

THESIS

ASSESSING POST-FIRE TREE REGENERATION AND FOREST CONVERSION
ACROSS AN ELEVATIONAL GRADIENT IN SOUTHERN COLORADO

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Amanda K. Hastings

Department of Forest and Rangeland Stewardship

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Master's Committee:

Advisor: Camille Stevens-Rumann

Paula Fornwalt

Monique Rocca

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ABSTRACT

ASSESSING POST-FIRE TREE REGENERATION AND FOREST CONVERSION ACROSS AN ELEVATIONAL GRADIENT IN SOUTHERN COLORADO

Increased wildfire activity, with anticipated novel climate scenarios, raises concerns about forest resilience— particularly in semi-arid regions of the western US. Specifically in southwestern US and Southern Rocky Mountain forests, lack of conifer seed sources and shifts in temperature or precipitation post-wildfire may limit the recruitment of dominant conifer species. Meanwhile, hotter and drier conditions may promote the proliferation of resprouting angiosperm species, resulting in vegetative type conversions. To better understand forest susceptibility to type conversion following wildfire, I assessed early vegetation assembly 3 years post-fire, in sites that burned at low and high severity and spanned a climatic gradient in the Sangre de Cristo range of southern Colorado. Research sites were located in lower montane, upper montane, and subalpine forests, with relative dominances of *Pinus ponderosa*-*Pseudotsuga menziesii*; *Abies concolor*-*Pinus contorta*-*Populus tremuloides*; and *Abies lasiocarpa*-*Picea engelmannii*-*Pinus flexilis*-*Pinus aristata*; respectively. I quantified post-fire tree seedling densities and other site-specific attributes to evaluate a) how do burn severity and forest type influence early post-fire tree regeneration, b) are these forest types undergoing conversions? and c) if so, what factors are driving type-conversion?

In this early assessment, I found concerns of forest conversion may be warranted for lower montane forests, with greater abundances of deciduous tree-shrub species, *Quercus gambelii* and *Robinia neomexicana*, and high shrub cover. Meanwhile, upper montane forests are

likely regenerating to a similar forest composition, with early *Populus tremuloides* dominance and *Pinus contorta* regeneration. For both lower and upper montane forest types, conifer regeneration was positively correlated with legacies of low-moderate severity fire, such as overstory cover and litter/woody debris. Meanwhile, subalpine tree regeneration was driven by site-climate and topographic position, regardless of fire severity. In subalpine forests, this study suggests early post-fire conifer regeneration may be dominated by xeric and drought-tolerant species, *Pinus flexilis*, *Pinus aristata*, and *Pinus contorta*, where decades may pass before the establishment of shade-tolerant species characteristic of this forest type. Across all forest types, greater time is required in the post-fire period to predict ultimate recovery trajectories. However, this study serves as one of the first within southern Colorado to evaluate post-fire regeneration across a full elevational gradient and multiple forest types within a single fire footprint.

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INTRODUCTION

Fire is a fundamental ecological force that has long shaped and promoted the health of the Earth's terrestrial ecosystems, including fire-adapted forests of western North America. Examples of ecosystem processes and components affected by fire include post-fire successional trajectories, nutrient cycling, hydrology, carbon dynamics, and native biodiversity conservation (Abella and Fornwalt 2015, Parks et al. 2018, Turner 2010). However, global climate change has led to an increase in the severity and extent of wildfires in recent decades (Abatzoglou and Williams 2016, Parks et al. 2016, Parks and Abatzoglou 2020). Climate-associated shifts— such as rising temperatures, decreased snowpack, drought, and greater fuel aridity— have facilitated increases in fire incidence and severity, warranting concern that fire activity will push beyond the historical range of variability with projected warming (Abatzoglou et al. 2021, Higuera et al. 2021).

Climate warming and associated shifts in fire regimes raise concerns about long-term vegetation change and ecosystem resilience (Coop et al. 2020, Guiterman et al. 2022, Higuera et al. 2021, Stevens-Rumann et al. 2018). Resilience is defined as an ecosystem's ability to recover to a state, similar in structure, composition, function, and feedbacks, to the pre-disturbance state (Holling 1973, Johnstone et al. 2016). Ecological legacies that persist following a disturbance event, and species traits and adaptations that are preserved over greater time and spatial scales, interact with environmental conditions to drive ecosystem recovery and are inherently tied to resilience (Johnstone et al. 2016). For conifer-dominated ecosystems of the western US, forest resilience is dependent upon sufficient tree regeneration (Johnstone et al. 2016, Stevens-Rumann et al. 2018), and can be further assessed at the community level with relative abundances of other

plant functional groups (Abella and Fornwalt 2015, Fornwalt and Kaufmann 2014, Stevens-Rumann and Fornwalt 2019).

Of the factors impacting seedling regeneration post-fire, seed availability from surviving reproductive trees has been shown to be a primary driver (Chambers et al. 2016, Kemp et al. 2016, Stevens et al. 2021, Stevens-Rumann and Morgan 2019, Wooten et al. 2022). Previous research has demonstrated a strong negative relationship between tree seedling density and distance to the nearest living seed source trees and/or low severity patch/refugia (Donato et al. 2016, Falk et al. 2022, Stevens-Rumann and Morgan 2019). Species with adaptive life history traits lending to aerial seedbanks or greater dispersal, such as *Pinus contorta* (lodgepole pine) with facultative serotiny (Coop et al. 2020, Falk et al. 2022) or *Pinus flexilis* (limber pine) with secondary dispersal by birds (Coop and Schoettle 2009), may have greater success reestablishing post-fire. However, for many obligate-seeding conifer species common to the western US, dispersal (commonly via wind) is limited (Coop et al. 2020, Falk et al. 2022); thus, even a single surviving tree within the interior of increasingly common large high-severity patches can provide irreplaceable function (Stevens et al. 2021).

Post-fire climate also strongly influences forest recovery, where unusually hot and dry conditions, from rising temperatures and increased evaporative demand, can lead to reduced seedling regeneration (Coop et al. 2020, Davis et al. 2019a, Hessburg et al. 2019, Urza and Sibold 2017, Stevens-Rumann et al. 2018). For a majority of tree species, juvenile seedlings have a narrower climatic niche in comparison to adult trees (Dobrowski et al. 2015, Rodman et al. 2020b). Canopy loss by wildfire can further exacerbate inhospitable conditions for seedling germination and survival due to increased solar exposure at the surface and soil warming/drying (Davis et al. 2019b, Wooten et al. 2022). Furthermore, topographic factors, such as aspect, heat

load index, and elevation, are additional drivers of regeneration (Stevens-Rumann and Morgan 2019). Specifically in dry forest types, conifer seedling densities are commonly greater on north-facing slopes and higher elevations (i.e., wetter sites; Rodman et al. 2020a). Interannual climate variability also influences post-fire recovery in conifer forests, with regeneration being less likely in fires followed by abnormally dry periods (Davis et al. 2019a, Rodman et al. 2020a).

Conifer establishment, growth, and survival can also be impacted by post-fire vegetation in terms of competition, facilitation, and microsite modification (Rodman et al. 2020a). Resprouting, as exhibited in many woody angiosperm species, allows rapid regrowth from buds in response to significant biomass loss and is commonly described as an adaptation to high-severity fire (Falk et al. 2022). Soil seed banking, especially common in taxa such as graminoids, forbs, and shrubs, enables these plant functional groups to dominate, at least initially, in post-fire landscapes (Falk et al. 2022). Some shrub and herbaceous species exhibit adaptations to disturbance, such as smoke- or heat-induced germination (Falk et al. 2022, Keeley et al. 2011, Pausas and Keeley 2014, Pausas and Keeley 2009). Understory plant cover can facilitate seedling survival or establishment by creating favorable microsite conditions in harsh post-fire environments, yet hinder seedling establishment via competition at high densities (Coop and Schoettle 2009, Wooten et al. 2022). Additional factors can have variable effects at the microsite level, such as coarse woody fuels that can either inhibit plant growth or serve as nurse objects ameliorating otherwise harsh conditions (Wooten et al. 2022).

When disturbances undermine the longstanding resilience of forested ecosystems, ecosystem transitions can occur— with either temporary or persistent changes in composition, structure, and trajectories— and may be referred to as conversion (Davis et al. 2020, Falk et al. 2022, Guiterman et al. 2022). Conversion takes on a myriad of forms, such as shifts in dominant

species, replacement of individual species, rapid changes in species distributions, or transitions in dominant plant functional type (Coop et al. 2020, Falk et al. 2022, Parks et al. 2019). More specifically, fire-driven forest conversion is a two-fold process, consisting of major vegetation change mediated by high-severity fire and reduced post-fire conifer recruitment (Coop et al. 2020, Stevens-Rumann and Morgan 2019). As an example, a growing body of literature demonstrates high-severity fires have induced tree mortality and subsequent expansion of resprouting deciduous species, like *Quercus gambelii* (gambel oak) and *Robinia neomexicana* (New Mexico locust; Coop et al. 2016, Guiterman et al. 2018), in dry, mixed conifer forests of the western US. Vigorous resprouting of broadleaf, deciduous species has the potential to impede or suppress regeneration by outcompeting conifer seedlings via limitations in light and water (Guiterman et al. 2018). Whether or not these transitions indicate alternative stable states or seral states in ecosystem succession is uncertain (Guiterman et al. 2018). However, enduring vegetation changes and novel ecosystem types can be expected to become increasingly common as a consequence of anthropogenic climate change, land-use change, and altered disturbance regimes (Guiterman et al. 2022).

Predictions of post-fire vegetation reassembly are inherently difficult with rapid global change and unknowns surrounding future climatic variability (Abella and Fornwalt 2015, Rodman et al. 2019). However, patterns of new tree establishment in the post-disturbance environment may provide early insights of climate change impacts (Rodman et al. 2020a). While long-term monitoring is well-recognized as a research need in ecological forecasting, the first few years of regeneration post-disturbance can serve as the best available indicator of future trajectories, proving useful for management decisions and restoration efforts (Gill et al. 2017). Furthermore, previous studies have found short-term regeneration patterns are often highly

correlated with long-term regeneration patterns (Coop et al. 2010, Gill et al. 2017, Stevens-Rumann and Morgan 2019).

The purpose of this study was to assess early post-fire regeneration and susceptibility to conversion across 3 different forest types along an elevational gradient in southern Colorado. I addressed three primary research questions: a) how do burn severity and forest type influence early post-fire tree regeneration? b) are these forest types undergoing conversions? and c) if so, what factors are driving type-conversion or shifts in dominant species?

I predicted that, across the entire elevational gradient, conifer regeneration would generally be low in the early post-fire period. In sites where conifer seedlings were present, I hypothesized conifer seedling densities would be better predicted by forest type, than by burn severity. I expected higher conifer densities in forest types with dominant species whose life history traits, such as serotiny or drought tolerance, lend to successful regeneration post-fire. Meanwhile, I hypothesized the effect of burn severity on broadleaf, deciduous tree densities would be dependent upon forest type. For example, I predicted high severity fire would have stimulatory effects for species such as *Quercus gambelii* or *Robinia neomexicana* in lower elevation forest types, but not necessarily for *Populus tremuloides* (quaking aspen) in higher elevation forest types.

In terms of potential susceptibility to type-conversions or shifts in dominant species, I predicted early evidence of conversion to either shrub- or deciduous-dominance in lower montane, dry-mixed conifer forest types would be present in the study. I also predicted higher abundances of deciduous species, *Populus tremuloides*, over coniferous tree seedlings in upper montane and subalpine, mesic-mixed conifer forest types in the early post-fire period. Of the

factors influencing risk of conversion, I hypothesized that distance to seed source of dominant conifer species, site heat load index, and fire severity would be most impactful.

METHODS

Study Area

The Spring Creek Fire burned in the Sangre de Cristo range of southern Colorado in 2018 (Figure 1.2). The fire burned 43,724 ha from 2,106 m to 3,528 m in elevation— across nearly a full elevational gradient characteristic of the forests within the region. Forests in the Sangre de Cristos occupy a broad elevational band between 2000 m to 3650 m (Allen and Peet 1990, Marshall 2019). Mean annual precipitation increases with elevation (Allen and Peet 1990, Baker 1944, Johnson and Cline 1965).

The lowest elevations in the region are occupied by *Pinus edulis* (pinyon pine) and *Juniperus monosperma* (juniper) woodlands (Marshall 2019). Lower montane, dry-mixed conifer forests at lower elevations are largely comprised of *Pinus ponderosa* (ponderosa pine), *Pseudotsuga menziesii* (Douglas-fir), and *Quercus gambelii*, and to a lesser extent, *Abies concolor* (white fir) and *Pinus flexilis* (Marshall 2019, Wooten et al. 2022). Historically, lower montane forests had relatively open-canopy structures with substantial understory plant communities shaped by frequent, low severity fire (Hessburg et al. 2019, Schoennagel et al. 2004). At higher elevations along the climatic gradient, *Populus tremuloides* and *Pinus contorta* are found throughout upper montane, mesic-mixed conifer forests (Margolis et al. 2007, Marshall 2019). Upper montane forest types in the region are characterized by historical mixed-severity fire regimes with stand-replacing patches (Hessburg et al. 2019, Hurteau et al. 2014, Margolis et al. 2011, Margolis and Balmat 2009). Species comprising subalpine forests at the highest elevations below treeline include *Picea engelmannii* (Engelmann spruce), *Abies lasiocarpa* (subalpine fir), and on southwest facing aspects, *Pinus aristata* (Rocky Mountain bristlecone pine) and *Pinus flexilis* (Margolis et al. 2007). Subalpine forests in the region

historically experienced infrequent, stand-replacing fires (Margolis et al. 2011, Schoennagel et al. 2004).

Study sites were located within the San Isabel National Forest and on privately owned lands, spanning 2,595-3,206 m in elevation. Across study sites, average January minimum temperatures range between -10.9 °C and -7.7 °C and average July maximum temperatures range between 21.8 °C and 25.5 °C. Total annual precipitation falls between 382 mm and 619 mm (1991-2020 normals from Parameter-elevation Regressions on Independent Slopes Model [PRISM]). Across the elevational gradient, annual precipitation and growing season precipitation averaged over post-fire years (2019-2021) were lower than 30-year normals, while climatic water deficit was higher in post-fire years (Table 1.1; Table 1.2).

Site Selection

I identified areas that burned at low and high severity with dNBR (differenced Normalized Burn Ratio)-derived fire severity data from Monitoring Trends in Burn Severity (MTBS.gov). I used Environmental Site Potential (landfire.gov) data as a proxy for forest types throughout the burn perimeter to identify potential study sites (Figure 1.1). I then verified burn severity and forest type classification with field observations. Forest types were classified based upon dominant pre-fire overstory tree species and elevation. Lower montane sites were located between 2500-2700 m and dominated by *Pinus ponderosa* and *Pseudotsuga menziesii*. Upper montane sites were classified by *Pinus contorta*-*Populus tremuloides* dominance, spanning 2900-3010 m in elevation. Subalpine sites were dominated by *Abies lasiocarpa*, *Picea engelmannii*, and *Pinus aristata*, and located between 3150-3250 m. Species of wider ecological amplitude, such as *Pinus flexilis*, *Abies concolor*, and *Pseudotsuga menziesii*, were commonly present across multiple forest types; however, the dominant tree species for each forest type

comprised $\geq 80\%$ basal area. Sites with 80-100% tree mortality were classified as high severity, while sites with $< 60\%$ tree mortality were classified as low severity.

Within each forest type, I established site pairs including one low severity site and one high severity site (n= 34). For each site pair, I aimed to keep topographic characteristics consistent; elevation ranged within 75 m and slope within 20%. Aspects between 135° and 315° were characterized as xeric, while aspects falling outside this range were characterized as mesic (Stevens et al. 2019). I established paired sites on slopes with the same aspect category (either xeric or mesic). All sites were established at least 50 m apart from one another and 50 m from a road or trail.

Sampling Design and Field Measurements

For each site, we (please refer to Acknowledgements section for list of field crew members) established a 0.08 ha plot. I recorded topographic measurements for each site at plot center, including geographic coordinates, elevation, slope (%), and aspect (degrees). I calculated a heat load index from direct solar radiation from slope, aspect, and latitude (McCune and Keon 2002, Stevens-Rumann et al. 2018). We measured the distance to the nearest living mature conifer from plot center, using a logger's tape or laser rangefinder (limited to < 500 m). When the distance to seed source exceeded the limit of the rangefinder, the distance was recorded as greater than 500 m. To quantify pre- and post-fire forest structure, we recorded the species, diameter at breast height (1.37 m; DBH), crown base height (for living trees), and tree decay class (modified from Forest Inventory and Analysis National Core Field Guide, USDA 2020) for overstory trees within the entire plot where $DBH \geq 12.7$ cm; trees were also tagged.

We established four 16.1 m transects extending from plot center in the four cardinal directions. We utilized point intercept sampling along transects to quantify percent cover of understory vegetation by functional group (graminoid, forb, shrub, tree), and forest floor substrate (bare ground, rock, litter, woody debris, or other living organisms: moss, lichen, fungi) for a total of 127 points per site. On a subset of sites, we recorded canopy cover each meter along transects for a total of 63 observations per site to calculate percent canopy cover (n=24).

We quantified seedling densities within 2.5 m, 6.9 m, 10 m, or 16.1 m radius subplots dependent upon our initial observations of regeneration in the plot, aiming to capture a count of approximately 20 post-fire conifer seedlings or deciduous stems within the regeneration subplot. We also walked throughout each site and recorded the presence or absence of post-fire conifer seedlings. Herein, I use the term “conifer” to refer to evergreen, needle-leaved, gymnosperm species within the Pinaceae family and “deciduous” to capture deciduous, broad-leaved, angiosperm tree species in Fabaceae, Fagaceae, and Salicaceae families. We did not distinguish between new germinants and resprouts in deciduous tree species (Wooten et al. 2022). We classified regeneration by species commonly classified as tree-shrubs, *Robinia neomexicana* and *Quercus gambelii*, as deciduous tree regeneration. For a subset of sites (n=24), we established a 6.9 m radius circular subplot to measure coarse woody debris (1000-hr, size class >7.62 cm) (Sikkink and Keane 2008). For all coarse woody debris within the subplot, we measured the length and diameter at either end of log. In scenarios where a downed log extended beyond the subplot, we recorded the log diameter at the subplot edge. We were unable to obtain coarse woody debris and canopy cover measurements in subalpine sites (n=10) due to time constraints and a blowdown event in the following year when attempting to return and complete measurements.

Statistical Analyses

I used R software for statistical analysis and data visualization (R Core Team 2021-2023). For all analyses, I assessed significance at a $\alpha=0.05$ level. To evaluate tree regeneration in response to burn severity and forest type, I grouped tree species ($n=11$) according to seed storage structure, conifer or deciduous, and performed analyses on the two larger tree groups. I used forest type, burn severity category, and the interaction between forest type and burn severity as predictor variables. I used a zero-inflated Poisson regression model to evaluate conifer seedling densities and a two-way analysis of variance (ANOVA) to assess deciduous seedling densities (with square-root transformation) as a function of each predictor variable across all sites ($n=34$). I performed Tukey-HSD adjusted comparisons with the emmeans package in R (Length 2022) to identify differences for each tree group, conifer and deciduous, across all predictors. Each statistical model for either conifer densities or deciduous densities was chosen based upon the distribution of the data. I visually assessed diagnostic plots of the residuals to test model assumptions for both analyses.

To evaluate post-fire vegetation structure and other site-specific factors influencing regeneration, I used non-metric multi-dimensional scaling (NMS) ordinations in the vegan package in R (Oksanen 2022). I subset sites by forest type to account for expected compositional differences (Lower montane, $n=13$; Upper montane, $n=10$, Subalpine, $n=10$). As a metric for community structure, I wanted to evaluate tree species densities relative to percent cover by understory functional groups (graminoids, forbs, shrubs). To account for the difference in units between seedling densities and percent cover, I relativized by the maximum value for each variable. Within each relativized column, values ranged from 0 to 1, where 1 would be the

maximum density per tree species or maximum percent cover per functional group observed in the subset of sites for each forest type.

I then conducted ordinations based upon Euclidean distances as if each tree species and each plant functional group were their own “taxon.” Euclidean distance served as the best distance metric for these analyses, given percent cover by each functional group corresponded to cover by a collection of species versus individual species. To assess potential factors driving conversion, I fit site-specific environmental vectors onto these ordinations and assessed squared correlation coefficients (r) between NMS axes and each vector. Site-specific variables included heat load index, live basal area, canopy cover, coarse woody debris, substrate, and the average distance to the nearest conifer seed source by species.

Supplemental to the analyses listed above, I also evaluated the relative cover of plant functional groups in response to burn severity and forest type across all sites ($n=34$). I used two-way analyses of variance (ANOVA) to evaluate mean cover by graminoids, forbs, shrubs, and tree seedlings as a function of forest type, burn severity, and the interaction between the two predictor variables. To test assumptions of normality and homogeneous variance, I visually assessed diagnostic plots of the residuals. I used a square root transformation for graminoid, shrub, and tree seedling cover to better fit model assumptions. For all functional group categories, I performed Tukey-HSD adjusted comparisons to identify differences between groups.

RESULTS

Tree regeneration

The effect of burn severity on conifer seedling densities varied with forest type ($\chi^2=1365.0$, $p<0.001$; Figure 1.3b). In lower montane sites, the mean conifer density was 278 seedlings/ha in low severity sites, exceeding a mean density of 18 seedlings/ha in high severity sites ($p<0.001$). For upper montane sites, the mean conifer density in low severity sites was greater than high severity sites at 7,046 seedlings/ha and 384 seedlings/ha, respectively ($p<0.001$). In contrast, high severity subalpine sites showed greater regeneration with a mean density of 63 seedlings/ha, relative to low severity subalpine sites with 21 seedlings/ha ($p<0.001$).

Pinus contorta exhibited the most regeneration of all conifer species; seedlings were present across all forest types (Figure 1.3a). *Pinus contorta* seedlings were present in 4 upper montane sites, as well as 2 lower montane sites and 1 subalpine site, where *Pinus contorta* previously did not comprise the pre-fire overstory. *Pseudotsuga menziesii* was found in all forest types and more specifically, on 4 out of 19 sites, where mature *Pseudotsuga menziesii* trees were present. *Pinus flexilis* and *Pinus aristata* seedlings were present in 4 out of 10 sites, and 1 out of 6 sites where they previously comprised the pre-fire overstory, respectively. New germinants of *Pinus ponderosa*, *Abies lasiocarpa*, and *Picea engelmannii* were not found on any sites.

Deciduous seedlings were present in all sites, apart from 2 subalpine sites. Forest type was a significant predictor of deciduous densities ($F=11.286$, $p<0.001$; Figure 1.3b); however, burn severity ($F=3.168$, $p=0.086$; Figure 1.3b) was not. The effect of burn severity did not vary with forest type ($F=1.031$, $p=0.37$). The mean deciduous seedling density was higher in lower

montane sites at 8032 seedlings/ha and lower in subalpine sites at 815 seedlings/ha. The mean deciduous density (3569 seedlings/ha) in upper montane sites did not differ significantly from lower montane and subalpine sites.

Out of deciduous species, *Quercus gambelii* was the most abundant, with mean densities of 6317, 55, and 0 seedlings/ha in lower montane, upper montane, and subalpine sites, respectively (Figure 1.3a). *Populus tremuloides* was the only deciduous species present in all three forest types. Increasing along the elevational gradient, mean *Populus tremuloides* densities were 397 seedlings/ha in lower montane sites, 3513 seedlings/ha in upper montane sites, and 815 seedlings/ha in subalpine sites (Figure 1.3a). Lastly, *Robinia neomexicana* was only found in lower montane sites, with mean densities of 1935 seedlings/ha in high severity and 700 seedlings/ha in low severity sites.

Cover by tree seedlings— including both conifer and deciduous— varied by forest type ($F=12.260$, $p<0.001$; Figure 1.7), but not burn severity ($F=0.140$, $p=0.710$; Figure 1.7). Mean percent seedling cover was significantly lower in subalpine sites at 1.8% and higher in lower montane sites at 9.9%. Percent seedling cover in upper montane sites was 4.2% and not significantly different than the other two forest types. Deciduous densities comprised the major component of tree seedling cover; therefore, this pattern mirrors that which was observed with deciduous densities in response to burn severity and forest type.

Site-specific factors influencing community composition and vulnerability to conversion

For all ordinations across forest types, only environmental vectors with significant ($\alpha>0.05$) correlations are shown (Figure 1.4 -1.6). The ordination using Euclidean distances for the lower montane community matrix converged with a two-dimensional solution (stress =

0.109, non-metric $R^2 = 0.988$; Figure 1.4). Axis 1 separated plant groups by reproductive strategy, where arboreal cone-bearing species— such as *Pinus contorta* and *Pseudotsuga menziesii*— increased along axis 1, while most soil seed-banking, vegetative, or resprouting species decreased (apart from *Populus tremuloides*). Axis 2 was related to fire severity, where sites with low severity, post-fire legacies increased along the axis. This is echoed by strong, positive correlations between axis 2 with live basal area ($r = 0.932$, $p=0.039$; Figure 1.4) and litter/woody debris cover ($r = 0.964$, $p=0.007$; Figure 1.4). Furthermore, the correlation between axis 2 and burn severity trended towards significance ($r=0.194$, $p=0.062$).

For upper montane sites, the ordination using Euclidean distances converged on a two-dimensional solution (stress = 0.090, non-metric $R^2 = 0.992$, Figure 1.5). Canopy cover and litter/woody debris cover were strongly correlated with both NMS axes, where correlations with both environmental variables were negative with axis 1 ($r = -0.557$, $p=0.011$; $r= -0.346$, $p=0.004$; Figure 1.5) and positive with axis 2 ($r = 0.717$, $p=0.011$; $r= 0.726$, $p=0.004$; Figure 1.5). Axis 1 was related to a gradient in light availability, canopy structure, and substrate. Species that typically thrive on sites with high solar radiation (e.g. south-west facing slopes, open-canopy), such as *Pinus flexilis*, increased along the axis, while more shade tolerant species, such as *Pseudotsuga menziesii* decreased. Meanwhile, axis 2 separated sites by fire severity, where all high severity sites were below the zero horizon and decreased along the axis, while most low severity sites increased.

Similar to the other two forest types, the ordination based on Euclidean distances for subalpine sites converged on a solution with two dimensions (stress = 0.087, non-metric $R^2 = 0.992$; Figure 1.6). There were strong, positive correlations between heat load index with both axes (axis 1, $r= 0.730$, $p=0.016$; axis 2, $r= 0.683$, $p=0.016$). Meanwhile, for both axes, there were

very weak correlations with burn severity (axis 1, $r = 0.064$, $p=0.673$; axis 2, $r = -0.161$, $p=0.673$). Axis 1 was driven by regeneration of conifer species and plant group reproductive strategy. Where all conifer species densities increased along axis 1, cover by graminoids, forbs, shrubs, and *Populus tremuloides* densities decreased. Axis 2 was strongly influenced by a single mesic, subalpine site where *Pinus contorta* seedlings were found. *Pseudotsuga menziesii*, *Pinus flexilis*, and *Pinus aristata* seedlings increased along axis 2, while *Pinus contorta* seedlings appeared well below the zero horizon in the ordination. *Populus tremuloides* and the remaining plant functional groups: graminoids, forbs, and shrubs were distributed about the zero horizon for axis 2; meanwhile, forbs appeared closer in ordination space to high severity sites.

Post-fire vegetation cover across functional groups

Graminoid cover varied by burn severity ($F = 14.064$, $p < 0.001$; Figure 1.7), but not forest type ($F = 0.019$, $p = 0.982$; Figure 1.7). The interaction between burn severity and forest type was not significant in graminoid cover ($F = 0.344$, $p = 0.712$). Mean percent cover by graminoids was over four times higher in low severity versus high severity sites, at 15.6% and 3.7%, respectively. Of graminoid species, Poaceae spp. had the highest mean percent cover at 8.7%, followed by Cyperaceae spp. at 3.1% (Table 1.3).

Forb cover varied by forest type ($F = 8.062$, $p = 0.002$; Figure 1.7), but not burn severity ($F = 0.053$, $p = 0.820$; Figure 1.7). There was not a significant interaction between forest type and burn severity in forb cover ($F = 0.314$, $p = 0.733$). Mean percent forb cover was significantly higher in lower montane sites at 36.2% versus the other two forest types. Mean percent forb cover was not statistically different between versus upper montane and subalpine sites, at 24.5% and 17.0%, respectively. Frequently encountered understory forb species included *Arnica cordifolia*,

Alyssum simplex, Fabaceae spp., *Chenopodium album*, *Descurainia sophia*, *Oreochrysum parryi*, and *Penstemon strictus* (Table 1.3).

The effect of burn severity on shrub cover varied with forest type ($F=3.480$, $p=0.045$; Figure 1.7). Mean percent shrub cover was highest in high severity, lower montane sites at 7.6%, followed by low severity, lower montane sites at 5.4% and low severity, upper montane sites at 6.8%. Within upper montane and subalpine forest types, low severity sites had significantly higher shrub cover than high severity sites within the same forest type. Frequently encountered shrub species included *Arctostaphylos uva-ursi*, *Mahonia repens*, *Rosa woodsia*, *Symphoricarpos rotundifolius*, and *Vaccinium myrtillus* (Table 1.3).

DISCUSSION

Following a large disturbance event, such as wildfire, public land managers and private landowners are often times called to make decisions about how to promote forest recovery within the burn footprint in the first several years post-fire. This study serves as one of few recent studies (Rodman et al. 2020a, Rodman et al. 2020b, Wooten et al. 2022) monitoring early post-fire conifer regeneration in south-central Colorado. Furthermore, this research contributes to the growing body of literature on vegetation type conversion, particularly in the Southern Rockies ecoregion and the Southwestern US (Figure 1.2; Coop et al. 2016, Coop et al. 2020, Davis et al. 2020, Falk et al. 2022, Guiterman et al. 2022, Guiterman et al. 2018). By establishing sites across the entire elevational band characteristic of forest types in the Sangre de Cristo subrange, this study is also unique to the region in assessing short-term post-fire recovery in upper montane and subalpine forest types— where previous studies in these higher elevation forests typically span longer time scales (Coop et al. 2010, Coop and Schoettle 2009, Margolis et al. 2011, Margolis et al. 2007). With novel climate scenarios anticipated and uncertainties surrounding regeneration patterns post-disturbance, studies that span elevational and biophysical gradients— such as Allen et al. 1991, Kemp et al. 2016, Margolis and Balmat 2009, Marshall 2019, and this study—are invaluable as researchers and land managers seek to understand how these forests are currently changing and how these forests might change in the future.

It is worth noting that literature on vegetation type conversions commonly discusses vegetation change that is temporally enduring and maintained through fire-vegetation-climate feedbacks (Coop et al. 2020, Davis et al. 2020); however, reburns and longer time scales were outside the scope of this study. Given this research focuses on forest recovery following a single fire event, I used the following metrics to assess forest vulnerability and early indicators of

conversion: conifer seedling regeneration, the relative abundances of other plant functional groups, and site-specific characteristics that may influence successful conifer seedling establishment and/or proliferation of notable deciduous tree or tree-shrub species.

Lower montane forests

For lower montane forests, results of this study suggest areas following high severity fire may be more at risk to conversion from conifer-dominated forests to dominance of deciduous tree-shrubs, particularly *Quercus gambelii* and to a lesser extent, *Robinia neomexicana*. This finding is consistent with a wealth of literature focused on similar forest types within southern Colorado and northern New Mexico (Coop et al. 2020, Coop et al. 2016, Guiterman et al. 2018, Guiterman et al. 2022, Rodman et al. 2020). Resprouting tree-shrubs, such as *Quercus gambelii* and *Robinia neomexicana*, exhibit not only greater resilience to drought and fire, but also competitive growth advantages over conifer seedlings (Guiterman et al. 2018, Marshall and Falk 2020). Under historical conditions in lower montane forests, low severity, frequent fire and high levels of shade from overstory conifers likely limited growth of coexisting tree-shrubs, such as *Quercus gambelii* (Guiterman et al. 2018). However, in their study investigating fire history and long-term persistence of *Quercus gambelii* shrubfields in lower montane forests in the region, Guiterman et al. 2018 concluded that conifer to tree-shrub transitions after high severity fire more likely represent an alternative stable state versus a seral stage in conifer forest succession. Warmer, drier conditions in the future and increases in fire activity suggest greater vulnerability to fire-catalyzed vegetation change in years to come for Southwestern US and Southern Rockies lower montane forests.

This study underscores the importance of climatic suitability in post-fire tree regeneration and the benefits of low severity fire in lower montane forests. Successful conifer establishment,

by dominant species such as *Pinus ponderosa* and *Pseudotsuga menziesii*, has been shown to be dependent upon parent tree survival (with closer proximity to seed source trees), understory composition (competition or facilitation), and microclimate modification by overstory cover (Guiterman et al. 2022, Rodman et al. 2020a). While I did not find any post-fire *Pinus ponderosa* seedlings in this study, regeneration by conifer species, *Pseudotsuga menziesii* and *Pinus contorta* was correlated with legacies of low severity fire— such as live basal area and cover by litter/woody debris. These results are consistent with studies that have found post-fire microsite conditions, such as accumulated litter and early successional plant cover, help limit soil warming and drying and may promote seedling germination (Wooten et al. 2022). Additional research has also demonstrated low severity fire limits reductions in recruitment due to high climatic water deficit, for both *Pinus ponderosa* and *Pseudotsuga menziesii*, versus high severity fire (Davis et al. 2023).

In southwestern US and southern Rocky Mountain forests, *Pinus ponderosa* has been described as having episodic regeneration events, associated with cool, wet years (Stevens-Rumann and Morgan 2019); therefore, the lack of regeneration observed in this study could indicate delayed recruitment versus regeneration failure (Stevens-Rumann et al. 2022). In their recent study focused on recovery following 15 fires, spanning 1988-2010, in the same region, Rodman et al. 2020a found five peak years of seedling establishment coincided with above-average moisture availability. Predicting future precipitation patterns is inherently difficult; however, abnormally moist years in a warmer climate may promote post-fire regeneration on sites previously absent of seedlings (Stevens-Rumann and Morgan 2019) and must be taken into consideration when assessing conversion in lower montane forests.

While fire exclusion over the 20th century has resulted in increased stand density across a variety of forest types, postfire management is especially challenging in low elevation, frequent fire forests given large departures from historical pre-fire forest structure (Stevens et al. 2021). This study contributes to the ongoing discussion of the importance of low severity fire in ameliorating the impacts of climate change and the benefits of using it as a management tool.

Upper montane forests

For upper montane forests, the abundant resprouting of *Populus tremuloides* observed in this study, particularly following high severity wildfire early in the post-fire period, is congruent to previous research (Margolis et al. 2007, Romme et al. 2001). Rapid resprouting by *Populus tremuloides* within high severity burn patches in southwestern US upper montane forests is well documented (Margolis et al. 2007); however, does not necessarily imply long-term forest type conversion. Within mesic, mixed conifer forests of the Sangre de Cristo Mountains, large even-aged *Populus tremuloides* stands are considered to be a seral stage in successional pathways (Margolis et al. 2007, Margolis et al. 2013). The general successional pathway is described as “conifer-aspen-conifer”, proceeding from mature conifer-dominance pre-fire, rapid resprouting by *Populous tremuloides* post-fire, reestablishment by conifer seedlings, and mature conifers overtopping *Populous tremuloides* (Margolis et al. 2007). In the late 20th century, late successional dominance by conifers was of concern due to substantial declines in *Populus tremuloides* cover (Bartos 2001, Margolis et al. 2007); however, shifts in fire activity in the region may be reversing this trend and contributing to decreased conifer seedling establishment (Margolis et al. 2007).

Similar to the observations in this study, current research has demonstrated adequate *Pinus contorta* regeneration, even with little to no regeneration of other species (Stevens-

Rumann and Morgan 2019); however, it is possible *Pinus contorta* may undergo substantial declines with future climate change and fire activity (Davis et al. 2023, Guz et al. 2021, Stevens-Rumann and Morgan 2019). The results of this study suggest that areas most conducive to *Pinus contorta* seedling establishment are those with higher canopy cover, live basal area, and litter/woody debris. Within the Spring Creek fire perimeter, Wooten et al. 2022 found canopy cover on low severity burned areas increased soil moisture and decreased soil temperatures—conditions previously described as favorable to conifer recruitment (Davis et al. 2019a, Davis et al. 2019b, Petrie et al. 2016).

While successful, but limited, *Pinus contorta* regeneration is projected in the future, there is also concern that fire return intervals in years to come may be shorter than time to reproduction for conifer species (Turner et al. 2019). Previous studies have shown severe drought is strongly associated with fire occurrence within upper elevation mixed-conifer forests (Margolis et al. 2007), with the most areas burned in years of extreme seasonal climate conditions (Higuera et al. 2021, Sibold et al. 2006). Researchers have already projected continued warming in coming decades will push fire activity within similar forest types (at more northern latitudes) beyond the historical range of variability (Higuera et al. 2021). Therefore, disequilibrium and risk of vegetation conversion in this forest type may be predominantly dependent on time between subsequent fires.

Subalpine forests

For subalpine forests, my findings of higher densities of drought-tolerant conifer species, including *Pinus flexilis*, *Pinus aristata*, and *Pinus contorta*, over drought-intolerant species, *Abies lasiocarpa* and *Picea engelmannii*, in the early post-fire period is consistent with previous studies (Schapira et al. 2021a). Previous studies have shown moisture availability, (Andrus et al.

2018, Schapira et al. 2021a, Schapira et al. 2021b), seed dispersal (Coop and Schoettle 2009), and topographic position (Coop et al. 2010), to be particularly influential in post-fire subalpine tree recruitment. Both *Picea engelmannii* and *Abies lasiocarpa* seedlings are sensitive to post-fire moisture stress (Schapira et al. 2021a), which can be exacerbated in large burn patches and drought conditions (Coop et al. 2010, Schapira et al. 2021a). Meanwhile, *Pinus flexilis* and *Pinus aristata* commonly occupy areas beyond the physiological tolerances of other conifer tree species, such as windswept ridges, or rocky, xeric slopes (Coop and Schoettle 2009). *Pinus aristata* seeds are winged and small enabling wind-dispersal, while *Pinus flexilis* seeds are heavier and dispersed by Clark's nutcrackers, whereby seeds reach open sites (e.g., exposed interiors of large burns; Coop and Schoettle 2009). These attributes exhibited by both species—in terms of seed dispersal and physiological tolerances—enable early colonization following high-elevation, stand-replacing burns (Coop and Schoettle 2009).

The commonly described successional pathway on xeric sites in the subalpine zone involves initial establishment by five-needle pines, *Pinus flexilis* and *Pinus aristata*, followed by a protracted succession to *Picea engelmannii* and *Abies lasiocarpa* (Coop et al. 2010). In this study, I found heat load index was the primary driver in early community composition and regeneration on subalpine sites, likely attributable to the greater presence of xeric species. Meanwhile, *Picea engelmannii* is typically the first to establish on mesic sites, followed by slow infilling by *Abies lasiocarpa* (Coop et al. 2010). Furthermore, successional stages with abundant resprouting by *Populus tremuloides*, similar to those in southwestern US upper montane forests, are also characteristic of subalpine forests in the regions, but with different dominant conifer species (Margolis et al. 2007). Thus, the high post-fire densities of *Populus tremuloides* observed

in this study are consistent with other research in the region (Coop et al. 2010, Margolis et al. 2007).

Previous studies spanning longer time scales have demonstrated the initial post-fire cohort, with greater numbers of drought-tolerant conifer seedlings and resprouting *Populus tremuloides*, may be distributed over decades (Margolis et al. 2011). While no post-fire *Picea engelmannii* and *Abies lasiocarpa* seedlings were found in this study, Coop et al. 2010 observed prolific regeneration of both species 30 years post-fire and little post-fire regeneration by *Pinus aristata* and *Pinus flexilis*. Thus, findings from this study do not present significant departures from previously described successional trajectories, or vegetation type conversions, for subalpine forests. However, current literature emphasizes the potential vulnerability of subalpine tree species to climate change (Malone et al. 2018, Schapira et al. 2021a, Schapira et al. 2021b).

In this study, *Pinus contorta* regeneration was observed in one high severity subalpine site, despite no adult *Pinus contorta* trees within the site or upslope of the site (personal observation). Distances to live *Pinus contorta* seed source trees exceeded 1000m; therefore, regeneration was likely attributable to aerial seed banking in dead trees lower in elevation. While *Pinus contorta* showed greater regeneration on low severity sites— with overstory structure that potentially contributed to microclimatic buffering— in lower and upper montane sites, *Pinus contorta* seedlings in this single subalpine site regenerated successfully on bare mineral soil. Previous research in areas at higher latitudes has demonstrated *Pinus contorta* regenerates effectively on bare mineral soils (Harvey et al. 2016, Schapira et al. 2021b). Which presents the question as to whether increases in elevation or latitude and microclimate buffering effects may present similar moisture and temperature conditions suitable to *Pinus contorta* growth.

Species distribution models suggest climate-induced range shifts may be facilitated by wildfire (Hill et al. 2021), with some western US tree species predicted to shift upward in elevation with future climatic conditions (Halofsky et al. 2018). It is impossible to assess whether *Pinus contorta* establishing at higher elevations is a distinctive trend from a single site in this study; however, future studies with greater sample size may be able to detect or infer if range shifts are occurring. In the event lower elevation species with different fire regimes shift upwards in elevation, this could lead to novel species assemblages and forest development (Malone et al. 2018). Understanding how species ranges may change across various forest types, regions, and disturbance types, will be essential to ecosystem management in years to come (Donato et al. 2016, Stevens-Rumann and Morgan 2019).

Overall, generally little to no conifer regeneration across the elevational gradient is consistent with previous studies focused on conifer-dominated forests of the western US (Stevens-Rumann and Morgan 2019). This study further emphasizes the importance of climatic conditions and the variability of temperature and moisture requirements between conifer species across different forest types (Petrie et al. 2016, Stevens-Rumann and Morgan 2019).

Research Limitations

As discussed previously, the fact that I collected data early in the post-fire period serves as a research advantage; however, it simultaneously limits my ability to assess the ultimate recovery trajectories of the forests. Stevens-Rumann et al. 2022 discuss the need to consider temporal and spatial scales specific to each forest type when assessing regeneration scenarios. If the post-fire observation period is too short to effectively observe regeneration establishment, delayed regeneration may be misclassified as regeneration failure (Stevens-Rumann et al. 2022). Thus, for this study, it is too early to constitute no conifer regeneration on some sites as

regeneration failure. Simultaneously, in sites where deciduous densities drastically exceed conifer densities, ultimately there is uncertainty as to whether this pattern will persist long-term. However, when leveraged with preexisting literature spanning longer time scales, it is possible to infer likely recovery scenarios. Furthermore, this study will persist as a record in time to be referenced with later studies, thus enabling future researchers to assess long-term recovery.

Future research evaluating water balance metrics specifically pertaining to plant stress, such as climatic water deficit, soil moisture, or actual evapotranspiration, could help further predict vegetation patterns and susceptibility to fire-driven conversion in semi-arid landscapes (Rodman et al. 2020a). Previous research has demonstrated that interannual climate variability within the first 3-years postfire is important in postfire vegetation trajectories (Rodman et al. 2020a). Unfortunately, statistical downscaling of climatological data was outside the scope of this study. The spatial proximity of sites did not allow for differentiation between sites, when using high-resolution gridded climate data, such as PRISM or Terraclimate data (800 m or ~4km resolution, respectively); therefore, I was unable to integrate important climate variables as predictors in my analyses. Additional studies spanning multiple years could further assess the influence of interannual climate variability in successful conifer regeneration and overall community composition. Ultimately, there is uncertainty as to whether the patterns I observed in this study may remain consistent or become amplified in the hotter, drier conditions projected in the future.

Lastly, while not within the scope of this study, these forests are experiencing a myriad of other compounding or interacting disturbances— such as *Dendroctonus ponderosae* (mountain pine beetle) and *Dendroctonus rufipennis* (spruce beetle) outbreaks, *Cronartium ribicola* (white pine blister rust) disease in *Pinus aristata* and *Pinus flexilis*, as examples. Future research

focusing on the effects of the multiple disturbances and their interactions could expand upon this study as well as preexisting literature (Coop et al. 2010, Malone et al. 2018, Schapira et al. 2021a).

Conclusions

Concerns of potential conversion to shrublands or deciduous-dominated forests, with abundant *Quercus gambelii* and *Robinia neomexicana* resprouting, may be more warranted in lower montane versus upper montane and subalpine forests. Given dominance by *Populus tremuloides* has been previously described as a seral stage in the successional pathway of upper montane southwestern US forests, this study does not suggest substantial change to dominant species in this forest type. In subalpine forests, I observed higher abundances of five-needle pines, *Pinus flexilis* and *Pinus aristata*, that are more tolerant to xeric or harsher climatic environments. Several decades may pass before substantial development of canopy ensues and promotes the growth of shade tolerant species characteristic of these high elevation forests, such as *Abies lasiocarpa* and *Picea engelmannii*. Therefore, while I found early indicators of post-fire conversion in lower montane forest types, I did not find any clear departures from successional trajectories in upper montane or subalpine forest types 3 years post-fire.

Resources and funding are finite in the wake of wildfire. This study describes early regeneration patterns and indicators of potential vegetation conversion, so that land managers may identify areas suitable to seedling growth (whether planted or natural regeneration) or areas where promoting non-forested or novel forested ecosystems may be warranted— now and in the future climate. For all forest types, studies spanning multiple years or conducted later in the post-fire period will be instrumental in evaluating the compounding effects of wildfire, other disturbances, and warming trends to ultimately assess the resilience of these forests.

Table 1.1 Climate data for 30-year normals (1991-2020) averaged over sites within each forest type. Primary climate variables were retrieved from PRISM; derived (secondary) climate variables were retrieved from Terraclimate (Abatzoglou et al. 2018) datasets. Growing season variables were averaged over April-September for each year. VPD indicates vapor pressure deficit; CWD indicates climatic water deficit.

<i>Climate data</i>	Lower Montane	Upper Montane	Subalpine
Annual Precipitation (mm)	518.98	507.70	617.59
Growing Season Precipitation (mm)	54.34	49.11	56.61
Growing Season Minimum Temperatures (°C)	5.14	3.52	2.92
Growing Season Maximum Temperatures (°C)	19.99	18.22	16.87
January Minimum Temperatures (°C)	-8.39	-10.21	-10.85
July Maximum Temperatures (°C)	25.02	23.24	21.84
Minimum VPD (hPa)	1.84	1.56	1.50
Maximum VPD (hPa)	12.93	11.02	9.73
CWD (mm)	45.86	35.79	34.17

Table 1.2 Climate data for post-fire years (2019-2021) averaged over sites within each forest type. Primary climate variables were retrieved from PRISM; derived climate variables were retrieved from Terraclimate (Abatzoglou et al. 2018) datasets. Growing season variables were averaged over April-September for each year. VPD indicates vapor pressure deficit; CWD indicates climatic water deficit.

<i>Climate data</i>	Lower Montane	Upper Montane	Subalpine
Annual Precipitation (mm)	405.84	387.2	495.15
Growing Season Precipitation (mm)	40.84	35.81	40.49
Growing Season Minimum Temperatures (°C)	5.78	4.67	3.83
Growing Season Maximum Temperatures (°C)	19.78	18.76	17.33
January Minimum Temperatures (°C)	-8.12	-9.57	-10.67
July Maximum Temperatures (°C)	24.47	23.42	21.87
Minimum VPD (hPa)	2.26	1.92	1.71
Maximum VPD (hPa)	12.92	11.74	10.18
CWD (mm)	70.15	60.51	60.12

Table 1.3 List of commonly encountered species or genera within the study.

Species/Genus Name	Family
<i>Abies concolor</i>	Pinaceae
<i>Abies lasiocarpa</i>	Pinaceae
<i>Achillea millefolium</i>	Asteraceae
<i>Achnatherum nelsonii</i>	Poaceae
<i>Alyssum simplex</i>	Brassicaceae
<i>Antennaria parvifolia</i>	Asteraceae
<i>Antennaria rosea</i>	Asteraceae
<i>Arctostaphylos uva-ursi</i>	Ericaceae
<i>Arnica cordifolia</i>	Asteraceae
<i>Artemisia frigida</i>	Asteraceae
<i>Artemisia ludoviciana</i>	Asteraceae
<i>Astragalus crassicaarpus</i>	Fabaceae
<i>Astragalus flavus</i>	Fabaceae
Brassicaceae spp.	Brassicaceae
<i>Bromus ciliatus</i>	Poaceae
<i>Bromus inermis</i>	Poaceae
<i>Bromus tectorum</i>	Poaceae
<i>Campanula rotundifolia</i>	Campanulaceae
<i>Cerocarpus montanus</i>	Rosaceae
<i>Chamerion angustifolium</i>	Onagraceae
<i>Chenopodium album</i>	Amarathaceae
<i>Chenopodium capitatum</i>	Amarathaceae
Cirsium spp.	Asteraceae
<i>Clematis columbiana</i>	Ranunculaceae
<i>Corydalis aurea</i>	Papveraceae
<i>Cymopterus alpinus</i>	Apiaceae
<i>Cynoglossum officinale</i>	Borginaceae
<i>Danthonia parryi</i>	Poaceae
<i>Descurainia sophia</i>	Brassicaceae
<i>Dracocephalum parviflorum</i>	Lamiaceae
<i>Elymus elymoides</i>	Poaceae
<i>Elymus hispidus</i>	Poaceae
<i>Elymus trachycaulus</i>	Poaceae
Erigeron spp.	Asteraceae
<i>Erigeron speciosus</i>	Asteraceae
<i>Ericameria nauseosa</i>	Asteraceae
<i>Erigeron eximius</i>	Asteraceae
<i>Erysimum capitatum</i>	Brassicaceae
<i>Festuca arizoninca</i>	Poaceae
<i>Festuca thurberi</i>	Poaceae
<i>Fragaria virginiana</i>	Rosaceae
<i>Galium boreale</i>	Rubiaceae
<i>Heterotheca villosa</i>	Asteraceae
<i>Juniperus communis</i>	Cupressaceae

<i>Koeleria macrantha</i>	Poaceae
<i>Lappula occidentalis</i>	Boraginaceae
<i>Lathyrus arizonicus</i>	Fabaceae
<i>Lathyrus laetivirens</i>	Fabaceae
<i>Lupinus argenteus</i>	Fabaceae
<i>Mahonia repens</i>	Berberidaceae
<i>Medicago lupulina</i>	Fabaceae
<i>Muhlenbergia montana</i>	Poaceae
<i>Oreochrysum parryi</i>	Asteraceae
<i>Paxistima myrsinites</i>	Celastraceae
<i>Packera fendleri</i>	Asteraceae
<i>Penstemon strictus</i>	Scrophulariaceae
<i>Penstemon virens</i>	Scrophulariaceae
<i>Picea engelmannii</i>	Pinaceae
<i>Pinus aristata</i>	Pinaceae
<i>Pinus contorta</i>	Pinaceae
<i>Pinus flexilis</i>	Pinaceae
<i>Pinus ponderosa</i>	Pinaceae
<i>Poa nemoralis</i>	Poaceae
<i>Poa nervosa</i>	Poaceae
<i>Poa pratensis</i>	Poaceae
<i>Polygonum aviculare</i>	Polygonaceae
<i>Polygonum douglasii</i>	Polygonaceae
<i>Populus tremuloides</i>	Saliaceae
<i>Potentilla hippiana</i>	Rosaceae
<i>Pseudotsuga menziesii</i>	Pinaceae
<i>Quercus gambelii</i>	Fagaceae
<i>Ribes montigenum</i>	Grossulariaceae
<i>Robinia neomexicana</i>	Fabaceae
<i>Rosa woodsii</i>	Rosaceae
<i>Rubus idaeus</i>	Rosaceae
<i>Sedum lanceolatum</i>	Crassulaceae
<i>Senecio eremophilus</i>	Asteraceae
<i>Solidago multiradiata</i>	Asteraceae
<i>Symphoricarpos rotundifolius</i>	Caprifoliaceae
<i>Taraxacum officinale</i>	Asteraceae
<i>Thermopsis divaricarpa</i>	Fabaceae
<i>Vaccinium myrtillus</i>	Ericaceae
<i>Verbascum thapsus</i>	Scrophulariaceae
<i>Vicia americana</i>	Fabaceae

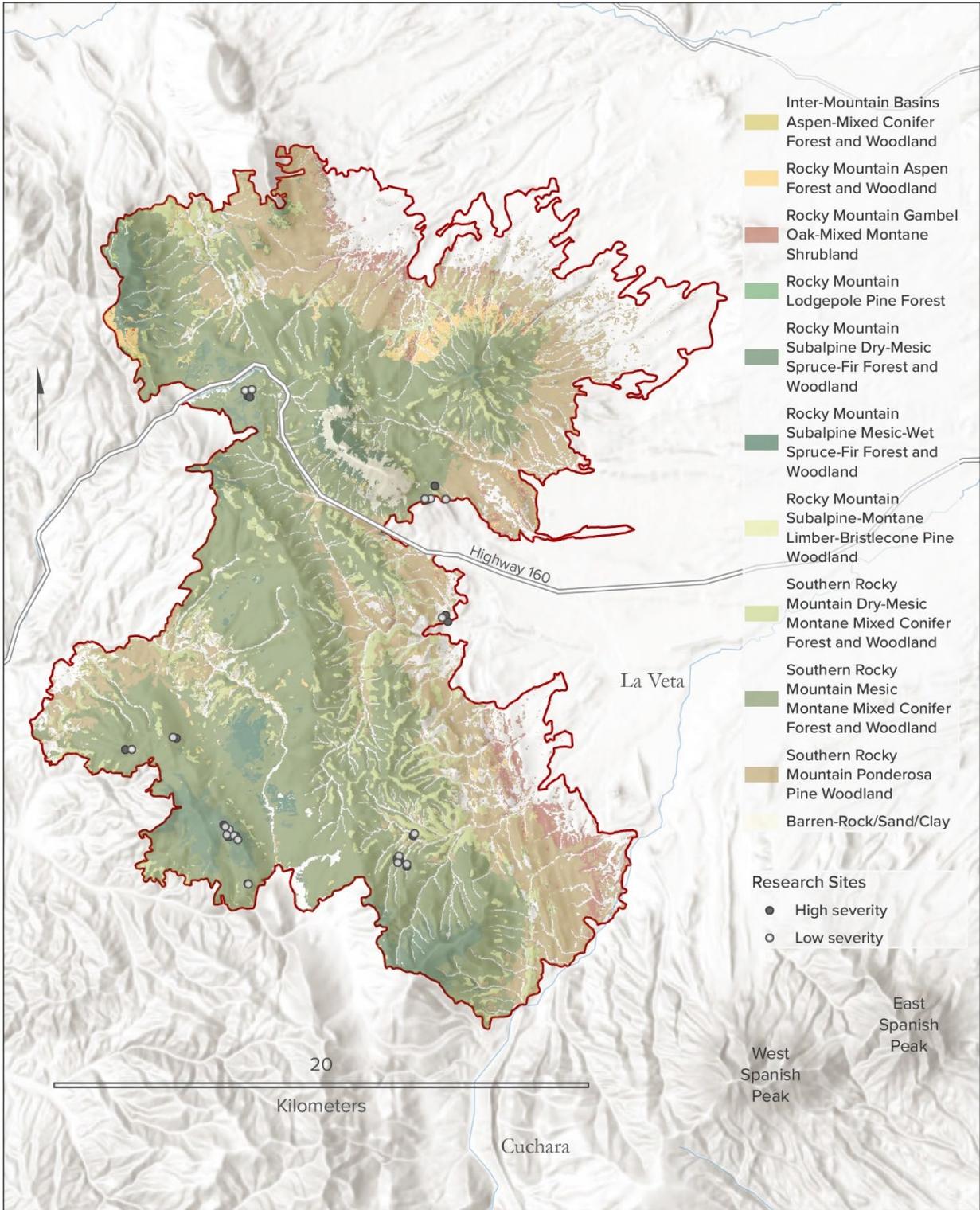


Figure 1.1 Map of the Spring Creek Fire perimeter and research sites (n=34). Fire perimeter data retrieved from the Monitoring Trends in Burn Severity program. Forest types listed in legend pertain to LANDFIRE Environmental Site Potential within the burn perimeter.



Figure 1.2 Locator map of the Spring Creek Fire in southern Colorado, US. Red symbology indicates the Spring Creek Fire burn perimeter. Light green and dark green symbology indicate different ecoregions: Southern Rockies and Arizona- New Mexico Plateau, respectively. Data retrieved from the Monitoring Trends in Burn Severity program and the Environmental Protection Agency.

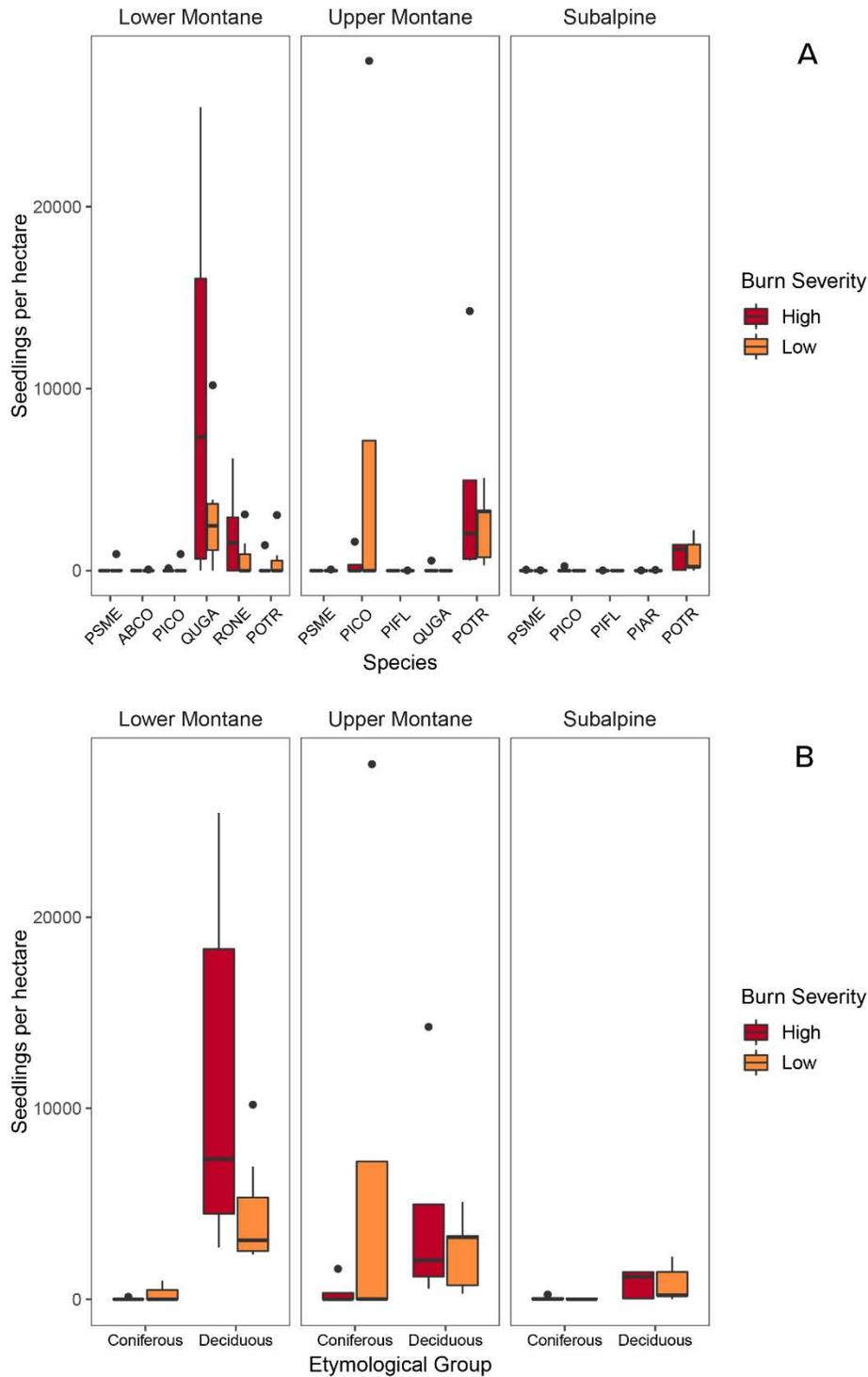


Figure 1.3 Post-fire tree seedling densities across all sites, split by forest type and colored by burn severity (n=34). a) Seedling densities by species: *Pseudotsuga menziesii* (PSME), *Abies concolor* (ABCO), *Pinus contorta* (PICO), *Pinus flexilis* (PIFL), *Pinus aristata* (PIAR), *Quercus gambelii* (QUGA), *Robinia neomexicana* (RONE), *Populus tremuloides* (POTR). b) Seedling densities by larger tree group: coniferous or deciduous.

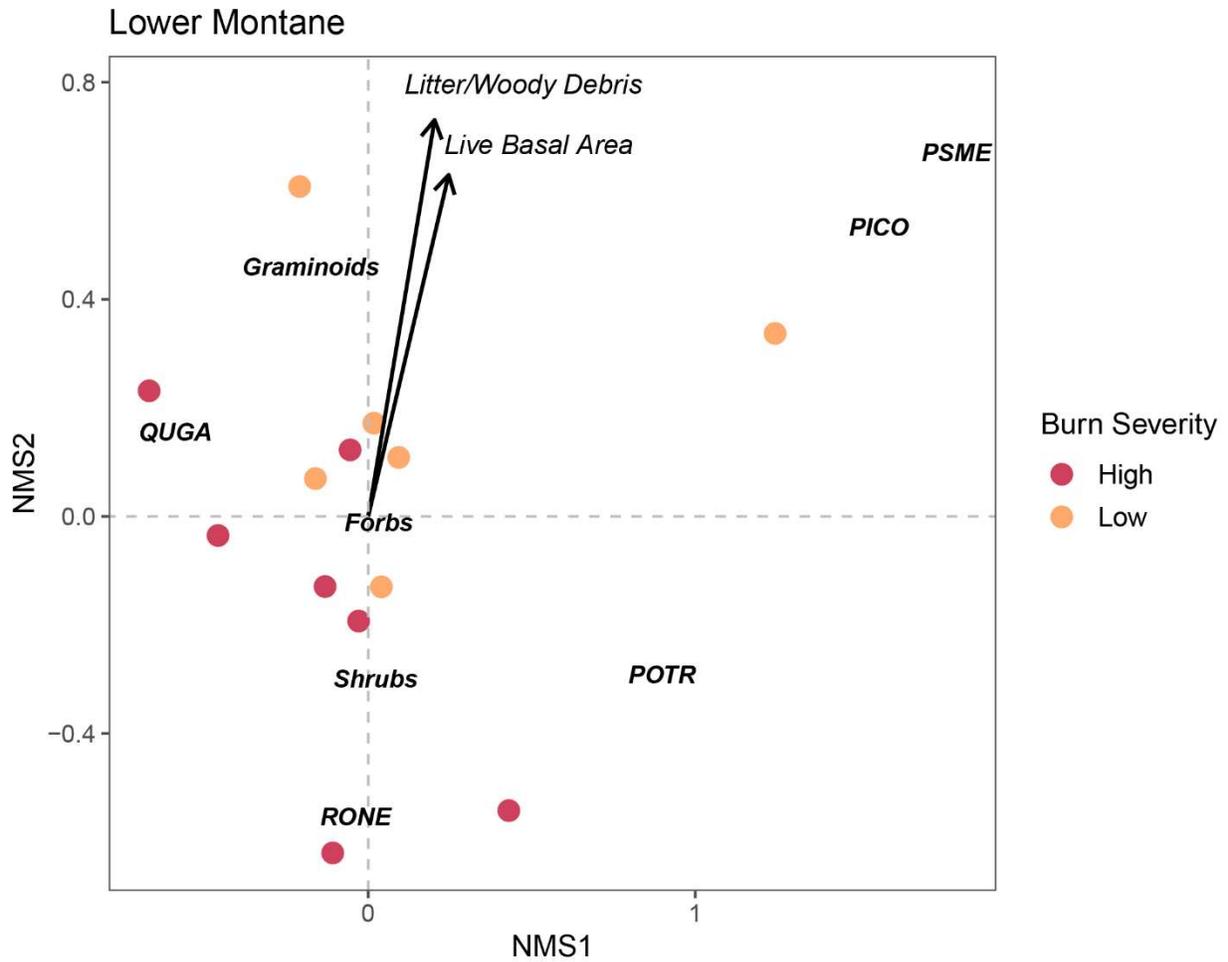


Figure 1.4 Nonmetric multidimensional scaling ordinations of overall community composition, including understory plant cover by functional group and tree seedling densities by species for lower montane sites. Text represents the center of each plant group in ordination space. Species names are listed by species code: *Pseudotsuga menziesii* (PSME), *Pinus contorta* (PICO), *Pinus Quercus gambelii* (QUGA), *Robinia neomexicana* (RONE), and *Populus tremuloides* (POTR). Environmental vectors with significant correlations ($\alpha=0.05$) with the overall ordination are shown.

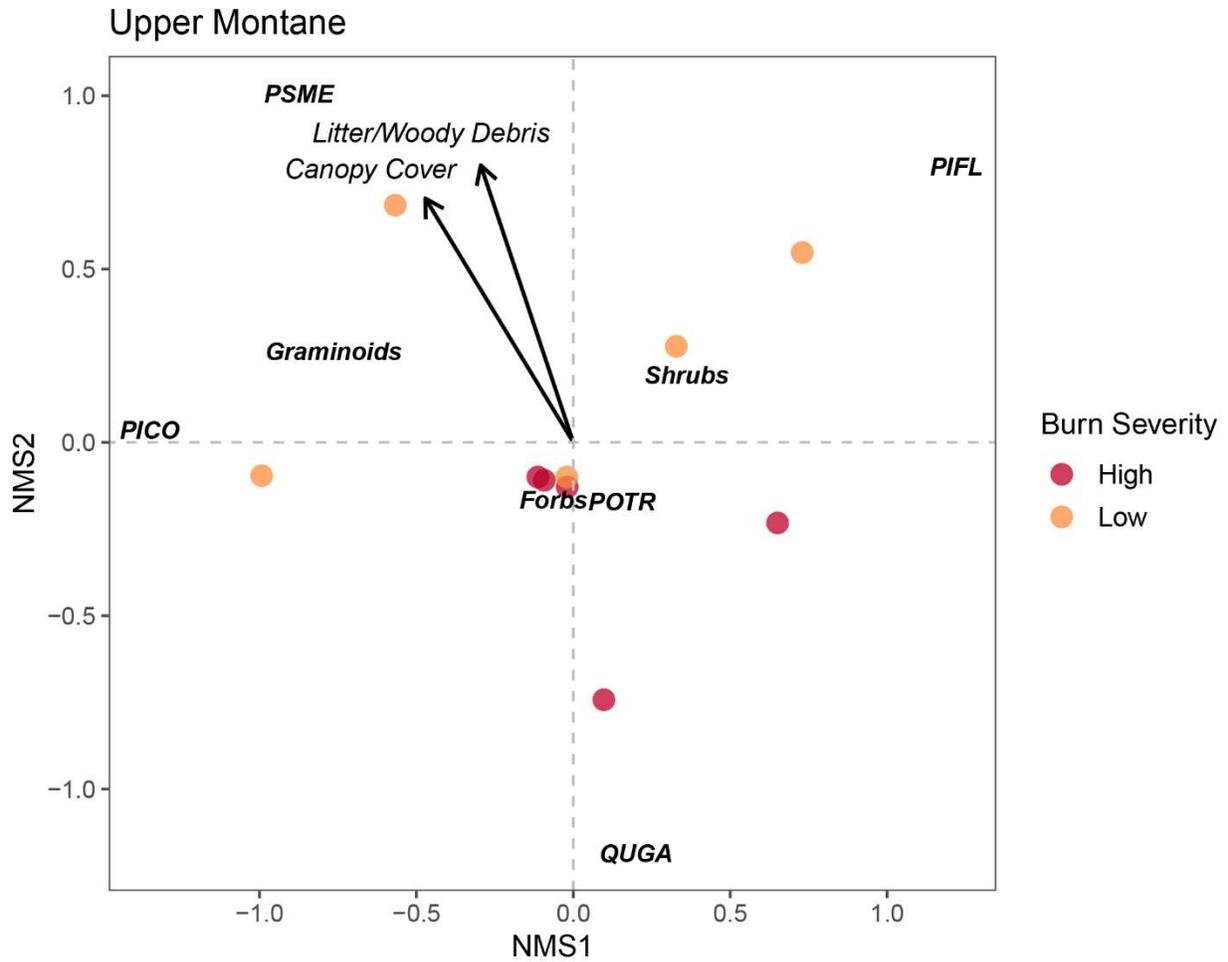


Figure 1.5 Nonmetric multidimensional scaling ordinations of overall community composition, including understory plant cover by functional group and tree seedling densities by species for upper montane sites. Text represents the center of each plant group in ordination space. Species names are listed by species code: *Pseudotsuga menziesii* (PSME), *Pinus contorta* (PICO), *Pinus flexilis* (PIFL), *Quercus gambelii* (QUGA), and *Populus tremuloides* (POTR). Environmental vectors with significant correlations ($\alpha=0.05$) with the overall ordination are shown.

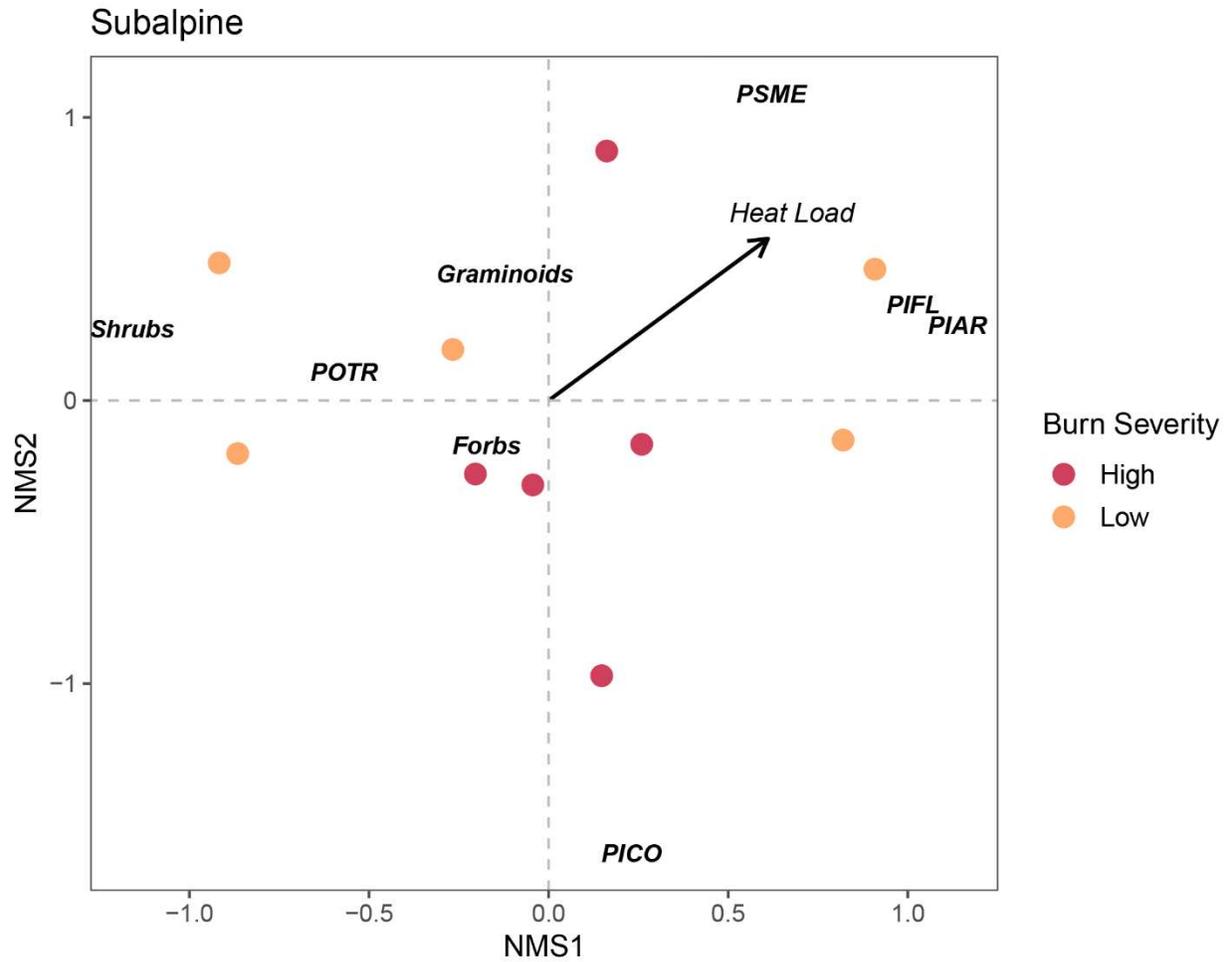


Figure 1.6 Nonmetric multidimensional scaling ordinations of overall community composition, including understory plant cover by functional group and tree seedling densities by species for subalpine sites. Text represents the center of each plant group in ordination space. Species names are listed by species code: *Pseudotsuga menziesii* (PSME), *Pinus contorta* (PICO), *Pinus flexilis* (PIFL), *Pinus aristata* (PIAR), and *Populus tremuloides* (POTR). Environmental vectors with significant correlations ($\alpha=0.05$) with the overall ordination are shown.

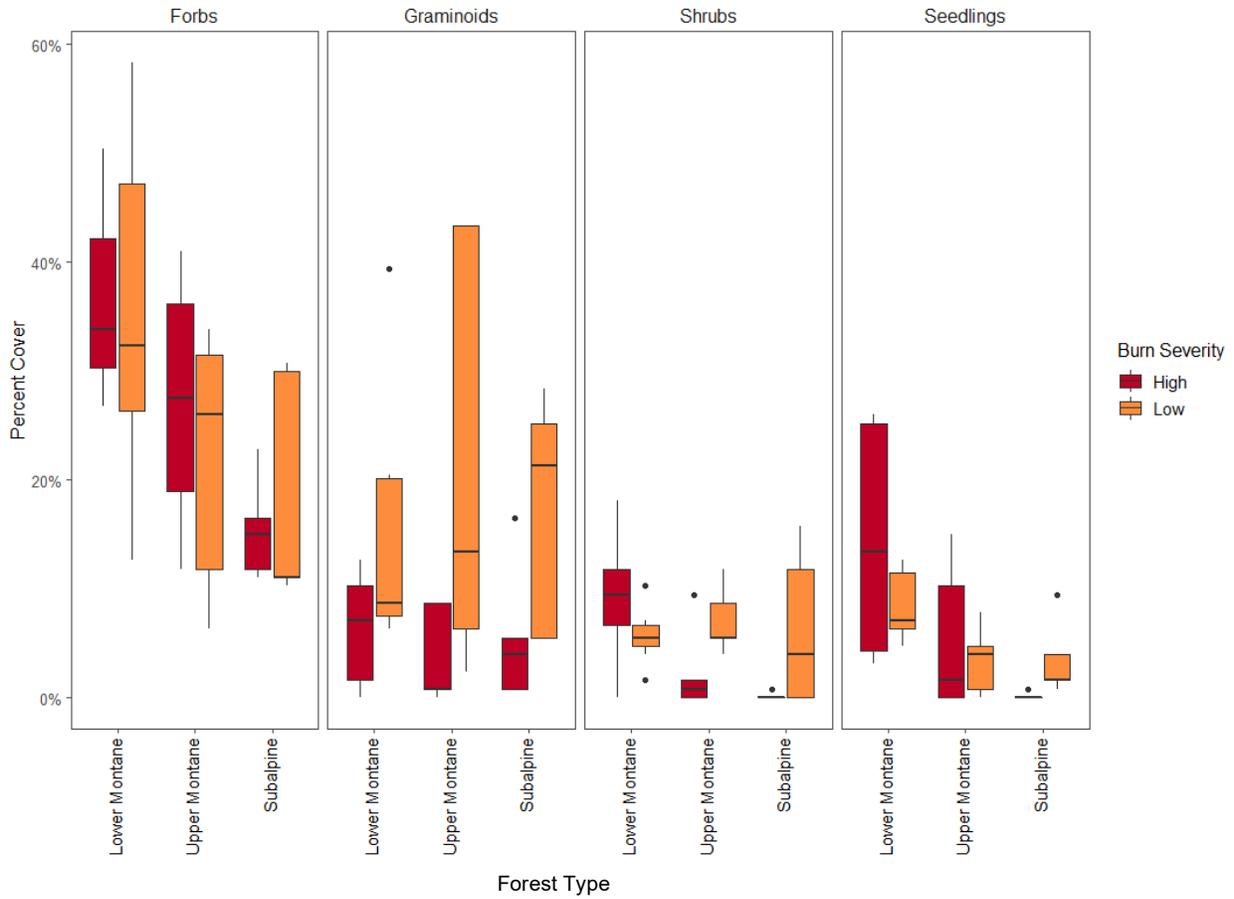


Figure 1.7 Percent cover of understory plants by functional group across all sites, separated by forest type and colored by burn severity (n=34).

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