover, cover of understory functional groups, and fuel loads also increased significantly over time (Table 2.3), as would be expected nine years post-fire. All surface covers, except NPV, had high within group agreement, whereas cover of understory functional groups and fuels had fairly low within group agreement, except for 1-hr fuels and litter which both had high within group agreement.

Table 2.3. Blocked multi-response permutation procedure (MRBP) tests comparing 2008 variables to 2016 variables. Boldface P-values denotes significance at the 95% confidence level, whereas boldface A-values are above 0.3 (strong within group agreement), and S.E. denotes the standard error within each group. NPV=Non-photosynthetic (dead or dormant) vegetation; CWD=coarse woody debris.

Variable Description	P	A	2008 Mean (S.E.)	2016 Mean (S.E.)
Tree Canopy Cover (%)	< 0.001	0.255	40.08(1.56)	26.68(3.19)
Live Tree Basal Area (m ² ha ⁻¹)	< 0.001	0.115	2.19(0.34)	9.54(1.14)
Dead Tree Basal Area (m ² ha ⁻¹)	< 0.001	0.063	1.34(0.2)	5.57(0.67)
Live Tree Density (stems ha ⁻¹)	< 0.001	0.214	298.57(42.1)	140.71(16.82)
Dead Tree Density (stems ha ⁻¹)	< 0.001	0.162	250(36.33)	52.86(6.32)
Live Sapling Density (stems ha ⁻¹)	0.036	0.012	104.29(49.25)	40(4.78)
Dead Sapling Density (stems ha ⁻¹)	< 0.001	0.181	994.29(176.2)	68.57(8.2)
Live Seedling Density (stems ha ⁻¹)	0.001	0.027	571.43(318.72)	236.43(28.26)
Dead Seedling Density (stems ha ⁻¹)	0.081	0.008	600(392.69)	7.14(0.85)
Green Cover (%)	< 0.001	0.488	5.54(0.68)	29.39(3.51)
NPV Cover (%)	0.003	0.052	49.74(2.67)	58.41(6.98)
Soil and Rock Cover (%)	< 0.001	0.421	40.7(2.66)	12.0(1.19)
Total Char Cover (%)	< 0.001	0.675	59.69(2.31)	7.34(0.88)
Moss, Lichen, and Fungi Cover (%)	< 0.001	0.122	1.76(0.78)	2.31(0.28)
Shrub Cover (%)	< 0.001	0.106	0.94(0.35)	6.53(0.78)
Graminoid Cover (%)	< 0.001	0.356	4.47(0.77)	14.15(1.69)
Forb Cover (%)	< 0.001	0.117	7.14(1.05)	10.92(1.31)
Invasive Cover (%)	< 0.001	0.151	0.1(0.09)	2.42(0.29)
Total Fuel Loads (Mg ha ⁻¹)	< 0.001	0.094	17.98(2.39)	30.07(3.59)
Fine Fuel Loads (Mg ha ⁻¹)	< 0.001	0.110	7.21(0.72)	11(1.31)
CWD (Mg ha ⁻¹)	0.002	0.053	10.78(3.19)	19.07(2.28)
100hr fuels (Mg ha ⁻¹)	0.008	0.034	1.69(0.42)	1.31(0.16)
10hr fuels (Mg ha ⁻¹)	0.001	0.055	0.66(0.12)	1.16(0.14)
1hr fuels (Mg ha ⁻¹)	< 0.001	0.410	0.02(0)	0.32(0.04)
Litter (Mg ha ⁻¹)	< 0.001	0.404	1.68(0.22)	6.08(0.73)
Duff (Mg ha ⁻¹)	0.052	0.019	3.16(0.41)	2.14(0.26)

Discussion

Most treated sites burned at low severity, reflecting the results of previous research that found that pre-fire fuel reduction treatments in fire-suppressed dry ponderosa pine forests reduce burn severity (Agee and Skinner 2005; Stephens *et al.* 2009; Fulé *et al.* 2012). Burn severity effects over time were successfully observed by LandTrendr analysis, with the most pronounced post-fire changes observed in untreated-high severity sites, which showed only a gradual increase and had still not recovered to pre-fire NBR levels nine years post-fire; NBR increased more rapidly in treated sites that burned at high severity, and had recovered to unburned/low NBR levels within four years after fire. Kennedy *et al.* (2010) also found that LandTrendr time series were effective at capturing disturbances and vegetation recovery in dry ponderosa pine forests in Washington and Oregon. Using LandTrendr, pre- and post-disturbance vegetation trends can be consistently monitored on a landscape level through time with more detail than is commonly feasible with field monitoring crews. However, field monitoring crews are critical for both interpreting and validating remotely-sensed data.

Biophysical attributes measured in 2008 and re-measured in 2016 were predicted by one-year post-fire dNBR, the strongest relationship being with tree canopy cover, similar to the findings of prior studies (Hudak *et al.* 2007; Lentile *et al.* 2009). Understory variables, except total fuel loads, were also predicted by dNBR, most notably total char cover. Lentile *et al.* (2009) found similar results after the 2000 Jasper Fire in the ponderosa pine dominated Black Hills of South Dakota, though percent live tree canopy cover was the most significant predictor of one-year post-fire dNBR in their study. What is notable about our study is that char cover was significantly predicted by the dNBR nine years post-fire, though the coefficient of determination was relatively low. This reinforces Lentile *et al.*'s (2009) findings and indicates that char cover can still be found in burned areas nine years post-fire, more notably in areas that burned at high severity, and thus can be used as an indicator of burn severity over time. One general rule of thumb used by managers for the longevity of treatment effectiveness is that treatments tend to last for 10-15 years (Agee and Skinner 2005). Most of the treated sites we observed were treated between one to twenty-one years prior to the Egley Complex yet were still successful at reducing burn severity in the area compared to untreated sites. However, Prichard *et al.* (2010) found higher burn severity in ponderosa pine stands that

had been recently thinned (15 years pre-fire) but where surface fuels had not yet been treated, as did Hudak *et al.* (2011b) in cold mixed conifer forest stands thinned the previous year but with fuel piles still remaining. This highlights the importance of surface fuel treatments in addition to thinning treatments. The success of fuel reduction treatments at reducing high severity in the Malheur National Forest might be because most of the treatment units intersected by the Egley Fire Complex (668 of 1041) had received multiple treatment entries, thus increasing treatment effectiveness.

Live and dead tree and sapling density were significantly affected by treatments but or dead tree basal area were not. The lack of basal area trends is likely because pre-commercial thinning treatments usually remove small diameter trees, which contribute little to overall tree basal area. Areas that burned at high severity, however, did reduce live tree basal area in both sample years and dead tree basal area in 2008. The lack of differences by treatment and severity found in standing dead tree basal area and tree density in 2016 can be attributed to many dead trees in high severity sites having fallen and become downed woody fuels, as previously discussed. Tree canopy cover, live and dead tree density, and live and dead sapling density all decreased over time, but tree basal area, both live and dead, increased over time, realizing management objectives of decreasing density and increasing tree basal area to improve fire resilience. However, it is possible that the smaller sampling plot used in 2016 (8 m radius instead of 11.3 m radius) led to reduced tree density and basal area measured in 2016 compared to 2008.

Seedling density, though, did not differ by treatment or severity in either sample year. The lack of differences between treatment and severity might be attributed to the amount of variability between untreated sites that burned at low severity. In 2016, though, the lack of differences seen between treatment and severity might be explained by post-fire planting efforts that took place between May 2010 and April 2015. Ten out of the seventy sites sampled had seedlings planted post-fire: four treated and six untreated. Eleven out of our seventy sites had an average distance to seed source over 60 m (unpublished data), where we would expect lower seedling density due to lack of a seed source (Kemp *et al.* 2016), but seven of these sites had been planted. This indicates a successful management decision to plant ponderosa pine seedlings in areas where conifer regeneration would have been slow, if

existent. The significant decrease in live seedling density from 2008 to 2016, might be attributable to reduced overstory protection of seedlings from drought, frost heaving, or other environmental stress (Schubert 1974).

The NPV cover fraction that includes both litter, duff, and FWD, likely was not completely consumed at untreated sites that burned at low severity and then accumulated from one-year post-fire to nine years post-fire. On the other hand, treated sites that burned with high severity had the lowest NPV cover, more exposed soil and rock cover, and less tree canopy cover, allowing vegetation to grow faster and more abundantly (Bartuszevige and Kennedy 2009b; Schwilk *et al.* 2009; Stephens *et al.* 2012b). Other studies have shown that thinning can cause soil disturbances (Korb *et al.* 2004; Stephens *et al.* 2012b), which might explain the higher soil and rock cover found in treated sites in 2008. However thinning has also been shown to increase FWD (Agee and Skinner 2005; Stephens *et al.* 2009) which may have been consumed in treated sites that burned at high severity, creating more soil and rock exposure (Graham *et al.* 1999; Hille and Stephens 2005).

Understory vegetation functional groups followed similar patterns as surface cover materials. The only functional group that was affected by severity in 2008 was shrub cover, which was higher in sites that burned with low severity than high severity. It is not uncommon for forb, graminoid, and shrub cover to decrease one- to three-years post-fire (Metlen *et al.* 2004; Collins *et al.* 2007; Knapp *et al.* 2007; Dodson *et al.* 2008) however, some studies have shown increases in understory vegetation cover (Armour *et al.* 1984; Moore *et al.* 2006; Ellsworth and Kauffman 2010). Metlen and Fiedler (2006) found that native plant cover was significantly lower initially post-fire (same year as the prescribed burn) than unburned sites, however found no differences in cover one- to three- years between burned sites and unburned sites in ponderosa pine/Douglas-fir forest near Missoula, MT. Armour *et al.* (1984) found that forb, graminoid, and shrub cover steadily increased one to three years following a prescribed fire in a ponderosa pine forest, with shrubs having the highest percent cover in sites that burned at high intensity. We found similar results nine years post-fire; with higher percent cover of shrub, graminoid, and forbs in sites that burned at high severity than sites that burned at low severity. The increase in percent cover of understory functional groups in high severity burned sites nine years post-fire suggests either vegetation

recovery or re-colonization within high severity burned sites in between sample years, trends which also apply to green surface cover, though the change in vegetation field collections methods may also account for increases seen. The increase in cover of all understory functional groups from 2008 to 2016, and the increasing trend of LandTrendr-derived NBR from 2008 to 2016 (Figure 2.4), indicative of vegetation cover, suggests vegetation recovery as well.

In 2016, we also found that untreated sites that burned at high severity had more invasive cover than sites that burned at low severity. Treatments have been shown to increasing invasive cover (Korb *et al.* 2004; Dodson and Fiedler 2006; Collins *et al.* 2007; Dodson *et al.* 2008; Stephens *et al.* 2012b) as well as high burn severity (Turner *et al.* 1997; Caprio *et al.* 1999; Keeley *et al.* 2003; Keeley 2006). Though treatments have been shown to increase soil disturbance leading to an increase in invasive cover (Korb *et al.* 2004; Stephens *et al.* 2012b), we found that high severity fire, which burned mostly in untreated sites, led to a higher cover of invasives than treatments.

Wildfires have been shown to cause vegetation shifts from forested to non-forested vegetation types (Savage and Mast 2005; Crotteau *et al.* 2013; Dodson and Root 2013; Coop *et al.* 2016). Savage and Mast (2005) found that in southwestern US ponderosa pine forests, high severity sites experienced a vegetation shift from ponderosa pine stands to shrub-dominated patches of pointleaf manzanita (*Arctostaphylos pungens* Kunth). One of the dominate shrubs in the Malheur National Forest is snowbrush ceanothus, and we found higher shrub cover particularly in treated sites that burned with high severity Gratkowski (1962) found that snowbrush ceanothus seeds are germinated by heat and Weiner *et al.* (2016) also found snowbrush ceanothus cover to be higher in areas that burned with high severity in sagebrush steppe and western juniper woodlands.

Fuel loads, while higher in low severity sites than high severity sites in 2008, were highest in sites that burned with high severity in 2016. By 2016, sites that experienced high tree mortality (high burn severity) had more downed woody debris accumulation (e.g., fallen snags) than low severity burned sites. Thus, higher surface fuel accumulations were not apparent after just one year but were after nine years. Other studies have shown tree mortality caused by high severity wildfire becoming heavy surface fuel accumulations at least three

years post-fire as well (Passovoy and Fulé 2006; Roccaforte *et al.* 2012; Stevens-Rumann *et al.* 2012). The lack of differences found in fuel loads between treated sites that burned at high severity and both treated and untreated sites that burned at low severity suggests that the Egley Fire Complex, following thinning efforts, lowered surface fuels much like a prescribed fire would have. It is important to note that fuel estimates were collected using slightly modified Brown's transects in 2008 (Brown 1974) and photoloads in 2016 (Keane and Dickinson 2007). We opted for the newer, photoload method (Keane and Dickinson 2007) of estimating surface fuel loads in 2016 to speed field sampling, and considering more recent research that showed the Brown (1974) method may fail to capture inherently high fuels variability in natural fuel beds (Keane *et al.* 2012; Vakili *et al.* 2016). However, Sikkink and Keane (2008) found photoload measurements to overestimate fuel loads (both fine and coarse fuels), especially when a site had high fuel loads ($>2 \text{ kg m}^{-2}$) in montane forests, which could be occurring here.

It is widely believed that with the past century of fire suppression, the accumulation of fuels in ponderosa pine forests has led to the increase in large, high severity fires seen today (Kilgore 1981; Covington and Moore 1994; Allen *et al.* 2002)(Kilgore 1981; Covington and Moore 1994; Allen *et al.* 2002). While fuel loads in our study did significantly increase from 2008 to 2016, high fuel loads were mostly in untreated sites that burned with high severity. This suggests that the Egley Fire Complex successfully reduced fuel loads for up to nine years post-fire, especially in areas that had been treated pre-fire and burned with low severity and may have met many objectives that Malheur National Forest managers hope to achieve from prescribed fire.

Conclusions

Mechanical fuel treatments implemented one to twenty-one years pre-fire were effective at reducing burn severity within a large wildfire. LandTrendr was an effective tool for monitoring vegetation recovery post-fire, and regression models of one-year post-fire dNBR significantly predicted biophysical attributes, both in 2008 and 2016, except total fuel loads. The interaction between time since treatment and one-year post-fire dNBR significantly predicted one-year post-fire tree canopy and understory vegetation cover; as burn severity

(one-year post-fire dNBR) and time since fire increased, one-year post-fire tree canopy and understory green vegetation cover decreased.

Treatments did not decrease tree canopy cover and basal area as much as burn severity did in 2008, however, treatments did reduce density of live trees and saplings. The lower tree and sapling density in pre-fire treated areas likely resulted in the significant reduction in burn severity on treated sites compared to untreated sites. Understory shrub, graminoid, forb, and invasive species cover measured nine years post-fire were higher in sites that burned with high severity, as a result of strong vegetation recovery or re-colonization in those sites. Fuel loads in 2016 were higher at untreated sites that burned with high severity than all other sites, including treated sites that burned at high severity, indicating that mechanical treatments, in conjunction with reducing burn severity, reduced surface fuel loads nine years post-fire.

The decrease in tree canopy cover and density of trees and saplings along with the increase in tree basal area from 2008 to 2016 reflects management objectives to reduce fuels via thinning small diameter trees while increasing canopy base height to increase fire resilience within the forest. Fuel loads measured in 2016 across the Egley Complex were higher than fuels measured in 2008, indicating post-fire fuel accumulation and suggesting a need for a repeated understory fuel treatment. These results support the implementation of fuel treatments to reduce fire effects in ponderosa pine forests and suggest that low severity wildfire can accomplish fuel reduction treatment objectives while not overly impacting overstory tree mortality.

CHAPTER 3: Effects on bee and flowering plant communities in a ponderosa pine forest ten years after a major wildfire event

Introduction

Bees are the most important insect pollinators for many flowering plant species in the United States (Ollerton *et al.* 2011; Winfree *et al.* 2011), being the primary pollinator for many natural (Tependino 1979; Biesmeijer *et al.* 2006; Brosi and Briggs 2013) and managed systems in the US (Delaplane and Mayer 2000; Klein *et al.* 2007). In the United States alone, 130 agricultural plants are bee pollinated (McGregor 1976). Honey bees (*Apis mellifera*) are the primary managed pollinator for agriculture in the United States, estimating to contribute US\$9 billion to US agriculture (Klein *et al.* 2007), however there are many native, wild bee pollinators that also contribute substantially to crops (Delaplane and Mayer 2000; Klein *et al.* 2007). The success of long-term stability in crop pollination by wild bees strongly depends on suitable land available for nesting and foraging (Koh *et al.* 2016). Though wild bee pollinators are critical for agricultural success (Winfree *et al.* 2011) and native biodiversity (Biesmeijer *et al.* 2006; Brosi and Briggs 2013), there is not much known about pollinator diversity within forested ecosystems or how natural disturbances, like wildfire, affect pollinator diversity (Koltz *et al.* 2018; Rivers *et al.* 2018).

Natural disturbances are important in many terrestrial ecosystems (Pyne *et al.* 1996; DeBano *et al.* 1998; Bowman and Johnston 2005), particularly in ponderosa pine forests. Fire has been shown to increase understory vegetation cover (Armour *et al.* 1984; Moore *et al.* 2006) in ponderosa pine forests as shown in Chapter 2. High severity wildfires in forested ecosystems, typically classified due to dramatic reductions in tree overstory caused by fire, thus reducing overstory canopy and exposing mineral soil (Keeley 2009), are typically followed by an increase in understory plant species cover (Armour *et al.* 1984; Moore *et al.* 2006; Ellsworth and Kauffman 2010) as demonstrated in the previous chapter. In fire-adapted ecosystems, like ponderosa pine forests, many understory vegetation species have strategies to adapt and compete after the overstory canopy and duff layers are consumed by fire (Bond and Van Wilgen 1996). Thus, there is often a temporary increase in understory plant richness and abundance following wildfires (Keeley 1987; Keeley *et al.* 2003; Dodge *et al.* 2019). The

increase in plant richness and cover caused by fire is expected to have important effects on local pollinators.

Although some bee genera nest above ground in twigs and stems (e.g. *Ceratina*, some *Xylocopa*, *Hylaeus*, and *Chilicola*, some *Megachile* sp.), most bees found in fire-prone areas are non-social (solitary) bees that nest in the ground (Ne'eman and Dafni 1999; Cane and Neff 2011). In order to survive lethal temperatures, nests need to be adequately insulated (Cane and Neff 2011). If nests are under thick litter layers, though, fires can cause the litter layers to smolder, extending the duration of heating on mineral soils (DeBano *et al.* 1979). In general, solitary bees prefer to nest in bare ground or soil banks. Cane and Neff (2011) found that *Osmia lignaria* and *Megachile rotundata* nests that were deeper than 5 cm were able to survive higher temperatures for longer durations. Most solitary bees place nest cells deeper than 10 cm, increasing chances of survival during wildfires. However, survival still depends on fire intensity; the higher the fire intensity, the more likely bee progeny will be killed (Cane and Neff 2011).

Little information is available describing fire effects on bee pollinators, particularly in fire-prone forested ecosystems (Ne'eman and Dafni 1999; Koltz *et al.* 2018; Rivers *et al.* 2018; Galbraith *et al.* 2019). There are no studies looking at long-term effects on bee pollinators in forested ecosystems or studies that correlate flowering plant species with bee pollinator species that I could find, which might have important implications for land managers wanting to rehabilitate burned areas threatened by invasive species.

Objectives

Given the lack of research on pollinator abundance and diversity following fires in ponderosa pine forests and the increase of large, high-severity fires in these habitats (Kaye *et al.* 2005; Fulé *et al.* 2012), the objectives of this study were to use vegetation data collected previously (Chapter 2) in combination with data collected on bees communities to: 1) determine differences in bee, flowering plants (hereafter plants), and flower abundance, richness, diversity, and evenness by summer months (June, July, and August) and by sites burned at high severity and unburned sites; 2) quantify differences in plants, flower, and bee communities (i.e. diversity and each species' abundance) in those same sites; 3) determine if there is a correlation between bee communities and both the plant and flower communities.

Because Burns, OR has rainy springs but hot and dry summers, I hypothesize bee, plants, and flowers will all be more abundant and diverse earlier in the summer than later in the summer, attracting more pollinators in the early summer compared to the late summer. I suspect that the decrease in tree canopy cover in high severity burned sites (as shown in Chapter 2) would allow more sunlight access to understory plants than in unburned sites and therefore high severity burned sites would have higher bee, plant, and flower abundance and diversity than unburned sites. I also hypothesize that the bee community (i.e. abundance and diversity) and the plant/flower community will be strongly correlated, mainly because of their co-dependence on each other, however, I suspect bees would be more attracted to plants with higher proportions of flowers, therefore I suggest the correlation between the bee community and the flower community will be stronger than the correlation between the bee community and the plant community.

Methods

Study Area

The study area was within the Malheur National Forest, approximately 55 km northwest of Burns, OR (43° 52' 50" N, 119° 38' 24" W). The Malheur National Forest occupies 688,000 hectares (ha) in the Blue Mountains of eastern Oregon and includes high desert grasslands, sagebrush (*Artemisia* spp. L.) steppe and juniper (*Juniperus occidentalis* Hook.) woodlands, ponderosa pine forests, and mixed conifer forests. Our study focused on the southern ponderosa pine forests of the Malheur National Forest. Mean monthly high temperature in the growing season (May through August) is 26°C and the mean monthly low temperature in winter (November through February) is -8°C. Mean annual precipitation is 279 mm (US Climate Data 2019), with the majority of precipitation accumulated between November and May and with less than 19 mm of precipitation accumulated between June and October. Elevation of study sites ranges from 1506 m to 1755 m above sea level. Common grass species included needlegrass (*Achnatherum* spp. P. Beauv.), squirreltail (*Elymus elymoides* (Raf.) Swezey), and Sandberg bluegrass (*Poa secunda* J. Presl). Forb species included common yarrow (*Achillea millefolium* L.), blue eyed Mary (*Collinsia* spp. Nutt.), and willowherb (*Epilobium* spp. L.). Invasives species included cheatgrass (*Bromus tectorum* L.), Canadian thistle (*Cirsium arvense* (L.) Scop.), and bull thistle (*C. vulgare* (Savi) Ten.).

Snowbrush ceanothus (*Ceanothus velutinus* Douglas ex Hook.), creeping barberry (*Mahonia repens* (Lindl.) G. Don), and antelope bitterbrush (*Purshia tridentata* (Pursh) DC.) were the most common shrubs within the study area (flowering species are listed in Appendix A).

The Egley Complex, comprised of three lightning-ignited fires, burned approximately 56,802 ha (Figure 3.1) from 7 to 21 July 2007 under low fuel moisture and extreme burning conditions. Burn severity strata were determined by the Monitoring Trends in Burn Severity (MTBS) program (Eidenshink *et al.* 2007), which used a Landsat 5 TM image from July 18, 2006 for the pre-fire image and an image from July 7, 2008 for the post-fire image to calculate dNBR. The dNBR was binned into two classes: unburned (-100 to 99 dNBR) and high (> 450, Eidenshink *et al.* 2007). Sites (n=14), were distributed within the Egley Fire Complex perimeter, either in unburned (n=7) or high severity (n=7) locations constrained by slope, aspect, and older tree age structure and proximity to a navigable road.

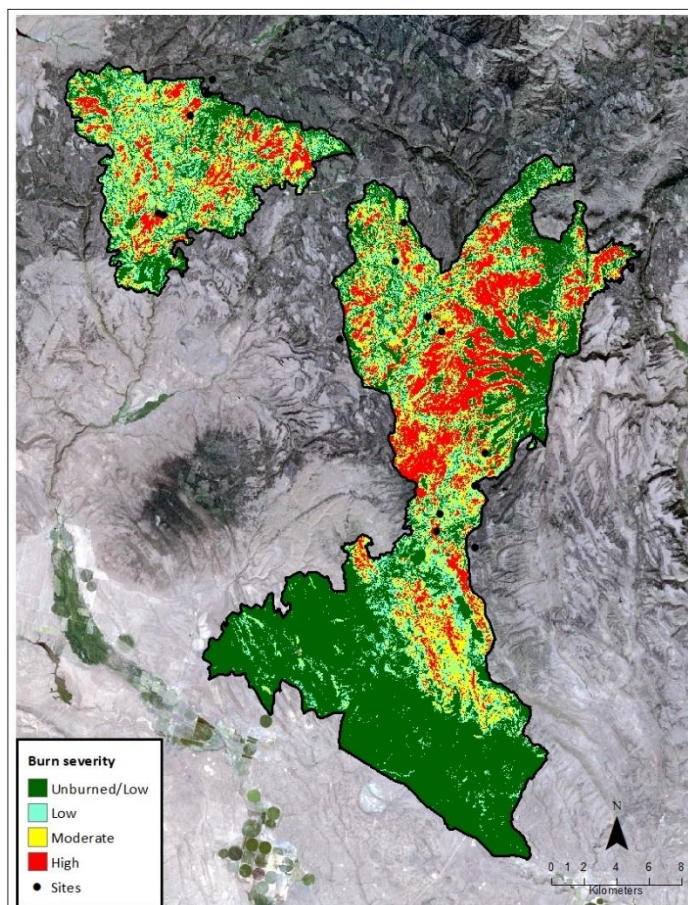


Figure 3.1. Egley fire complex located in eastern Oregon, showing distribution of the classified delta normalized burn ratio (dNBR) burn severity map (Finco *et al.* 2012).

Field Procedures

Field sites were established the first week of June and resampled the first week of July and August 2017, ten years post fire. Each site consisted of a central plot and four additional plots situated orthogonally 30 m from the center plot and oriented to the prevailing slope (Figure 3.2). At each field site, two 0.61 m tall shepherd's poles were placed at plot center, each with a Japanese beetle trap, one blue and one yellow (Figure 3.3) and left for six to eight days (Cook *et al.* 2011). On the bottom of one of the two traps, an iButton was mounted on a string, about 0.5 m from the ground, to collect temperature and relative humidity every four hours for each site. Temperature and humidity data considered in the analysis started at 6 am the morning after traps were placed and ended at 9 pm the night before traps were collected.

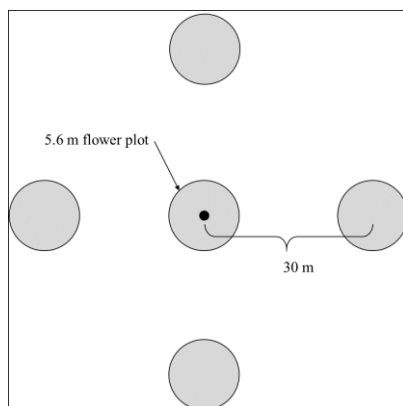


Figure 3.2. Field site layout (not drawn to scale) used at field sites in 2017



Figure 3.3. Yellow and blue Japanese beetle traps on shepherd's poles

At each site, tree canopy cover was estimated using a convex spherical densiometer facing the four cardinal directions around each plot. Flowering plants were counted at each of the five plots within a fixed radius of 5.6 m (1/100th of a hectare) and identified to species. Because the number of flowers on each plant varied widely, the number of flowers on each plant and number of species within the plot were also recorded (Grundel *et al.* 2010). Among insects collected in the traps, only bees were kept and identified to the finest taxon (family, genus, or species, listed in Appendix B).

Statistical Analysis

Variables collected at all five plot locations per field site were aggregated to the site level. Plant and flower density (plants/ ha, flowers/ ha, respectively) were calculated and used, along with bee counts for abundance and community analyses. An alpha level of 0.05 was set

for determining significance in all analyses. Abundance (sum of all specimens for each site) and richness (count of all specimen for each site) were tested by the Lilliefors (Kolmogorov-Smirnov) Test for Normality (Dallal and Wilkinson 1986) and found to be non-normally distributed. Therefore a Kruskal-Wallis test was used to determine differences in abundance and richness among months, and a Dunn's Test was used for pairwise comparisons (Table 3.1). A Kruskal-Wallis test was also used to determine differences in plant, flower, and bee abundance and richness between burned and unburned sites. To maintain trap color pairs per site, a paired Wilcoxon test was used to analyze bee abundance and richness differences between blue traps and yellow traps within each month and within burned and unburned sites within each month (R Core Team 2013).

Table 3.1. Objectives, hypothesis, and analysis used for each objective.

Objectives	Hypothesis	Analysis
1) Determine differences in bee, flowering plants (plants), and flower, abundance and richness by: a) summer month b) burned and unburned (fire) site c) trap color for bees	1) Bee, plants, and flower abundance will be higher in a) early summer months than later summer months b) high severity (burned) sites than unburned sites c) yellow traps than blue traps	1a) A Kruskal-Wallis and Dunn's pairwise tests among months 1b) A Kruskal-Wallis between burned and unburned 1c) A paired Wilcoxon -paired by trap color
2) Analyze differences in bee, plant, and flower diversity (both Shannon's and Simpson's) by; a) summer month b) burned and unburned site c) trap color for bees	2) Bee, plants and flower diversity will be more diverse a) earlier in the summer than later in the summer b) in burned sites than unburned sites c) in yellow traps than blue traps	2a) An ANOVA was used to determine differences in diversity among summer months 2b) A t-test was used to determine differences in diversity between burned and unburned sites 2c) A paired t-test was used to determine differences in diversity between blue and yellow traps
3) Evaluate differences in bee, flowering plant (plants), and flower community composition by; a) summer month (June, July, and August) b) burned (high severity) and unburned site c) trap color (yellow and blue) for bee communities	3) Bee, plant, and flower communities will be more abundant a) earlier in the summer (June) than later in the summer (August) b) in burned sites than unburned sites c) in yellow traps than blue traps	3a) An MRBP was used to determine differences in communities between summer months 3b) An MRPP was used to determine differences in communities between burned and unburned sites 3c) An MRBP was used to determine differences in bee communities and trap colors
4) Determine if the bee community and abundance correlate with plant or flower communities or abundance	4) The bee community will correlate with both the plant and flower communities but more so with the flower community than the plant community	4) A Mantel test was used to test correlations between the bee community and both the plant and flower communities A Spearman's correlation was used to test correlation between bee abundance and plant and flower abundance

To quantify species diversity, Shannon's Diversity (H' ; Shannon 1949), Simpson's Diversity (D ; Simpson 1949), and Pielou's Evenness (E_H ; Pielou 1966) were calculated at the site level. Shannon's Diversity is defined as:

$$H' = \sum p_i \ln p_i$$

where H' is the Shannon Diversity index and p_i is the relative abundance of a species within an area. Simpson's Diversity is defined as

$$1 - D$$

where D is the Simpson 'dominance' index. Evenness is defined as:

$$E_H = \frac{H'}{\ln S}$$

where E_H is the Pielou species evenness index, H' is the Shannon's Diversity index, and S is total species richness in an area. Shannon's Diversity was chosen to determine the diversity of all species found within the study area whereas Simpson's Diversity was chosen as an additional diversity measure to determine the diversity of common species with insensitivity to species richness (Smith and Wilson 1996) within the study area. Shannon Diversity index, Simpson Diversity index, and Pielou's Evenness were tested by the Lilliefors (Kolmogorov-Smirnov) Test for Normality (Dallal and Wilkinson 1986) and found to be normally distributed. An analysis of variance (ANOVA) was used to determine differences in both diversity indices and evenness of bees, plants, and flowers among summer months and a student's t-test was used to evaluate diversity differences between burned and unburned sites within each summer month. A paired student's t-test was used to determine differences in bee diversity between trap colors and within burn category, burned and unburned, by month (Table 3.1, R Core Team 2013).

To analyze differences in bee, plant, and flower community compositions among months, a non-parametric blocked multi-response permutation procedure (MRBP) blocked by month with Euclidean distance measure (PC-ORD v.7; McCune and Mefford 2016) was used. An MRBP provides the chance-corrected within-group agreement (A), which is the likelihood of homogeneity within groups that occurs by chance. If $A=1$, all variables are homogenous within groups, whereas if $A < 0$, there is more heterogeneity within groups than expected by

chance. If $A = 0$, then heterogeneity within groups equals what was expected by chance (McCune and Grace 2002). A multi-response permutation procedure (MRPP) was used to determine differences between burned and unburned sites within each month. To analyze bee community composition between trap colors while maintaining pairs, an MRBP was used again, this time blocked by trap color, within each month and within burned and unburned sites within each month (Table 3.1).

To determine whether bee abundance correlated with either plant abundance or flower abundance, a Spearman's rank-order correlation was used for total summer abundance and for abundance measured within each month (Table 3.1). For a more in-depth correlation analyses, a Mantel test was used to examine correlations between the bee community (i.e. bee diversity and abundance for each species) and both the plant and flower community for total summer months and each month (R Core Team 2013). The Mantel test is a multivariate statistical analysis method designed to test for correlation between two matrices (Mantel 1967; PC-ORD v.7; McCune and Mefford 2016).

For exploratory analyses, a permutation ANOVA (perMANOVA) was used to test significant interactions of temperature ($^{\circ}\text{C}$) and humidity (%) between summer months and unburned and high severity burned sites (PC-ORD v.7; McCune and Mefford 2016). Linear regression models were used to predict average monthly temperatures ($^{\circ}\text{C}$) and average monthly humidity (%) were fit as a function of tree canopy cover (%) measured in June 2017. To determine indicator species among bee, plant, and flower communities for each summer month (i.e. which species indicate certain environmental conditions seen in June, July, and August) and burned and unburned sites (i.e. which species are indicative to burned sites vs unburned sites) were present, an Indicator Species Analysis (ISA) was conducted on bee, plant, and flower species among summer months, burned and unburned sites within each month. An ISA was also conducted on for bee species between trap colors within each month and each burn category within each month to determine if there were bee species indicative to trap color. An ISA calculates the degree to which a species indicates a group based on the species constancy and distribution of abundance. The Dufrêne and Legendre (1997) method of indicator values was chosen because of its ability to analyze quantitative (opposed to binary) data. The significance of indicator values obtained from Dufrêne and Legendre (1997)

was evaluated by randomly reassigning sample units to groups and repeated through 4999 Monte Carlo permutations (PC-ORD v.7; McCune and Mefford 2016).

Results

Abundance and richness

There were no differences in bee abundance between summer months but there were significant differences in both plant and flower abundance (both Kruskal-Wallis chi-squared ≥ 9.95 , both $P \leq 0.001$, Figure 3.4), with August having lower plant and flower abundance than June and July (all Z-statistics ≥ 2.46 , all $P \leq 0.014$). Bee, plant, and flower richness all differed between summer months (all Kruskal-Wallis chi-squared ≥ 8.96 , all $P \leq 0.011$), with August having lower bee (bee: 4.0 ± 0.7), plant (plant: 3.57 ± 0.61 [mean \pm SE]), and flower richness (flower: 6.92 ± 0.89) than both June (bee: 7.64 ± 1.04 ; plant: 8.5 ± 0.84 ; flower: 12.5 ± 0.84) and July (all Z-statistics ≥ 2.46 , all $P \leq 0.014$; bee: 7.29 ± 0.81 ; plant: 7.07 ± 0.79 ; flower: 11.07 ± 0.79). Bee and plant abundance did not differ significantly between unburned/burned sites in June or July but were significantly higher in burned sites than unburned sites in August (both Kruskal-Wallis chi-squared ≥ 6.36 , both $P \leq 0.004$). Flower density was significantly higher in burned sites than unburned sites in both July and August (both Kruskal-Wallis chi-squared ≥ 6.21 , both $P \leq 0.013$). Bee abundance was significantly higher in yellow traps than blue traps in July ($w = 14.5$, $P < 0.001$, yellow traps: 16.7 ± 3.29 , blue traps: 4.15 ± 1.01) and August ($w = 35.5$, $P = 0.004$, yellow traps: 10.1 ± 2.61 , blue traps: 1.6 ± 0.59). Yellow traps also had higher bee abundance in both unburned and burned sites during both July and August (all $w \geq 2$, all $P \leq 0.040$, Figure 3.5, Table 3.2). Plant and flower richness, like abundance, did not differ between unburned/burned sites in June, but were higher in burned sites than unburned sites in July (plants in burned sites: 8.71 ± 0.97 and unburned sites: 5.43 ± 0.97 ; flowers in burned sites 13.0 ± 0.98 , flowers in unburned sites 9.14 ± 0.7) and August (all Kruskal-Wallis chi-squared ≥ 4.50 , all $P \leq 0.034$, plants in burned sites 5.0 ± 0.87 , and unburned sites: 2.14 ± 0.4 ; flowers in burned sites 7.86 ± 1.03 , and unburned sites 5.83 ± 1.47). Bee richness was higher in yellow traps (6.23 ± 0.78) than blue traps (3.69 ± 0.51) in July ($w = 39.5$, $P = 0.021$). Yellow traps (7.33 ± 0.71) also had higher bee richness than blue traps (4.5 ± 0.67) in burned sites sampled in July ($w = 4$, $P = 0.029$).

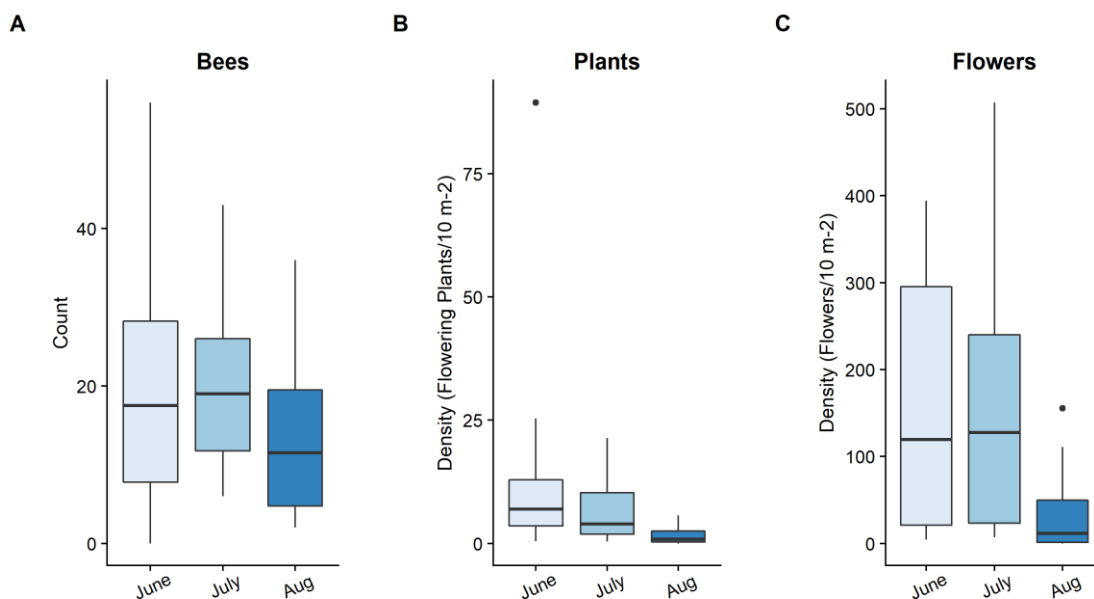


Figure 3.4. Abundance of bees (A), plants (B), and flowers (C) during June, July and August. Lower and upper hinge are the 25th and 75th percentile, respectively. Middle hinge is the median. Lower whisker is the smallest observation \geq to lower hinge $- 1.5 \times$ (upper hinge $-$ lower hinge) and the upper whisker is the largest observation \leq to upper hinge $+ ($ upper hinge $-$ lower hinge). Letters above upper whisker indicate significance of Dunn's pairwise comparisons. Note, plant and flower abundance are shown for 10 m² instead of hectares to simplify visualization.

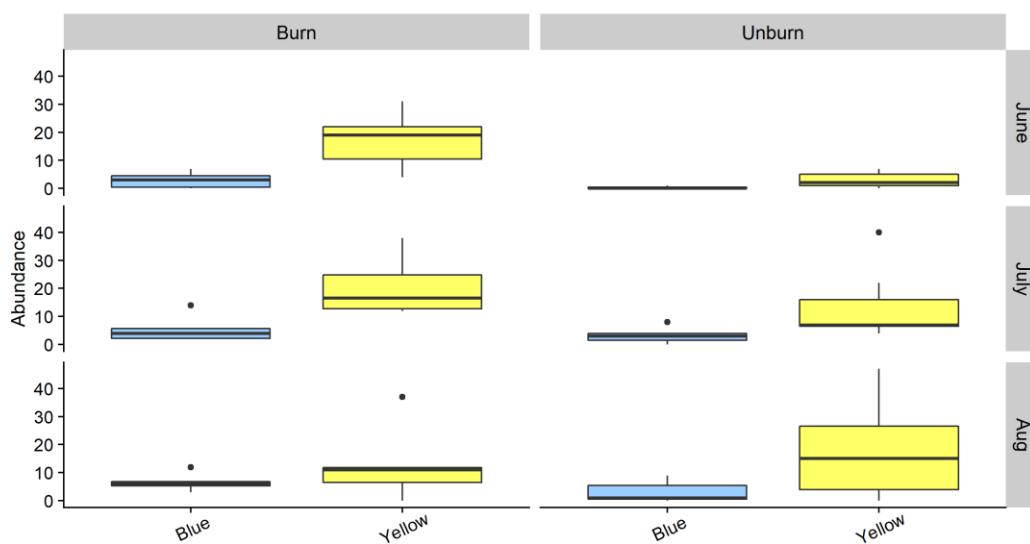


Figure 3.5. Abundance of bees in blue or yellow traps by month (June, July, and August) in unburned (0) and burned (4) sites. Lower and upper hinge are the 25th and 75th percentile, respectively. Middle hinge is the median. Lower whisker is the smallest observation \geq to lower hinge $- 1.5 \times$ (upper hinge $-$ lower hinge) and the upper whisker is the largest observation \leq to upper hinge $+ ($ upper hinge $-$ lower hinge). Letters above upper whisker indicate significance of pairwise Wilcoxon tests.

Table 3.2. Mean and standard error (SE) bee abundance and richness in blue and yellow traps by month (June, July, and August) in unburned and burned sites and the paired Wilcoxon Rank Sum and Signed Rank test w-statistic and P-value. Boldface denotes significance at the 95 % confidence interval.

Month	Sites	Blue Traps		Yellow Traps		Abundance		Richness	
		Mean Abundance (SE)	Mean Richness (SE)	Mean Abundance (SE)	Mean Richness (SE)	w	P	w	P
June	Unburned	3.14 (1.53)	2.86 (1.03)	17.57 (6.51)	5.29 (1.61)	10.5	0.080	15.5	0.270
	Burned	6.5 (1.23)	4.83 (0.31)	12.67 (5.22)	6.17 (1.64)	13	0.468	11.5	0.329
July	Unburned	3.14 (0.99)	3 (0.69)	13.71 (4.92)	5.29 (1.25)	5	0.015	14.5	0.218
	Burned	5.33 (1.86)	4.5 (0.67)	20.33 (4.2)	7.33 (0.71)	2	0.013	4	0.029
Aug	Unburned	0.29 (0.18)	0.57 (0.37)	3 (1.05)	1.57 (0.43)	6	0.040	13	0.116
	Burned	2.86 (1.01)	2.43 (0.75)	17 (3.47)	4.57 (0.75)	2.5	0.006	10.5	0.080

Diversity

Both Shannon's and Simpson's diversity indices of plants, flowers, and bees differed among months (all $F \geq 5.2$, all $P \leq 0.010$), but plants, flowers, and bee evenness did not differ between months. August had lower Shannon's diversity indices for plants, flowers and bees than June and July (all $P \leq 0.012$, Table 3.3). Shannon's diversity index for flowers was also lower in July than June ($P = 0.15$, Table 3.3). Simpson's diversity index for plants, flowers, and bees were also lower in August than in June (all $P \leq 0.007$, Table 3.3) and July for bees ($P < 0.001$, Table 3.3). Diversity did not differ between burned and unburned sites except for Shannon's diversity index for plants in August which was higher in burned sites (1.17 ± 0.2) than unburned sites (0.86 ± 0.15 ; $t = -2.4$, $P = 0.035$) and Shannon's diversity index for bees in June which was also higher in in burned sites (1.78 ± 0.1) than unburned sites (0.95 ± 0.23 ; $t = -23.3$, $P = 0.010$). Evenness did not differ among summer months or between burned and unburned sites except for flower evenness in July, which was higher in unburned sites (0.39 ± 0.06) than burned sites (0.26 ± 0.06 ; $t = 2.3$, $P = 0.04$) and for bees in June which were higher in burned sites (0.74 ± 0.02) than in unburned sites (0.43 ± 0.09 ; $t = -2.5$, $P = 0.043$). Bee diversity did not differ between trap colors for each month except for Simpson's diversity index in August, which was higher in yellow traps than blue traps (paired t-test, $P = 0.018$). Bee diversity did not differ between trap colors within burned or unburned sites either except for Simpson's diversity index, which was higher in blue traps than yellow traps in burned sites sampled in August (paired t-test, $P = 0.004$).

Table 3.3. Mean and standard error (SE) of Shannon's diversity index, Simpson's diversity Index and Pielou's evenness measure for flowering plants (plants), flowers, and bees found in June, July, and August.

		Shannon's Index	Simpson's Index	Pielou's Evenness
	Month	Mean (SE)	Mean (SE)	Mean (SE)
Plant	June	1.32(0.08)	0.63(0.03)	0.69(0.04)
	July	1.02(0.13)	0.49(0.05)	0.61(0.05)
	Aug	0.53(0.13)	0.37(0.08)	0.48(0.1)
Flower	June	1.09(0.1)	0.56(0.04)	0.47(0.03)
	July	0.7(0.11)	0.36(0.06)	0.32(0.05)
	Aug	0.32(0.08)	0.25(0.07)	0.17(0.04)
Bee	June	1.36(0.17)	0.69(0.05)	0.58(0.06)
	July	1.28(0.13)	0.6(0.05)	0.57(0.05)
	Aug	0.49(0.15)	0.24(0.07)	0.24(0.07)

Community Composition

All communities differed significantly among summer months (see Table 3.4 for results). Bee community composition did not differ between June and July but did differ between June and August and July and August. Both plant and flower communities differed among all months. Bee communities in burned sites were significantly different than in unburned sites in June (MRPP, $P < 0.001$, $A = 0.167$) and August (MRPP, $P = 0.002$, $A = 0.354$),) whereas plant communities differed between burned and unburned sites in July (MRPP, $P = 0.019$, $A = 0.132$) and August (MRPP, $P = 0.002$, $A = 0.272$). Flower communities also differed between burned and unburned sites, although only in August (MRPP, $P = 0.007$, $A = 0.176$). Bee communities were significantly different between trap colors within all summer months (all $P \leq 0.010$, all $A \geq 0.11$) and within burned and unburned sites (all $P \leq 0.029$, all $A \geq 0.19$) except burned sites in June.

Table 3.4. Blocked multi-response permutation procedure (MRBP) results between bee, plant, and flower communities and summer months (June, July, and August). Boldface denotes significance at the 95% confidence interval.

	Bees, A=0.167, P< 0.001		Plants, A=0.103, P< 0.001		Flowers, A=0.098, P< 0.001	
	A	P	A	P	A	P
June vs July	0.011	0.250	0.088	0.000	0.081	0.003
June vs Aug	0.262	< 0.001	0.098	0.001	0.096	0.001
July vs Aug	0.309	< 0.001	0.055	0.021	0.057	0.019

Correlation among Bees and Plants/Flowers

The bee community (i.e. diversity and abundance for each species) were significantly, though weakly, correlated with both plant and flower communities over all summer months (Mantel, plants; $P = 0.002$, $r = 0.184$, flowers; $P=0.015$, $r = 0.102$). However, bee communities did not correlate with plant and flower communities within each month. Bee abundance was significantly and strongly correlated with both plant and flower abundance over all summer months (Spearman's Rank Correlation, plants; $P < 0.001$, $\rho = 0.527$, flowers; $P < 0.001$, $\rho = 0.577$) and August (Spearman's Rank Correlation, plants; $P = 0.003$, $\rho = 0.729$, flowers; $P = 0.009$, $\rho = 0.672$). In June, bee abundance was also significantly and strongly correlated with flower abundance (Spearman's Rank Correlation, $P = 0.025$, $\rho = 0.594$).

Indicator species analysis

Bee, plant, and flower communities had significant indicator species for each of the summer months (ISA, all $P \leq 0.002$). Bee, plant, and flower communities did not have indicator species for burned or unburned sites in June but, plant and flower communities had significant indicator species for burned sites in July (ISA, both $P = 0.007$), and all communities had significant indicator species for burned sites in August (ISA, all $P \leq 0.040$, Table 3.6). There were no indicator species for unburned sites in any of the summer months. The bee community had significant indicator species for yellow traps over the summer (ISA, $P < 0.001$, Table 3.7). Although there were no significant indicator species for trap colors in June,

both July and August had significant indicator species for yellow traps (ISA, both $P \leq 0.016$). There were no indicator species for blue traps for any of the summer months.

Table 3.5. Significant (at the 95% confidence interval) Indicator Species Analysis (ISA) of bees, plants, and flowers between summer months.

	Month	Species	Mean (SE)	P
Bee Species, P=0.002	June	<i>Anthophora ssp.</i>	24.7 (7)	0.003
	June	<i>Habropoda ssp.</i>	10.5 (5.2)	0.032
	June	<i>Lassioglossium ssp.</i>	14.7 (5.94)	0.033
	July	<i>Bombus centralis</i>	11.6 (5.69)	0.028
	July	<i>Bombus edwardsii</i>	15.6 (6.44)	0.021
	July	<i>Bombus huntii</i>	12.1 (5.78)	0.009
	July	<i>Osmia ssp.</i>	31.1 (6.08)	0.008
	July	<i>Stelis ssp.</i>	14.3 (5.86)	0.033
	Aug	<i>Melissodes ssp.</i>	33.1 (6.74)	0.001
Plant Density P<0.001	June	<i>Antennaria neglecta</i>	10.4 (5.02)	0.028
	June	<i>Arnica cordifolia</i>	15.9 (6.64)	0.035
	June	<i>Eriophyllum lanatum</i>	17.4 (6.5)	0.048
	June	<i>Lomatium triternatum</i>	15.6 (6.79)	0.002
	June	<i>Microseris nutans</i>	13.8 (6.22)	0.015
	June	<i>Phlox longifolia</i>	10.9 (5.7)	0.028
	June	<i>Purshia tridentata</i>	12.9 (5.78)	0.008
	June	<i>Ribes cereum</i>	14.2 (6.1)	<0.001
	June	<i>Senecio integerrimus</i>	23.8 (7.41)	<0.001
	July	<i>Antennaria neglecta</i>	34.8 (9.01)	0.004
	July	<i>Erigeron foliosus</i>	20.7 (6.95)	0.002
	July	<i>Antennaria neglecta</i>	10.4 (5.10)	0.025
Flower Density P<0.001	June	<i>Arnica cordifolia</i>	15.5 (6.41)	0.03
	June	<i>Lomatium triternatum</i>	15.7 (6.94)	0.001
	June	<i>Microseris nutans</i>	13.9 (6.3)	0.016
	June	<i>Phlox longifolia</i>	11 (5.79)	0.027
	June	<i>Purshia tridentata</i>	13.3 (6.16)	0.007
	June	<i>Ribes cereum</i>	15 (6.58)	0.001
	June	<i>Senecio integerrimus</i>	24.3 (7.69)	<0.001
	July	<i>Achillea millefolium</i>	36.4 (9.8)	0.001
	July	<i>Erigeron foliosus</i>	22.1 (7.75)	0.002

Table 3.6. Significant Indicator Species Analysis (ISA) of bee, plant, and flower communities between burned and unburned sites within each summer month.

	Month	Species	Burn/Unburned	Mean (SE)	P
Bee Species	Aug, P= 0.007	<i>Melissodes</i>	Burned	54 (8.49)	0.002
Plant Species	July, P=0.007	<i>Achillea millefolium</i>	Burned	65 (13.84)	0.020
		<i>Erigeron foliosus</i>	Burned	44.9 (12.93)	0.013
Flower Species	Aug, P=0.040	<i>Achillea millefolium</i>	Burned	57.2 (10.95)	0.001
	July, P=0.007	<i>Achillea millefolium</i>	Burned	64.4 (13.43)	0.018
		<i>Erigeron foliosus</i>	Burned	44.6 (13)	0.013
	Aug, P=0.032	<i>Achillea millefolium</i>	Burned	58 (11.22)	0.001

Table 3.7. Significant Indicator Species Analysis (ISA) of bee communities between blue and yellow (Y) trap colors within each summer month.

	Species	Trap Color	Mean (SE)	P
Summer months	<i>Halictidae</i>	Y	9.2(2.94)	0.022
	<i>Megachile ssp</i>	Y	9.1(2.81)	0.003
	<i>Melissodes ssp</i>	Y	26.5(4.79)	0.000
	<i>Osmia ssp</i>	Y	31.8(4.92)	0.002
June	<i>Lassioglossum ssp</i>	Y	17.9(6.64)	0.038
	<i>Osmia ssp.</i>	Y	46.6(9.68)	0.006
July	<i>Megachile ssp</i>	Y	17.9(6.4)	0.040
	<i>Melissodes ssp</i>	Y	17.9(7.12)	0.037
	<i>Osmia ssp</i>	Y	53.2(7.03)	0.000
Aug	<i>Melissodes ssp</i>	Y	42.3(8.24)	0.002

Additional Environmental Variables

All monthly average temperatures (°C) differed significantly among summer months but did not differ between burned or unburned sites or the interactions between summer months and burned/unburned sites except for monthly average minimum temperature, which did differ among burn severity sites (Table 3.8, Figure 3.6). Specifically, the average minimum temperature in June was higher in unburned sites than burned sites (PerMANOVA P=0.0198, Figure 3.6A). Similarly, monthly average humidity differed significantly among summer months but did not differ between burned or unburned sites or among the interactions

between summer months and burned/unburned sites except monthly average minimum humidity which had a significant interaction between months and burned/unburned sites (Table 3.8, Figure 3.6). Monthly average minimum humidity in July was significantly higher in high burn severity sites than control sites (PerMANOVA $P=0.003$, Figure 3.6B) but did not differ between burn severity sites in June or August.

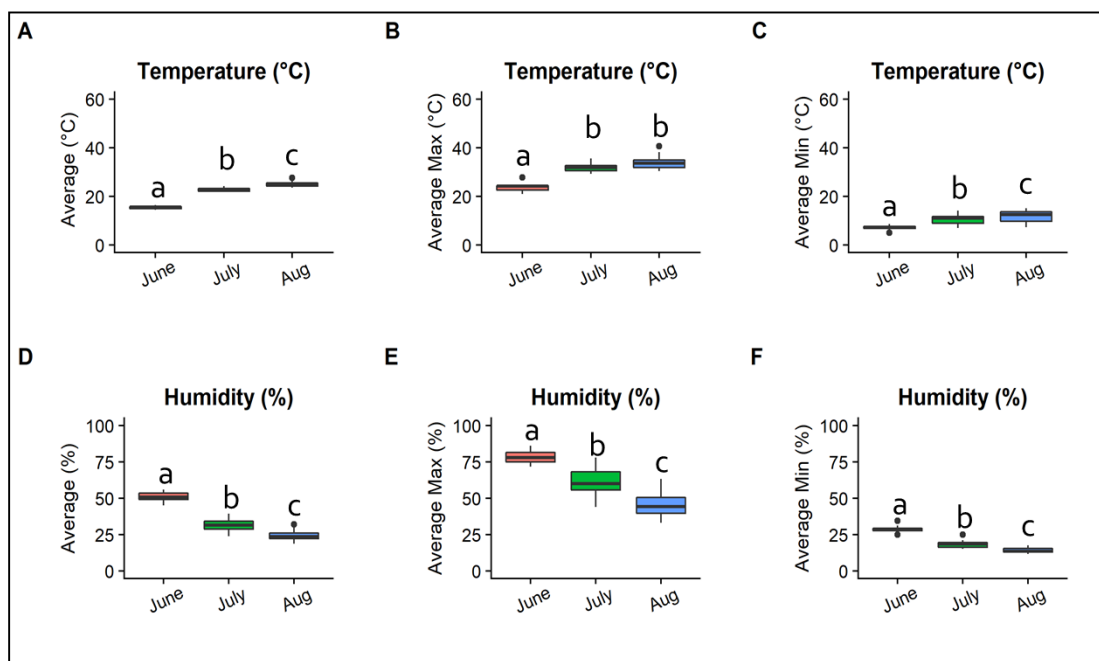


Figure 3.6. Average monthly temperature (A), average monthly max temperature (B), average monthly min temperature (C), average monthly humidity (D), average monthly max humidity (E), average monthly min humidity (F) for 2017 summer months June, July, August. Letters denote significance of Tukey multiple comparisons test between months.

Table 3.8. Permutation ANOVA results showing average monthly temperature and humidity interactions between summer months and burn severity (high severity or unburned sites).

Boldface denotes significance at the 95% confidence level.

	Month P	Severity P	Month: Severity P
Average Temperature (°C)	< 0.001	0.169	0.760
Average Max Temperature (°C)	< 0.001	0.101	0.425
Average Min Temperature (°C)	< 0.001	0.017	0.927
Average Humidity (%)	< 0.001	0.115	0.431
Average Max Humidity (%)	< 0.001	0.072	0.499
Average Min Humidity (%)	< 0.001	0.051	0.030

Linear regression models between monthly average temperatures of summer months and tree canopy cover revealed a significant relationship between canopy cover and June average temperature, but not for July and August (Figure 3.7). Linear regression models between average humidity of summer months and tree canopy had no significant results.

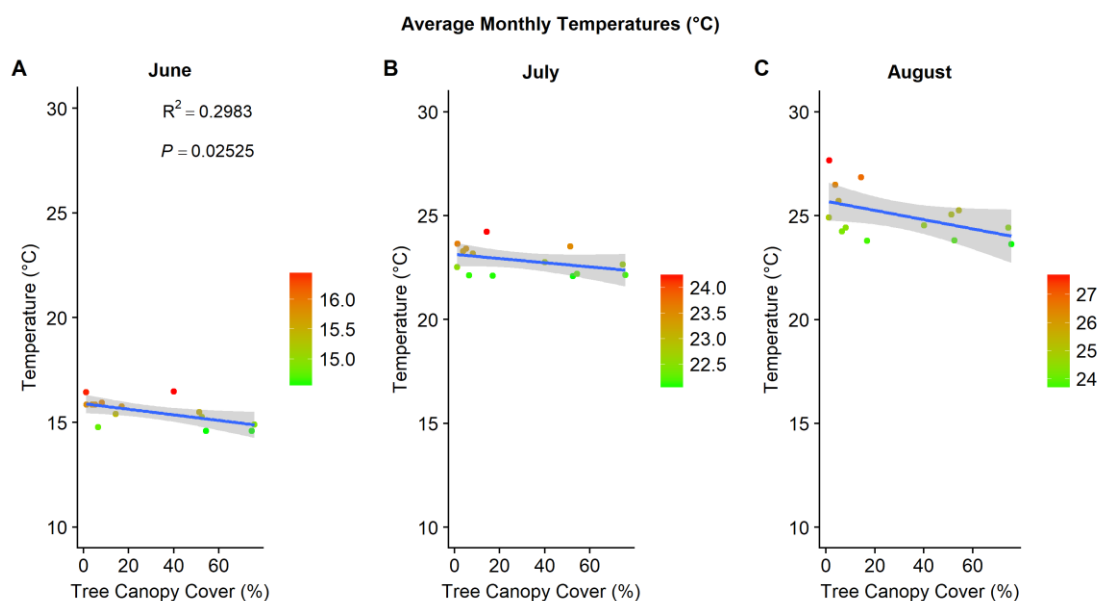


Figure 3.7. Linear regression models predicting percent tree canopy cover as a function of monthly average temperature (°C) for June (A), July (B), and August (C).

Discussion

Seasonality did not affect bee abundance but did affect bee richness and diversity, which decreased as the summer progressed. This indicates that there were fewer bee species present in August compared to June and July but were caught at high abundances. *Melissodes* (n =124 for August out of 163 total), being the only indicator bee species for August, suggests this as well. The strong -within-group agreement among bee communities sampled in August compared to June and July bee communities implies that there was more species overlap in June and July but not between June/July and August. This could be explained by lower bee diversity later in the summer. It is also possible that the bees caught are a poor representation of bees in the area at that time. Cane *et al.* (2000), in creosote bush ecosystems in northwest Arizona, found that pan traps poorly represented bee abundance and diversity in their study area compared to net sampling. Cane *et al.* (2000) suggests that pan traps are less attractive to foraging bees than flowers in the area and are therefore inversely proportional to the available flowers in bloom. It is possible that Japanese beetle traps are less attractive to foraging bees than flowers in the area as well.

Seasonality did affect plant and flower abundance, richness, and diversity, which also tended to decrease as the summer progressed, with August having the lowest plant and flower abundance, richness, and diversity. The higher temperatures seen in August compared to June and July might explain the lower plant, flower, and consequentially bee, abundance, richness, and diversity. Temperatures markedly increased from June to August whereas humidity decreased. It is possible that the higher temperatures and lower humidity later in the summer caused some flowering plant species to senesce. The lack of plant and flower indicator species in August is also indicative of early senescence (McCloud and Berenbaum 2000; Yoshie 2008).

Bee, plant, and flower abundance and richness all tended to be higher in burned sites than unburned sites, though only later in the summer. It could be that the rise in temperatures as the summer progressed caused shade-tolerant flowering species, more commonly found in unburned sites, to senesce earlier than shade-intolerant flowering species, more commonly found in burned sites. Most of the flowering plant and flower species analyzed in the ISA were indicative to June, meaning they were found at significantly higher abundances in June

compared to July and August. On the other hand, common yarrow (*Achillea millefolium* L.) and leafy fleabane (*Erigeron foliosus* Nutt.) were two flowering species that were indicative to burned sites later in the summer. Common yarrow is a shade-intolerant species (David and Raymond 1939) with late flowering phenology (U.S. Department of Agriculture, Forest Service 1937) so it is not surprising that it was found at higher abundance in burned sites that tended to have less tree canopy cover and higher temperatures. Romme *et al.* (2016) found that climate and substrate were the strongest drivers for understory plant community composition eleven years post-fire in a lodgepole pine (*Pinus contorta* Douglas ex. Loudon) forest. However, 25-years post-fire, re-growth of tree canopy was a significant driver for understory plant composition, leading to a decrease of annual plants and shade-intolerant forbs (Romme *et al.* 2016).

Similarly, Galbraith *et al.* (2019), found that fire severity was a strong predictor of bee and plant abundance in a mixed conifer forest of western Oregon. In addition to higher abundance of flowers to forage in severely burned areas ten years after fire, it is possible that the increase in coarse woody debris and more exposed soil found in high severity burned sites (Chapter 2) provided more nesting cavities for bees (E. Gorton Linsley 1958). The majority of bee genera caught in this study were ground nesters, though a few genera have species that nest in twigs and woody debris (E. Gorton Linsley 1958; Cane 1991, Appendix B), and thus would probably greatly benefit from additional debris and exposed soil along with higher flower abundance caused by high severity fire.

Diversity, on the other hand, did not tend to differ between burned and unburned sites, except Shannon's diversity for bees in June and plants in August which were both higher in burned than unburned sites. Shannon's diversity index tends to be more sensitive to rare species, or species measured at lower abundance than Simpson's diversity index (Peet 1974). The lack of significance in plant evenness measures, which accounts for richness, between burned and unburned sites is also an indication that Shannon's diversity is more sensitive to rare species. Though I hypothesized burned sites to have higher bee, plant, and flower diversity, it is not that surprising to see no differences in diversity between burned and unburned sites. This study was conducted ten years post-fire, which likely gave plant species

time to either re-sprout post-fire or colonize burned areas (Bond and Midgley 2001; Pausas and Keeley 2014).

Both plant and flower communities differed significantly between each month sampled, however the within group agreement was weak, suggesting flowering plant species were present in at least two of the months sampled, although in different abundance. It was surprising to see differences in bee communities between burned and unburned sites in June with a strong within group agreement, even though there were no differences in abundance or richness found. Because the MRPP analysis incorporates both diversity and abundance, it is possible that diversity explains most of the differences seen between burned and unburned sites, demonstrated by the higher Shannon's diversity and evenness measures for bees captured in burned sites compared to unburned sites in June.

Bee communities differed between yellow and blue traps, especially in burned sites, with yellow traps having higher bee abundance than blue traps, especially in burned sites. Diversity, however, did not differ between trap colors, except Simpson's diversity in August which was higher in yellow traps than blue. Simpson's diversity is more weighted by abundance, which might explain why it was significant and Shannon's diversity did not differ between traps (Peet 1974). Other studies have reported that different trap colors attract different species of bees, especially *Bombus* spp (Cane *et al.* 2000; Cook *et al.* 2011) and sometimes (Cane *et al.* 2000; Cook *et al.* 2011) different sexes (Leong and Thorp 1999). Therefore, even though there were no indicator species for blue traps in this study and more bees were caught in yellow traps, it may still be important to have both colors for abundance and diversity studies.

Though the relationships between bee abundance and both plant and flower abundance were strong, the relationships between the bee community and both the plant and flower community were weak. The weaker relationships between the communities as opposed to the abundance, might be explained by the robustness of the Mantel test. The Mantel correlated each bee species and their abundance to each plant and flower species and their abundance. Therefore, the significant though weak correlation means that the bee community is correlated to both the plant and flower community, though there were few, if any, specialized species present; most bee species were general pollinators. Therefore, if managers were interested in

increasing pollinators in the area, there are multiple flowering plant species options to seed and manage.

Conclusion

Though there is an abundance of studies on fire effects on plants, there are limited studies on fire effects on pollinators. This study on long-term fire effects on flowering plants and pollinators demonstrates how bee and plant communities vary over the summer and documents the importance of fire in increasing diversity and abundance within a dry ponderosa pine ecosystem. Given that little information is available on this topic, my study has led to more questions than answers, specifically questions related to short-term fire effects and the effects of low and moderate severity on flowering plants and pollinators. Further research on this topic could improve post-fire recovery efforts and potentially improve the use of native bees on agriculture pollination.

CHAPTER 4: Management Implications

Pre-fire fuel treatments effectively lowered the occurrence of high severity wildfire, likely due to successful reduction of pre-fire tree and sapling density and surface fuels, which supports the implementation of fuel-reduction treatments in dry ponderosa pine forests to reduce high severity wildfire effects. This study also demonstrates the changes in vegetation and fuels from one-year post-fire to nine years post-fire. Further, we suggest that low severity wildfire can meet prescribed fire management objectives of lowering surface fuel accumulations while not increasing overstory tree mortality.

This research provides new information about communities of bees and flowers in burned and unburned dry ponderosa pine forest. Seasonality affected bee, flowering plant, and flower richness and diversity, all of which decreased as the summer progressed. Severely burned sites had higher bee, flowering plant, and flower abundance later in the summer than unburned sites, however there were no differences in diversity suggesting ten years post-fire was an adequate time for bee and plant species to re-colonize burned areas. Furthermore, Japanese beetle traps were found to be a successful alternative to pan traps for collecting bees. Bee abundance was strongly correlated with both plant and flower abundance, though more so with flower abundance.

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APPENDIX A Flowering plant species found in Malheur National Forest. Codes are from the United States Department of Agriculture (USDA) plants data base (USDA, NRCS. 2019)

Month Captured	Functional Group	USDA Code	Species	Common Name		
June	Forb	AGRE	<i>Agoseris retrorsa</i>	Spearleaf agoseris		
		AGOSE2	<i>Agoserous species</i>	Agoserous		
		ANNE	<i>Antennaria neglecta</i>	Field pussytoes		
		ARCA7	<i>Arenaria capillaris</i>	Slender Mountain Sandwort		
		ASFI	<i>Astragalus filipes</i>	basalt mildvetch		
		BASA3	<i>Balsamorhiza sagittata</i>	Arrowleaf balsamroot		
		BASE2	<i>Balsamorhiza serrata</i>	Serrate balsamroot		
		ERBL	<i>Erigeron bloomeri</i>	scabland fleabane		
		FRVI	<i>Fragaria virginiana</i>	Virginia strawberry		
		LERE7	<i>Lewisia rediviva</i>	Bitter root		
		LIPA5	<i>Lithophragma parviflorum</i>	smallflower woodland-star		
		LOTR	<i>Lomatium sp</i>	Biscuitroot		
		LOTR2	<i>Lomatium triternatum</i>	Nineleaf biscuitroot		
		LUSE	<i>Lupinus silverback</i>	creeping silverback		
		MINU	<i>Microseris nutans</i>	Nodding microseris		
		PENST	<i>Penstemon sp.</i>	Penstemon		
		PHHO	<i>Phlox hoodii</i>	Spiny Phlox		
		PHLO	<i>Phlox longifolia</i>	Longleaf Phlox		
		SENEC	<i>Senecio sp.</i>	Groundsel		
		TAOF	<i>Taraxacum officinale</i>	Common dandelion		
		ZIVE	<i>Zigadenus venenosus</i>	Meadow deathcamas		
		June - July	Shrub	PREM	<i>Prunus emarginata</i>	bitter cherry
				PRVI	<i>Prunus virginiana</i>	Chokecherry
				RICE	<i>Ribes cereum</i>	Wax currant
		June - July	Forb	ANPA4	<i>Antenaria parvifolia</i>	small-leaf pussytoes
				ANRO2	<i>Antenaria rosea</i>	rosy pussytoes
				ARCO9	<i>Arnica cordifolia</i>	Heartleaf arnica
				CASTI2	<i>Castilleja sp</i>	Indian paintbrush
				CRAT	<i>Crepis atribarba</i>	Slender hawkbeard
				ERPU2	<i>Erigeron pumilus</i>	shaggy fleabane
				GEVI2	<i>Geranium viscosissimum</i>	Sticky purple geranium
				MARE11	<i>Mahonia repens</i>	creeping Oregon-grape
				POGL9	<i>Potentilla gradulosa</i>	Sticky cinquefoil
SEIN2	<i>Senecio integerrimus</i>			Lambstongue ragwort		

	Shrub	CEVE	<i>Ceanothus velutinus</i>	Snowbrush ceanothus
		PUTR2	<i>Purshia tridentata</i>	Antelope bitterbrush
June - August	Forb	PEDE4	<i>Penstemon deustus</i>	scabland penstemon
June-Aug	Forb	ACMI2	<i>Achillea millefolium</i>	Common yarrow
July	Forb	ALLIU	<i>Allium sp.</i>	Onion
		APCA	<i>Apocynum cannabinum</i>	Indian hemp
		ARSO2	<i>Arnica soria</i>	twin arnica
		COGR4	<i>Collimia grandiflora</i>	giant blue-eyed Mary
		CRAC2	<i>Crepis acuminata</i>	Tapertip hawksbeard
		DENU2	<i>Delphinium nuttallianum</i>	Twolobe larkspur
		ERFO2	<i>Erigeron foliosus</i>	leafy fleabane
		ERTE6	<i>Erigeron tener</i>	slender fleabane
		ERIOG	<i>Eriogonum sp.</i>	Buckwheat
		PEHU	<i>Penstemon humilis</i>	low beardtongue
		PESE12	<i>Penstemon seorsus</i>	shortlobe penstemon
		PHHE2	<i>Phacelia heterophylla</i>	varileaf phacelia
		SESE2	<i>Senecio serra</i>	senecio serra
		UCAR	<i>Unknown caryophyllaceae</i>	
		ULYC	<i>Unknown Litter</i>	Yellow
July - August	Forb	ERHE2	<i>Eriogonum heracloides</i>	parsnipflower buckwheat
		ERLA6	<i>Eriophyllum lanatum</i>	common wooly sunflower
		FRAL2	<i>Frasera albicaulis</i>	whitestem frasera
	Invasive	VETH	<i>Verbascum thapsus</i>	Common mullein
August	Forb	CHAN9	<i>Chamerion angustifolium</i>	Fireweed
		CIUN	<i>Cirsium undulatum</i>	Wavyleaf thistle
		ERFI2	<i>Erigeron filifolius</i>	Flett's fleabane
		EREL5	<i>Eriogonum elatum</i>	tall wooly buckwheat
		HISC2	<i>Hieracium scouleri</i>	Scouler's woollyweed
		SOLID	<i>Solidago sp.</i>	Goldenrod
		UNKAR	<i>Unknown Arnica</i>	

Flowering plant species found in the Malheur National Forest and when they were flowering. Codes are from the United States Department of Agriculture (USDA) plants data base (USDA, NRCS. 2019).

APPENDIX B Bee species captured in the Malheur National Forest.

Month Captured	Family	Species	Nesting Style
June	<i>Anthophoridae</i>	<i>Habropoda ssp</i>	Ground ^{vi}
	<i>Apidae</i>	<i>Bombus bifarius nearcticus</i>	Ground/burrow ^{vii}
		<i>Bombus morrisoni</i>	Ground/burrow ^{vii}
		<i>Bombus occidentalis</i>	Ground/burrow ^{vii}
		<i>Bombus vosnesenskii</i>	Ground/burrow ^{vii}
	<i>Megachilidae</i>	<i>Anthidum ssp.</i>	Ground/above-ground/wood ^{vii}
		<i>Dianthidium ssp.</i>	Ground/above-ground/wood ^{vii}
June - July	<i>Apidae</i>	<i>Bombus rufocinctus</i>	Ground/burrow ^{vii}
	<i>Megachilidae</i>	<i>Ashmeadiella ssp.</i>	Ground/nest cavities/wood ^{vii}
		<i>Heriades ssp.</i>	Ground/nest cavities/wood ^{vii}
		<i>Hoplitis ssp.</i>	Cavity ^{vi}
		<i>Stelis ssp.</i>	Ground/nest cavities/wood ^{vii}
June - Aug	<i>Anthophoridae</i>	<i>Epeolus ssp.</i>	
June - Aug	<i>Andrenidae</i>		Ground/burrow ^{vii}
		<i>Anthophoridae</i>	
		<i>Anthophora ssp.</i>	Ground ^{vi}
		<i>Melissodes ssp.</i>	Ground ^{ii, vi}
	<i>Apidae</i>	<i>Bombus edwardsii</i>	Ground/burrow ^{vii}
	<i>Halictidae</i>		
		<i>Agapostemon ssp.</i>	Ground ⁱⁱ
		<i>Halictus ssp.</i>	Ground ^{iv}
		<i>Lassioglossum ssp.</i>	Ground ^{iv, vi}
		<i>Megachilidae</i>	<i>Megachilie ssp.</i>
		<i>Osmia ssp.</i>	Wood/stems ^v , above ground ⁱ
July	<i>Apidae</i>	<i>Bombus ssp.</i>	Ground/burrow ^{vii}
		<i>Bombus appositus</i>	Ground/burrow ^{vii}
		<i>Bombus centralis</i>	Ground/burrow ^{vii}
		<i>Bombus crotchii</i>	Ground/burrow ^{vii}
		<i>Bombus huntii</i>	Ground/burrow ^{vii}
July – August	<i>Apidae</i>	<i>Bombus californicus consanguineus</i>	Ground/burrow ^{vii}
		<i>Bombus fervidus</i>	Ground/burrow ^{vii}

The table shows the bee species captured in the Malheur National Forest, which month bees were captured in the summer of 2017, and their nesting style.

ⁱ(Cane *et al.* 2007)

ii (Charles D. Michener 2007) – Tribe level nesting information

iii (Kim *et al.* 2006)

iv (Packer 1991)

v (Praz *et al.* 2008)^x Praz *et al.* 2008

vi (Roulston and Cane 2000)

vii (Triplehorn and Johnson 2005)^{*} Family level nesting information for *Megachilidae*, genus level nesting information for *Bombus* spp