Forest vulnerability to disturbances

Camille Stevens-Rumann, Forest and Rangeland Stewardship Colorado State University*

Paula Fornwalt, Rocky Mountain Research Station, Fort Collins, CO

*Camille Stevens-Rumann
C.Stevens-Rumann@colostate.edu
Department of Forest and Rangeland Stewardship
Colorado State University
1472 Campus Delivery
Fort Collins, CO 80523-1472
Phone: 602-509-5077

Section 1: Abstract

As ecosystems become more impacted by disturbances it is critical to understand how our natural communities are responding and what impact our management actions have on these ecosystem responses. In this study, we examined understory plant community responses to treatments and wildfires. We examined treatments as a low severity forest disturbance, while high severity fire represent high severity disturbance and low severity fire likely falling somewhere in between. We used plant functional types to understand how communities are changing and perhaps promoting certain groups of species. We sampled 67 plots in areas that experienced fuels reduction treatments between 2009-2013, low severity or high severity wildfire between 2010-2012, or that were untreated and unburned. Sampling was conducted in 2017 (6 plots) and 2018 (61 plots), 5-9 y post-disturbance. We found that understory plant cover increased with increasing severity of disturbance, as did species richness. Forbs, invasive forbs, and shrubs cover also increased with disturbance severity with the highest abundances on high severity burned areas. Moreover, overall community composition differed along the disturbance severity gradient, as well as along overstory structure, coarse wood cover, and elevational gradients. Plant communities are changing in response to disturbances and in these areas of mixed-use historically, and high human traffic currently, these changes are driven by changes in abundance of invasive species. Forest treatments should be approached with caution, though high severity fires present a greater risk to both forest structure and plant community shifts compared to forest treatments.

Section 2: Introduction

The effects of climate change are now beginning to be realized world-wide, generating considerable interest in understanding how our natural systems might be affected. Disturbances such as wildfires have long been known to influence plant communities in forested ecosystems west-wide, but when combined with a warmer climate, they may bring about novel impacts (Millar and Stephenson 2015, Bowman et al. 2017). As such, there is a critical need to understand how plant communities will respond to disturbances, and how we may facilitate resiliency to these stressors through management.

Multiple studies have demonstrated that warmer and drier conditions following recent disturbances like high severity forest fires may lead to tree regeneration failures, thereby decreasing forest resiliency (Rother et al. 2016, Stevens-Rumann et al. 2017). Other studies have demonstrated that species transitions are occurring following recent high severity forest fires not just in terms of trees but in terms of understory species as well, with species more tolerant of a warmer and drier climate favored (Stevens et al. 2015, Stevens et al. in review). These studies utilized the biogeographic affinity of individual species in plant communities, or the climatic tolerances of taxa based on the regions and time periods under which they evolved and diversified (Wiens & Donoghue 2004), to examine whether species originating in warmer and drier climates were more favored by high severity fire than those originating in cooler and wetter climates. Thus, this approach allows for an evolutionary explanation for species preferences and dominance under certain site and climatic conditions (Stevens et al. 2015).

However, topography and other local features can strongly alter these transitions. These local features can potentially buffering the effects of changing climate and creating microclimate refugia that act to slow community transition for hotter and drier communities (Dobrowski 2010; Rapacciuolo et al. 2014; Spasojevic et al. 2014), or conversely accelerate or exacerbate these changes on south facing slopes (Kemp et al. 2016). Thus, there may be expansions of some ecosystem types and species, while a reduction in others. However, the extent to which this is already occurring is poorly understood with minimal research about these changing ecosystems on the Front Range of Colorado.

As a warmer climate begins to play a larger role in shaping our landscapes it is important to promote management actions that may improve the longevity of our much loved ecosystems, identify refugia for those most vulnerable individuals, and begin the conversation and acceptance that many of our ecosystems may look differently over the coming decades. In this study we utilized a range of fuel reduction management actions performed on Boulder County and City of Boulder properties, as well as wildfires that burned on County and City properties, with two primary objectives: 1) Examine how in forested ecosystems both overstory and understory species are already changing as a result of management actions and wildfires. 2) Determine the biogeographic affinity for dominant plant species on both City and County properties and how they changed as a result of the disturbance

Section 3: Methods

Field data collection

We conducted our field work in ponderosa pine (*Pinus ponderosa*) and dry mixed conifer sites on and surrounding City of Boulder and Boulder County lands (Figure 1). Sites fell into one of four disturbance classes: 1) control, 2) fuel treatment, 3) low to moderate severity wildfire, and 4) high severity wildfire. Class one sites were in unburned and untreated stands. Class two sites were in stands unburned by wildfire, but treated by fuels reduction treatments (including thinning and restoration treatments). Treatments were performed between 2009 and 2013. Class three sites were untreated prior to wildfire, but burned at low to moderate severity with less than 80% canopy mortality. Class four sites were untreated prior to wildfire and burned at high severity, with high canopy mortality (>80%). Class three and four sites were in areas that burned in the 2010 Fourmile Canyon Fire, the 2010 Dome Fire, and the 2012 Flagstaff Fire. We established 13 control sites, 16 treatment sites, 14 low severity sites and 18 high severity sites; these sites were established and subsequently measured in 2018. We supplemented these sites with an additional three control and three fuel treatment sites that had been previously established and measured on Boulder County lands in 2017 (Briggs et al. 2017).

We conducted measurements at each site in a 0.04-ha circular plot. Four transects radiated from plot center in the cardinal directions (sensu Briggs et al. 2017), along which we recorded all vascular understory plant species and substrate types (e.g., litter, bare ground, fine

(<7.6 cm diameter) wood, coarse (>7.6 cm diameter) wood) encountered at 100 evenly-spaced observation points. We also conducted a complete inventory of all understory species present in the entire 0.04-ha plot. Unknown plants were collected for later identification. While most plants were ultimately identified to the species level (varieties and subspecies were not distinguished), some were only identified to the genus level or were not identified at all, because key morphological characteristics were not sufficiently developed. All plants identified to the genus level are hereafter also referred to as species. We subsequently assessed the growth form and nativity for understory species using the USDA Plants Database (2018) and local botanical keys (e.g., Harrington 1964; Ackerfield 2018). We also subsequently used Raven and Axelrod's (1978) tome on the evolutionary origin of the California flora to assign understory species a biogeographic affinity of either north-mesic or south-xeric (sensu Stevens et al. 2015; Stevens et al. in prep). North-mesic species were in families or genera that Raven and Axelrod (1978) classified as north temperate elements of the California flora, while south-xeric species were in families or genera that they classified as Madrean-Tethyan, California Floristic Province, warm temperate, or desert elements.

Additionally, we measured all overstory (>1.4 m tall) trees in the 0.04-ha plots for diameter at breast height, species and height. Elevation, aspect, and slope were also taken at each site.

Data analysis

We investigated how various measures of understory plant richness and cover varied among the four disturbance classes using JMP (SAS Institute Inc. 2007). Total richness was calculated by tallying the number of species per 0.4-ha plot. Total cover was calculated by summing the cover of all species along each transect and averaging across the four transects per plot. Richness and cover for functional groups defined by growth form and nativity (i.e., native graminoid, native forb, native shrub, invasive graminoid, invasive forb, invasive shrub) and by biogeographic affinity (i.e., north-mesic and south-xeric) were calculated in a similar manner. To understand total and functional group richness and cover responses to disturbance classes, we used one-way analysis of variance, with disturbance class as the predictor variable. When an overall difference among classes was detected (α=0.050), we used a Tukey's HSD test to identify pairwise differences between them. We also examined differences in overstory tree density and basal area and in substrate cover among disturbance classes to provide insight into where differences in understory community may be driven by changes in overstory structure versus perhaps a response to the disturbance class itself.

We used non-metric multi-dimensional scaling (NMS) ordination and multi-response permutation procedures (MRPP) in PC-ORD (MjM Software Design 2016) to investigate whether the four disturbance classes differed in overall understory plant community composition. These analyses were conducted following the recommendations of McCune and Grace (2002). We used our species cover data in the analyses, with species found in the plot inventories but not along the transects assigned a nominal cover of 0.25%. We omitted species occurring in <5% of the plots to reduce noise in the dataset. To conduct the NMS ordination analysis, we first assessed the dimensionality of the dataset by running 250 ordinations with real data and 250 ordinations with randomized data using a step-down in dimensionality procedure and a random starting configuration. Each run used the Sørensen distance measure, a maximum of 500 iterations, and a stability criterion of 0.00001. We identified the optimal preliminary configuration as the one that had a significant (α=0.050) p-value and that minimized the number of dimensions in the solution while also minimizing stress, a measure of "badness of fit." Then, we conducted a final ordination run with the optimal preliminary configuration used as the starting configuration. Last, we rigidly rotated the final configuration to align disturbance class with axis one, with the classes ranked along our disturbance gradient from least disturbed to most disturbed (i.e., 1 = control, 2 = thinned, 3 = low severity fire, 4 = high severity fire), and we calculated the Pearson's R^2 correlation between ordination axes and environmental variables including treatment, elevation, aspect, live overstory tree density and basal area, and cover by substrate type. We overlaid environmental variables that were strongly correlated (R^2 >0.250) with one or more axes on the ordination as vectors. We used the Sørensen distance measure to conduct the MRPP analysis. Following a significant (α=0.050) overall test, we conducted pairwise tests between disturbance classes and used a Bonferoni correction to account for multiple comparisons (α= 0.050/6 =0.008).

Results

We identified 268 different species in our plots. Of those, 45 appeared on at least a third of the plots (Table 1). An additional 65 species only occurred on only one plot. Species richness, or total number of species per plot, increased across the disturbance gradient with the highest mean species per plot on low and high severity burned plots ($F=2.29$, $P=0.040$). Overstory live tree density varied significantly among disturbance types ($F=22.12$, $P<0.001$), with the highest density in control plots with a density of 820 trees ha^{-1}, followed by low severity burned plots and mechanically treated plots which did not vary from one another at densities of 289 trees ha^{-1} and 303 trees ha^{-1} respectively. Only two plots in our high severity disturbance type had any living trees, for an overall mean live tree density of 44 trees ha^{-1}.

In large part, control and treated areas were similar compared to low severity and high severity sites which were significantly different from unburned sites, in terms of understory species metrics. Percent total understory vegetation cover increased with increasing disturbance severity, with significantly higher percent cover on low and high severity burned sites, compared to treated and control sites ($F=19.08$, $P<0.001$; Figure 2a). Additionally, high severity burned areas had significantly higher bare ground or rock substrate ($F=27.56$, $P<0.001$; Figure 2b) and significantly lower litter cover compared to low severity fire as well as treated and control areas ($F=24.84$, $P<0.0001$; Figure 2c). The difference in cover was predominantly driven by increases in total forb, total shrub, total graminoids, and invasive forb frequency across the disturbance gradient, with the highest average frequency of both native and invasive forb cover and shrub cover in high severity burned areas ($F>6.6$, $P<0.0006$; Figure 3). Total graminoid cover did vary significantly across among disturbance types ($F=3.56$, $P=0.0191$), while invasive graminoid cover, similarly had the highest mean cover on burned areas, however this trend was only marginally significant ($F=2.73$, $P=0.053$; Figure 3d).

Richness followed similar patterns. Low and high severity burned sites had significantly more species richness than control sites ($F=3.63$, $P=0.0175$) and this was driven by an increase in exotic species ($F=5.87$, $P=0.0014$) not native species ($F=1.05$, $P=0.38$). By growth form, graminoid, forb, and shrub richness varied among the four disturbance types but with different patterns. Shrub richness was greatest on low severity sites and did not vary among high severity, treated, and control ($F=3.21$, $P=0.029$). Graminoid richness was highest in treated sites and did not vary among the low and high severity burned sites and control sites ($F=3.05$, $P=0.035$). Forb richness was highest in low and high severity burned sites and did not vary between control and treated sites ($F=5.19$, $P=0.003$).

Biogreographic affinity varied by cover but not richness among disturbance types. Cover of both north-mesic species and south-xeric species was highest on high severity burned sites, likely because total cover was also highest on these sites ($F>7.27$, $P<0.003$). When examining the proportion of north-mesic and south-xeric cover, compared to total cover there is a significant decrease in north-mesic species at low and high severity sites compared to control and treatments ($F=3.11$, $P=0.030$). Neither north-mesic species richness nor south-xeric species richness varied among disturbance types ($F<1.45$, $P>0.230$). However, there were many species that were unable to be assigned a biogeographic affinity using Raven and Axelrod (1978). In the case of cover, this "unknown affinity" group represented on average anywhere from 14-33% of the mean total cover per disturbance type with individual plots having as much as 70% of cover with unknown affinity.

We expected certain functional groups to be most prone to thrive in highly disturbed areas, such as invasive species (McGlone et al. 2009, Fornwalt et al. 2010, McGlone et al. 2010). We had a total of 40 invasive or non-native graminoids and forbs. Of these *Verbascum thapsus, Taraxacum officinale, Poa pratensis,* and *Lactuca serriola* occurred on more than 40 of our plots, while *Tragopogon dubius* and *Bromus tectorum* occurred on 57 and 58 of our 67 plots, respectively. Only two control plots had no non-native species observed. We saw an increase in invasive graminoids and forbs along the disturbance gradient; however, only the invasive forbs increased significantly at an $\alpha=0.050$ level. While treated areas experienced an increase in invasive plant cover and number of invasive species, burned areas were more substantially affected. Incidence of invasive species during complete inventory of species also varied significantly with an average of five invasive species per plot in control sites, eight species in treated areas and ten in both low and high severity burned sites ($F=15.90$, $P<0.001$). Thus, manager consideration of the risks of smaller increases in invasive plants following treatments and the possibility of lower severity wildfires, should one occur, must be weighed against the possibility of high severity fire that may also result in the establishment and spread of invasive plants.

The NMS ordination analysis produced a three dimensional solution that explained 75% of the variation in the understory plant community composition dataset (stress=15.928; Figure 4). Axes 1, 2, and 3 accounted for 22, 30, and 23% of the variation, respectively. Plots appeared to separate in ordination space somewhat by disturbance class, with control plots appearing to be most similar in composition to treated plots and least similar to high severity fire plots. This visual assessment was supported by the strong correlation between ordination axis one and ranked disturbance class ($R^2=0.655(+)$) and by the results of our MRPP analysis (Figure 4). Ordination axis one was also strongly correlated with coarse wood cover ($R^2=0.282(+)$), live overstory tree basal area (($R^2=0.623(-)$), and live overstory tree density (($R^2=0.357(-)$). Meanwhile, ordination axis two was strongly correlated with elevation ($R^2=0.356(+)$).

Discussion

We expect that the primary drivers of these community differences are the differences in overstory structure due to either the treatments or the wildfires, as others have shown (Springer et al. 2018). However, given that we saw many differences in both richness and cover between treated sites and low severity burned sites in spite of similar overstory structure, aspects of the disturbance type itself are likely influencing the subsequent plant community. This may be, in part, due to the differences in litter cover that can inhibit plant growth (Xiong and Nilsson 2001) and was much more abundant in treated areas than either high or low severity burned areas. Additionally the wildfire itself may stimulate plant growth, or release more seeds for germination compared to a mechanical treatment.

Given that the degree of overstory reduction has been shown to relate to the increased prevalence of species adapted to warmer and drier climates (Stevens et al. 2015, Stevens et al. in prep), we expected that such species would be promoted the most at our high severity sites.

Unfortunately, we have been unable to definitively evaluate this hypothesis because we have not yet been able to assess the biogeographic affinity for all species encountered on our sites -- our proposed approach for characterizing climatic preferences. Similar to Stevens et al. (2015) and Stevens et al. (in prep), our main source of information for determining biogeographic affinity was Raven and Axelrod (1978), which describes the evolutionary origins of the families and/or genera comprising the California flora. While there is substantial overlap between the floras of the City and County of Boulder and California at the family and/or genus level, the City/County of Boulder's flora also contains many elements not found in California. 142 species or 31% of the total species on our sites could not be assigned a biogeographic affinity. Moreover, the flora of the City/County of Boulder also contained many invasive species, which are typically not included in studies of biogeographic affinity. We will continue to search for other sources of biogeographic affinity information, and/or explore other methods for assessing species' climatic preferences.

Overall we found substantial differences in communities following both mechanical treatments and wildfires. In part the difference was a result of canopy openings that allowed the release of numerous plant species, however we also observed significant differences in plant cover between low severity burned areas and treated areas that did not correspond to differences in overstory. Instead the higher plant cover in low severity sites were likely a result of the decrease in litter cover compared to mechanical treatments and the higher proportion of bare ground substrate. We also observed a significant increase in the number of non-native species as well as the cover of non-native species as a result of this plant release. This study demonstrates the need for careful treatment implementation and fire effects mitigation in areas of both mixed past land use and continued high human use, to prevent invasion of non-native species.

References

Ackerfield, J. (2015) Flora of Colorado. Botanical Research Institute of Texas Press, Fort Worth, Texas, USA.

Bowman D.M., Williamson, G.J., Abatzoglou, J.T., Kolden, C.A., Cochrane, M.A. & Smith, A.M. (2017) Human exposure and sensitivity to globally extreme wildfire events. Nature Ecology & Evolution 1, 0058.

Briggs, J.S, Fornwalt, P.J. & Feinstein, J.A. (2017) Short-term ecological consequences of collaborative restoration treatments in ponderosa pine forests of Colorado. Forest Ecology and Management 395, 69-80.
Dobrowski, S.Z. (2010) A climatic basis for microrefugia: the influence of terrain on climate. Global Change Biology 17, 1022–1035.
Fornwalt, P.J., Kaufmann, M.R., & Stohlgren T.J. (2010) Impacts of mixed severity wildfire on exotic plants in a Colorado ponderosa pine–Douglas-fir forest. Biological Invasions 12, 2683-2695.
Fornwalt, P.J. & Kaufmann, M.R. (2014) Understory plant community dynamics following a large mixed severity wildfire in a *Pinus ponderosa-Psuedotsuga menziesii* forest, Colorado, USA. Journal of Vegetation Science 25, 805-818
Harrington, H.D. (1964) Manual of the Plants of Colorado, 2nd ed. Swallow Press, Chicago, Illinois, USA.
Intergovernmental Panel on Climate Change (2016) Climate change synthesis report. Cambridge University Press, Cambridge, UK.
Kemp, K.B., Higuera, P.E. & Morgan, P. (2016) Fire legacies impact conifer regeneration across environmental gradients in the US northern Rockies. Landscape Ecology 31, 619–636.
McCune, B. & Grace, J.B. (2002) Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon, USA.
McGlone C.M., Springer J.D., & Covington W.W. (2009) Cheatgrass Encroachment on a ponderosa pine forest ecological restoration project in northern Arizona. Ecological Restoration 27, 37-46.
McGlone C.M., Stoddard M.T., Springer J.D., Daniels M.L., Fule P.Z., & Covington W.W. (2012) Nonnative species influence vegetative response to ecological restoration: two forests with divergent restoration outcomes. Forest Ecology and Management 285, 195-203.
Millar, C.I. & Stephenson, N.L. (2015) Temperate forest health in an era of emerging megadisturbance. Science 349, 823–826.
MjM Software Design (2016) PC-ORD Version 7.04. Gleneden Beach, OR.
Rapacciuolo, G., Maher, S.P., Schneider, A.C., Hammond, T.T., Jabis, M.D., Walsh, R.E., Iknayan, K.J., Walden, G.K., Oldfather, M.F., Ackerly, D.D. & Beissinger, S.R. (2014) Beyond a warming fingerprint: individualistic biogeographic responses to heterogeneous climate change in California. Global Change Biology 20, 2841–2855.
Raven, P.J. & Axelrod, D. (1978) Origin and Relationships of the California Flora. CA, University of California Press, Berkeley, CA.
Rother, M.T. & Veblen, T.T. (2016) Limited conifer regeneration following wildfires in dry ponderosa pine forests of the Colorado Front Range. Ecosphere 7, e01594.
SAS Institute Inc. (2007) JMP Version 7. Cary, NC.
Spasojevic, M.J., Damschen, E.I. & Harrison, S. (2014) Patterns of seed dispersal syndromes on serpentine soils: examining the roles of habitat patchiness, soil infertility and correlated functional traits. Plant Ecology & Diversity 7, 401–410
Springer J.D., Huffman D.W., Stoddard M.T., Sanchez Meador A.J., & Waltz A.E.M. (2018) Plant community dynamics following hazardous fuel treatments and mega-wildfire in a warm-dry mixed-conifer forest of the USA. Forest Ecology and Management 429, 278-286.

Stevens, J.T., Safford H.D., Harrison, S., & Latimer A.M. (2015) Forest disturbance accelerates thermophilization of understory plant communities. Journal of Ecology 10, 1253-1263.
Stevens, J.T., Miller, J.E.D, & Fornwalt, P.J. (In prep.). Fire severity and changing composition of forest understory plant communities.
Stevens-Rumann, C.S., Kemp, K., Higuera, P., Harvey, B., Rother, M., Donato, D., Morgan, P., & Veblen, T. (2017) Evidence for declining forest resilience to wildfires under climate change. Ecology Letters doi: 10.1111/ele.12889
USDA NRCS (2018) The PLANTS database, Version 3.1 (http://plants .usda.gov) National Plant Data Center, Baton Rouge, LA, USA.
Wiens, J.J. & Donoghue, M.J. (2004) Historical biogeography, ecology and species richness. Trends in Ecology & Evolution 19, 639–644.
Xiong S.J., Nilsson C. (1999) The effects of plant litter on vegetation: a meta-analysis. Journal of Ecology 87, 984-94.

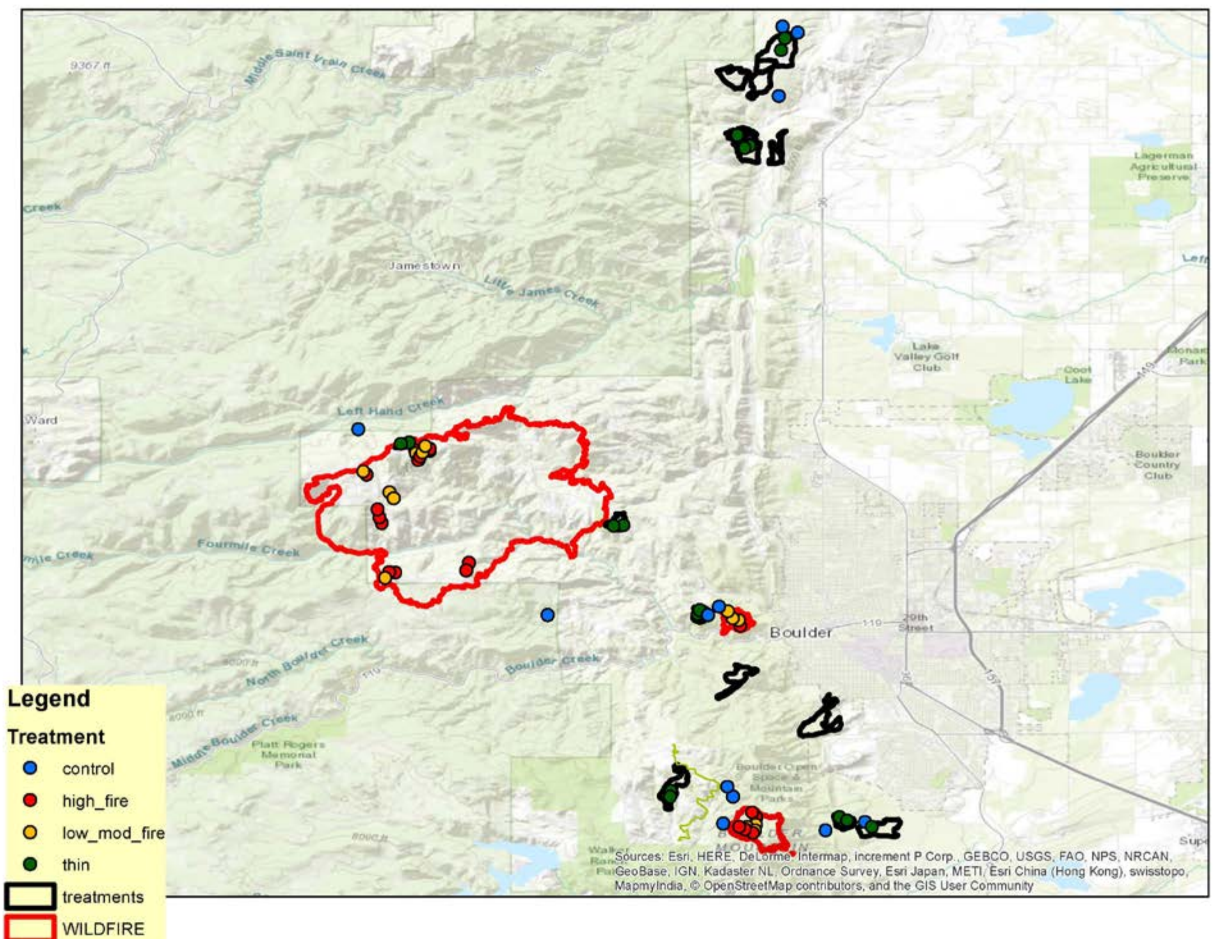

Figure 1: Wildfires (red) and thinning or forest restoration treatments (black) that were used for site selection for study areas. Control plots (blue) in nearby areas to treatments and wildfires, high severity sites are indicated with red points, low severity points in yellow and treated areas in green.

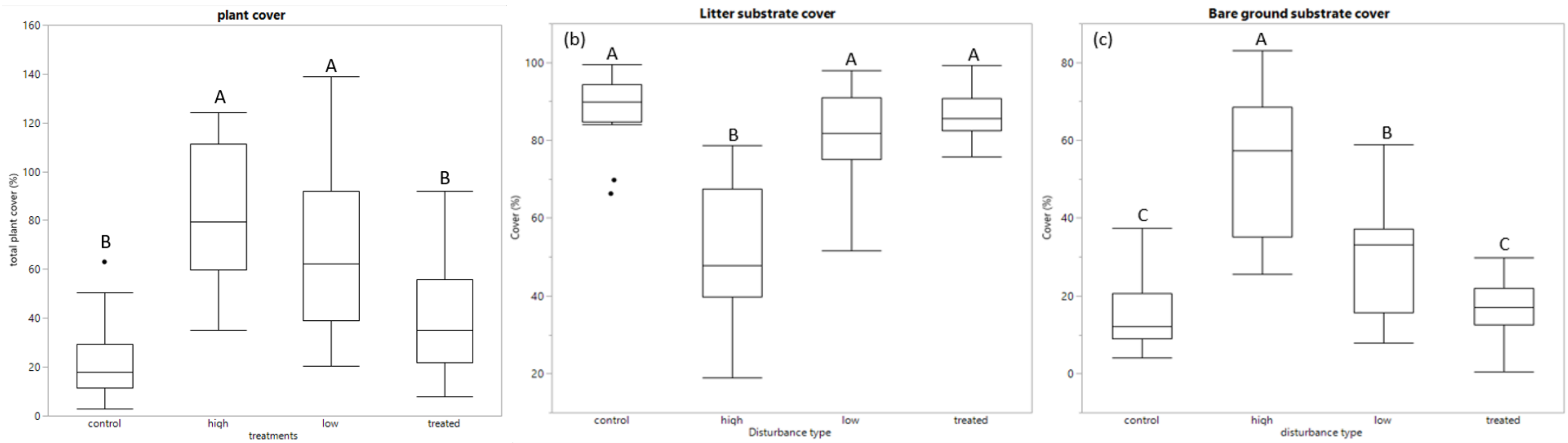

Figure 2: box plots show mean and quartiles in cover among the four disturbance types (control, high severity, low severity, and non-burning treatments). (a) indicates percent total cover of all plants, (b) indicates litter substrate cover, and (c) shows bare ground and rock substrate cover. Letters above each figure show results of a Tukey's HSD test; significant differences are indicated by different letters.

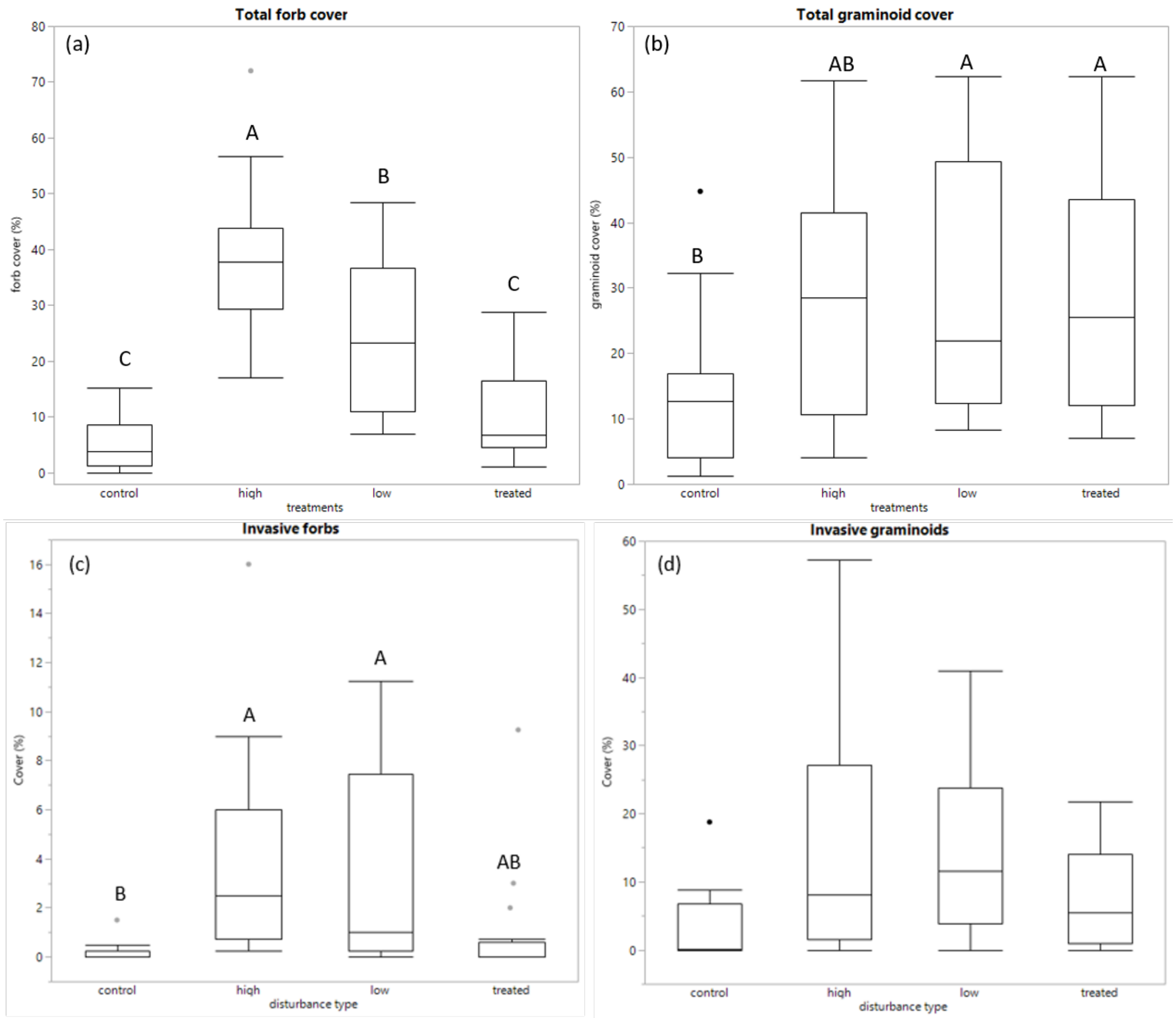
Total forb cover
(a)
forb cover (%)
treatments
control
high
low
treated
C
A
B
C
Total graminoid cover
(b)
graminoid cover (%)
B
AB
A
A
Invasive forbs
(c)
Cover (%)
disturbance type
B
A
A
AB
Invasive graminoids
(d)

Figure 3: box plots show mean and quartiles in cover a among the four disturbance types (control, high severity, low severity, and non-burning treatments). (a) cover of total forbs, (b) indicates cover of total graminoids, (c) indicates cover of non-native forbs, while (d) indicates cover of non-native graminoids. Letters above each figure show results of a Tukey's HSD test; significant differences are indicated by different letters.

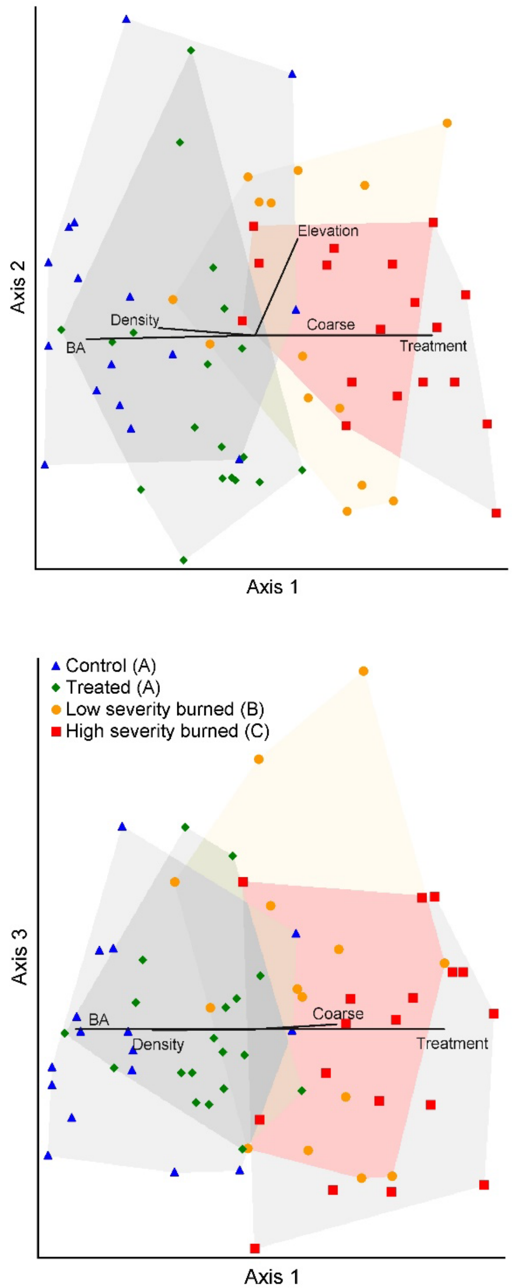

Figure 4. Axis 1 versus 2 (top) and axis 1 versus 3 (bottom) of a nonmetric multidimensional scaling (NMS) ordination analysis of understory plant community composition at control, thinned, low severity fire, and high severity fire plots. Plots for each disturbance class are grouped by shaded convex hulls. Environmental variables that were strongly correlated (R^2>0.250) with one or more axes are overlaid on the ordination as vectors (BA = overstory live tree basal area; density = overstory live tree density; coarse = coarse wood cover). Letters in parentheses in the legend indicate results of a multi-response permutation procedures (MRPP) analysis; significant compositional differences are indicated by different letters.

Table 1: Forty-five most common species or genera, as well as the number of plots on which the species was found.

Species	**# of plots**
Carex	67
Heterotheca villosa	64
Artemisia ludoviciana	62
Rock	60
Bromus tectorum	58
Tragopogon dubius	57
Elymus elymoides	53
Artemisia frigida	52
Penstemon virens	52
Poa pratensis	51
1000 hr fuel	50
Achillea millefolium	50
Verbascum thapsus	50
Pinus ponderosa	49
Campanula rotundifolia	48
Lactuca serriola	48
Solidago	48
Taraxacum officinale	48
Ceanothus fendleri	47
Ribes cereum	46
Leucopoa kingii	45
Symphyotrichum porteri	42
Koeleria macrantha	41
Poa compressa	40