Prescribed fire shrub consumption in a Sierra Nevada mixed-conifer forest

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Abstract

Live shrubs in forest understories pose a challenge for mitigating wildfire risk with prescribed fire. Factors driving shrub consumption in prescribed fires are variable and difficult to explain. This study investigated spatial patterns and drivers of Sierra Nevada mixed-conifer forest shrub consumption in prescribed fires through analysis of high-resolution imagery taken before and after prescribed fire. We applied a spatially explicit, generalized additive model to assess tree cover and coarse woody material as potential drivers of shrub consumption. Shrub cover in two experimental stands prior to burning was 38% and 59% and was 36% and 45% one-year post burn. In both stands shrub patch density increased, while area-weighted mean patch size and largest patch index decreased. Increased local percent cover of coarse woody material was associated with increased shrub consumption. These findings provide information for prescribed fire managers to help better anticipate shrub consumption and patchiness outcomes under similar conditions.

KEYWORDS:
High resolution imagery, Teakettle Experimental Forest, mixed-conifer, fire hazards, fuel treatments, coarse woody debris
INTRODUCTION

Shrubs are an essential ecosystem component of forested environments in the western United States and are important for wildlife, nutrient cycling, and biodiversity (Hunter 1990; North et al. 2016). However, shrubs can be strong competitors for soil moisture, which can limit tree establishment and growth (Fowells and Stark 1965; McDonald and Fiddler 1989). Disturbances which open forest canopies, such as fire, increase light availability on the forest floor and promote shrub establishment and growth. Furthermore, fire stimulates seed germination and re-sprouting of many Mediterranean-climate shrub species, which in combination with canopy disturbance, can lead to prolific shrub establishment and growth (Collins et al. 2019; Stephens et al. 2020).

The use of prescribed fire to reduce fuel loads and mitigate wildfire risk has a long history in western North American forests, but long-term and large-scale implementation has yet to occur (Biswell 1989; North et al. 2012). There are numerous studies which describe the ecological and wildfire hazard reduction impacts of prescribed fire in mixed-conifer forests (e.g., Fernandes and Botelho 2003; Battaglia et al. 2008; Stephens et al. 2009). There is some information on longer-term forest understory responses following prescribed fire (e.g., Goodwin et al. 2018), but similar information on fuel dynamics is comparatively lacking. This information can be particularly important to managers in areas where prescribed fire facilitated major fuel changes (i.e. timber litter to shrub- or grass-dominated). While a transition to grass as the dominant fuel type may be relatively benign or beneficial from a wildfire hazard standpoint, a transition to a shrub fuel type can be problematic (Coppoletta et al. 2016). Under wildfire conditions, shrubs can exacerbate surface fire intensity, as well as facilitate the movement of fire from the surface to the canopy. However, like other live fuels, shrubs can be challenging to burn...
in prescribed fires, which tend to be conducted under moderate fire weather conditions (Ottmar et al. 2016). Understanding shrub consumption and responses to repeated prescribed burns will be important as the need for large-scale prescribed fire is increasingly recognized in western North American forests (USDA-USDI 2014).

Shrub consumption in prescribed fires can be highly variable and there are few studies which quantitatively investigate this variability (Prichard et al. 2017). Furthermore, live forest understory fuels have been generally overlooked in many prescribed fire studies (Agee and Skinner 2005). Shrub consumption is impacted by their live moisture content which in some cases can inhibit fire spread (Stephens et al. 2009). This study addresses this knowledge gap by not only describing the spatial patterns of shrub consumption during prescribed fire, but also identifying the factors associated with consumption. Specifically, we investigate how coarse woody material (CWM) and tree cover relate to shrub consumption. CWM can burn for long durations, which may release enough heat to allow for ignition and spread through live shrubs, even under prescribed fire conditions (Tappeiner et al. 2015). Conifer tree cover may influence shrub consumption through deposition of needles and branches, which, at low moisture contents, can facilitate ignition and fire spread (Andreu et al. 2012). Conversely, shading from tree cover can result in higher live fuel moisture of shrubs due to reduced evaporative demand on the plant and the soil (Ma et al. 2010). Using high-resolution imagery collected before and after prescribed fire within a long-term southern Sierra Nevada study area, we investigated (1) how do the spatial patterns in shrub distribution change from pre- to post-prescribed fire?; (2) is CWM a driver of shrub consumption; and (3) is tree cover a driver of shrub consumption? (4) is topographic wetness index (TWI) a predictor of shrub consumption?
METHODS

Study site

This study was conducted at the Teakettle Experimental Forest, located in the southern Sierra Nevada, California. Teakettle is a 1300-ha old-growth mixed-conifer forest and is located at 36° 58’ N and 119° 2’ W with elevations varying from 2,000 to 2,800 m. It has a Mediterranean climate and receives an average of 134 cm of precipitation annually (North et al. 2002, Innes et al. 2006). The mixed-conifer forests at Teakettle are composed of Jeffrey pine (Pinus jeffreyi), sugar pine (Pinus lambertiana), incense-cedar (Calocedrus decurrens), white fir (Abies concolor), and black oak (Quercus kellogii) (North et al. 2002). Shrub species include mountain whitethorn (Ceanothus cordulatus), bush chinquapin (Chrysolepis sempervirens), pinemat manzanita (Arctostaphylos nevadensis), green leaf manzanita (A. patula), snowberry (Symphoricarpos mollis), sticky currant (Ribes viscosissimum), Sierra gooseberry (R. roezlii) and hazelnut (Corylus cornuta). Mountain whitethorn and bush chinquapin are the most abundant shrub species (North et al. 2002). Historical fire occurrence reconstructed in this area determined a mean return interval for individual trees of 17 years (range of 3 to 115 years) (North et al. 2005). The last widespread fire occurred in 1865. From 1865 to the present, there were two small wildfires that burned within the Teakettle watershed.

Our study took advantage of a long-term experiment which was implemented in 1998 and has been maintained and monitored through the present. The experiment was designed to investigate the effects of thinning and prescribed burning on Sierra Nevada mixed-conifer forests. The study was conducted in two 4 ha units which had two prescribed fires and one thinning treatment. The two units had different thinning treatments applied: one received an understory thin, retaining approximately 40% canopy cover while the other unit received
overstory thin which was much heavier (Goodwin et al. 2020). The understory thin removed trees between 25 and 76 cm at diameter at breast height (DBH). On average this left 44 trees ha\(^{-1}\) with an average DBH of 91 cm (North 2002). The overstory thin removed trees greater than 25 cm while retaining on average 18 trees ha\(^{-1}\) regularly spaced 20-25 m apart, with an average DBH of 103 cm (North et al. 2007).

Both sites were subjected to a prescribed burn in 2001 and again in October 2017, to imitate the mean-historic interval for the area (Goodwin et al. 2020). Objectives for the prescribed fires were to replicate fire effects of the historical fire regime with flame heights <2 m from consumption of surface and ladder (<25 cm DBH) fuels. Prescribed fires were conducted by Sierra National Forest personnel under the following general prescription parameters: 10-15\% 10-hr fuel, 50-75\% relative humidity, 0-10 °C air temperature, and 0-5 m s\(^{-1}\) wind speed. Both prescribed burns were conducted after the first fall precipitation (2 cm in 2001 and 1.2 cm in 2017), with actual daytime temperatures of 10-15°C and relative humidity ranging from 25\% (afternoon) to 70\% (3am) (Innes et al. 2006; North pers. observation). During both burns, shrubs resisted combustion unless larger (> 100 hr) surface woody fuels were present and caught fire (North pers. observation). In 2017, the precipitation was 36 cm above the 30-year average with a z-score of 0.86, the temperature was 0.33 degrees Celsius above the 30-year average with a z-score of 0.52. In 2018, the precipitation was 27 cm below the 30-year average with a z-score of -10.86, the average temperature was the same as 2017 (PRISM Climate Group 2020). Both areas are similar in aspect (178-195 AZM), slope (5-6 degrees) and elevation (2024-2042 m). Canopy cover in 2017, as estimated from allometric equations for crown radius (Gill et al. 2000), was 18\% and 19\% for understory and overstory thin units, respectively.
Data Collection

Remotely sensed imagery and on-the-ground measurements were used to assess pre- and post-burn vegetation and surface fuel conditions. We collected the imagery with a hexacopter unmanned aerial system in June 2017 and 2018 at each of the two 4 ha sites. The unmanned aircraft system (UAS) carried a Sony a6000 camera (Sony Corporation, Tokyo, Japan) with a 19 mm prime lens. We used post processed kinematic (PPK) positioning for the image centroids using a pair of EMLID Reach global navigation satellite system (GNSS) receivers (www.emlid.com): one on the UAS which was triggered by the camera shutter, and one positioned on a nearby ridge as a concurrent base station. We post-processed the base station location using rapid ephemeris timings from a nearby CORS site in RTKLib (v2.4.3,http://www.rtklib.com/). All flight planning was conducted using the open-source software Mission Planner (v1.3), within visual line of sight and at 120 m above ground level, with 85% front and 80% side image overlap. These flight plans generated around 110 images 4 ha unit and resulted in a ground sample distance of roughly 2 cm per pixel. We then converted the images to 16-bit linear TIFF files in Python3.6 and used Agisoft Metashape for structure from motion (SfM) processing to generate an orthomosaic. Each image has a ground resolution of just under 2 cm.

High spatial resolution of the UAS imagery (Figure 1) allowed us to visually map and delineate individual shrubs and shrub clusters with segmentation using ArcMap 10.6.1 (Esri, Red-lands, California, USA). This digitizing was conducted by two analysts. Analysts worked on separate plots, though care was taken to ensure the two analysts were calibrated with each other including each analyst outlining a subsection of the other’s pre- and post-fire imagery. Although no quantitative metrics were used in the comparison of the two analysts’ work, based on
qualitative visual inspections of shrub patch delineation there was high agreement. We created a
spatial layer of shrub consumption by differencing pre- and post-fire shrub cover maps. CWM
was also mapped manually with on-screen digitizing of the pre-fire imagery. Although this
approach has the potential of being biased because it was only capable of identifying logs which
were exposed from the shrub layer, we believe the 2 cm resolution of the imagery allowed for
relatively consistent detection of CWM (>30 cm diameter). Furthermore, the complete (wall to
wall) coverage of our imagery is an improvement over field-based methods of mapping, for
which complete coverage would have been impractical. An overstory tree cover layer was
created using a geolocated stem map, for which all trees were mapped and measured prior to the
2017 burn (Goodwin et al. 2020). The stem map includes information such as tree species and
DBH. We used allometric equations from Gill et al. (2000) to approximate the crown area for
each individual tree. The allometric equations were used instead of the imagery because it was
difficult to delineate the canopies in some portions of the imagery due to shadows (Figure 1).

**Data Analysis**

FRAGSTATS (McGarigal and Marks 2012) was used to characterize the spatial patterns
of shrub cover prior to and following the second prescribed fires and to quantify change in shrub
cover after prescribed fire. The moving window summary used for the metric computation
applied the 8-cell neighborhood rule for all the raster files. Three metrics were chosen to describe
spatial patterns of shrubs pre- and post-burn: patch density, the number of patches per hectare
(PD- patch ha⁻¹), largest patch index, the percentage of area of the largest shrub patch (LPI- %),
and area-weighted mean patch size, which gives perspective on landscape structure by weighting
the larger patches more heavily than the simple area mean (AREA_AM- \( \text{m}^2 \)) (McGarigal et al. 2012, Turner and Gardner 2015).

The remainder of the analysis was done in \( \text{R 3.6.1} \) (R Core Team 2020). We fit a Generalized Additive Model (GAM) to explore the potential influence of three factors on shrub consumption in the second prescribed fires: topographic wetness index (calculated from a DEM), percent cover of CWM (as detected in UAV imagery), and percent tree cover (from field-based stem map). To calculate TWI, we used a 1 m digital elevation model (DEM) derived from airborne LiDAR (Fricker et al. 2019). Then using a moving window summary, we reduced the resolution of the DEM to 5m to eliminate noise. We used RSAGA package version 1.3.0 (Brenning et al. 2018) to calculate TWI. We created 1m resolution rasters, the same resolution as the DEM, for the shrub pre- and post-prescribed fire, CWM (presence and absence), tree cover (presence and absence), and burn (pre-fire shrub minus post fire shrub) layers. Using a moving window summary, we assessed the percentage of tree cover and the percentage cover of CWM within a 25m x 25m square (Hagen-Zanker 2006). This window size was chosen because it was the average length of clusters of canopies.

A smoothing parameter was chosen using generalized cross-validation, and the models were fit using the package \texttt{mgcv} version 1.8-23 in the \texttt{R} statistical computing environment (Wood 2011). A GAM was chosen specifically to account for spatial autocorrelation in the response variable (shrub consumption) by fitting two splines on the geographic location of the pixels (one spline for the x direction and one spline for the y direction in the raster grid). Modeling the data in this fashion accounts for spatial trends in the data exterior to the parameters of interest and exhibited as clusters of large residuals (Cressie 2015). To understand the effect of spatial autocorrelation, we created two semivariograms, with and without the spatial splines. We employed model selection to determine which of the factors explored were important in driving
shrub consumption. Initially, we looked at univariate models, then we looked at the addition of the variables of percent cover of CWM, percent tree cover, and TWI. We ranked potential models using the Akaike information criterion (AIC) (Eilers and Marx 1996).

RESULTS

Overall shrub cover prior to burning (second prescribed fire) was 38% in the understory and 59% in the overstory thinning units. Following burning, overall shrub cover decreased to 36% in the understory and 45% in the overstory thinning units. Prior to burning there were 16 logs ha$^{-1}$ in the understory treatment and there were 55 logs ha$^{-1}$ in the overstory treatment. The prescribed fire changed the shrub spatial patterns from pre- to post-prescribed fire (Figure 2). PD increased substantially following the burn in both treatment units, for overstory thin PD increased 1605 patches ha$^{-1}$ and understory thin increased 1016 patches ha$^{-1}$. The LPI and AREA AM decreased in both units (Figure 3). Overstory LPI decreased by 43% and understory LPI decreased by 12%, while overstory AREA-AM decreased by 640m$^2$ and understory AREA-AM decreased by 160 m$^2$. Taken together, these indicate prescribed fire modestly reduced overall shrub cover by breaking up the largest patches, resulting in many more small patches.

Semi variograms for model iterations with and without spatial splines demonstrated a decrease in spatial dependence when a spatial spline was included (Figure A1). As a result, we included a spatial spline as a model parameter. The best fitting model had an adjusted r-squared of 0.38, and included linear variables of percent cover of CWM, tree cover, and TWI (Table A1, A2). All variables were sufficiently independent, with a correlation $\leq .7$ (Figure A2). CWM had a positive effect on shrub consumption, while TWI, and to a lesser extent tree cover, were negatively related to shrub consumption (Figure 4).
DISCUSSION

Shrub Patch Spatial Change

Shrub consumption patterns following prescribed fire (second entry) varied across the two thinning units and resulted in spatial shrub changes. Shrub consumption differences between the two thinning treatments may have been influenced by shrub patch structure (Figure 3). The overstory thin unit had more continuous larger shrub patches that may have facilitated fire spread, while the understory thin unit had less continuous smaller patches that may have inhibited fire spread (Finney et al. 2010). It is worth noting that these different patterns of shrub establishment and growth following initial implementation of thinning and prescribed fire was likely due to the greater reductions in tree density in the overstory thin relative to the understory thin (Zald et al. 2008). Another potential cause for the increased consumption in the overstory thin unit was the higher log density in that unit which may have allowed for longer heating duration on adjacent shrubs and consequently more efficient combustion of the shrubs (Brown et al. 2003; Rabelo et al. 2004). Other studies have similarly found that shrub consumption is increased with the presence of CWM and surface fuels in Sierra Nevada forests (Kauffman and Martin 1990; Lutz et al. 2017).

Despite the strong difference in consumption, both units had similar responses in the metrics from pre- to post-fire: increased in patch density, and reductions in area-weighted mean patch size and in largest patch index (Figure 3). Taken together, these indicate prescribed fire modestly reduced overall shrub cover by breaking up the largest patches, resulting in more small patches, which was more pronounced in the overstory thin unit. However, the different levels of shrub consumption also corresponded with different levels of shrub regrowth following the
second prescribed fire (Figure 2). The link between consumption and regrowth is not entirely clear but is perhaps worth investigation in future work.

**Drivers of Shrub Consumption**

CWM, tree cover, and TWI were all important drivers of shrub consumption, suggesting that consumption is limited by both fuel and local moisture availability. The positive relationship between CWM and shrub consumption (Figure 4) is likely a product of the greater fire residence time and heat release associated with higher loads of CWM (Brown et al. 2003; Rabelo et al. 2004). Both would allow for greater spread in shrubs under the milder weather and fuel moisture conditions associated with prescribed fire.

The modestly negative relationship between tree cover and shrub consumption, and the different effect between the two thinning types at the higher tree cover (Figure 4) are difficult to explain. This is particularly true given the similar overall tree canopy cover estimates for the two units. It is possible that the different pre-fire shrub cover patterns, i.e., larger, more continuous patches in the overstory thin, partially explain this tree cover-treatment interaction. Fire spread and ultimately shrub consumption may have been aided by fuel deposition from nearby trees (Cansler et al. 2019) where shrub cover was more patchy (understory thin), whereas in areas with great shrub continuity (overstory thin) the trees were local disruptions in the continuity, which may have limited spread and consumption nearer to trees. Alternatively, the microclimates associated with the shading of tree canopies could increase the moisture content of those shrubs and this would reduce their combustibility. These assertions are very speculative at this point and would require more focused attention in future studies to fully investigate these potential interactions.
Using the tree cover without differentiating between tree species may have limited the effectiveness of this analysis. With regard to needle drape on shrubs in particular, it is far more likely that pines would have a stronger influence than firs due to the structure of the needles. Single-needled fir’s create dense fuel beds while pines with longer needles and higher terpene content create more flammable fuel beds, and previous studies have shown overstory pine to be an important driver of fuel consumption (Fonda et al. 1998). Also, tree cover variability does not account for the effect of wind on needle dispersal, meaning that being close to the trees does not necessarily mean there will be more needles in the fuel bed of shrubs.

The negative relationship between TWI and shrub consumption is suggestive of an underlying relationship between fine-scale moisture availability and fuel moisture (Meigs et al. 2020). It is possible that under the more moderate fire weather conditions associated with prescribed fire greater fine-scale moisture availability, as indicated by higher TWI values at 5 m spatial resolution, increases live fuel moisture to a point that inhibits fire spread. Further research with replicated study units is needed for a more robust investigation of this hypothesis.

Our work is somewhat limited by the lack of field validation to support the imagers used. Shading from tree canopies created some uncertainty in delineating shrub patches. Field-based mapping of shrubs near trees would have helped understand this uncertainty and possible approaches for accounting for it. However, the overall area obfuscated is very small due to the low canopy cover, making this only a slight limitation. Other factors that were not included in the model such as fire behavior and climatic variables, might have helped explain deviance in the data. Ultimately, more experiments are needed to isolate these factors and their impact on shrub consumption. UAS imagery looks at changes in shrub cover which can be attributed to
consumption and growth; though, we are unable to control for differences in growth potential and actual growth which can be constrained by climatic variables.

Management Implications and Conclusions

Silvicultural methods that increase patchiness of shrubs may reduce fire intensity and ultimately fire-caused mortality of overstory trees. However, it is unclear what level of patchiness is needed to ensure overstory resistance to fire. Areas with a higher proportion of CWM have an increased amount of shrub consumption. Understanding the factors driving shrub consumption as well as the patterns they create may help managers more effectively design and implement fuel treatments and provide better estimates of potential shrub consumption following prescribed burning. Information from this study could be used to refine burning prescriptions to better meet understory objectives and could be used by modelers to predict the responses of shrubs and coarse wood to prescribed fires.

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Declarations

Competing interests

The authors declare there are no competing interests
Author Contributions

MJ conceived of and designed the study, analyzed data, and wrote the paper. BC, SS, MH, and MN contributed to study design, analytical approaches, and writing. FM and HN analyzed the aerial imagery and contributed to writing. JL did statistical analysis and contributed to writing. DK did the image processing and contributed to writing. All authors read and approved the final manuscript.

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Data Availability

Data used in this study is not currently publicly available.

REFERENCES

Agee, J. K., and Skinner, C.N. 2005. Basic principles of forest fuel reduction treatments. Forest Ecology and Management 211:83–96.

Andreu, A. G., Shea D., Parresol, B.R., and Ottmar, R.D. 2012. Evaluating fuel complexes for fire hazard migration planning in the southeastern United States. Forest Ecology and Management 273: 4-16

Battaglia, M. A., Smith F.W., and Sheperd, W.D. 2008. Can prescribed fire be used to maintain fuel treatment effectiveness over time in Black Hills ponderosa pine forests? Forest Ecology and Management 256:2029–2038.

Biswell, H. H. 1989. Prescribed burning in California wildland vegetation management.

University of California Press, Berkeley, CA.
Brenning, A., Bangs, D., and Becker, M. (2018). RSAGA: SAGA Geoprocessing and Terrain Analysis. R package version 1.3.0. https://CRAN.R-project.org/package=RSAGA

Brown, J. K., Reinhardt, E. D., and K. A. Kramer. 2003. Coarse woody debris: Managing benefits and fire hazard in the recovering forest. Page RMRS-GTR-105. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft. Collins, CO.

Cansler, C. A., Swanson, M. E., Furniss, T.J., Larson, A.J., and Lutz, J.A. 2019. Fuel dynamics after reintroduced fire in an old-growth Sierra Nevada mixed-conifer forest. Fire Ecology 15:16.

Cressie, N. A. C. 2015. Statistics for spatial data. Statistics for spatial data. John Wiley & Sons, Ltd. pp.1-26

Collins, B. M., Stephens, S.L., and York, R.A. 2019. Perspectives from a long-term study of fuel reduction and forest restoration in the Sierra Nevada. Tree Rings 29:7-9.

Coppoletta, M., Merriam, K. E., and Collins, B.M. 2016. Post-fire vegetation and fuel development influences fire severity patterns in reburns. Ecological Applications 26:686–699.

Eilers, P. H. C., and Marx, B.D. 1996. Flexible smoothing with B-splines and penalties. Statistical Science 11:89–121.

ESRI 2020. ArcGIS Pro: Release 2.6.0. Redlands, Ca. Environmental Systems Research Institute.

Finney, M. A., J. D. Cohen, I. C. Grenfell, and K. M. Yedinak. 2010. An examination of fire spread thresholds in discontinuous fuel beds. International Journal of Wildland Fire 19:163-170.
Fricker, G.A., N.W. Synes, J.M. Serra-Diaz, M.P. North, F.W. Davis, and J. Franklin. 2019. More than climate? Predictors of tree canopy height vary with scale in complex terrain, Sierra Nevada, CA (USA). Forest Ecology and Management 434: 142-153.

Fonda R.W., Bellanger L.A., and Burley, L.L. 1998. Burning characteristics of western conifer needles. Northwest Science 72: 1–9.

Fowells, H. A., and Stark, N.B. 1965. Natural regeneration in relation to environment in the mixed conifer forest type of California. General Technical Report PSW-24, U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, CA, USA.

Gill, S. J., Biging G.S., and Murphy, E.C. 2000. Modeling conifer tree crown radius and estimating canopy cover. Forest Ecology and Management 126:405–416.

Goodwin, M. G., North, M.P., Zald, H.S.J., Hurteau, M.D. 2018. The 15-year post-treatment response of a mixed-conifer understory plant community to thinning and burning treatments. Forest Ecology and Management 429: 617-624.

Goodwin, M. G., North M.P., Zald, H.S.J., Hurteau, M.D. 2020. Changing climate reallocates the carbon debt of frequent-fire forests. Global Change Biology doi:10.1111/gcb.15318.

Hagen-Zanker, A. 2006. Map comparison methods that simultaneously address overlap and structure. Map comparison methods that simultaneously address overlap and structure 8:165–185.

Hunter, M. L. 1990. Wildlife, forests, and forestry. Principles of managing forests for biological diversity. Wildlife, forests, and forestry. Principles of managing forests for biological diversity.
Innes, J., North, M. and Williamson, N. 2006. Effect of thinning and prescribed fire restoration treatments on woody debris and snag dynamics in a Sierran old-growth mixed-conifer forest. Canadian Journal of Forest Research 36: 3183-3193.

Kauffman, J.B., and Martin, R. E., 1990. Sprouting shrub response to different seasons and fuel consumption levels of prescribed fire in Sierra Nevada mixed conifer ecosystems. Forest Science 36, 748–764.

Lutz, J.A., Furniss, T.J., Germain, S.J., Becker, K.M.L., Blomdahl, E.M., Jeronimo, S.M.A., Cansler, C.A., Freund, et al. 2017. Shrub Communities, Spatial Patterns, and Shrub-Mediated Tree Mortality following Reintroduced Fire in Yosemite National Park, California, USA. Fire Ecology 13, 104–126. https://doi.org/10.4996/fireecology.1301104

Ma, S., Concilio, A., Oakley, B., North, M., and Chen, J. 2010. Spatial variability in microclimate in a mixed-conifer forest before and after thinning and burning treatments. Forest Ecology and Management 259: 904-915.

McGarigal, K., Cushman S.A., and Ene, E. 2012. FRAGSTATS v4: spatial pattern analysis program for categorical and continuous maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following web site: http://www.umass.edu/landeco/research/fragstats/fragstats.html

McDonald, P. M., and Fiddler, G. O. 1989. Competing vegetation in ponderosa pine plantations: ecology and control. General Technical Report PSW-113, U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, CA, USA.
Meigs, G. W., Dunn, C.J., Parks, S.A., and M. A. Krawchuk, M. A. 2020. Influence of topography and fuels on fire refugia probability under varying fire weather conditions in forests of the Pacific Northwest, USA. Canadian Journal of Forest Research 50:636-647.

North, M., Oakley, B., Chen, J., Erickson, H., Gray, A., Izzo, A., Johnson, D., Ma, S., et al. 2002. Vegetation and ecological characteristics of mixed-conifer and red fir forests at the Teakettle Experimental Forest. Page PSW-GTR-186. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA.

North, M., Hurteau, M., Fiegener, R., and Barbour, M. 2005. Influence of fire and El Niño on tree recruitment varies by species in Sierran mixed conifer. Forest Science 51: 187-197.

North, M., Innes J., and Zald, H. 2007. Comparison of thinning and prescribed fire restoration treatments to Sierran mixed-conifer historic conditions. Canadian Journal of Forest Research 37: 331-342.

North, M.P., Collins, B.M., and Stephens, S.L. 2012. Using fire to increase the scale, benefits and future maintenance of fuels treatments. Journal of Forestry 110: 392-401.

North, M., Collins, B.M., Safford, H.D., and Stephenson, N.L. 2016. Chapter 27: Montane forests. Pages 553-577 in H. Mooney and E. Zavaleta, editors. Ecosystems of California University of California Press, Berkeley, CA, USA.

Ottmar, R. D., Hiers, J.K., Butler, B.W., Clements, C.B., Dickinson, M.B., Hudak, A.T., O’Brien, J.J., Potter, et al. 2016. Wood. Measurements, datasets and preliminary results from the RxCADRE project – 2008, 2011 and 2012. International Journal of Wildland Fire 25:1.
Prichard, S. J., Kennedy, M.C., Wright, C.S., Cronan, J.B., and Ottmar, R.D. 2017. Predicting forest floor and woody fuel consumption from prescribed burns in southern and western pine ecosystems of the United States. Data in Brief 15:742–746.

PRISM Climate Group, 2020. Time Series Values for Individual Locations. Accessed 29 December 2020. http://prism.oregonstate.edu

R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rabelo, E. R. C., Veras, C.A. G., J. A. Carvalho, E. C. Alvarado, D. V. Sandberg, and Santos, J.C. 2004. Log smoldering after an amazonian deforestation fire. Atmospheric Environment 38:203–211.

Stephens, S.L., Moghaddas, J.J., Ediminster, C., Fiedler, C.E., Hasse, S., Harrington, M., Keeley, J.E., McIver, et al. 2009. Fire treatment effects on vegetation structure, fuels, and potential fire severity in western U.S. forests. Ecological Applications 19: 305-320.

Stephens, C. W., Collins, B.M., and Rogan, J. 2020. Land ownership impacts post-wildfire forest regeneration in Sierra Nevada mixed-conifer forests. Forest Ecology and Management 468:118161.

Tappeiner, J. C., Bailey, J.D., Harrington, T.B., and Maguire, D.A. 2015. Fire and Silviculture. Pages 316–349 Silviculture and Ecology of Western U.S. Forests. 2nd edition. Oregon State University Press, Corvallis.

Turner, M. G., and Gardner, R.H., 2015. Landscape Metrics. Pages 97–142 Landscape Ecology in Theory and Practice: Pattern and Process. Second. Springer, New York.
USDA-USDI. 2014. The National Strategy: The final phase in the development of the National Cohesive Wildland Fire Management Strategy.

http://www.forestsandrangelands.gov/index.shtml.

Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society: Series B (Statistical Methodology) 73:3–36.

Zald, H. S. J., Gray, A.N., North M., and Kern, R. A. 2008. Initial tree regeneration responses to fire and thinning treatments in a Sierra Nevada mixed-conifer forest, USA. Forest Ecology and Management 256:168–179.
Figure 1. Examples of imagery before (A and C) and after (B and D) the 2017 prescribed fire in the understory unit in the Teakettle Experimental Forest demonstrating contrasting levels of shrub consumption within the unit. Images are paired with (A) and (B) capturing an area with substantial shrub consumption, while (C) and (D) show minimal consumption. This map was created using ESRI ArcGIS Pro 2.6.0 and basemap data from
Figure 2. Shrub cover for the two study units before and after prescribed fire. The unit outlined in orange is the understory unit and the unit outlined in green is the overstory unit. The shrubs depicted in orange burned, shrubs in dark green are new growth, and shrubs in light green are unchanged from pre to post burn. The map and basemap were generated using ESRI (2020).
Caption: Figure 3. Shrub pattern change in the two different-treatments units comparing shrub patch characteristics pre and post prescribed fire. Variables investigated are patch density (PD- patch ha⁻¹), largest patch index (LPI- %), area-weighted mean patch size (AREA_AM- m²), and percentage cover (% cover).
Figure 4. Probability of burn and (left) percent cover of CWM (%), (right) tree cover (%), and (bottom) TWI (m²m⁻¹) where 1 represents 100% probability of burn and 0 represents no probability of burn. The points at 1 and 0 are the observations of pixels burned or unburned. The horizontal axis is the local percent cover within a 25 m by 25 m window for percent cover of CWM and tree cover and a 5 m by 5 m window for TWI.
APPENDIX 1

Figure A1: Semivariograms (Left) a semivariogram without the spatial spline incorporated into the GAM (Right) a semivariogram with a spatial spline incorporated into the GAM. Both graphs are semivariance by distance in meters and show the change in autocorrelation between the two models.

APPENDIX 2

Table A1: GAM Output. Output of model where TC is percent cover of tree cover, CWM is percent cover of coarse woody material, and TWI is topographic wetness index. TC and CWM are in percent, TWI was probability of burn m$^{-2}$m$^{-1}$.

|        | Std. coeff. | Std. error | t-value | p-value |
|--------|-------------|------------|---------|---------|
| Intercept | -3.690      | 0.236      | -15.658 | <0.01   |
| TC      | -0.004      | 0.001      | -4.353  | <0.01   |
| CWM     | 0.10        | 0.009      | 11.000  | <0.01   |
| TWI     | -0.099      | 0.043      | -2.295  | 0.02    |

APPENDIX 3

Table A2. GAM Fitting. The single variables represent the univariate analysis of percent cover CWM (coarse woody material), percent cover of TC (tree cover), and TWI (topographic wetness index). CWM and TC had units of % and TWI has units of probability of burn m$^{-2}$m$^{-1}$.

| GAM Function | AIC  | R$^2$ |
|--------------|------|-------|
| CWM          | 18284| .358  |
| TC           | 18381| .353  |
| TWI          | 18403| .352  |
| TC + CWM + TWI | 18261| .385  |

APPENDIX 4

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Figure A2: Correlation of Predictor Variables. Our cut off for correlation was .7, and no variable were close to that.