SEVERITY OF SHORT-INTERVAL REBURN MEDIATES COMPOSITIONAL SHIFTS IN FIRE-ADAPTED MONTANE SHRUBLANDS

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**Abstract**

Montane chaparral is a shrub community dependent on fire for its persistence in areas where it intergrades with the dry mixed-conifer forests of northern California. In these fire-prone regions, irregular patterns of mixed-severity fire on the landscape historically created forest gaps and clearings where shrublands could persist. Decades of fire exclusion facilitated the invasion of conifer forests into these gaps, reducing the extent of shrub-dominated ecosystems. Evidence exists that large, stand-replacing wildfires of recent years may be reversing this trend in some areas. Previous studies have documented vegetative type-conversion to chaparral occurring where high-severity fire has eliminated forest cover. These state shifts are especially persistent in short-interval reburn areas, where conifer regeneration is often limited, and fire-adaptive strategies of chaparral species allow for post-fire shrub dominance. As an ecosystem, chaparral is well known to be tolerant of high-severity fire, though species typical to this ecosystem possess divergent post-fire regenerative strategies, and each species’ response to wildfire severity and frequency can differ according to these adaptations. These regeneration mechanisms are often broadly grouped into species that rely on soil seed banks for post-fire germination, and species that store carbohydrates in underground structures to facilitate post-fire sprouting. While burn severity- and interval-dependent vegetative shits are well studied, little attention has been given to the influence of differential severity and frequency on the species assemblages of these subsequent plant communities, given the divergent adaptive strategies that occur. In order to assess the influence of adaptive strategy and burn severity on shrub community dynamics, we examined shrub abundance and species composition across a spectrum of burn severity combinations in a 9,000 ha reburn area with a 12-year interval between wildfires in the Lassen National Forest, CA. Our results indicate that chaparral species with the capacity to resprout after stand-replacing wildfire are advantaged over those that depend on fire-cued germination from latent seedbanks following repeated high-severity fires.

**Introduction**

Fire regimes in the northwestern United States have been dramatically impacted by changing climatic patterns and the consequences of past fire exclusion (Agee 1993, Schoennagel et al. 2017). Recent studies have documented increases in the frequency, severity and extent of wildfires as well as changes in the spatial patterns of burn area (Westerling et al. 2006, Miller et al. 2009, Stevens et al. 2017). In regions where past natural and anthropogenic fires were of mixed or low severity, the increased incidence of large, stand replacing wildfires is well outside of the historic range of variability (Taylor 2000, Hessburg et al. 2005, Mallek et al. 2013). This departure from historic norms [Higher incidence of wildfire on the landscape] has, in turn, resulted in increased occurrence of reburns, where wildfires burn inside of the boundaries of previous fires. This phenomenon is concerning to land managers, due to the largely unknown ecological ramifications, and has recently become a focus of fire research.

Although some authors have found that previous wildfires limited the extent and severity of reburns (Parks et al. 2014, Stevens‐Rumann and Morgan 2016), other studies have observed self-reinforcing effects of repeated wildfires (Collins et al. 2009, Coppoletta et al. 2016, Harvey et al. 2016, Lauvaux et al. 2016): these effects were often mitigated by initial fire severity and fire interval. Initial fire severity, time since fire and vegetation are frequently cited as the most important determinants of reburn outcomes (Harvey et al. 2016, Grabinski et al. 2017, Harris and Taylor 2017). High-severity wildfires can alter successional pathways, especially in naive ecosystems, such that conversions to alternative vegetative states occur. Examples of these type conversions exist in a variety of ecosystems (Odion et al. 2010, Knox and Clarke 2012, Collins and Roller 2013). The legacies of these extreme events can exhibit strong temporal persistence, influencing not only post-fire vegetation and fuels, but even promoting (pushing the system towards) the creation of novel fire regimes. This shift occurs via positive feedbacks, where initial high severity begets subsequent high severity, fueled in large part by fire-mediated vegetative state shifts. Some authors have proposed that frequent, severe reburns advance ecological thresholds, beyond which vegetation is permanently altered and previous ecosystems are unlikely to return (Falk 2013, Tepley et al. 2017, Stevens‐Rumann et al. 2018).

These post-fire state shifts and feedbacks have been observed when stand-replacing wildfires facilitate the conversion of dry mixed-conifer forests of northeastern California to montane chaparral shrublands (Collins and Roller 2013, Coppoletta et al. 2016, Lauvaux et al. 2016). In this fire-prone region, irregular vegetative patterns resulting from mixed-severity fires historically created gaps and clearings where shrub-dominated communities could persist. Decades of fire exclusion facilitated the invasion of conifer forests into these gaps, reducing the extent of chaparral ecosystems (Lauvaux et al. 2016). Chaparral often re-establishes where overstory mortality is high, and this resurgent dominance is reinforced with subsequent burns (Coppoletta et al. 2016)

These communities are composed of species that are highly tolerant of severe disturbance by fire, and display varying adaptive strategies that allow for post-fire dominance through rapid recolonization and regeneration.

While many studies have examined fire-mediated shifts from forest to chaparral-dominated landscapes, and the self-reinforcing nature of these vegetative changes, information is lacking as to how repeated wildfires influence species composition, especially where high-severity fire is self-perpetuating. Changes in plant community composition can have lasting impacts on flammability, reburn potential and severity, and habitat value into the future (citations!). In order to study the interactive effects of burn severity in two wildfire events on species composition, we surveyed the mid-story across a gradient of burn severity combinations, in a short-interval reburn area in northern California. Using these data, we asked the following questions: 1) Were there compositional shifts in the mid-story across severity gradients? 2) did certain species drive these changes? 3) are there fire-adaptive trait differences between species that were associated with particular severity combinations? We hypothesized that differences in species’ regeneration strategies would influence species assemblages following short-interval reburn along a gradient of burn severities.

**Methods**

*Study Area*

This study was conducted within the intersection of the Storrie (2000) and Chips (2012) Fire extents in the southern Cascade Range in the Lassen National Forest in northern California, USA. Soils of the site are typically young and of volcanic origin, but also include granitic soils in the southernmost portion of the study area, where the Cascades and Sierra Nevada intersect (Kliewer 1994). Climatic patterns are Mediterranean, with warm dry summers, and cool, wet winters, during which 95% of the annual precipitation is received (Kliewer 1994). Elevations range from 900 to 1800 m above sea level (asl), with steep slopes dominating the terrain. Forest cover type in the study area is classified as Sierra Nevada Mixed Conifer (McDonald 1980). Common overstory species are ponderosa pine (*Pinus ponderosa* var. *ponderosa* C. Lawson), sugar pine (*Pinus lambertiana* Douglas), coast Douglas-fir, white fir, incense-cedar (*Calocedrus decurrens* (Torr.) Florin), and California black oak. Common shrub species are deerbrush (*Ceanothus integerrimus* Hook. & Arn.), greenleaf manzanita (*Arctostaphylos patula* Greene), snowbrush (*Ceanothus velutinus* Douglas ex Hook. var. *velutinus*), Sierra gooseberry (*Ribes roezlii* Regal var. *roezlii*), mountain whitethorn (*Ceanothus cordulatus* Kellogg), and trailing snowberry (*Symphoricarpos mollis* Nutt.).

The Storrie Fire burned approximately 23,000 ha in the Lassen and Plumas National Forests (hereafter “Lassen” and “Plumas”) in August of 2000. The Chips Fire burned approximately 30,000 ha in the same area, beginning in the Feather River Canyon of the Plumas, and quickly spreading onto the Lassen in August of 2012. The Chips Fire burned into the perimeter of the Storrie Fire, creating an overlapping reburn area of approximately 9,900 ha. Both wildfires burned at a mix of severities, allowing sampling across a spectrum of combined burn severity strata. Data collection occurred in the summer of 2015, three years after the Chips Fire, and 15 years after the Storrie Fire.

*Field Sampling*

Ninety-one plots were established inside and adjacent to the 9,900 ha reburn area, ranging in elevation from 900 to 1400 m asl. Our sampling design used Monitoring Trends in Burn Severity project (MTBS, www.mtbs.gov) classifications of burn severity for the Storrie Fire area (unburned, low, moderate, and high), and then paired these with the same classes of Chips Fire severity, for a total of 16 possible burn severity combinations (i.e., unburned-unburned, unburned-low, unburned-moderate, etc.; Figure 1). We selected plots randomly within the previously defined strata using ArcGIS (ESRI, Redlands, California, USA). Plots were located at least 10 m from roads and trails to avoid edge issues. We further excluded areas with evidence of subsequent post-fire management activity (e.g., post-fire salvage, fuel mastication).

Species and height were recorded for all woody plant species >10 cm and <137 cm tall within a 4.2 m radius (56.48 m2 area) circular plot. Two orthogonal crown diameter measurements were taken for each individual, and used to calculate relative percent cover for each species. Tree seedlings and saplings were recorded in the following height categories: 10-25 cm or 25-50 cm for seedlings and 50-75 cm, 75-137 cm, and >137 cm but ≤2.5 cm DBH for saplings.

**Results**

Indicator species analysis:

cov.ind <- multipatt(cover2, cluster = cat, control = how(nperm = 999), duleg = T)

> summary(cov.ind, indvalcomp = T)

Multilevel pattern analysis

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Association function: IndVal.g

Significance level (alpha): 0.05

Total number of species: 12

Selected number of species: 6

Number of species associated to 1 group: 6

List of species associated to each combination:

Group high/high #sps. 1

A B stat p.value Indicator Value

**CECO 0.2258 0.8333 0.434 0.018 \* 18**

Group high/un #sps. 1

A B stat p.value

CEVE 0.5361 0.1667 0.299 0.805

Group low/low #sps. 2

A B stat p.value

**QUKE 0.4423 1.0000 0.665 0.001 \*\*\* 44**

CEPR 0.4685 0.3333 0.395 0.603

Group mod/low #sps. 1

A B stat p.value

**PILA 0.3836 0.6667 0.506 0.043 \* 26**

Group mod/un #sps. 2

A B stat p.value

ARPA 0.3472 0.5000 0.417 0.236

PIPO 0.7462 0.1667 0.353 0.898

Group un/low #sps. 2

A B stat p.value

RIRO 0.2853 0.6000 0.414 0.360

SYMO 0.3719 0.4000 0.386 0.241

Group un/mod #sps. 1

A B stat p.value

**CEIN 0.1391 1.0000 0.373 0.002 \*\* 14**

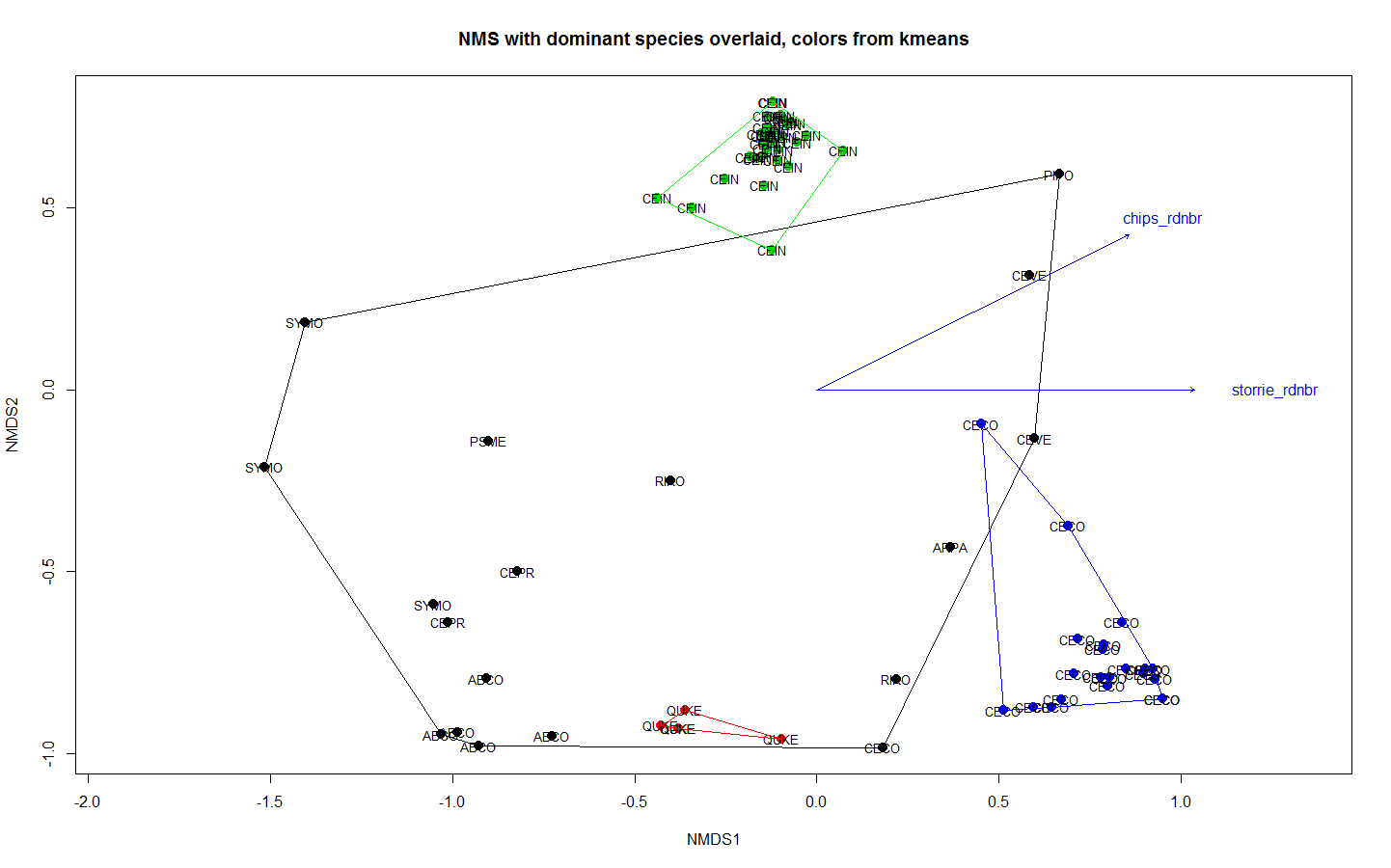
Group un/un #sps. 2

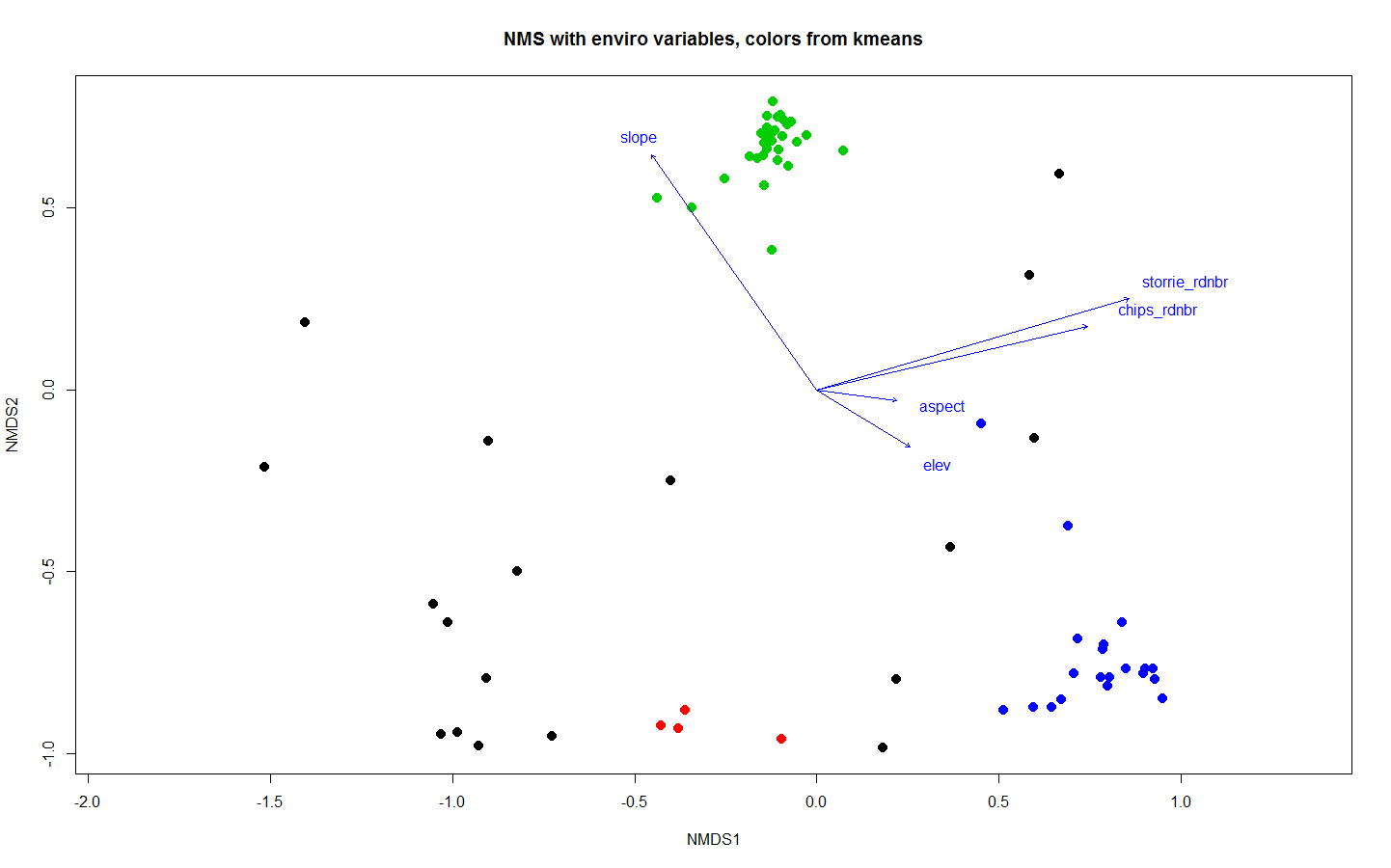
A B stat p.value

**PSME 0.8800 0.5000 0.663 0.013 \* 44**

**ABCO 0.4128 0.7500 0.556 0.013 \* 31**

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On the second plot, only storrie, chips, and elevation are significant:

NMDS1 NMDS2 r2 Pr(>r)

storrie\_rdnbr 0.96005 0.27984 0.3302 0.001 \*\*\*

chips\_rdnbr 0.97352 0.22862 0.2407 0.001 \*\*\*

aspect 0.99127 -0.13184 0.0204 0.461

elev 0.85060 -0.52581 0.0377 0.263

slope -0.57585 0.81755 0.2589 0.001 \*\*\*

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Signif. codes: 0 ‘\*\*\*’ 0.001 ‘\*\*’ 0.01 ‘\*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Permutation: free

Number of permutations: 999

Here’s the code I’m using for the permanova:

#PERMANOVA of cover data

library(tidyverse)

library(vegan)

library(devtools)

#data frame of response variables (ALL common species Relative cover values)

cover2 <- read.csv(file="C:/Users/dnemens/Dropbox/CBO/chaparral/center data/data sheets/coverRel.csv")

# dataframe of predictor variables (rdnbr, plot names & categories)

cover <- read.csv(file="C:/Users/dnemens/Dropbox/CBO/chaparral/center data/data sheets/cover1.csv")

#creates vector of storrie/chips severity combination

cat <- as.factor(cover$SC)

#B-C distance matrix

cov.dist <- vegdist(cover2, method = "bray")

#PERMANOVA

#simple test for overall effect

try1 <- adonis(cover2~cat, data = cover2)

try1

Call:

adonis(formula = cover2 ~ cat, data = cover2)

Permutation: free

Number of permutations: 999

Terms added sequentially (first to last)

Df SumsOfSqs MeanSqs F.Model R2 Pr(>F)

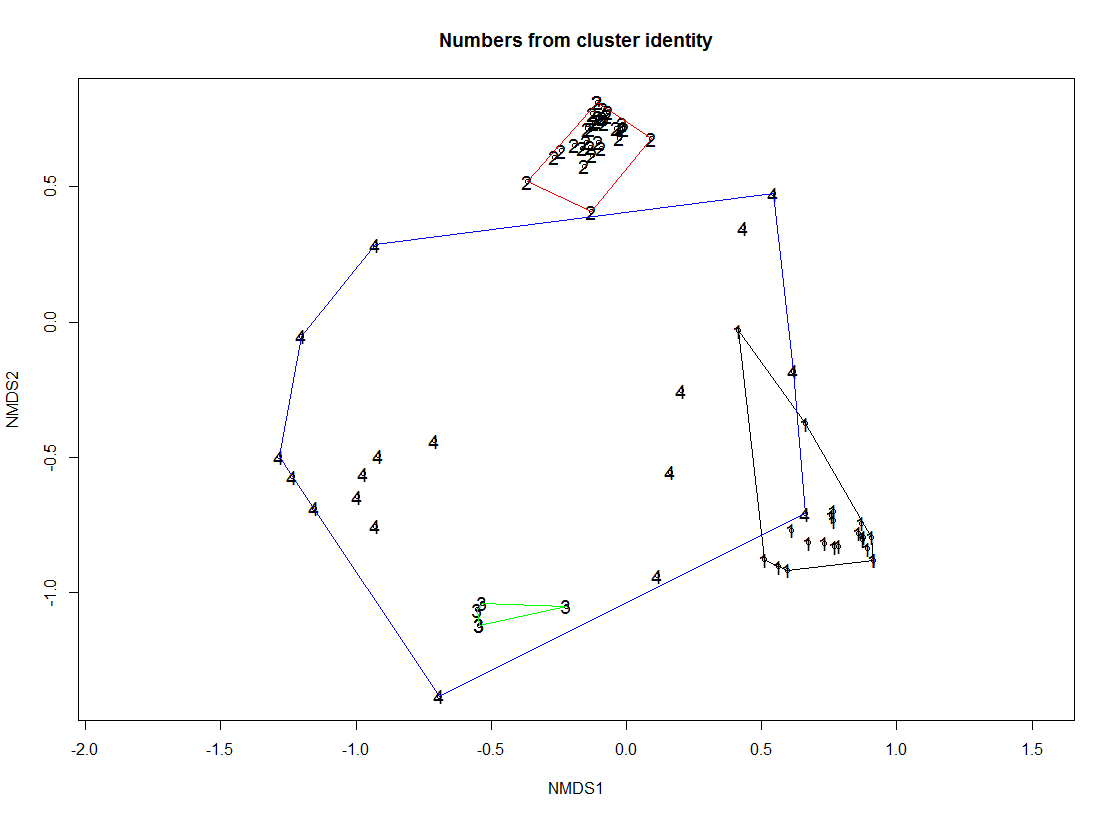
cat 15 10.420 0.69468 2.7005 0.35069 0.001 \*\*\*

Residuals 75 19.293 0.25725 0.64931

Total 90 29.714 1.00000

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Signif. codes: 0 ‘\*\*\*’ 0.001 ‘\*\*’ 0.01 ‘\*’ 0.05 ‘.’ 0.1 ‘ ’ 1

This is the code I found for multiple comparisons:

x <- betadisper(cov.dist, k$cluster)

anova(x)

tx <- TukeyHSD(x)

tx

Tukey multiple comparisons of means

95% family-wise confidence level

Fit: aov(formula = distances ~ group, data = df)

$group

diff lwr upr p adj

2-1 -0.081643125 -0.1689599 0.005673602 0.0754836

3-1 -0.086683217 -0.2317947 0.058428271 0.4040499

4-1 0.433666341 0.3273878 0.539944877 0.0000000\*

3-2 -0.005040092 -0.1411134 0.131033199 0.9996704

4-2 0.515309467 0.4217481 0.608870802 0.0000000\*

4-3 0.520349559 0.3713970 0.669302091 0.0000000\*

Literature cited

Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C.

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.

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

Falk, D. A. 2013. Are Madrean ecosystems approaching tipping points? Anticipating interactions of landscape disturbance and climate change. Pages 40-47 *in* Merging science and management in a rapidly changing world: Biodiversity and management of the Madrean Archipelago III and 7th Conference on Research and Resource Management in the Southwestern Deserts; 2012 May 1-5; Tucson, AZ. Proceedings. RMRS-P-67. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Grabinski, Z. S., R. L. Sherriff, and J. M. Kane. 2017. Controls of reburn severity vary with fire interval in the Klamath Mountains, California, USA. Ecosphere **8**.

Harris, L., and A. H. Taylor. 2017. Previous burns and topography limit and reinforce fire severity in a large wildfire. Ecosphere **8**:e02019--n/a.

Harvey, B. J., D. C. Donato, and M. G. Turner. 2016. Burn me twice, shame on who? Interactions between successive forest fires across a temperate mountain region. Ecology **97**:2272--2282.

Hessburg, P. F., J. K. Agee, and J. F. Franklin. 2005. Dry forests and wildland fires of the inland Northwest USA: Contrasting the landscape ecology of the pre-settlement and modern eras. Forest Ecology and Management **211**:117--139.

Kliewer, G. F. 1994. Soil survey of Lassen National Forest Area, California. USDA Forest Service, Pacific Southwest Region, NRCS.

Knox, K. J. E., and P. J. Clarke. 2012. Fire severity, feedback effects and resilience to alternative community states in forest assemblages. Forest Ecology and Management **265**:47-54.

Lauvaux, C. A., C. N. Skinner, and A. H. Taylor. 2016. High severity fire and mixed conifer forest-chaparral dynamics in the southern Cascade Range, USA. Forest Ecology and Management **363**:74--85.

Mallek, C. M., H. Safford, J. Viers, and J. D. Miller. 2013. Modern departures in fire severity and area vary by forest type, Sierra Nevada and southern Cascades, California, USA. Ecosphere **4**:1--28.

McDonald, P. M. 1980. California black oak. Page 122 *in* F. Eyre, editor. Forest cover types of the United States and Canada. Society of American Foresters, Washington, D.C.

Miller, J. D., H. D. Safford, M. Crimmins, and A. E. Thode. 2009. Quantitative Evidence for Increasing Forest Fire Severity in the Sierra Nevada and Southern Cascade Mountains, California and Nevada, USA. Ecosystems **12**:16-32.

Odion, D. C., M. A. Moritz, and D. A. DellaSala. 2010. Alternative community states maintained by fire in the Klamath Mountains, USA. Journal of Ecology **98**:96--105.

Parks, S. A., C. Miller, C. R. Nelson, and Z. A. Holden. 2014. Previous Fires Moderate Burn Severity of Subsequent Wildland Fires in Two Large Western US Wilderness Areas. Ecosystems **17**:29--42.

Schoennagel, T., J. K. Balch, H. Brenkert-Smith, P. E. Dennison, B. J. Harvey, M. A. Krawchuk, N. Mietkiewicz, P. Morgan, M. A. Moritz, R. Rasker, M. G. Turner, and C. Whitlock. 2017. Adapt to more wildfire in western North American forests as climate changes. Proceedings of the National Academy of Sciences **114**:4582-4590.

Stevens, J. T., B. M. Collins, J. D. Miller, M. P. North, and S. L. Stephens. 2017. Changing spatial patterns of stand-replacing fire in California conifer forests. Forest Ecology and Management **406**:28--36.

Stevens‐Rumann, C., and P. Morgan. 2016. Repeated wildfires alter forest recovery of mixed‐conifer ecosystems. Ecological applications **26**:1842-1853.

Stevens‐Rumann, C. S., K. B. Kemp, P. E. Higuera, B. J. Harvey, M. T. Rother, D. C. Donato, P. Morgan, and T. T. Veblen. 2018. Evidence for declining forest resilience to wildfires under climate change. Ecology letters **21**:243-252.

Taylor, A. H. 2000. Fire regimes and forest changes in mid and upper montane forests of the southern Cascades, Lassen Volcanic National Park, California, U.S.A. Journal of Biogeography **27**:87--104.

Tepley, A. J., J. R. Thompson, H. E. Epstein, and K. J. Anderson‐Teixeira. 2017. Vulnerability to forest loss through altered postfire recovery dynamics in a warming climate in the Klamath Mountains. Global change biology **23**:4117-4132.

Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. Science **313**:940--943.