

THESIS

FOREST TYPE AND BURN SEVERITY AFFECT UNDERSTORY RESPONSE TO
HISTORIC WILDFIRES

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Kate Weimer

Department of Forest and Rangeland Stewardship

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Master's Committee:

Advisor: Camille Stevens-Rumann

Monique Rocca
Troy Ocheltree

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ABSTRACT

FOREST TYPE AND BURN SEVERITY AFFECT UNDERSTORY RESPONSE TO HISTORIC WILDFIRES

The fire season of 2020 was unprecedented in the Western US. In one summer, three different fires individually broke the record of Colorado's largest wildfire. Understanding the recovery following these unprecedented events can lend insight into the compounding effects of wildfire and climate change. Reorganization of the understory community after disturbance can indicate changes in conditions not yet reflected in tree communities. Understory dynamics also affect watershed characteristics and wildlife, so knowledge about the influence of wildfire on understory plants is crucial. The purpose of this study is to determine if a trend toward thermophilization is being shown in understory vegetation following 4 different wildfires in 2020 and to compare the relative importance of burn severity, forest type, and other environmental factors on understory community composition. We found a trajectory toward thermophilization in high elevation forests that burned with high severity. We also found that drivers of community composition varied by forest type. These findings help assess how wildfire is affecting plant communities in the 21st Century and highlight where future management concerns may be.

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Colorado State University acknowledges, with respect, that the land we are on today is the traditional and ancestral homelands of the Arapaho, Cheyenne, and Ute Nations and peoples. This was also a site of trade, gathering, and healing for numerous other Native tribes. We recognize the Indigenous peoples as original stewards of this land and all the relatives within it. As these words of acknowledgment are spoken and heard, the ties Nations have to their traditional homelands are renewed and reaffirmed. CSU is founded as a land-grant institution, and we accept that our mission must encompass access to education and inclusion. And, significantly, that our founding came at a dire cost to Native Nations and peoples whose land this University was built upon. This acknowledgment is the education and inclusion we must practice in recognizing our institutional history, responsibility, and commitment.

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Introduction

Warmer temperatures, increasing drought, and extreme weather events have been observed and continue to be projected on a global scale (Intergovernmental Panel on Climate Change, 2022). At the same time, wildfires are increasing in size and frequency (Abatzoglou et al., 2021). In fire-prone forests, the combined effects of wildfire and climate change pose questions about forest longevity and the ability of the ecosystem to recover from disturbance. Forest understory vegetation dynamics influence watershed characteristics, tree regeneration, and wildlife habitat (Balandier et al., 2022). Thus, an understanding of understory dynamics is essential for predicting and responding to the effects of future wildfires. In disturbed forest systems of the 21st Century, one common trend of understory community change is toward thermophilization.

Thermophilization is a process in which the relative abundance of warm-adapted taxa in a given area increases due to a warming climate, especially in combination with disturbances. Thermophilization has been described in numerous studies including tropical, temperate and boreal forests and mountain plant communities (eg. Bertrand et al., 2011; Fadrique et al., 2018; Gottfried et al., 2012; Lenoir et al., 2010; Savage & Vellend, 2015) as well as in other taxonomic groups such as butterflies, fishes and birds (Cheung et al., 2013; Devictor et al., 2012; Gaüzère et al., 2017). Many of these quantify thermophilization using the concept of biogeographic affinity. Biogeographic affinity describes the general climatic tolerances of taxa based on the climatic conditions of the time and place where they evolved or diversified. Because there is evidence of correspondence between biogeographic affinity and plant functional traits (Ackerly, 2003), a community with taxa of diverse biogeographic histories may have a greater range of ecological strategies available. For example in California, north-temperate derived lineages tend to have a

higher specific leaf area and to occupy colder ranges, while lineages with a more tropical history show a significantly higher seed size (Ackerly, 2003). Ackerly (2004) suggests biogeographic history as an important feature associated with trait evolution. Thermophilization along elevational gradients raises questions about the longevity of cold, high-elevation plant communities (Gottfried, 2012), while thermophilization in disturbed areas raises questions about biodiversity loss (Stevens et al, 2019). Raven and Axelrod (1978) describe the biogeographic affinity of California's plant taxa, where about half of modern flora come from lineages that diversified in northern, temperate, mesic regions. Most of the other half come from lineages that diversified in southern, fire-prone, xeric regions. This distinction sets the stage for studying the effects of climate on community composition.

As climatic conditions become warmer and drier, redistribution of species ranges has already begun and is expected to continue (Feeley et al., 2020). Areas that previously supported a given taxon may no longer be able to, while areas that were once unsuitable may become suitable for said taxon. The concept of "climatic debt" is used to describe the lag between changes in ambient temperature and changes in species composition (Bertrand et al., 2011, 2016, Richard et al., 2020). In other words, while climate drives change in species distributions, some taxa are unable to keep up with this pace of change. In forest communities, thermophilization is hastened by disturbance that opens the canopy, including wildfire, prescribed fire, and fuel reduction treatments (Stevens et al, 2015, 2019, Dietz et al., 2020, Richard et al., 2020, Zellweger et al., 2020). Disturbances like these decrease the climatic debt. The lag between climate change and plant community change can indicate a lag of extirpation of more cold-tolerant species if they do not advance to colder locations. An increased rate of thermophilization decreases the climatic debt, as it indicates plant communities are keeping pace with the rate of

change. Disturbance to the canopy hastens thermophilization. There is some evidence that the likewise is also true, and closure of the forest canopy can “buffer” the effects of warming, slowing the pace of thermophilization (De Frenne et al., 2013). However, the vegetation in an area which experienced an abrupt opening of the forest canopy can remain more thermophilic than a similar undisturbed area, even as shade and light conditions return to their previous state (Dietz et al., 2020).

Johnstone et al. (2016) propose the concept of “resilience debt,” which refers to misalignment of a disturbance with system’s adaptations to historical disturbance cycles. An increase in resilience debt could be caused by a change in disturbance regime, a change in the conditions required for recovery, or community changes that affect the adaptations, individuals, and materials (such as propagules) that shape a system’s response to disturbance. Johnstone et al. (2016) use the framework of “safe operating space” to describe acceptable levels of stressors or disturbances that allow an ecosystem to recover from disturbance. Resilience debt becomes apparent after a disturbance, when a system is pushed outside its safe operating space. Recovery to its past state is no longer possible, and a state transition occurs.

Microclimate is the main driver of thermophilization for understory vegetation (Zellweger et al., 2020). In mixed conifer forests of the Sierra Nevada, the microclimate variables affected by different combinations of thinning and burning include monthly mean air temperature, soil surface temperature, soil temperature at 15 cm depth, relative humidity, water vapor deficit of air, soil volumetric moisture at 15 cm depth, daily sum of photosynthetically active radiation, and wind speed (Ma et al, 2010). Ma et al (2010) suggest that microclimate variability is very high within a forest and driven primarily by elevation and canopy cover. This is consistent with the findings of Bertrand et al. (2011), who demonstrated differing rates of

thermophilization between lowland and mountainous vegetation communities in Europe, as well as De Frenne et al. (2013, 2019) who have demonstrated the thermal buffering capacity of forests globally. De Frenne et al. (2015) have also shown that warming alone may not result in a high rate of thermophilization, but the combination of warming temperature and increased light radiation will. The effects of herbivory on thermophilization are not well studied in North America, though Richard et al. (2021) demonstrate that large herbivores' effects on the shrub layer in French forests have little to no effect on microclimate or thermophilization, unlike changes to overstory canopy characteristics. Almost unanimously in the literature, microclimate is the primary driver of thermophilization, and microclimate is controlled by canopy cover. Where canopy is disturbed by fire, understory microclimate becomes hotter and drier due to increased solar radiation, and is also affected by the resultant change in albedo due to ash and char.

Historic disturbance regimes - and modern divergences from them - vary between the forest types included in this study. The differences in fire regime and life history of different forest types of the southern Rocky Mountains are necessary context for understanding post-disturbance changes with the framework of resilience debt. Ponderosa pine forests occur at the lowest elevation and are the most xeric of the forest types in which this study takes place. They have historically had a frequent but regionally variable fire regime, with a fire return interval on the order of 7-50 years (Brown et al., 2020). Because of fire suppression, these forests tend to be denser today than their historical norm. One would expect the resilience debt to be high in ponderosa forests. Their ahistorically dense canopy is misaligned with the current fire regime (Chambers et al., 2016), undermining resilience. Therefore, sudden disturbance to the canopy, such as by wildfire, might trigger a rapid thermophilic response from the understory community.

Lodgepole pine are higher in elevation than ponderosa and have historically had a fire return interval of 75-300 years (Brown et al., 2020). Fire suppression policies have not removed lodgepole pine from its historic fire regime to the degree that they have ponderosa pine. Finally, subalpine forests are the highest elevation and most mesic of the forest types we study. Historically they have had a long fire return interval of 100-600 years (Brown et al., 2020). Modern subalpine forests are not far outside their historic fire regime, if at all. Their understory community is likely to thermophilize following canopy disturbance, but their resilience debt is likely not as severe as in lower elevation forests.

The fire season of 2020 was unprecedented in the western US. In one summer, three different fires individually broke the record of Colorado's largest wildfire, previously held by the Hayman Fire of 2002. Understanding the recovery following these events can lend insight into the compounding effects of wildfire and climate change. Using four different 2020 wildfires across a gradient of forest type, burn severity, and canopy cover, we seek to answer three questions:

1. How do forest type, burn severity, and year affect the ratio of warm-xeric to cool mesic taxa in a burned forest?

H1: Within a given forest type, the proportion of warm-xeric to cool-mesic taxa will be greater in high severity burn areas than low severity burn areas. There are two reasons why this seems a likely outcome. First, high severity burn areas have a greater degree of canopy disturbance and the understory in these areas typically receives more solar radiation than in low severity burn areas. Second, high severity burn areas have experienced more consumption of the understory and soil seed bank, so we expect more local extinctions and more opportunity for entry of new species to these areas. Additionally, the difference in proportion of warm-xeric to cool-mesic taxa between burn severities will be greatest in ponderosa pine, which is furthest outside its

historic disturbance regime and likely carries the greatest resilience debt. We expect to see the least difference in the subalpine forest type, which are barely, if at all, outside their historic fire regime. Accordingly, we expect that the biogeographic affinity in different burn severities of lodgepole pine will fall between the other two forest types. We expect that in all forest types and burn severities, the 2nd year post fire will show a higher ratio of warm-xeric taxa than the first as the community reorganized in the first few years following disturbance. In the 2nd year post fire, there will have been more time for colonization of ruderal taxa, which in this region are more likely to have a warmer biogeographic affinity than longer-lived taxa.

2. What other factors influence the ratio of warm-xeric to cool-mesic taxa?

H2: We expect the sites with less canopy cover to have a higher ratio of warm-xeric to cool-mesic taxa. This hypothesis is based on various research indicating that the degree of thermophilization is driven by canopy cover. We also expect that south facing slopes will have a higher ratio of warm-xeric taxa as they experience hotter, drier conditions than north facing slopes.

3. How do forest type, burn severity, and other environmental factors influence community dissimilarity?

H3: We expect the drivers of community dissimilarity to be similar to those driving thermophilization. We expect more similar communities within sites, as they occur in the same forest type and geographic area. Within a site we expect burn severity, canopy cover, and northness to be drivers of community dissimilarity.

Methods

Study Area

Ninety-two research plots were placed in four wildfire scars across three forest types. Forest types included subalpine spruce-fir (*Picea* spp. and *Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), and ponderosa pine (*Pinus ponderosa*). Plots were established in 2021 and revisited in 2022. Plot elevations ranged from 2178 to 3284 m. Each of these fires – the Mullen Fire, Cameron Peak Fire, Calwood Fire, and East Troublesome Fire - occurred in 2020 and burned forests of the southern Rocky Mountains. The Mullen Fire burned 176,878 acres between September 17 and October 23, 2020. Our plots in the Mullen fire scar are in the Medicine Bow National Forest. The Cameron Peak Fire burned 208,760 acres between August 13 and November 5, 2020. The Calwood Fire burned 10,106 acres between October 17 and October 28, 2020. Our plots in the Cameron Peak Fire and Calwood Fire are in the Roosevelt National Forest. Finally, the East Troublesome Fire burned 193,812 acres between October 14 and November 4, 2020. Our plots in the East Troublesome Fire are in the Arapahoe National Forest (Figure 1). A combination of Burned Area Emergency Response (BAER), soil burn severity maps, and on-the-ground scouting were used to determine suitable plot locations. To establish a plot in a given forest type, the plot area must contain greater than 80% basal area of that forest type. For example, in a spruce-fir plot, at least 80% of the basal area must be comprised of spruce and fir trees. Additionally, plot criteria included: less than 35% slope and at least 50 m from a road. For a plot to be considered low to moderate severity, it must have had at least one green-canopied tree within the 0.04 ha plot area in 2021. For a plot to be considered high severity, it had to have 100% tree mortality and be at least 100 m from a green-canopied tree (Figure 2). Within areas meeting selection criteria, we established sites of 12 plots with equal

representation of “high severity” and “low to moderate severity” plots. These 12 plots were placed in close proximity but no less than 50 meters from one another, paired so that there were 6 high severity and 6 low to moderate severity plots per site. Due to time constraints, the subalpine site in the Cameron Peak fire has 5 high severity and 4 low to moderate severity plots, which site comprises 9 rather than 12 plots. Elevation ranged from 2178 to 3261 m across all forest types (Table 1). Unburned control plots were not included in this study. Unburned areas within the fire scars typically had been recently burned or treated or had some other stand condition that would prevent them from being a good control for this study, while unburned areas outside the fire scars were in most cases so far from our selected areas that they could not reasonably be considered part of the same site.

Specific plot locations were chosen by walking a random number of meters towards a random azimuth. In some locations, there were stumps evidencing past management treatment. We tried to avoid having stumps in the plot and took note where it was unavoidable. Additionally, we avoided placing plots in areas with adult aspen (*Populus tremuloides*), to decrease the likelihood of the understory being dominated by aspen shoots in the first few years of recovery.

One additional site of 9 plots was established in 2022 to improve evenness of sampling across forest type. Sites were distributed across the four wildfires and were somewhat dependent on both availability of public land and dominant forest types across the fire footprint. We had 1 site in the Calwood Fire, 1 in the East Troublesome Fire, 2 in the Mullen Fire, and 5 in the Cameron Peak Fire.

Data Collection

Aspect, slope, and elevation data were recorded for each plot. Understory composition was assessed by recording the presence of every tree, forb, graminoid, and shrub, in each 0.4 ha plot. Non-vascular plants were not included in the survey due to challenges in identification. Unknown taxa were collected for later identification. Individuals lacking distinctive parts were classified to the genus level, but most taxa were identified to the species level. Taxa identified to the genus level include *Carex* spp, *Solidago* spp, and *Vaccinium* spp. A small proportion of taxa could not be identified to the genus level and are disregarded in our measures of richness and composition but included in estimates of percent cover.

Percent cover was estimated through measurements on a line point intercept (LPI). LPI measurements were taken on 8 transects, with 25 points beginning 1.8 m from plot center, radiating from plot center in the cardinal and ordinal directions (Figure 3). At each point, the substrate and any plant species present were recorded. Points along the transect were measured 0.3 m apart.

Canopy cover was measured by walking along the North-South transect with a densitometer and recording the presence or absence of canopy every 0.3 m. Species was recorded for live trees and dead branches of live trees, while dead “hits” were classified in their own category.

Data classification and analysis

We constructed a summary table to compare canopy cover, mean species richness, percent cover, and non-native percent cover between burn severities, forest types, and years since fire. For each of these summaries, we created a generalized linear model with the question of

interest as the response variable and burn severity, forest type, and year as predictors. We used the emmeans package in R (Lenth, 2021) to conduct pairwise comparisons using the Tukey adjustment.

In order to determine the ratio of warm-xeric to cool-mesic taxa, we classified every taxon in the data into one of those two categories. We used the biogeographic classifications of Raven and Axelrod (1978), grouping taxa from the California Floristic Province (CFP), Madro-tertiary (MaT), and Warm Temperate Desert (WTD) into the warm-xeric category, and grouping Arcto-Tertiary (AT) as cool-mesic (*sensu* Stevens et al., 2019). 303 unique taxa were contained in our dataset. 276 of these were classified to the species level and 27 to the genus level. Many of these species exactly matched California-based datasets where biogeographic affinity had already been classified (Harrison and Grace, 2007; Raven and Axelrod, 1978; Stevens et al., 2015), while others were a match at the genus level. For those taxa in families or genera not found in Raven and Axelrod (1978), we assigned biogeographic affinities using affinities of close phylogenetic relatives (*sensu* Stevens et al. 2019). Of 303 taxa, 21 (7%) we were unable to confidently categorize as warm-xeric or cool-mesic. In addition to classifying the biogeographic affinity of each taxon in our dataset, we classified whether they are native or introduced using the USDA Plants Database (USDA, NRCS, 2022). There were 17 taxa which we could not confidently identify as native or introduced, which are included as “unknown.” This case only applies to taxa that were identified to the genus level, in a genus which contains both native and introduced species.

In order to compare the relative proportion of biogeographic affinities across forest type and burn severity class, we calculated a ratio of warm-xeric to cool-mesic taxa for each plot. We fit a generalized linear model (GLM) with the ratio of warm-xeric to cool-mesic taxa as the

response variable and with year, forest type and burn severity as predictors. We conducted an ANOVA with type III sums of squares and used pairwise comparisons with a Tukey adjustment to look at differences between the 12 combinations of burn severity, forest type, and year. We also conducted a one-tailed t test to determine if the ratio of thermophilic taxa was higher in high severity burn areas than low to moderate severity burn areas in both the first and second year post-fire.

To address our questions about other variables affecting the ratio of thermophilic taxa, we fit a generalized linear mixed model (GLMM) using the lme4 package in R (Bates et al., 2015). We fit a model with canopy cover, heat load index (McCune & Keon, 2002, McCune, 2007), northness, eastness, and elevation as random effects and retained variables with significant p values (<0.05). The model with the lowest Aikake information criterion (AIC) included eastness as a random effect and fire as a fixed effect. Eastness is a sine transformation of aspect which transforms it into a continuous gradient with values near 1 facing east and values near -1 facing west. Similarly, northness is a cosine transformation of aspect with values near 1 facing north and values near -1 facing south. Heat load index is an estimate of potential annual direct incident radiation using latitude, slope, and aspect as inputs.

To assess community composition in the 2nd year post-fire, we used non-metric multidimensional scaling (NMDS) for each forest type. We also calculated a distance-based MANOVA (perMANOVA) with Bray–Curtis dissimilarity distance measure to compare the similarities of plant communities, using site as a blocking factor. We assessed for environmental variables explaining the NMDS axes, including burn severity UTM Easting, UTM Northing, elevation, canopy cover, northness, and eastness.

Results

Canopy cover was highest on average in low severity lodgepole plots and lowest in high severity plots of spruce-fir (Table 1). Canopy cover was significantly higher in low severity burn areas than high severity burn areas for spruce-fir ($p < 0.01$) and lodgepole pine ($p < 0.01$) but not ponderosa pine. Mean species richness per plot was highest in ponderosa pine and lowest in spruce-fir, with no significant differences between low and high severity burn areas within a forest type. High severity burned lodgepole and high and low severity burned ponderosa pine saw significant increases in both warm-xeric and cool-mesic taxa between the first and second years post-fire. Within forest types, there was a significant difference in understory percent cover between high and low severity burn areas in spruce-fir ($p = 0.03$) but not for lodgepole or ponderosa pine. The only significant difference in percent cover of non-native species is between high severity spruce-fir and low severity ponderosa pine ($p = 0.05$).

Our first hypothesis on the effects of year, burn severity, and forest type on the proportion of thermophilic taxa is partially supported. There was a significant three-way interaction between year, burn severity, and forest type ($p = 0.040$) (Table 2). In the second year post-fire, there was a higher ratio of warm-xeric taxa in high severity burn areas than low severity ones for spruce-fir ($p = 0.013$) and lodgepole ($p = 0.040$) forest types but not for ponderosa ($p = 0.938$) using a one-tailed t test. For the first year post-fire, there is no evidence that any forest type has a higher ratio of thermophilic taxa in high severity burn areas using a one-tailed t test. We find the same significant differences using pairwise comparisons from the GLM (Figure 4). Ponderosa pine had the highest ratio of thermophilic taxa of the forest types, with no significant difference between years or between burn severities (Figure 4). In lodgepole pine in the second year post-fire, high severity burn areas had a significantly higher ratio of

warm-xeric taxa than they did in the first year post-fire, while low to moderate severity burn areas showed no significant difference between years. Spruce-fir shows the same trend, with high severity burn areas having a higher ratio of warm-xeric taxa in the second year post-fire than the first, but no significant difference between years in low to moderate severity burn areas.

Our second hypothesis on canopy cover and northness affecting the ratio of warm-xeric to cool-mesic taxa was not supported. Canopy cover did not have a significant effect on the ratio of biogeographic affinity in any model, nor did northness. However, the model showed that eastness has a marginally significant influence on biogeographic affinity, with more westerly aspects having a higher ratio of warm-xeric to cool-mesic taxa ($p = 0.065$).

Our third hypothesis on the drivers of community dissimilarity was also partially supported. In NMDS ordination analyses we found different drivers of dissimilarity in different forest types. In ponderosa pine, elevation ($R^2 = 0.15$, $p = 0.01$) and burn severity ($R^2 = 0.07$, $p < 0.001$) were significant drivers of community dissimilarity (Table 3, Figure 5). For lodgepole pine, burn severity ($R^2 = 0.03$, $p = 0.05$) and UTM northing ($R^2 = 0.04$, $p = 0.07$) were marginally significant drivers of dissimilarity (Table 4, Figure 6). Finally, in spruce-fir, elevation ($R^2 = 0.07$, $p < 0.05$) was significant and canopy cover was a marginally significant ($R^2 = 0.76$, $p = 0.07$) driver of community dissimilarity (Table 5, Figure 7).

Discussion

The proportion of warm-xeric to cool-mesic taxa increased in high severity burn areas in high elevation forests from the first to the second year post-fire and drivers of community dissimilarity varied by forest type. We draw three major conclusions from this work. First, the changes in biogeographic affinity in lodgepole pine and spruce-fir indicate a trajectory of thermophilization which is not seen in ponderosa pine, suggesting influence of their relative life histories. Second, percent cover and species richness increased in all forest types and burn severities between the first and second year post-fire. Third, western aspects showed a higher ratio of thermophilic taxa compared to other aspects, while burn severity, elevation, canopy cover, and UTM northing were drivers of dissimilarity in different forest types. Most literature on resilience debt focuses on trees, while we focus on the understory plant communities as elements of the ecosystem that confer or diminish resilience using Johnstone et al.'s (2016) framework of resilience debt. Reorganization of shorter-lived understory communities following fire offers insight into conditions that may not yet be reflected in tree communities, and can indicate the presence or absence of resilience debt.

Understanding the role of year, burn severity and forest type

Spruce-fir forests historically burned in infrequent, high severity, stand-replacing fires (Brown et al., 2020, Schoennagel et al., 2004), and decades of fire suppression have not changed the severity. However, there is evidence from the southern Rockies that frequency may be increasing (Higuera et al. 2021). A shift in frequency from 200-300 years to 117 years (Higuera et al. 2021) but no shift in severity may not result in conditions outside the “safe operating space” of tree regeneration, though that is yet to be seen in this early post-fire period. However, when considering the full plant community of spruce-fir forest, there may be a mismatch

between ecological memory and current disturbance regime, indicating a resilience debt as these communities move to hotter and drier climatically adapted species. Very few species of warm-xeric biogeographic affinity were seen in low severity burn areas in the first year post-fire, suggesting that the forest had very few warm-xeric species before fire. The change in conditions caused by canopy opening may facilitate colonization by shade intolerant species which are also more likely to be warm-xeric species. To summarize, the mostly cool-mesic affinity of spruce-fir understory communities may make them susceptible to more drastic change with sudden canopy opening.

Lodgepole pine, which in our analysis showed a significant difference in biogeographic affinity between low and high severity areas, likely has a similar dynamic to spruce-fir, especially considering the historically and currently dense growth pattern of this forest type (Brown et al., 2020). Unlike spruce-fir forests, however, much of the lodgepole forest that burned at high severity in 2020 is already seeing significant seedling regeneration (Chambers et al., 2021). De Frenne et al (2019) demonstrated that closure of the forest canopy can slow the effects of a warming climate on understory communities. So while there appears to be a trajectory toward increased thermophilization in lodgepole pine, it is likely to be more ephemeral than that of spruce-fir as the overstory canopy grows in.

By contrast ponderosa pine forests are more arid and experience warmer temperatures than higher elevation forest types. For most of their history, their understories have experienced open, sunny conditions. Early post-fire proportions of warm-xeric taxa in ponderosa pine communities in other studies were similar to the proportions observed here (Stevens et al., 2019). The ponderosa forests studied here had a higher ratio of warm-xeric taxa than other forest types across severities, suggesting these forests had a greater diversity of biogeographic affinities

before fire as well. It is possible that the pre-existing diversity of biogeographic affinities in ponderosa pine makes the understory more resilient to canopy disturbance. While the overstory community shows evidence of resilience debt after high severity wildfire (Chambers et al., 2016, Rother & Veblen, 2016, Stevens-Rumann et al., 2018), the understory may still be within its safe operating space. In the future we may see greater divergence in these communities but in the near term there is little difference between high and low severity burn areas.

Across all forest types and burn severities percent cover and number of species increased from the first to the second year post-fire (Table 1, Figure 8). Stevens et al (2019) have shown that colonizing warm-xeric taxa can typically be observed within the first year post fire in mixed ponderosa pine – Douglas fir (*Pseudotsuga menziesii*) forests of Colorado, and that colonizing warm-xeric taxa persist for at least 10 years after the fire. If these trends hold true in other forest types, then we can expect that high severity burn areas in high elevation forests will continue to have an elevated ratio of warm-xeric taxa relative to low severity burn areas and unburned forest. In ponderosa pine, we did not observe differences between low and high severity burn areas in either year one or year two, though longer-term trends are yet to be understood. Following wildfire in western conifer forests, it is typical for species diversity and vegetation cover to continue to increase for 10 to 20 years (Webster & Halpern 2010; Shive et al 2013). Recolonization of locally extinct cool-mesic and shade- or fire- intolerant taxa is possible, but is constrained by dispersal abilities and a possible mismatch of environmental tolerances with post-fire conditions. Further monitoring of the trajectory of community composition is recommended for these research sites.

Influence of other site conditions

In our analysis, canopy cover did not significantly affect thermophilization despite our expectations. There are a few possible explanations for this. Our selection criteria for low versus high severity burn areas likely predisposed high severity plots to have less canopy cover than low severity. So it is possible that severity is explaining a proportion of the impact of canopy cover in our models. The second possibility is that there will be an effect of canopy cover in future years, but the communities have not fully reorganized to match site conditions of this new post-fire environment. Interestingly, canopy cover was significantly greater in low severity burn areas than high severity burn areas in lodgepole pine and spruce-fir but not ponderosa pine forest, in both the first and second year post-fire.

The degree of thermophilization had a marginally significant negative correlation with eastness, with west-facing slopes having a more warm-xeric biogeographic affinity. In the northern hemisphere, western aspects receive afternoon sun and so frequently see hotter, drier conditions than more east-facing aspects. They also tend to have a less dense canopy than eastern and northern aspects (Beers et al., 1966), with more solar radiation reaching the understory. We had good representation of aspects in all forest types and burn severities, though they were not normally distributed. For example, sites with low severity ponderosa pine are skewed with low values for northness, indicating most slopes of this type face south. This is both a function of where we could find suitable sampling areas, and the fact that north-facing slopes of ponderosa pine often see encroachment from Douglas fir, and thus would not meet our selection criteria for ponderosa pine forest type.

Drivers of community dissimilarity

In our PERMANOVA analyses, drivers of community dissimilarity varied by forest type. While canopy cover was not a driver of thermophilization, it was a marginally significant driver of community composition in spruce-fir forest (Table 5, Figure 5). Elevation was a driver of community dissimilarity in spruce-fir and ponderosa pine but not lodgepole pine, even though all forest types had a similar range of elevations (Table 1). With more years of data collection, this dataset can be used to address the question of whether plant taxa are migrating upward along elevational gradients in burned areas, which is a possible response to warmer and drier conditions.

Limitations and management implications

Several limitations are evident in this study. First, our research plots were established after the wildfires occurred. Instead of using pre- to post-wildfire data which would reveal information about the relative contributions of colonization and extirpation, we are limited to comparing communities between different burn severities in a post-fire environment. Second, we had difficulty in finding areas of lodgepole pine and spruce-fir forests that burned with low severity. For some sites, the only low severity areas we could find were the edges between burned and unburned forest, which could limit the usefulness of conclusions drawn about low severity burn areas of lodgepole and spruce-fir. In other cases it is hard to say if there were existing differences in pre-fire stand conditions that drove the fire to burn differently in these places. Finally, we rely on the floristic classifications of Raven and Axelrod (1978), which pre-date phylogenetic methods. However, Raven and Axelrod's classifications align with contemporary plant distributions among California's ecoregions (Ackerly 2009, Harrison and Grace, 2007), correspond with functional traits (Ackerly, 2003), and have been used by Stevens

et al. (2015, 2019) to study disturbance effects in mixed conifer forests of Colorado and California.

These findings lead us to a few management recommendations. These systems are in a period of rapid change, and further monitoring is needed to see how they continue to respond to wildfire. We do not recommend intervention in understory response unless invasive species start to become a problem. Tree regeneration is likely going to be a major factor in what the understory looks like in the future, so we recommend continued monitoring and to consider planting in areas where there is not evidence of tree regeneration but tree canopy is desired. To reduce the loss of forest resilience caused by the compounding effects of wildfire and climate change, we recommend swift and decisive action to address the climate crisis.

Trees account for a very small percentage of the biodiversity of forest vegetation communities. Because grasses, forbs, and shrubs have shorter lifespans than trees, reorganization of understory communities may be an indicator of conditions not yet reflected in tree communities. Responses of understory communities to wildfire lend insight into resilience to future disturbance. Declines in cool-mesic taxa are an issue of conservation concern, as they can decrease stand-scale diversity and overall biodiversity, including species which may have economic or cultural importance. Additionally, the correlation of biogeographic affinity with functional traits such as specific leaf area, water use efficiency, and seed size (Ackerly, 2003) raises questions about species niches being filled in future forests. However, increasing thermophilization of the understory community is also an indication that the communities are reorganizing in response to current conditions, which can confer resilience to climate change and future wildfire disturbance.

Tables and Figures

Table 1: Plot elevation and vegetation characteristics with the first year post-fire listed first and second year post-fire listed second. Standard errors are included in parentheses. Superscripts represent groups with Tukey adjustment ($\alpha = 0.05$).

Forest Type	Ponderosa		Lodgepole		Spruce-fir	
Severity	High	Low/Mod	High	Low/Mod	High	Low/Mod
Elevation range (m)	2178-2627	2305-2597	2539-2964	2450-2775	2775-3258	2831-3261
% Cover of forest canopy	11.8 (4.6) ^a 19.9 (3.9) ^{abc}	31.7 (4.6) ^{abcde} 25.9 (5.6) ^{abcde}	22.6 (3.8) ^{abcd} 17.9 (3.8) ^{ab}	42.9 (3.8) ^e 38.6 (3.8) ^{de}	16.7 (3.8) ^{ab} 13.2 (3.8) ^a	37.8 (4.3) ^{cde} 34.9 (4.3) ^{bcd}
Species per plot (mean)	17 (3) ^{bcd} 39 (2) ^{gh}	32(3) ^{efg} 46 (2) ^h	9 (2) ^{ab} 26 (2) ^{def}	18 (2) ^{bcd} 33 (2) ^{fg}	6 (2) ^a 13 (2) ^{abc}	18 (2) ^{bcd} 21 (3) ^{cde}
% Cover of vegetation	0.9 (5.5) ^a 24.5 (4.6) ^{bc}	12.8 (5.5) ^{abc} 35.5 (4.9) ^c	1.4 (4.5) ^a 17.5 (4.5) ^{abc}	15.6 (4.5) ^{abc} 33.8 (4.5) ^c	2.7 (4.5) ^a 10.6 (4.5) ^{ab}	21.4 (4.7) ^{abc} 34.1 (5.0) ^c
% Cover of non-native spp.	0.1 (1.9) ^a 1.9 (1.1) ^a	3.0 (1.3) ^a 5.2 (1.2) ^a	0.0 (1.7) ^a 0.4 (1.1) ^a	1.5 (1.3) ^a 3.2 (1.1) ^a	0.3 (2.6) ^a 0.0 (1.3) ^a	0.1 (1.6) ^a 1.1 (1.3) ^a
Warm-xeric species per plot (mean)	3.6 (0.6) ^{bc} 8.7 (0.5) ^e	7.3 (0.6) ^{de} 11.1 (0.5) ^f	0.8 (0.5) ^a 5.8 (0.5) ^{cd}	2.4 (0.5) ^{ab} 5.9 (0.5) ^d	0.6 (0.5) ^a 2.2 (0.5) ^{ab}	1.6 (0.5) ^{ab} 1.9 (0.5) ^{ab}
Cool-mesic species per plot (mean)	11.42 (2.0) ^{abc} 27.6 (1.7) ^{fg}	22.0 (2.0) ^{def} 31.5 (1.8) ^g	6.6 (1.6) ^a 18.2 (1.6) ^{cde}	14.4 (1.6) ^{bce} 24.6 (1.6) ^{efg}	5.2 (1.6) ^a 10.3 (1.6) ^{ab}	15.0 (1.7) ^{bce} 18.1 (1.9) ^{bcd}

Table 2: Output of 3-way ANOVA with Type III Sums of Squares for 1st and 2nd year post-fire. Proportion of warm-xeric to cool-mesic taxa is the dependent variable. There is a significant interaction between severity and year, forest type and year, and a three-way interaction between the three variables. Significant p values are represented in bold. Marginally significant ($\alpha = 0.1$) p values are marked with an asterisk.

	Sum Sq	Df	F values	Pr(>F)
Severity	0.031	1	2.461	0.118
ForestType	0.548	2	21.838	<0.001
Phase	0.465	1	37.026	<0.001
Severity:ForestType	0.018	2	0.726	0.485
Severity:Year	0.078	1	6.182	0.014
ForestType:Year	0.246	2	9.819	<0.001
Severity:ForestType:Year	0.082	2	3.272	0.040
Residuals	2.284	182		

Table 3: Output of permutational multivariate analysis of variance (PERMANOVA) analysis of the axis values of the NMDS ordination in relation to eastness, northness, canopy cover, elevation, UTM Easting, UTM Northing, and burn severity for the ponderosa pine forest type. df = degrees of freedom, SS = sums of squares, MS = mean squares, F = F value per permutation. p values calculated based on 10,000 permutations. Significant p values are represented in bold (alpha = 0.05). Terms were added sequentially first to last and site was used as a blocking factor.

	df	SS	R^2	F	p
Elevation	1	0.82	0.15	7.42	0.01
Canopy Cover	21	3.31	0.60	1.43	0.11
Burn Severity	1	0.44	0.07	3.96	<0.001
Eastness	1	0.13	0.02	1.18	0.43
Northness	1	0.17	0.03	1.55	0.20
UTME	1	0.11	0.02	0.98	0.73
UTMN	1	0.09	0.01	0.83	0.73
Residual	4	0.44	0.08		
Total	31	5.51	1.00		

Table 4: Output of permutational multivariate analysis of variance (PERMANOVA) analysis of the axis values of the NMDS ordination in relation to elevation, canopy cover, burn severity, eastness, northness, UTME and UTMN for the lodgepole pine forest type. df = degrees of freedom, SS = sums of squares, MS = mean squares, F = F value per permutation. p values calculated based on 10,000 permutations. Significant p values are represented in bold (alpha = 0.05). Terms were added sequentially first to last and site was used as a blocking factor. Marginally significant (alpha = 0.1) p values are marked with an asterisk.

	df	SS	R^2	F	p
Elevation	1	1.11	0.15	8.29	0.53
Canopy Cover	25	4.83	0.64	1.44	0.26
Burn Severity	1	0.26	0.03	1.91	0.05*
Eastness	1	0.09	6.05	0.66	0.88
Northness	1	0.09	0.01	0.68	0.83
UTME	1	0.28	0.01	2.08	0.28
UTMN	1	0.34	0.04	2.56	0.07*
Residual	4	0.54	0.07		
Total	35	7.54	1.00		

Table 5: Output of permutational multivariate analysis of variance (PERMANOVA) analysis of the axis values of the NMDS ordination in relation to eastness, northness, canopy cover, elevation, UTM Easting, UTM Northing, and burn severity for the spruce-fir forest type. df = degrees of freedom, SS = sums of squares, MS = mean squares, F = F value per permutation. p values calculated based on 10,000 permutations. Significant p values are represented in bold (alpha = 0.05) and marginally significant p values (alpha = 0.1) are marked with an asterisk. Terms were added sequentially first to last and site was used as a blocking factor.

	df	SS	R²	F	p
Elevation	1	0.53	0.07	4.11	< 0.05
Canopy Cover	23	5.50	0.76	1.87	0.07*
Burn Severity	1	0.18	0.02	1.37	0.31
Eastness	1	0.22	0.03	1.74	0.30
Northness	1	0.27	0.04	2.10	0.11
UTME	1	0.17	0.02	1.30	0.33
UTMN	1	0.12	0.02	0.93	0.63
Residual	2	0.26	0.04		
Total	31	7.23	1.00		

Table 6: The 20 most abundant taxa from the 2nd year post-fire. Count indicates how many of the 100 plots visited in 2022 had a given taxon present.

Species Code	Scientific Name	Count	Biogeographic affinity
CAREX	<i>Carex</i> L.	96	cool-mesic
CHAN9	<i>Chamerion angustifolium</i> (L.) Holub	73	warm-xeric
TAOF	<i>Taraxacum officinale</i> F.H. Wigg.	72	cool-mesic
SOLID	<i>Solidago</i> L.	57	cool-mesic
EPBR3	<i>Epilobium brachycarpum</i> C. Presl	50	warm-xeric
LASE	<i>Lactuca serriola</i> L.	50	cool-mesic
ACMI2	<i>Achillea millefolium</i> L.	49	cool-mesic
POPR	<i>Poa pratensis</i> L.	49	cool-mesic
CAPU	<i>Calamagrostis purpurascens</i> R. Br.	46	cool-mesic
CIAR4	<i>Cirsium arvense</i> (L.) Scop.	46	cool-mesic
ARCO9	<i>Arnica cordifolia</i> Hook.	44	cool-mesic
PEVI3	<i>Penstemon virens</i> Pennell ex Rydb.	44	cool-mesic
ROWO	<i>Rosa woodsii</i> Lindl.	44	cool-mesic
VACCI	<i>Vaccinium</i> L.	44	cool-mesic
CHFR3	<i>Chenopodium fremontii</i> S. Watson	42	warm-xeric
POFI3	<i>Potentilla fissa</i> Nutt.	42	cool-mesic
CHLE4	<i>Chenopodium leptophyllum</i> (Moq.) Nutt. ex S. Watson	41	warm-xeric
ARUV	<i>Arctostaphylos uva-ursi</i> (L.) Spreng.	40	cool-mesic
COAU2	<i>Corydalis aurea</i> Willd.	38	cool-mesic
SEER2	<i>Senecio eremophilus</i> Richardson	37	cool-mesic
HATR	<i>Harbouria trachyleura</i> (A. Gray) J.M. Coulter & Rose	36	cool-mesic

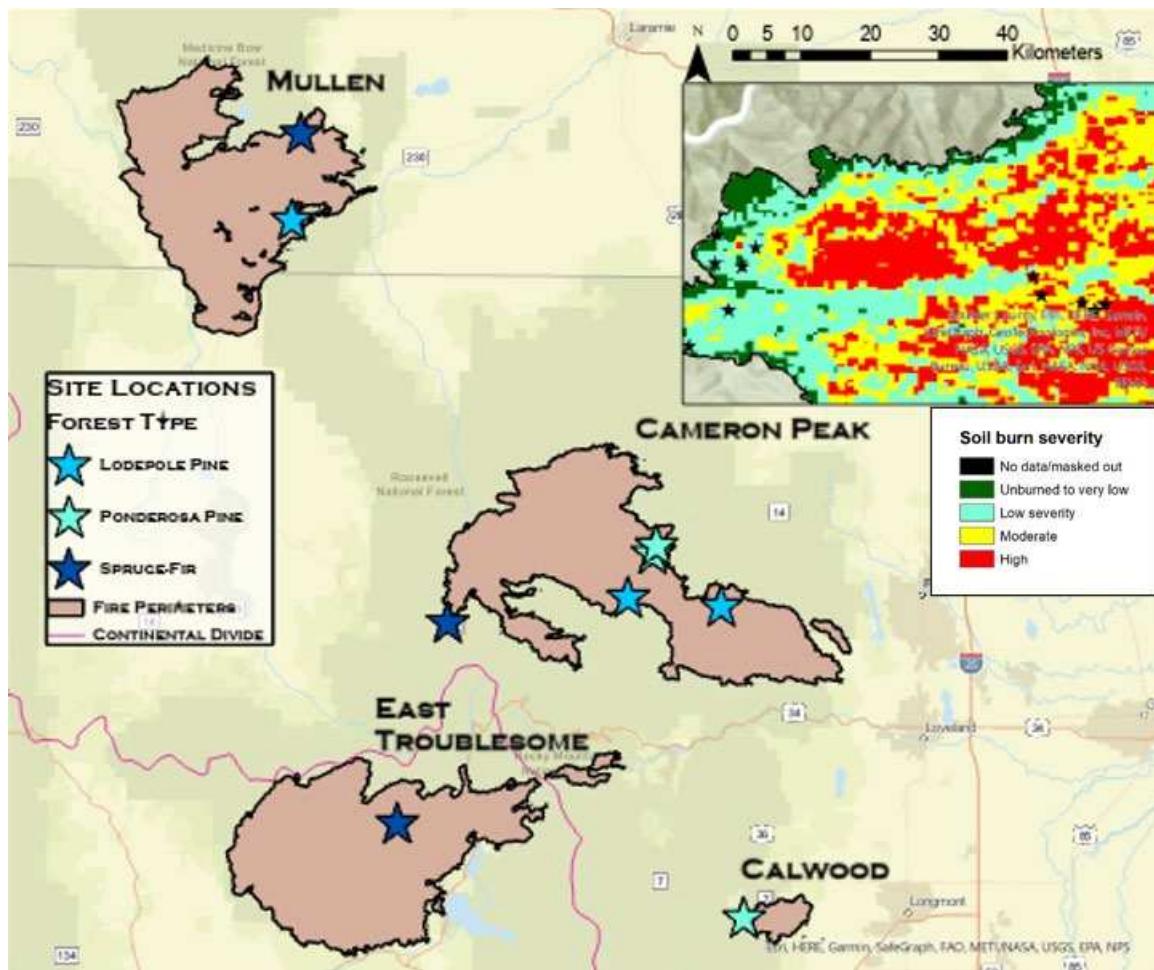


Figure 1: Map of research site locations within 4 fire perimeters. Site locations were selected in National Forests, less than 1 mile from a road for ease of access. Inset map shows a portion of the Calwood fire soil burn severity map (USDA, 2021) with research plots denoted as black stars.



Figure 2: Side by side comparison of a low severity plot and a high severity one for each forest type. Ponderosa pine is on top, followed by lodgepole and then spruce-fir. All photos were taken in the Cameron Peak Fire.

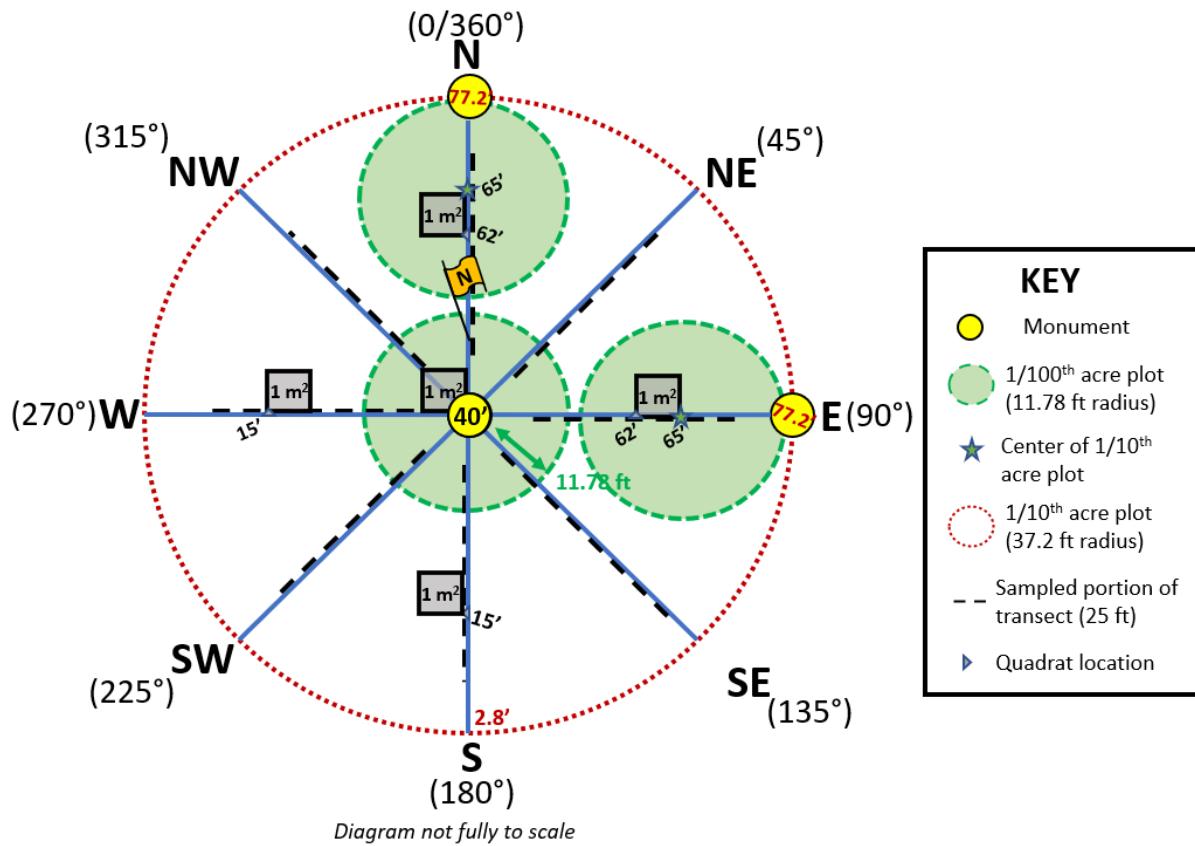


Figure 3: Diagram of plot layout.

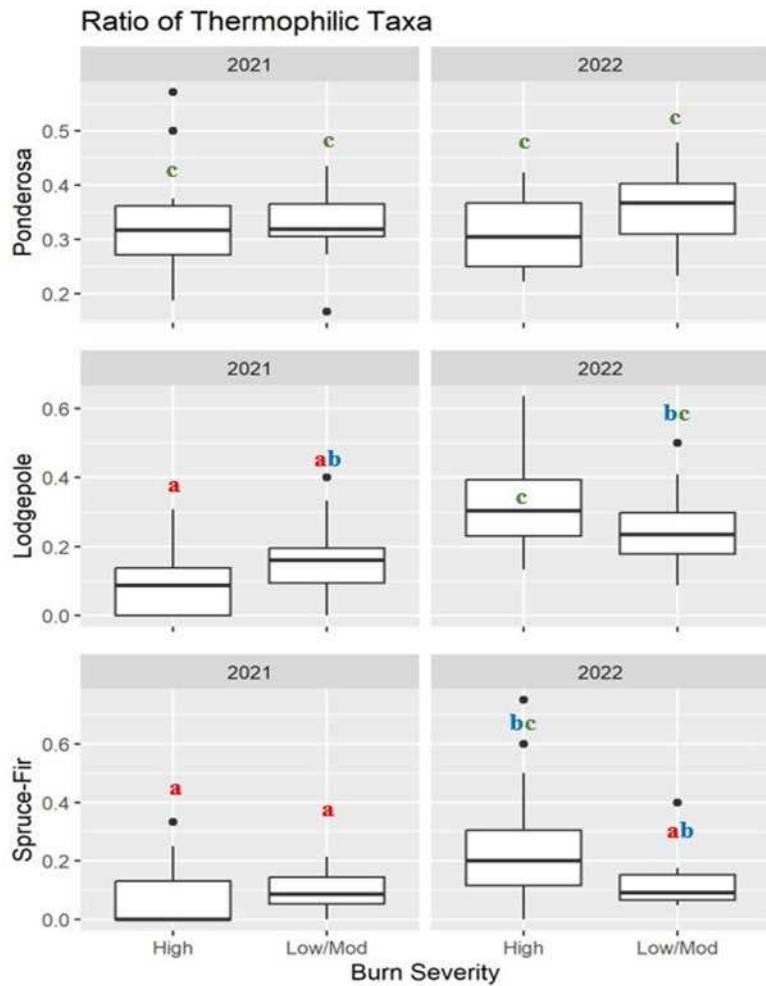


Figure 4: Ratio of thermophilic taxa in forests, grouped by forest type, year, and burn severity. Different letters represent a significant difference ($\alpha = 0.05$) in ratio of warm-xeric to cool-mesic taxa using a type III ANOVA on a generalized linear model with thermophilic ratio as the response variable and burn severity, forest type, year, and an interaction of burn severity, forest type, and year as predictors, with Tukey adjustment.

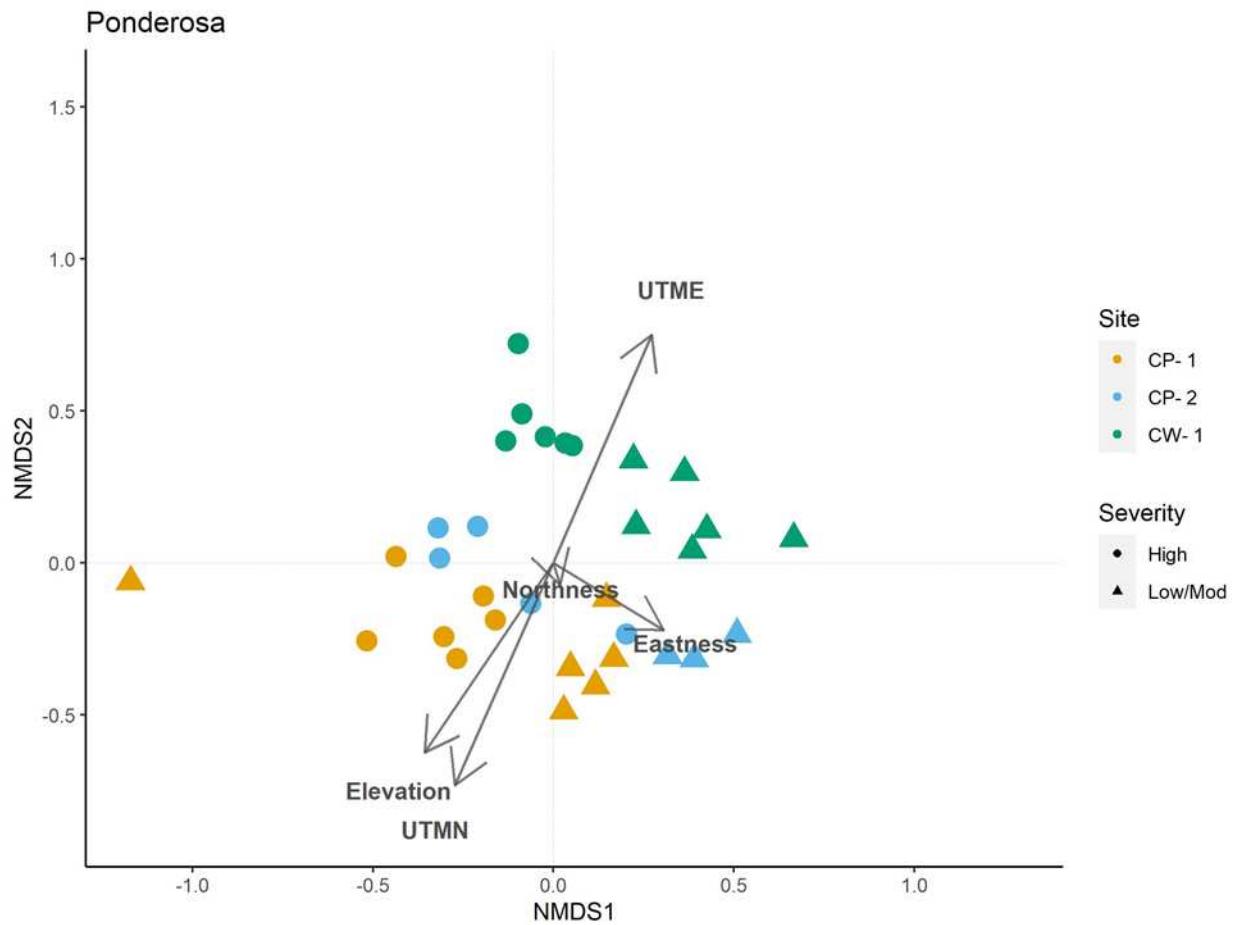


Figure 5: NMDS ordination analysis including all plots in ponderosa pine forest in the second year post-fire. CP denotes the Cameron Peak Fire and CW denotes the Calwood Fire. UTME represents easting and UTMN represents northing.

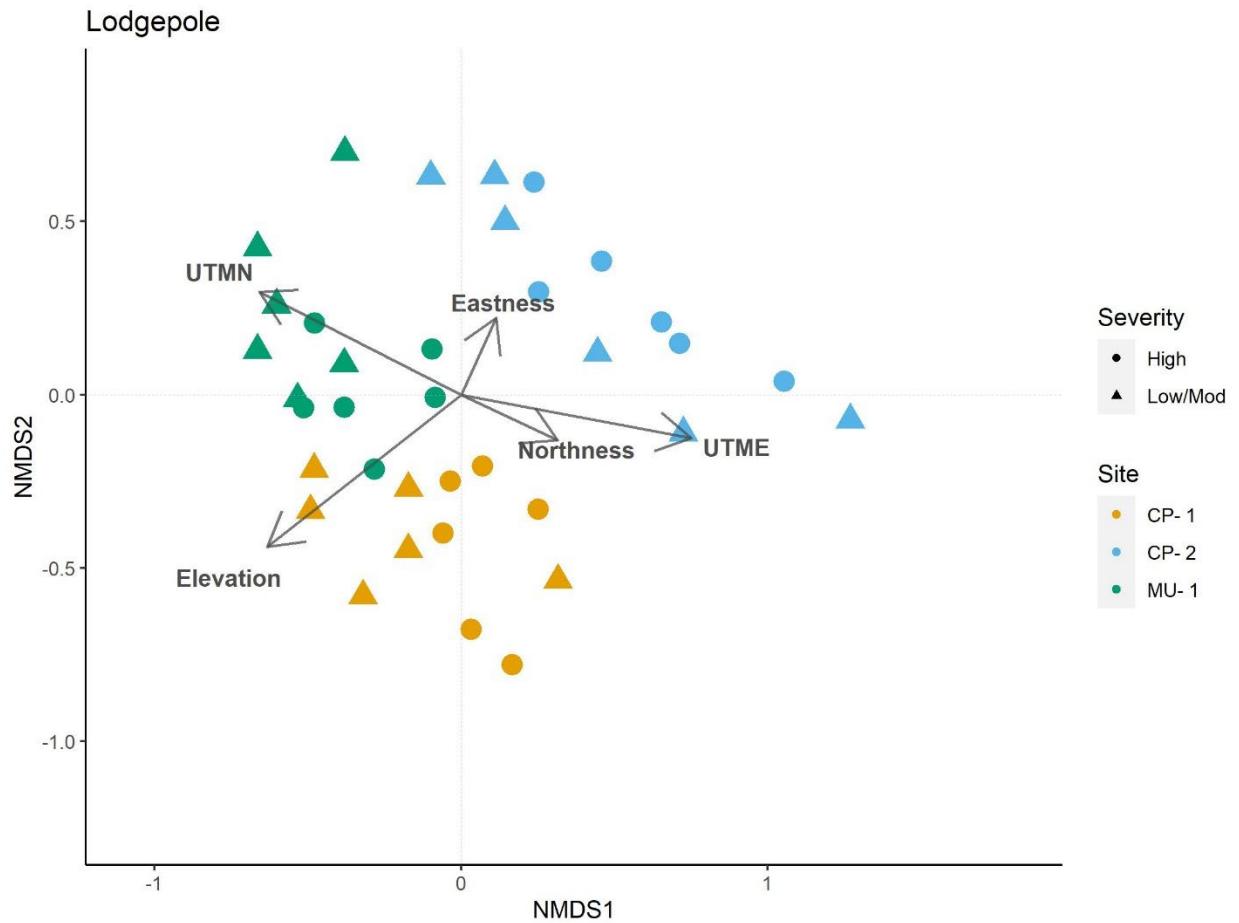


Figure 6: NMDS ordination analysis including all plots in lodgepole pine forest in the second year post-fire. CP denotes the Cameron Peak Fire and MU represents the Mullen Fire. UTME represents easting and UTMN represents northing.

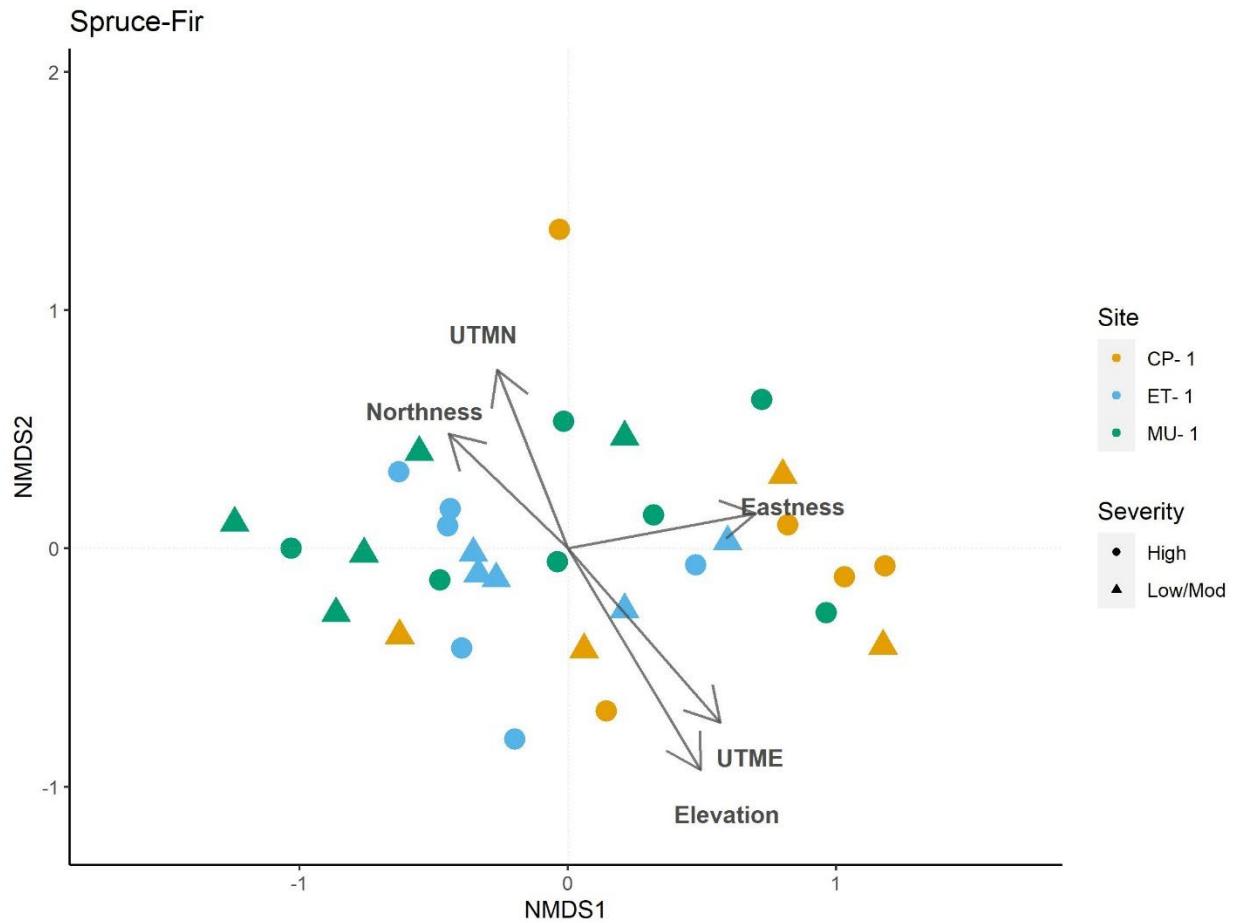


Figure 7: NMDS ordination analysis including all plots in spruce-fir forest in the second year post-fire. CP denotes the Cameron Peak Fire, ET denotes the East Troublesome Fire, and MU denotes the Mullen Fire. UTME represents easting and UTMN represents northing.



Figure 8: Side by side comparison of the same plot in the first year post-fire (left) and second year post-fire (right), demonstrating an increase in percent cover. This plot is in a ponderosa pine forest in the Cameron Peak Fire.

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