Tracking the Vegetative Compositional Changes 4 Years After the Rim Fire in Yosemite National Park

Andrew Capistrano

ABSTRACT

The Rim Fire burned through 257,314 acres of the Stanisluas National Forest and Yosemite National Park, California from August 15 to October 23, 2013. In 2017, I measured total plant canopy cover, plant species richness and plant composition of areas of high and low burn sites. The total understory plant canopy cover was significantly higher in areas of high severity (p-value: 0.000278). Overall, there was high richness of non-native forb and graminoids species at higher severity sites but the cover was unexpectedly low at <3% across all severities. There were also no significant differences in exotic forb and graminoid cover between high and low burn severities sites. Areas of high severity burns did have significantly higher shrub cover compared to low severity sites were deerbrush (*Ceanothus integerrimus*) and cheatgrass (*Bromus tectorum*). In addition, NMDS analysis similarly identified deerbrush, whitethorn, cheatgrass and rat-tail as the vegetative differences between the high severity sites, any long-term impacts of high severity fires on the plant community requires continued monitoring of the sites.

KEYWORDS

Fire Regime, high-severity fire, community structure, cover by life form, indicator species analysis

INTRODUCTION

Fire suppression and fire exclusion over the past century have severely altered the structure and dynamics of the forests across the Sierra Nevada in California, making the forests more susceptible to forest pests and diseases. Specifically, canopy densities of many Sierra Nevada forests have increased to an alarming level resulting in a large fuel build-up that causes uncharacteristically large wildfires (Goulden and Bales 2014) The increase in the frequency of these large wildfires has altered the post-fire plant communities, allowing for a more ideal habitat for exotic species to invade (Crawford et al. 2001). The overall shift in forest dynamics resulting from fire suppression and exclusion is generally characterized by increased stand densities, smaller average tree diameters, increased proportions of shade tolerant tree species, and elevated surface fuel loads, relative to historical or pre-European settlement forest conditions (Flower and Gonzalez-Meler 2015). Wildfires in these fuel loads can pose a large problem for post-fire regeneration and may cause increased damage to the soil. This affects water repellency rates and disturbs the soil microbial community, thus hindering post-fire understory vegetative growth (Debano 2000).

Wildfires can cause a change in dominant vegetation in the forest that can potentially become irreversible, as there is a strong correlation between the burn severity of the fire and postfire shrub recovery (Crotteau et al. 2013). High severity burned areas increased shrub cover more than lower severity burned areas by more than three times in the 2000 Storrie fire (Crotteau et al. 2013), where *Ceanothus* spp. grew rapidly. The loss of foundational species during the Storrie fire, such as the *Pinus ponderosa*, due to the high severity of the fire has altered forest community's structure allowing for more invasive species to persist and degrade native habitat (White et al. 1996). In terms of seedling regeneration, roughly half of all regeneration in the Mixed Conifer Forest type were *Abies* seedlings, whereas pre-fire regeneration consisted of majority *Pinus* spp. (Crotteau et al. 2013). The change in seed dynamics is a good indicator of evolving forest dynamics and environmental changes (Shive et al. 2013) and can affect the vulnerability of a growing site and thus post-fire climate in the first growing season can significantly impact forest regeneration (Az-Delgado and Lloret 2017). Monitoring long-term changes in vegetation is essential in understanding the shifts the landscape might undergo. High severity fires pose a problem for vegetative recovery with at all levels of ecosystem interactions. Fire severities can influence the re-establishment of re-sprouting species and the mortality of different plant species (Lentile et al. 2007). Factors such as soil, climate, elevation and pre-wildfire treatments can significantly affect the post-fire vegetative growth potential. High severity fires also have a potential to create a homogenous landscape which affect the richness and mediating abilities of these microbial soil communities (Certini 2005), altering the landscape for post-fire vegetative growth. In addition, the soil microorganisms in the soil post-fire heavily affect the regenerative composition and structure of the plant community (Hart et al. 2005). In addition, plant regeneration sources may be from onsite seeds, off-site seeds, or from re-sprouting structures which indicates that the plant recovery dynamics are highly site specific (Collins and Roller 2013). Although the forest structure at the over-story level in response to a wildfire has been well studied, the understory vegetative responses across a fire severity gradient needs to be monitored over a longer period.

Forests in North America are traditionally managed for maximizing timber yield. However, managers have started to recognized the ecological benefits that come with fuel reduction treatments. For the past few decades, Yosemite National Park has experienced a reintroduction of prescribed fire into their management strategy (Collins et al. 2011). An increasing number of studies (Schoennagel et al. 2004, Stephens et al. 2012) demonstrating that pre-wildfire fuel treatments such as prescribed fire can reduce fire severity in certain areas. The treatments generally reduce the severity of the fire by reducing the surface fuels, tree density and canopy connectivity (Shive et al. 2013). However, the influences of extreme fire weather conditions and geological factors result in high-severity fires even in treated regions. Pre-fire treatment will likely have an effect on post-wildfire vegetative recovery in both low-severity burn sites and high-severity burn sites, yet the understory effects are still unknown.

This study examines the plant cover and plant composition changes, across a burn severity gradient, four years after the Rim Fire in California to evaluate changes in understory community structure after a high-severity fire coupled with the frequency of fuel reduction treatment. This study serves as a baseline report for future research to have reference for long term monitoring assessments. I hypothesize that (i) higher burn severity areas will have a significant increase in post-fire understory plant canopy cover and (ii) more woody shrub species will have regenerated in high burn severity areas than in low severity areas. If true, the competition for water and

resources in higher burn severity areas will be extremely high, making it harder for conifer seedlings to establish on the site. I collected understory plant cover across 22 variably-burned sites. This data set provides me with adequate information to analyze the relationship between burn severity and understory cover coupled with the effects of the fuel reduction treatments.

METHODS

Study site

Yosemite National Park



Figure 1. Map of Yosemite National Park and the boundaries of the Rim Fire. The red dots symbolize the established plots that were visited in the summer of 2017.

Yosemite National Park is located in the central Sierra Nevada, California USA (37.8651° N, 119.5383° W; Figure 1). This region has a Mediterranean climate where precipitation ranges from 800 mm to 1720 mm year to year (Collins and Roller 2013). Yosemite National Park has a history of moving towards a more progressive fire regime by managing wildfires to return to their natural fire return interval of 6.8 years. The frequency and intensities of the implemented prescribed fires are very similar to historical fires (Collins and Stephens 2007). Treatments such as mechanical thinning and prescribed fire have reduced the fire severity of subsequent wildfires by reducing surface fuels, tree density and the canopy connectivity (Shive et al. 2013). Fire severity is broadly characterized as low (patches with <25% over-story tree mortality), moderate (patches with 25-74% over-story tree mortality) or high (patches with 75-100% over-story tree mortality).

There are four main vegetation types in the study area: ponderosa pine (*Pinus ponderosa*), sugar pine-white fir (*Pinus lambertiana–Abies concolor*), Jeffrey pine (*Pinus jeffreyi*), and red fir (*Abies magnifica*) (Lydersen et al. 2014). Prior to suppressing fire in the park, most of the forest types were dominated by tree species that were fire tolerant. This includes species such as ponderosa pine, sugar pine, and Jeffery pine (Collins and Stephens 2007). From the 1900s to the early 1970s suppressing fire was the dominant public policy which facilitated for white-fir, a less fire tolerant species, to dominate the landscape. As a result, the suppression of fire created nearly continuous canopy forest with significant fuel laddering (Collins et al. 2009). The homogenous landscape also led to the decrease of vigor in the forest thus making it more susceptible towards additional stressors.

Rim fire

The Rim Fire burned in fall of 2013, the second year of the extreme drought in California, and it was the largest wildfire recorded in the Sierra Nevada. The fire started on the 17th of August and was not contained until 23 October 2013 (Figure 2). It burned 104,131 ha of the Stanislaus National Forest and Yosemite National Park. The wildfire burned through the study area from the 26 August to 20 September and produced a mixed severity burn. The Rim Fire burned through the study area under relatively moderate weather conditions with burning index values ranging from 65-82 (Kane et al. 2015). Furthermore, the southern edge of the fire was burned because of management-ignited backfire from fire suppression efforts.



Figure 2. Map of the spread of the Rim Fire each day from the ignition point. The left inset shows the where the rim fire was located in the continental USA.

Data collection

Burn severity and treatment history

To determine severity post-fire, I used the Relative Difference Normalized Burn Ratio (RdNBR) (Az-Delgado and Lloret 2017), which is available from the Monitoring Trends in Burn Severity (MTBS) project (Eidenshink et al. 2007). RdNBR estimates the effects of fire on the abiotic environment and vegetation through Lidar data. It measures the immediate impacts of fire and ecosystem responses up to a year post-fire (Duffy et al. 2007). A high RdNBR value signifies a decrease in photosynthetic material and an increase in ash, carbon and exposed soil. RdNBR values have been found to be most correlated with field data when determining fire severity (Duffy et al. 2007). In addition, it is very sensitive to changes in living vegetation and moisture as the near-infrared channel and mid-infrared channels that RdNBR uses are particularly attuned to detecting those changes respectively. I extracted the treatment history data from a raster file sent by Kristen Shive (senior fire ecologist of Yosemite National Park) using ARCMAP. Because these

plots were established in 1997, I calculated the times burned at each low-severity burned areas to determine the relationship with cover type.

Shrub and herbaceous cover layer

To monitor the herbaceous and shrub layer, we visited 20 of the variably burned FMH plots. We laid out two 50m transects at each site, one from Q4 to Q1 and one from Q3 to Q2 (Figure 3). I recorded the vegetation species, ground material cover type, and height of shrub at 0.3 meter increments. I used a 2m pole to the height and counted each species only once at each point intercept even if the pole touches it more than once. If the pole did not touch any vegetation, I recorded the substrate it hit. This method is necessary to determine the dominant shrub in the landscape and necessary to calculate percentage shrub cover at each plot.



Figure 3. Plot layout used for by the park services to monitor their permanently established plots.

Data analysis

To determine the plant cover type in relation to pre-fire treatment and burn severity, I performed a two-way Permutational analysis of variance (PERMANOVA) test on burn severity

(high, low) and pre-fire treatment (times burned). I used the Bray-Curtis dissimilarity measure with 999 permutations, with an alpha level of 0.05. I then analyzed the difference among univariate response variables such as total plant cover, tree regeneration cover, shrub cover, forb cover, graminoid cover, exotic forb cover, and exotic forb cover using Euclidean distance. If the interactions were significant, I conducted subsequent PERMANOVA for the treatments within severity class.

To graphically display the community data by severity and treatment, I used vegan package (Oksanen et al. 2017) non-metric multidimensional scaling (NMDS) in R studio. The purpose of NMDS is to reduce information from multiple dimensions to just a few. I conducted 250 runs with the real data and chose the final number of axes based on the stress levels <0.15 with the p-values <0.05. Finally, I also used the indicspecies package (De Cáceres and Legendre 2009) in R studio to identify indicator species for each severity type. Species with indicator values >0.25 and a p-value <0.05 were considered indicator species based on a Monte Carlo test.

RESULTS

Understory response by cover type

The forb/herb cover, shrub, and graminoid cover were all higher in high severity areas compared to low severity areas (Table 1; Figure 2). The number of times burned significantly (p-value: 0.00246) reduced burn severity. For the total understory plant cover, there was a significant interaction with burn severity (p-value: 0.000278) where total understory plant cover was higher in high-severity burned areas compared to low-severity burned areas. The shrub understory component was the most abundant component of the high-severity area plant community and it was significantly (p-value: 0.0000343) higher in high-severity burned areas compared to low-severity burned areas. The total shrub cover comprised 32% of the total understory plant canopy. Within the low-severity burn class there also a significant (p-value: 0.0257) interaction between the frequency of treatment and the reduction in shrub cover.

Shrub dominance was also indicated by two species: *Ceanothus integerrimus* and *Ceanothus cordulatus*. Graminoid cover was the second highest cover type out of the understory plant canopy layer and it was significantly (p-value: 0.002) higher in high-severity burned areas

compared to low-severity burned areas. It comprises 8.74% of the total understory plant canopy. Although the forb/herb cover was higher in high-severity burned areas compared to low-severity burned areas, it was not significant (p-value: 0.134). However, it did comprise 7.4% of the total understory plant canopy. Tree regeneration cover was significantly (p-value: 0.001) higher in low-severity burned areas compared high-severity burned areas. Species richness was significantly higher in high-severity areas than in low-severity areas (p-value: 0.001). Both are primarily driven by greater forb richness in higher-severity areas where were approximately 85 forb species were found whereas only 17 forb species were found in low-severity areas. In addition, exotic species richness is also significantly (p-value: 0.006) higher in high-severity areas than in low-severity areas.

 Table 1. Summary table of the p-values from PERMANOVA test for severity and the frequency of treatment.

 The significance level is at alpha=0.05 and is denoted by bold in the table.

Response Variables	Severity	Frequency of treatment
Total plant cover	0.000278	0.0248
Shrub cover	0.00000343	0.0257
Forb Cover	0.134	0.767
Graminoid cover	0.002	0.431
Tree regeneration cover	0.001	0.91
Species Richness	0.001	0.0994
Exotic Species Richness	0.006	0.109



Figure 4. Bar graph of the average percentage cover and richness values for each burn severity class. These graphs show (a) Exotic species richness, (b) Species richness, (c) Tree regeneration cover, (d) Forb & herb cover, (e) Understory plant cover, (f) Shrub cover, and (g) Graminoid cover by severity class. The scales differ for each graph.

Vegetative community response

Plant community composition

Within the high severity class, *Ceanothus integerrimus* and *Bromus tectorum* were the only significant indicator species. *Ceanthus integerrimus* had an indicator value of 83.7 and a p-value of 0.003. *Bromus tectorum* had an indicator value of 66.8 and a p-value of 0.036. Within the low severity class, *Abies concolor* seedlings and *Gilia capitata spp. mediomontana* were the only significant indicator species. The *Abies conocolor seedlings* had an indicator value of 82.7 and a p-value of 0.024. *Gilia capitata spp. mediomontana* had an indicator value of 82.1 and a p-value of 0.018.

Table 2. Summary of the indicator species for each cover type by burn severity class. Species with indicator	
values >25 and a p-value <0.05 are in bold.	

	Graminoid		Forb	Shru	b
	Severity		Severity	Seve	rity
High		High		High	
	Bromus tectorum		Lactuca seeriola		Ceanthus integerrimus
	Vulpia myuros		Epilobium brachycarpum		Ceanothus cordulatus
	Elymus glaucus ssp. Glaucus		Phacelia heterophylla ssp. virgata		Arctostaphylos patula
			Madia elegans ssp. elegans		Ericameria arborescens
			Conyza canadensis		
			Gilia capitata ssp. mediomontana		
			Lupinus albicaulis		
			Stephanomeria virgata ssp. pleurocarpa		
			Viola lobata ssp. lobata		
			Cirsium vulgare		
			Calystegia malacophylla ssp. malacophylla		
Low		Low		Low	
	Gayophytum diffusum ssp. parviflorum		Iris hartwegii ssp. hartwegii		Ribes roezlii var. roezlii
	<i>Poa</i> unknown #1		Hieracium albiflorum		
			Lotus crassifolius var. crassifolius Lupinus breweri var. breweri		

The richness of non-native species was significantly higher (p-value: 0.006) in high-severity burned areas with an average of 13 counts of exotic species at each site. This difference was

indicated primarily by the presence of three species, *Bromus tectorum, Vulpia myuros* and *Lactuca serriola*. In high severity plots, 6 out of the 21 plots had *Bromus tectorum*, 6 out of 21 plots had *Vulpia myuros* and 6 out of 21 plots had *Lactuca serriola*. Although cover values were relatively low, the prevalence of two of these species reflects their designation as a significant indicator species of high severity areas (see Table 2).

Community structure

There are total six species of understory plants that drive the difference between the composition in a high-severity burn site compared to a low-severity burn site (Figure5). This stress of the NMDS ordination is 0.033 with two convergent solutions found after 20 tries. Species such as *Ceanothus integerrimus, Elymus glaucus ssp. glaucus, Madia elegans ssp. elegans, Vulpia myuros,* and *Bromus tectorum* are highly correlated with different axes. The graph shows that there is separation between high-severity burned areas negatively correlated with NMDS 1 influenced by the high relative abundances of *Ceanothus integerrimus, Elymus glaucus ssp. glaucus, Madia elegans ssp. elegans, Vulpia myuros,* and *Bromus tectorum* positively correlated with NMDS 2 and the high relative abundances of *Ceanothus cordulatus* negatively correlated with NMDS 2. The gradient may be due to some other unmeasured environmental variable. There is a clear separation between high-severity burned sites and low severity burned sites along NMDS. Sites with high relative abundance of *Ceanothus integerrimus, Elymus glaucus ssp. glaucus, Madia elegans ssp. elegans, Vulpia myuros* and *Bromus tectorum* are correlated in the direction of high severity burned areas and high relative abundance of *Abies concolor* seedlings correlates in the direction of low-severity burned areas.



Figure 5. NMDS ordination separating high-severity burned areas and the low-severity burned areas by different understory plant species.

DISCUSSION

Fire severity largely impacted the post-fire vegetation pattern. Four years post-fire I observed a large difference between low-severity burned areas and high-severity burned areas for most of the vegetation characteristics measured. In high-severity areas, resources have been made available as a result of the loss of some of the foundational species (Ellison et al. 2005) resulting in a higher mean understory plant canopy cover. This increase in cover is consistent with observations made on the Rodeo–Chediski fire in Arizona (Kuenzi et al. 2008) and also in agreement with my first hypothesis that higher burn severity areas will have a significant increase in post-fire understory plant canopy cover. Mt results also demonstrate a prominence of shrubby understory species highlighted by the appearance of 4 shrubs (*Ceanthus integerrimus, Ceanothus cordulatus, Arctostaphylos patula* and *Ericameria arborescens*) as indicator species. As a result,

much of the high severity areas have been converted to shrub-dominated communities because of the few to no overstory trees at the site as well as high shrub cover.

Understory vegetative response by cover type

Regeneration strategies of the different plant species provide insight into the interaction between fire severity and vegetative response. The total understory plant cover was higher in high severity burn areas compared to low severity burn areas with the shrub understory component the highest in high severity burn areas. Higher burn severity can significantly affect the plant cover or richness if the burn results in the consumption or mortality of more perennial structures. However, higher severity fires can create positive effects such as greater resource availability, greater openings for recruitment and greater stimulation for germination of fire-dependent species (Keeley et al. 2005)

Forb species responded consistently in increasing richness and cover across all highseverity burned areas. Litter depth and the different light environment have always been important predictors pertaining to this response (Keeley et al. 2005). The deeper accumulation of litter has the potential to limit the recruitment of plant species that prefer to establish on mineral soil (Hyde et al. 2016). However, this is one of the environmental variables that I did not analyze so I cannot justify its significance in altering the understory vegetative response. The greater the fire severity the greater the chance resources can become available due to the reduction in the density of competing tree roots (North et al. 2005) and the conversion of organic to mineral nitrogen (Lewis et al. 2006). Annual species that with strategies such as long distance dispersal and rapid growth have the potential to benefit from these areas of high-resource availability (Keeley et al. 2005).

Shrubs species typically positively responded to increasing fire severity, with increasing richness and cover. This response is evident through results identifying *Ceanothus integerrimus* as an indicator species for a high-severity site. For opportunistic seed-bank taxa such as *Ceanothus*, the increasing severity typically leads to a greater rate of germination if there are already seeds present in the soil (Huffman and Moore 2004). Some established plant species have the ability to resprout after fire as well, so unless intensities exceed a lethal threshold, any variation of severities of future fires may have a little effect on the survival and abundance of these shrub species (Shive et al. 2013).

14

Perennial forbs and graminoids responded only minimally to fire severity. This lack of response is because graminoids are such a highly diverse group of plant species. They all exhibit a diverse range of regenerative strategies in response to burning (Keeley 2009). Many perennial forb species are very tolerant of fire, however some are adapted to shade or deep accumulation of litter (Bales et al. 2011) and may be more sensitive to burning or to moisture stress. In contrast, perennial graminoids were uncommon as they had few mechanisms for dispersal (Keeley et al. 2005), limiting their ability to respond to the variation in fire severity.

Plant community response

The mixed conifer forest in the southern Sierra Nevada is very patchy creating high resource heterogeneity. This patchiness is often the explanation for a diverse plant community structure (North et al. 2005). In addition, changes in water, light, and nutrient availability have also been linked to influencing the composition and cover of understory plants (Hyde et al. 2016). However, low resource quantity, as opposed to resource heterogeneity, is associated with a higher diversity of understory plant species (Lydersen et al. 2013) but this might not be true in the mixed conifer forests of the Sierra Nevada. Highly diverse herb communities usually occur when soil moisture is high and low-diversity shrub communities usually occupy resource-poor microsites. Temporal changes in water availability and differences in plant functional group make it difficult to differentiate the effects of resource quantity and heterogeneity on the understory diversity.

Pre-wildfire treatment

Past disturbance history can influence the understory richness and structure of a site. Prefire treatment had little effect on the exotic species responses but it had several impacts on other response variables in the study area. However, significant differences occurred in total plant cover and plant community composition by pre-wildfire treatments like prescribed burns which demonstrates that severity along with pre-fire treatments can influence and drive post-fire vegetative communities. Treatment effect on total understory plant cover is likely to have major implications for post-fire reforestation. However, these small differences can probably be accounted for by pre-existing plant community than by actual wildfire or treatment itself. Yosemite National Park has been managed for logging prior to its induction into the national parks system which may have contributed to the low post-fire response by exotics (Miller et al. 2012). Management practices such as prescribed burning has the potential to increase non-native species due to the disturbance but it does not have the extensive detrimental effects as a severe wildfire (Rew and Johnson 2010)

Limitations and future directions

This study was done under severe drought conditions. The effects of drought coupled with pre-wildfire fuel treatments on the understory characteristics have yet to be explored. Also, frequency of treatment was not able to be included because I did not survey a control plot. Nonetheless, my results supported the continued application of management practices that reduces fuels such as burning treatments. In the future, it would be more feasible to compare treatments types such as mechanical treatments and fire treatment similar to what (Schwilk et al. 2009) did in the fire-and fire surrogate study. To resolve the debate between resource heterogeneity and resource quantity, re-measurements should be a priority when and where existing plots burn in the future. These treatments are important in maintaining the persistence of a mixed conifer forest. Finally, the important difference in vegetation response by pre-fire treatment within severity class demonstrated that landscapes burned under a given severity class may not be alike.

Conclusion

High-severity burned areas are characterized by higher understory plant canopy cover compared to low-severity burned areas and have mostly shrub colonizing species indicator species. However, exotic plant species cover, as well as perennial forb and graminoid cover, were not significantly higher in high severity areas compared to areas classified as low severity. Although the study was only conducted four years post fire, other studies have observed a rapid increase of exotic species within 2 to 3 years following a wildfire (Crawford et al. 2001). Thus, determining the factors that are responsible for community-scale plant diversity in the mixed conifer forests of California is a multifaceted problem. The main important factors to consider are: (1) disturbance history; (2) species-specific regenerative response to disturbance events; (3) environmental niche

specialization between life forms; (4) resource availability; (5) resource heterogeneity across a landscape. Although the diversity of plant species in these forested sites appears driven by non-equilibrium processes, it is important to consider that residual species that persist after fire can act to colonize a site due its species-specific niche specialization (Burkle et al. 2015).

ACKNOWLEDGEMENTS

Firstly, I would like to thank Kristen Shive, a PhD student in the Scott Stephens lab at the University of California, Berkeley and the Chief Fire ecologist of Yosemite National Park, for allowing me to analyze the data from the Parks. Secondly, I would also like to thank my mentor Scott Stephens for initially helping me to kick-start my project. Thirdly, I want to thank Patina Mendez for helping me throughout the way in terms of analyzing my data and also for helping me to gain confidence in my scientific writing abilities. Lastly, I would like to thank the wider ESPM community, my fellow environmental science peers (especially Zoe Klein, Camila Quintana, and Ziyu Li), my forestry peers as well my friends, my partner Mary Mcdonnell, my dad Domingo Capistrano and my mom Ester Capistrano for helping me throughout this journey.

WORKS CITED

- Az-Delgado, R. D., and F. Lloret. 2017. International Journal of Remote Sensing Influence of fire severity on plant regeneration by means of remote sensing imagery. International Journal of Remote Sensing 248:1751–1763.
- Bales, R. C., J. W. Hopmans, A. T. O'Geen, M. Meadows, P. C. Hartsough, P. Kirchner, C. T. Hunsaker, and D. Beaudette. 2011. Soil Moisture Response to Snowmelt and Rainfall in a Sierra Nevada Mixed-Conifer Forest. Vadose Zone Journal 10:786.
- Burkle, L. A., J. A. Myers, and R. T. Belote. 2015. Wildfire disturbance and productivity as drivers of plant species diversity across spatial scales. Ecosphere 6:art202.
- Certini, G. 2005. Effects of fire on properties of forest soils: a review. Oecologia 143:1-10.
- Collins, B. M., R. G. Everett, and S. L. Stephens. 2011. Impacts of fire exclusion and recent managed fire on forest structure in old growth Sierra Nevada mixed-conifer forests. Ecosphere 2:art51.
- Collins, B. M., J. D. Miller, A. E. Thode, M. Kelly, J. W. van Wagtendonk, and S. L. Stephens. 2009. Interactions Among Wildland Fires in a Long-Established Sierra Nevada Natural Fire

Area. Ecosystems 12:114–128.

- Collins, B. M., and G. B. Roller. 2013. Early forest dynamics in stand-replacing fire patches in the northern Sierra Nevada, California, USA. Landscape Ecology 28:1801–1813.
- Collins, B. M., and S. L. Stephens. 2007. Managing natural wildfires in Sierra Nevada wilderness areas. Frontiers in Ecology and the Environment 5:523–527.
- Crawford, J. A., C.-H. A. Wahren, S. Kyle, and W. H. Moir. 2001. Responses of Exotic Plant Species to Fires in Pinus ponderosa Forests in Northern Arizona. Journal of Vegetation Science 12:261–268.
- Crotteau, J. S., J. Morgan Varner, and M. W. Ritchie. 2013. Post-fire regeneration across a fire severity gradient in the southern Cascades. Forest Ecology and Management 287:103–112.
- Debano, L. F. 2000. The role of fire and soil heating on water repellancy in wildland environments: a review. Journal of Hydrology 231–232:195–206.
- De Caceres, M., Legendre, P. (2009). Associations between species and groups of sites: indices and statistical inference. Ecology, URL http://sites.google.com/site/miqueldecaceres/
- Duffy, P. A., J. Epting, J. M. Graham, T. S. Rupp, and A. D. Mcguire. 2007. Analysis of Alaskan burn severity patterns using remotely sensed data. International Journal of Wildland Fire 16:277–284.
- Eidenshink, J., B. Schwind, K. Brewer, Z.-L. Zhu, B. Quayle, and S. Howard. 2007. A project for monitoring trends in burn severity. Fire Ecology Special Issue 3.
- Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliott, C. R. Ford, D. R. Foster, B. D. Kloeppel, J. D. Knoepp, G. M. Lovett, J. Mohan, D. A. Orwig, N. L. Rodenhouse, W. V Sobczak, K. A. Stinson, J. K. Stone, C. M. Swan, J. Thompson, B. Von Holle, and J. R. Webster. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Front Ecol Environ 3:479–486.
- Flower, C. E., and M. A. Gonzalez-Meler. 2015. Responses of Temperate Forest Productivity to Insect and Pathogen Disturbances. Annual Review of Plant Biology 66:547–569.
- Goulden, M. L., and R. C. Bales. 2014. Mountain runoff vulnerability to increased evapotranspiration with vegetation expansion.
- Hart, S. C., T. H. DeLuca, G. S. Newman, M. D. MacKenzie, and S. I. Boyle. 2005. Post-fire vegetative dynamics as drivers of microbial community structure and function in forest soils. Forest Ecology and Management 220:166–184.
- Huffman, D. W., and M. M. Moore. 2004. Responses of Fendler ceanothus to overstory thinning, prescribed fire, and drought in an Arizona ponderosa pine forest. Forest Ecology and Management 198:105–115.

- Hyde, K. D., K. Jencso, A. C. Wilcox, and S. Woods. 2016. Influences of vegetation disturbance on hydrogeomorphic response following wildfire. Hydrological Processes 30:1131–1148.
- Kane, V. R., C. A. Cansler, N. A. Povak, J. T. Kane, R. J. Mcgaughey, J. A. Lutz, D. J. Churchill, and M. P. North. 2015. Mixed severity fire effects within the Rim fire: Relative importance of local climate, fire weather, topography, and forest structure. Forest Ecology and Management 358:62–79.
- Keeley, J. E. 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. International Journal of Wildland Fire 18:116–126.
- Keeley, J. E., C. J. Fotheringham, and M. Baer-Keeley. 2005. Factors affecting plant diversity during post-fire recovery and succession of mediterranean-climate shrublands in California, USA. Diversity Distributions 11:525–537.
- Kuenzi, A. M., P. Z. Fulé, and C. H. Sieg. 2008. Effects of fire severity and pre-fire stand treatment on plant community recovery after a large wildfire. Forest Ecology and Management 255:855–865.
- Lentile, L. B., P. Morgan, A. T. Hudak, M. J. Bobbitt, S. a. Lewis, A. M. S. Smith, and P. R. Robichaud. 2007. Post-Fire Burn Severity and Vegetaion Response Following Eight Large Wildfires Across the Western United States. Fire Ecology Special Issue 3:91–108.
- Lewis, S. A., J. Q. Wu, and P. R. Robichaud. 2006. Assessing burn severity and comparing soil water repellency, Hayman Fire, Colorado. Hydrological Processes 20:1–16.
- Lydersen, J. M., M. P. North, and B. M. Collins. 2014. Severity of an uncharacteristically large wildfire, the Rim Fire, in forests with relatively restored frequent fire regimes. Forest Ecology and Management 328:326–334.
- Lydersen, J. M., M. P. North, E. E. Knapp, and B. M. Collins. 2013. Quantifying spatial patterns of tree groups and gaps in mixed-conifer forests: Reference conditions and long-term changes following fire suppression and logging. Forest Ecology and Management 304.
- Miller, J. D., B. M. Collins, J. A. Lutz, S. L. Stephens, J. W. van Wagtendonk, and D. A. Yasuda. 2012. Differences in wildfires among ecoregions and land management agencies in the Sierra Nevada region, California, USA. Ecosphere 3:art80.
- North, M., B. Oakley, R. Fiegener, A. Gray, and M. Barbour. 2005. Influence of light and soil moisture on Sierran mixed-conifer understory communities. Plant Ecology 177:13–24.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., and H. Wagner, (2017). vegan: Community Ecology Package. R package version 2.4-5. https://CRAN.Rproject.org/package=vegan
- Rew, L. J., and M. P. Johnson. 2010. Reviewing the Role of Wildfire on the Occurrence and Spread of Invasive Plant Species in Wildland Areas of the Intermountain Western United

States. Invasive Plant Science and Management 3:347–364.

- Schoennagel, T., T. T. Veblen, and W. H. Romme. 2004. The Interaction of Fire, Fuels, and Climate across Rocky Mountain Forests. BioScience 54:661–676.
- Schwilk, D. W., J. E. Keeley, E. E. Knapp, J. McIver, J. D. Bailey, C. J. Fettig, C. E. Fiedler, R. J. Harrod, J. J. Moghaddas, K. W. Outcalt, C. N. Skinner, S. L. Stephens, T. A. Waldrop, D. A. Yaussy, and A. Youngblood. 2009. The national Fire and Fire Surrogate study: effects of fuel reduction methods on forest vegetation structure and fuels. Ecological Applications 19:285–304.
- Shive, K. L., C. H. Sieg, and P. Z. Fulé. 2013. Pre-wildfire management treatments interact with fire severity to have lasting effects on post-wildfire vegetation response. Forest Ecology and Management 297:75–83.
- Stephens, S. L., J. D. McIver, R. E. J. Boerner, C. J. Fettig, J. B. Fontaine, B. R. Hartsough, P. L. Kennedy, and D. W. Schwilk. 2012. The Effects of Forest Fuel-Reduction Treatments in the United States. BioScience 62:549–560.
- White, J. D., K. C. Ryan, C. C. Key, and S. W. Running. 1996. Remote Sensing of Forest Fire Severity and Vegetation Recovery. Int. J. Wildland Fire 6:125–136.