EARLY SERAL MIXED-CONIFER FOREST STRUCTURE AND COMPOSITION

FOLLOWING A WILDFIRE REBURN IN THE SIERRA NEVADA

By

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ABSTRACT

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Before the era of modern fire suppression, California's northern Sierra Nevada

mixed-conifer and yellow pine forests were self-regulating; recurring short-interval, low-

mixed severity wildfires maintained forest structure and composition, which in turn

exerted bottom-up controls on subsequent wildfires. As a result of fire suppression, and

coupled with the effects of climate warming and other anthropogenic disturbances, the

fundamental structure of mixed-conifer and yellow pine forests has shifted. Wildfires

may now be increasing in size, severity, and frequency across western North America.

However, little is known about the post-fire impacts of repeat wildfire on a forest after a

long era of suppression. In this study, I report findings regarding early successional

vegetation of Sierra Nevada mixed conifer forests that experienced two large wildfires,

the Storrie Fire (in 2000) and the Chips Fire (in 2012). These wildfires burned within the

historic fire frequency window for this ecosystem, but much of the forest within their fire

footprints had not burned for at least 100 years beforehand. I addressed three questions:

(1) how does wildfire affect plant community structure and composition among yellow

pine and mixed-conifer forests?; (2) do fire severity and fire frequency interact to

influence post-fire vegetation conditions?; and (3) are post-fire responses similar between

forests that have burned once, twice, or have not burned in the past century, or that have

burned at high, moderate, or low severity? In 2014, I sampled 74 plots in the Plumas and

Lassen National Forests. Of these plots, 50 plots were sampled from three fire severity

classes and two fire frequencies in and around the Chips Fire (2012). A portion of the

Chips Fire had reburned the Storrie Fire (2000), affording the opportunity to compare

them to post-fire effects of a single burn on fire-suppressed forests at the same stage of

post-fire succession. I also collected data in 24 unburned plots to contrast fire-suppressed

plots with plots that experienced wildfire.

Wildfire decreased tree density but also decreased available seed sources, which

can limit tree regeneration in high severity fire or reburns. Increased tree mortality also

produced greater fuel loading in reburns compared to single burns, though burned plots

exhibited less fuel loading and fuel connectivity than unburned plots. I also observed that

wildfire diversified species composition in single burns, increasing species richness,

evenness, and diversity. However, reburning plots appeared to reduce species richness,

causing reburns to exhibit richness similar to unburned plots. Still, reburn plots only

shared about half of its species with unburned plots, and 13% of species were exclusive

to reburns. My study was limited to a particular time (two years post-fire), and post-fire

effects may become more pronounced as early seral communities continue to respond to

the effects of the wildfire. Nonetheless, my results indicate that wildfire can produce

forest structure and composition that is dramatically different from fire-suppressed

mixed-conifer forests. Though it is unknown whether ecological processes can be

restored by just one or two wildfire events within a short time-span in fire-suppressed

landscapes, the post-fire conditions observed in my study have begun to resemble pre-suppression conditions by exhibiting reduced tree densities, lower fuel loads, and enhanced species diversity, especially at low to moderate fire severities. Because post-fire vegetation response is a stochastic and long-term process, understanding the effects of wildfire reintroduction and reburn will likely take multiple observations.

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INTRODUCTION

Wildfire is an important ecological process that plays an integral role in shaping many terrestrial ecosystems (Agee, 1993; Bond and van Wilgen, 1996). This dominant disturbance influences vegetation structure and composition by stimulating or inhibiting productivity of plants, creating heterogeneity in fuel structure size and spatial distribution, increasing available nutrients and light, regulating pests and disease, and by altering ecosystem services (Sugihara et al., 2006). While the impacts of individual fire events on vegetation have been well-studied (e.g., Sugihara, 2006; Donato et al., 2009a; Swanson et al., 2011; Collins and Roller, 2013; Crotteau et al., 2013; Miller et al., 2016), much less is known about how post-fire dynamics can influence the impacts of subsequent fires ("reburns") in the same areas. Post-fire succession and the influence of biological legacies such as dead and downed trees can impose bottom-up controls on the behavior of subsequent reburns (Tuner and Dale, 1998; Peterson, 2002; Agee, 2005; Thompson and Spies, 2010). Given that forest wildfires appear to be increasing in size, severity, and frequency across much of the western United States (Miller et al. 2009b; Westerling et al., 2006; Mallek et al., 2013; van Mantgem et al., 2013; Steel et al., 2015; Westerling, 2016), understanding the effect of reburns on forest landscapes is crucial for evaluating ecosystem resilience and employing successful land management (Gray and Franklin, 1997; Thompson et al., 2007; Donato et al., 2009b; Webster and Halpern, 2010; Coppoletta et al., 2016; Stevens-Rumann and Morgan, 2016).

In California's northern Sierra Nevada, mixed-conifer and yellow pine forests have evolved with a fire regime characterized by moderately short fire return intervals (5 to 25 years, with a mean of 11-16 years) and low to mixed severities (Sugihara et al., 2006; Van de Water and Safford, 2011). Wildfires here were historically "self-regulating"; typically, fires were relatively small in size due to recurring reductions in fuel loading and spatial continuity (Agee, 1993; Moody et al., 2006; Collins et al., 2009, Odion et al., 2014). This regime exhibited heterogeneous horizontal and vertical structure with low tree densities and a diverse array of fire-adapted plant species (Hessberg, 2007; North et al., 2009; van de Water and Safford, 2011). However, the United States' national land management policy of the past century has been largely defined by fire suppression. As a result of suppression, and coupled with the effects of climate warming, extensive logging, and other anthropogenic disturbances, the fundamental structure of mixed-conifer and yellow pine forests has shifted (Parsons and DeBenedetti, 1979; Westerling et al., 2006; Beaty and Taylor, 2008; Gedalof, 2011; Safford and Stevens, *in press*). Surface fuels loadings are higher, and tree densities have increased as smaller trees have reduced the number and size of canopy gaps (Collins et al., 2011; Safford et al., 2012). As such, shade-tolerant plant species are outcompeting the previous fire-adapted understory and overstory, reducing overall diversity (Ansley and Battles, 1998; Barbour et al., 2007; Knapp et al., 2013).

In addition to the well-known impacts of fire suppression on contemporary fires, there is growing concern that current forest structure may also exacerbate the potential for subsequent stand-replacing fires in areas that have burned recently (i.e., "reburns")

(Harris and Taylor, 2015; Coppoletta et al., 2016; Stevens-Rumann and Morgan, 2016). However, little is known about the post-fire impacts of repeat wildfires in forests after a long era of suppression (Donato et al., 2009b, Webster and Halpern, 2010; Parks et al., 2014). Without recurring fire, the legacies of previous fires on mixed-conifer and yellow pine ecosystems have diminished over time, the self-regulating concept has been interrupted, and dramatically altered successional pathways have occurred (Parsons and DeBenedetti, 1979; Peterson, 2002; Westerling et al., 2006).

In this study, I report my findings of a natural experiment regarding the early seral communities of Sierra Nevada mixed conifer forests that experienced two large wildfires, the Storrie Fire (2000) and the Chips Fire (2012). These wildfires burned 12 years apart, within the historic fire frequency window for this ecosystem, but much of the forest within their fire footprints had not burned for at least 100 years beforehand. I asked: (1) how does reintroducing wildfire affect plant community structure and composition among yellow pine and mixed-conifer forests?; (2) do fire severity and fire frequency interact to influence post-fire vegetation conditions?; and (3) are post-fire responses similar between forests that have burned once, twice, or have not burned in the past century, or that have burned at high, moderate, or low severity? Most studies investigating reburns to date have been conducted using remote sensing techniques (e.g., Collins et al., 2009; Thompson and Spies, 2010; Parks et al., 2014), but relatively few have used data collected on the ground (Webster and Halpern, 2010; Coppoletta et al., 2016). My study used 74 field plots in which I examined tree, fuel, and species composition characteristics. Unlike other reburn studies, my research compared post-fire

effects across all burn severities, not just high severity. My study area also burned as a result of late-summer wildfires, as opposed to burning in prescribed fires which may have more artificial conditions or could potentially ignite outside of the typical fire season when it's safer for humans and more easily controlled. Additionally, the effect of time-since-fire is equal across all fire frequencies in my study, which offers insight into how wildfire affects landscapes that experienced a single burn as compared to a reburn. Lastly, although the study did not take place in a wilderness area, I was able to survey areas whose structure remained relatively unaltered by management treatments, eliminating the need to account for confounding effects and affording us the opportunity to isolate the effects of wildfire from other disturbances.

MATERIALS AND METHODS

Study Area

I conducted my study within and adjacent to the 2012 Chips Fire in the Plumas and Lassen National Forests in California's northern Sierra Nevada (approximate center 40.09ºN and 121.18ºW; Fig. 1). The Chips Fire was ignited by lightning on July 29, 2012 and quickly burned over 30,500 ha of public and private land with varying fire severity. A portion of the Chips Fire overlapped almost half (45%) of the Storrie Fire of 2000 (FRAP, 2014). The Storrie Fire was human-caused, inadvertently ignited by railroad track repair on August 17, 2000, and resulted in 22,687 ha burned with varying fire severity. The Chips and Storrie Fires are both located in the North Fork Feather River watershed, which exhibits high spatial complexity, steep slopes and sharply undulating terrain. The region is characterized by a Mediterranean climate, with warm, dry summers and cold, wet winters during which most of the year's precipitation accumulates. I limited my study to mixed-conifer and yellow pine forests found at 1200-2000 m elevation (Safford et al., 2013). Common tree species included Jeffrey pine (*Pinus jeffreyi*), ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), Sierra lodgepole pine (*Pinus contorta* var. *murrayana*), white fir (*Abies concolor*), red fir (*Abies magnifica*), Douglas fir (*Pseudotsuga menziesii*), and incense-cedar (*Calocedrus decurrens*). Common shrubs species were California lilac (*Ceanothus cordulatus, C. velutinus, C. integerrimus*), manzanita (*Arctostaphylos patula, A. nevadensis*), huckleberry oak

(*Quercus vaccinifolia*), bush chinquapin (*Chrysolepis sempervirens*), and currant (*Ribes roezlii, R. cereum* var. *cereum, R. nevadense*). Soil composition is variable in the Plumas and Lassen National Forests, with volcanic, granitic, and ultramafic parent materials found across the study area (Jennings et al., 1977). For my research, I avoided sampling on ultramafic soils due to its unique effect on forest productivity, composition, and recovery from disturbance (Safford and Harrison, 2004; Safford and Mallek, 2011; DeSiervo et al., 2015).

From May to August of 2014, I installed 74 permanent fixed-radius circular plots to assess post-fire effects on forest structure and composition. I created a 400-m grid across my study area using ESRI ArcGIS 10.1, with the top row beginning a random distance in from the edge. I then stratified my sampling based on several criteria. About 25 plots were established for each of three fire frequency groups: (1) in forest disturbed only by the Chips Fire ("single burn"), (2) in forest where the Chips Fire reburned the earlier Storrie Fire (reburn), and (3) in the Control ("unburned") outside the Chips perimeter. Unburned plots were located within a 1 km buffer surrounding the Chips Fire to provide a baseline for comparing the structure and composition after a single burn or reburn to that found in an area of continued fire suppression. Within each burned group, a near-equal number of plots ($n = 8$ or 9) was selected in high-, moderate-, or low- severity patches in the Chips Fire; for the unburned plots, all 24 plots experienced no fire (Table A1).

Aside from the Chips and Storrie Fires, all plots experienced no other fires (wildfire or prescription burn) nor confounding management treatments such as logging

or thinning since 1900, according to historical USDA Forest Service polygons available in CalFire FRAP Mapping geodatabase and the USFS Region 5 Forest Service Activity Tracking System (FACTS) geodatabase, respectively. In addition, my plots were selected from areas at least 50 m from any road, active or decommissioned, and I explicitly selected plots on a wide range of slopes (<60%), aspects, slope positions, and elevations that could be mirrored in each fire frequency group.

Fire severity was determined prior to sampling using the Composite Burn Index (CBI), a geospatial product derived from the Relative differenced Normalized Burn Ratio (RdNBR) created from bands 4 and 7 of pre- and post-fire LANDSAT Thematic Mapper imagery (Key and Benson, 2006; Miller and Thode, 2007; Miller et al., 2009a). I used CBI from 'immediate' imagery (captured within 30-45 days of wildfire containment; Miller and Quayle, 2015) for both the Chips and Storrie Fires, since no 'extended' imagery (captured about one year post-fire; Miller and Quayle, 2015) was available for the Chips Fire. In the field, I then ground-truthed the remotely sensed Chips Fire severity using ocular estimates of percent vegetation burned based on a condensed version of severity classes from the National Park Service Fire Monitoring Handbook (Table 1).

My analyses explored whether my measurements of post-fire response differed based on fire frequency, Chips fire severity, or the interaction of the two variables. While Coppoletta et al. (2016) demonstrated that the severity of the Storrie Fire in part influenced the severity of the Chips Fire, my study included only fire frequency. The plots I sampled were selected based on Chips fire severity. Due to logistical challenges and post-fire treatment from the Storrie Fire implemented before the Chips Fire, I was not

able to sample every combination of pre- and post-Chips fire severity (Table A1). Thus,

consolidating all previous severities into a single fire frequency resulted in a more robust

sample size and greater statistical power. Although this adds more uncertainty to my

results, my study fills an important information gap in wildfire ecology. Additionally,

within my reburned plots ($n = 50$), previous (Storrie) fire severity was only mildly

correlated with Chips fire severity, with both fire severities measured as RdNBR ($r = 0.21$). However, my plots' correlation between Chips fire severity and previous fire

severity is weaker than what Coppoletta et al (2016) found in their study within the

Storrie-Chips reburn using a multiple linear regression models with a greater sample size

($n = 126$, $R^2 = 0.39$).

Data Collection

In all of my plots, I employed an 'extensive' version of the USDA Forest Service

Pacific Southwest Region 5 Common Stand Exam sampling protocol to collect data on

trees, fuels, vegetation composition, species composition, and site attributes (Safford,

2012). I used the USDA Forest Service Pacific Southwest Region 5 Post-fire

Regeneration Plot Protocol to sample tree regeneration (Safford and Welch, 2011). Each

plot center served as the nucleus for three nested concentric plots: a 4.4 m radius (~60-m^2

plot) was used to collect tree regeneration data; an 11.3 m radius (~400-m^2 plot) was used

to collect tree, fuels, and understory data; and an additional 16 m radius (~800-m^2)

"donut" surrounding the smaller plots allowed us to incorporate additional plant species

at a larger plot scale. All plots were at least 400 m apart to minimize the effects of spatial autocorrelation on my study. At each plot, I recorded slope, slope position, and aspect, to ground-truth my sampling stratification as well as correct for the influence of slope on analyses.

Trees

Individual saplings (tree species with DBH <7.6 cm but a height >1.37 m) and tree seedlings in my 60-m^2 plots were counted and identified to species. I used Franklin's guide (1961) to identify the species of younger seedlings (trees <1.37 m tall). Seedlings were categorized as being overtopped by shrubs or not overtopped. I recorded the height, mortality status, and DBH where applicable of all saplings and the tallest seedling for each species per plot. Seedlings and saplings were aged by counting bud scars and subtracting the current year.

For all trees $\geq$7.6 cm diameter at breast-height (DBH) in my 400-m^2 plots, I recorded the species, DBH, and mortality status ("live" or "dead") of each tree. For live trees, I also recorded the crown base height, defined as the lower limit of the canopy fuel stratum or the tip of the lowest hanging live branches so that the inclination of the branches is taken into account when measuring height (Garcia et al., 2011).

Fuels

Surface fuel loading was assessed by laying out four Brown's transects (Brown, 1974), radiating in the cardinal directions from the centers of my 400-m^2 circular plots. Starting at the edge of the plots and heading toward the middle, I tallied one-hour (diameter = 0.0-0.64 cm), 10 hour (0.64-2.5 cm), and 100 hour (2.5-7.6 cm) fuels for the first 2 m, and only 100 hour fuels for the subsequent 2 m for each 11.3 m transect. For coarse woody debris that crossed anywhere along the transects, I recorded diameter at the intersection and length. Decay class (sound/rotten) of every coarse woody debris log was determined by the persistence of bark or twig retention, texture, shape, and wood color. Additionally, at both the starting point and 4 m in from the starting point, I sampled fuel height, litter depth, and duff depth.

Composition

In my 400-m^2 plots, I estimated surface ground cover with values summing to 100%. Categories included areal covers of bare soil, rock, coarse woody debris, and litter. I also collected data about areal vegetation cover and species composition. Because I collected all data during only one field season, I were unable to visit plots more than once to gain a full inventory of plant species present at the different stages of the year. To mitigate potential phenological disparity and improve botanical consistency in my surveys, I sampled plots in all fire frequency groups each week, starting at my lower elevations and working my way higher as the season progressed. I identified all live plants present in my 400-m^2 plot and 800-m^2 donut to species using the current Jepson

Manual nomenclature (Baldwin et al., 2012). I categorized each species by origin

("native" and "nonnative") based on the Jepson Manual and Calflora

(http://www.calflora.org/), and USDA Forest Service's Fire Effects Information System

(FEIS, 2016). Plants that could not be identified in the field were collected and later

identified to species or assigned a family in the lab. I estimated vegetation cover and

modal heights for each live species, as well as the following live lifeforms overall: trees,

shrubs, forbs, and graminoids. I also estimated cover for each lifeform based on height

class, separating values by mortality class ("live" or "dead"): trees ≥1.8 m, trees <1.8 m,

shrubs ≥1.8 m, shrubs 1.8–0.5 m, shrubs ≤0.5 m. Vegetation cover estimates were

recorded to the nearest 5% for values greater than 10%. If a plant was present in a plot

but had <1% areal cover, I recorded that plant as having "trace" (0.5%) cover. Vegetation

cover estimates could sum to >100% due to crown overlap.

Uncertainty

The methods of the USDA Forest Service protocols I employed heavily rely on

observer skill and ocular estimates, therefore the aptitude of the observers may be one of

several sources of uncertainty in my study. A number of checks were developed to

maximize accuracy and precision of those estimates. At the beginning of the field season,

all field crews conducting post-fire surveys in the Sierra Nevada using the USDA Forest

Service protocols convened for a multi-day training where field technicians calibrated

their estimates of cover and fire severity, among other mensuration methods. Also, cover

was estimated by thresholds, typically to the nearest 10%, to mitigate uncertainty (Korhonen et al., 2006). The results of my study are from a single season and usually conducted by the same two crew members working together, so estimation error and inter-plot precision did not suffer from turnover of personnel. Additionally, my plots were selected based on pseudo-random stratification using spatial products which themselves contained uncertainty. For example, both the remotely-sensed fire severity CBI rasters from USDA Region 5 and the Digital Elevation Models from the United States Geologic Survey from which we extracted slope, elevation, and aspect had resolution of 30 m and a spatial error of 15 m. Not all roads or trails ever created in the Plumas and Lassen National Forests were included in a vector file from the USDA Forest Service Region 5, and the spatial error of roads that did exist in the database was largely unreported. While the thresholds used to determine fire severity in geospatial products like CBI and RdNBR have been heavily calibrated across California (Miller et al., 2009a; Miller and Quayle, 2015), I still ground-truthed fire severity and all other stratification factors as best and thoroughly as possible, and plot locations were relocated as necessary to capture a full spectrum of topographic characteristics, forest management, and desired fire severities. The ground-truthed fire severity and fire frequency were included in my analyses.

Perhaps the greatest source of uncertainty in this study comes from the fact that it involved surveying wildfires. Wildfires are natural experiments, and therefore cannot be replicated (Wiens and Parker, 1995). Weather is unmanipulable but is an important driver of fire behavior, which influences severity (Sugihara, 2006). In fact, Coppoletta et al.,

(2016) found weather to be the most influential predictor of reburn fire severity. Also, the conditions of a landscape are also unique to each wildfire, are unique to the sampling date, and will never be exactly the same again at a given location. While my study is unique even if all my plots were resurveyed at a later date or a near-by wildfire reburn was surveyed two years post-fire, my study still contributes the larger body of knowledge about wildfire ecology and forest management by illuminating the natural range of variation in post-fire response from various fire frequency scenarios.

In natural experiments, sampling cannot be entirely randomized (Wiens and Parker, 1995). Tobler's First Law of Geography suggests that things on a landscape that are closer are likely to be more similar than things that are distant (Tobler, 1970; Anselin and Bera, 1998; Plant, 2012). The GPS unit I used to demarcate plot center of the plots I sampled in the field was a Trimble Juno 3B. This unit had sub-meter accuracy capabilities, though weather, topographic, and temporal conditions rarely allowed for the fine-grained resolution capture of plot center coordinates. Even post-processing the collected geospatial data typically did not achieve sub-meter accuracy, instead typically ranging from 2-60 m. Despite accuracy error, I ensured my plots were at least 400 m apart to reduce spatial autocorrelation. Even so, spatial autocorrelation between forest mensuration plots located within Sierra Nevada mixed-conifer forests could be minimal due to landscape-scale heterogeneity, even in fire-suppressed areas (van Mantgem and Schwilk, 2009). Additionally, "single-time" study designs like mine that are from only one survey comparing impact and reference sites are less affected by pseudo-replication (i.e., multiple patches of the same fire severity within a wildfire's footprint) than other

study designs, although single-time designs assume that other natural factors can influence post-fire response (Wiens and Parker, 1995).

Data Analysis

All analyses were done using R Statistical Software (R Core Team, 2016). I conducted a series of tests using frequentist statistics to explore the differences in response between fire severities, fire frequencies, and their interactions. All data were tested for normality and heteroscedasticity of residuals. Where needed, I transformed data before using parametric tests or used equivalent nonparametric tests. When appropriate, I conducted Scheirer-Rary-Hare tests and rank-based Tukey's Honest Significant Differences (Tukey's HSD) tests (Table 4), which were executed in R following the methods outlined in Dytham (2011) and Sokal & Rohlf (2012). Two-way permutational multivariate analysis of variance (perMANOVA) tests were executed using the "vegan" package in R (R Core Team, 2016).

Since my tests involved multiple comparisons, I employed Holm or Bonferroni adjustments of the alpha level ($p = 0.05$) to reduce Type I error. When possible, I used Holm (1979) adjustments, because Holm is more powerful and less conservative than Bonferroni (Aickin and Gensler, 1996), which is especially beneficial because my nonparametric tests are already very conservative (Dytham 2011).

Trees

       To explore if the tree composition in this study is dominated by species that are typically associated with fire suppression, tree species were classified as either shade-tolerant or shade-intolerant (FEIS, 2016; Safford and Stevens, *in press*). Shade-tolerant species were likely favored by conditions arising from fire suppression: less fire-tolerant species that could grow with less available light. Conversely, shade-intolerant species were typically fire-tolerant or fire-dependent at maturity, and typically grew in more open, xeric conditions where available light was not as limited. The species I placed in my shade-tolerant plant group were: white fir (*Abies concolor*), red fir (*Abies magnifica*), Douglas fir (*Pseudotsuga menziesii*), and incense-cedar (*Calocedrus decurrens*). The species in my shade-intolerant plant group were: Jeffrey pine (*Pinus jeffreyi*), ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), and Sierra lodgepole pine (*Pinus contorta* var. *murrayana*). Hardwoods were rarely present in my plots (<1% of all trees or seedlings counted). Therefore, hardwoods were excluded from my analyses.

       Only 6% of the tree seedlings counted were >2 years old, signifying that the vast majority (94%) of regeneration present occurred following the Chips Fire. Therefore, I analyzed all seedlings together. Slope corrections of stem densities following Abella et al. (2004) were necessary because my fixed-radius plots were sampled across a range of slope gradients; a plot's horizontal area decreases as slope gradient increases, thereby imposing spurious restrictions on how many stems can fit in a plot regardless of any other biotic or abiotic factor (Abella et al, 2004). I calculated slope-corrected seedling density

(stems ha^{-1}), then back-transformed seedling density to counts for the 400-m^2 plot for my analyses to reduce the variance and overdispersion per-hectare calculations exhibited. I tested if the seedling density was different between live shade-tolerant or shade-intolerant plant groups using a Mann-Whitney-U test. I then performed a Scheirer-Ray-Hare test to see if the of proportions seedlings that were shade-tolerant and shade-intolerant differed by fire severity, fire frequency, or their interactions. Next, I conducted a two-way analysis of variance (ANOVA) on total seedling density with a log transformation to see if count differed between fire severity, fire frequency, or their interaction, followed by a Tukey's HSD post hoc test with a Holm adjustment.

To calculate the tree density (stems ha^{-1}) of live shade-tolerant, live shade-intolerant trees, and all dead trees ("snags") in each plot, I applied the same slope corrections (Abella et al., 2004). I also calculated the basal area (m^2 ha^{-1}) for each tree, the total sum of live basal area for shade-tolerant and shade-intolerant plant groups in each plot, as well as the total sum of snags in the plot regardless of shade preference. I tested if the basal area or tree density was different between live shade-tolerant or shade-intolerant plant groups using Mann-Whitney-U tests. I then conducted separate Scheirer-Ray-Hare tests for each plant group and snags, examining if basal area or tree density differed by fire severity, fire frequency, or their interaction. I followed the analyses with post hoc tests using Tukey's HSD with a Holm adjustment on data ranks.

Fuels

Surface fuels in each fuel class were summed per transect, and converted to fuel loadings (mg ha^{-1}) using Brown's method (1974) which includes slope correction. The fuel loadings of the four transect were then averaged so that each plot had an average sum of every fuel class. I tested for differences in fuel loading of all fuel size classes (1-hour, 10-hour, 100-hour, coarse woody debris) between fire severities, fire frequencies, and their interaction using a two-way multiple analyses of variance (MANOVA) with Pillai's trace statistic. Fuels data were square root-transformed to address issues of normality. To investigate which levels of fire severity and fire frequency significantly differed while also accounting for the correlation of loadings between fuel classes, I conducted two-sample Hotelling's T^2 tests with a Bonferroni adjustment.

Litter and duff depths were also summed for each transect and averaged per plot. I conducted separate tests for litter and duff because there was a lower correlation between their measured depths ($r = 0.40$). I did not combine litter and duff depths into one value because litter and duff have different contributions to fire behavior (Sugihara et al., 2006). Litter depth was log-transformed and analyzed with a two-way ANOVA, followed by Tukey's HSD post hoc test with a Holm adjustment. The differences in duff depth among fire severity, fire frequency, or their interaction were assessed using a Scheirer-Ray-Hare test, which is a multifactorial extension to the Kruskal Wallis test. I then conducted Tukey's HSD with a Holm adjustment as duff depth's post hoc test using data ranks.

Fuel strata gap is defined here as the distance from the top of the surface fuel bed to the lower limit of the canopy fuel stratum (Cruz et al., 2004; Garcia et al., 2011). I

calculated fuel strata gap as the physical distance between a plot's average crown base height of trees and the plot's modal height of the surface fuel stratum with the greatest areal cover, or the modal height of the tallest surface fuel stratum when that stratum's areal cover was $\geq$ 5% (Scott and Reinhardt, 2005; Mitsopoulous and Dimitrakopoulos, 2007; Garcia et al., 2011). Garcia et al. (2011) found that using a more conservative cover (e.g. $\geq$10%) provided worse estimates of canopy fuel characteristics in mixed-conifer stands in the United Kingdom than did my 5% cover threshold. Additionally, fuel strata gap was determined using only live fuels (Van Wagner, 1977; Helms, 1998; Scott and Reinhardt, 2001; Cruz et al., 2004). Nonetheless, dead woody stems and bark lichen have the ability to act as ladder fuels, so a potential error term was unaccounted for in my commonly-accepted calculations of fuel strata gap (Cruz et al., 2004; Garcia et al., 2011). Sapling presence usually did not affect calculations of fuel strata gap, as the vast majority of my plots did not have live saplings. Only 5% ($n = 4$) plots had $\geq$ 5 live saplings, where I used average sapling height as the height of the surface fuel stratum. These same five plots also had a shrub layer under the saplings. Shrubs have the potential to carry fire from the ground to the sapling canopy, and therefore reinforced justification for using average sapling height in calculations of fuel strata gap for these few plots. Figures of the raw tree canopy base height data revealed that high severity fire was strongly associated with no or minimal live crown base height. Therefore, excluded high severity plots from my analysis of fuel strata gap. I assessed if fuel strata gap (sans high severity) differed between fire severity and fire frequency or their interaction using a two-way ANOVA.

Without high severity, data met the assumptions of normality and no transformation was needed. Tukey's HSD with a Holm adjustment served as my post hoc test.

Composition

I evaluated the differences in ground cover between fire severity, fire frequency, the interaction of these independent variables using perMANOVA using the Bray-Curits distance. For post hoc tests, I conducted pairwise perMANOVA with a Holm adjustment, following Abrizu (2016).

Because graminoid cover was <3% in all fire severity × fire frequency categories, its areal cover was added to forb cover. This total herbaceous cover was then assessed in tangent with the other vegetation covers. I used a perMANOVA to assess whether vegetation cover differed between fire severity, fire frequency, and their interaction. The Bray-Curtis distance was employed in the perMANOVA, and 999 permutations were run. The post hoc test was pairwise perMANOVA with the same settings as the original vegetation cover perMANOVA.

In my assessments of community composition metrics, I used relative cover of each plant species present per plot. I then used the "vegan" package in R (Oksanen et al., 2009, *in* R Core Team, 2016) to calculate richness, Pielou's evenness, and the Shannon-Wiener diversity index of each plot's vegetation composition. To determine if response differed between fire severity, fire frequency, or the interaction of these independent variables, I analyzed these three community metrics separately using two-way ANOVA

and Tukey's HSD post hoc test; no transformation was needed because assumptions of normality were met.

RESULTS

Trees

In my study, total shade-tolerant seedling density was 14 times higher than total shade-intolerant seedling density ($U = 4102.5$, $p < 0.001$; Fig. 2A). In fact, shade-intolerant seedlings comprised only 7% of the total seedlings (325 stems out of 4970 seedlings counted in the 74 60-m^2 plots; Table 3). However, wildfire significantly increased the proportion of shade-intolerant seedlings ($H_{3, 67} = 12.42$, $p = 0.001$) (Table 4), where the proportions of shade-intolerant seedlings in plots that experienced moderate and high severities were on average 10 times greater than in unburned plots (mean $_{\text{moderate}}$ $_{\text{and high severity}} = 0.32 \pm 0.07$ s.e., mean $_{\text{unburned}} = 0.03 \pm 0.01$ s.e.; $p < 0.01$, and $p = 0.05$, respectively). Total seedling density in single burns was significantly higher than in unburned plots ($F_{3, 67} = 5.92$, $p = 0.001$), with seedling densities increasing in low and moderate fire severities, and decreasing in high fire severity (Fig. 2, Table 3). In general, reburns had dramatically lower total seedling densities than in unburned plots or single burns ($F_{1, 67} = 8.81$, $p < 0.01$; Fig. 2, Table A6), and seedling densities in high severity plots were on average less than half that in other severities ($p \leq 0.03$; Fig. 2, Table A6).

Like seedling density, shade-tolerant tree (DBH ≥ 7.6 cm) density was much higher than shade-intolerant tree density, often quadruple or more the density of shade-intolerant trees ($U = 4122.5$, $p < 0.001$; Fig. 3, Table 3). Shade-tolerant tree density displayed an inverse relationship with fire severity ($H_{3, 67} = 56.75$, $p < 0.001$) as each

progressive severity exhibited significantly lower shade-tolerant tree density ($p < 0.01$ for all pairwise severity comparisons), ranging from an average of 720 trees ha^{-1} ($\pm$ 73 s.e.) in unburned plots and plummeting to an average of 0.0 trees ha^{-1} ($\pm$ 0 s.e.) in high severity plots (Fig. 3, Table 3 and 4). The density of shade-intolerant tree density was greatest in unburned plots, averaging 147 trees ha^{-1} $\pm$ 43 s.e., but fell to an average of 3 ha^{-1} $\pm$ 2 s.e. in high severity plots ($H_{3,\,67} = 17.16$, $p < 0.001$). Especially compared to single burns and unburned plots, reburns contained very few live sun-tolerant trees regardless of reburn severity ($H_{1,\,67} = 3.76$, $p = 0.05$; Fig. 3, Table 3 and 4). Snag density was significantly different by both severity ($H_{3,\,67} = 21.11$, $p < 0.001$) and fire frequency ($H_{1,\,67} = 17.04$, $p < 0.001$) (Fig. 3, Table 3 and 4). In single burns, snag density linearly increased as severity treatments became more severe, with plots that experienced a single burn of high severity having about three times the snag density of unburned plots (Fig. 3). Reburns had only slightly more snags ($p = 0.09$) than unburned plots, and actually had a somewhat lower snag density in high severity-reburn plots compared to moderate severity-reburn plots.

Basal area of both shade-tolerant and shade-intolerant live trees in unburned plots was higher than in reburns and single burns, or moderate and high fire severities. However, snag basal area in reburns and single burns was about 250% higher than in unburned plots ($p < 0.001$; Fig. 3, Table 3 and 4).

Fuels

Fuel loading in unburned plots was double or even triple that in plots that burned ($F_{3,\,67}$ = 24.33, p = 0.001; Fig. 4 and A4, Table 3). Fine fuels (1-hour, 10-hour, and 100-hour fuels) decreased by 50% or more as severity increased from unburned to moderate, with reburns exhibiting somewhat higher fine fuel loads (1-hour: $F_{2,\,67}$ = 2.78, p = 0.07; 10-hour: $F_{2,\,67}$ = 2.67, p = 0.08). Yet, fine fuel loads tended to increase by about 50% in high severity compared to moderate severity (Fig. 4, Table 3). Within high severity plots, reburns had lower 1-hour and 10-hour fuel loads than single burns, but somewhat higher fuel loads than single burns in the 100-hour size class. Reburns had consistently higher fuel loads of coarse woody debris than single burns regardless of burn severity ($F_{1,\,67}$ = 3.36, p = 0.07), averaging almost double the fuel load of single burns (mean $_{\text{Reburn}}$ = 29.98 mg ha^{-1} ± 7.57 s.e., mean $_{\text{Single burn}}$ = 16.97 mg ha^{-1} ± 6.05 s.e.), but these fuel loads were still lower than in unburned plots (mean $_{\text{Unburned}}$ = 53.87 mg ha^{-1} ± 10.66 s.e.). Across all fuel class sizes, unburned plots had about triple the fuel load of reburns, and typically over triple the fuel load of single burns.

Compared to burned plots, unburned plots had over double the litter depth ($F_{3,\,67}$ = 12.63, p < 0.001), over quadruple the duff depth ($H_{3,\,67}$ = 51.64, p < 0.001) and about half the fuel strata gap ($F_{2,\,52}$ = 22.17, p < 0.001) of burned plots (Fig. 4, Table 3 and 4). Plots that experienced moderate fire severity had the second-greatest litter depth (mean = 3.3 cm ± 0.9 s.e.), more than those in low severity (mean = 2.4 cm ± 0.3 s.e.) or high severity (mean = 1.5 ± 0.4 s.e.). Reburns had somewhat less litter than single burns across all severities (mean $_{\text{Reburn}}$ = 1.9 cm ± 0.03 s.e., mean $_{\text{Single burn}}$ = 2.9 cm ± 0.6 s.e.). Unburned plots had on average 4.1 cm (± 0.5 s.e.) of duff, while the vast majority of

burned plots had scant amounts of duff (<1 cm $\pm$ $\leq$0.1 s.e.). Plots in reburns and plots that experienced moderate fire severity had a greater fuel strata gap than in single burns and low severity plots. A Welch two-sample t-test revealed that at moderate severity, single burns have significantly higher fuels strata gaps than reburns (mean $_{\text{Single burn, moderate severity}}$ = 12.5 m $\pm$ 1.4 s.e, mean $_{\text{Reburn, moderate severity}}$ = 19.6 m $\pm$ 2.0 s.e.; t = -2.89, df = 12.897, p = 0.01).

Composition

By far, the greatest areal cover of bare soil and exposed rock occurred in high severity plots, with mean covers of 15% $\pm$ 4 s.e. and 34% $\pm$ 6 s.e., respectively, compared to <2% $\pm$ 1 s.e. bare soil and <10% $\pm$ 3 s.e. rock cover in in low, moderate, and unburned plots ($F_{3, 67}$ = 24.33, p = 0.001, Table 4), with reburns possessing double the cover of these substrates than single burns and 8 times their cover in unburned plots ($F_{1, 67}$ = 24.33, p = 0.001; Fig. 5, Table 3 and 4). In this early seral stage of a post-fire landscape (2 years after the Chips Fire), litter cover decreased as severity increased, with reburns having less areal litter cover than single burns (mean = 65% $\pm$ 6 s.e.) compared to mean = 84% $\pm$ 5 s.e., respectively). The litter cover in plots experiencing high severity fire was half that in the other severities. Woody debris cover increased slightly as severity increased, which could be attributed to greater tree damage and mortality associated with higher fire severities, including mortality from the Storrie Fire. Unburned plots had twice as much coarse woody debris cover as reburns, and reburns had twice as much coarse

woody debris cover as single burns. Still, average woody debris cover of any fire severity or frequency was <7% ± 1 s.e..

Overall, overstory tree cover and total vegetation cover drastically diminished in plots with higher fire severity while herb cover and shrub cover increased in high severity plots ($F_{3, 67} = 22.86$, $p = 0.001$; Fig. 6, Table 3 and 4). Reburns consistently exhibited lower overstory tree cover than single burns (mean = 20% ± 4 s.e. vs mean = 35% ± 7 s.e., respectively). Shrub cover decreased as severity increased from unburned (mean = 10% ± 3 s.e.) to low (mean = 3% ± 1 s.e.) to moderate (mean = 2% ± 1 s.e.), then sharply increased in high severity (mean = 20% ± 5 s.e.). Reburns had somewhat less shrub cover than single burns, except in high severity where reburns had greater cover, though this difference was not significant according to a Mann-Whitney-U test. Additionally, of all the tree seedlings I counted ($n > 4000$), only two were overtopped by shrubs. Herb cover increased steadily as severity increased, with unburned plots having only 2% cover (± 0 s.e.) on average, whereas high severity had 8% average cover (± 3 s.e.). Reburns at low severity had the greatest herb cover, but exhibited otherwise comparable herb cover with single burns. Total areal vegetation cover trends resembled those of overstory tree cover. However, reburns had higher total vegetation cover than overstory tree cover due to higher levels of shrub and herb cover amidst an open canopy, especially in plots that experienced high fire severity.

This study's 74 plots contained a total of 215 observed plant species, with 58 species occurring in ≥ 5% of plots (Table A5). 63% of taxa were shared by all fire frequencies, 9% were unique to unburned plots, 25% were found only in single burns,

and 13% were exclusive to reburns, with herbs mainly accounting for the differences. The species overlaps between fire frequencies was around 45%: unburned plots shared 39% of species with single burns, and half of its species with reburns; single burns and reburns exhibited a 46% overlap.

At least one nonnative plant was found in 54% of plots (40 out of 74 plots). Only 4% of unburned plots (1 of 24 plots) had at least one nonnative. However, the percentage of plots with at least one nonnative rose dramatically in burned areas: 84% of plots experiencing a single burn had at least one nonnative (21 of 25 plots). Reburns also had a high amount of plots with at least one nonnative species (72%, or 18 out of 25 plots), but presence was lower than that of single burns. Nonnative presence was dominated by three species: cheatgrass (*Bromus tectorum*), rattail fescue (*Festuca myuros*), and sweetclover (*Melilotus albus*). Still, areal cover of any nonnatives in each plot was very low (mostly <2%).

Fire severity and fire frequency had significant or marginally significant effects on all species composition metrics tested (Table 4). In general, reburns exhibited lower values for species composition metrics than single burns, with more pronounced differences in high severity (Fig. 7, Table 3). However, reburns and single burns were not significantly different except for a marginal significance ($p = 0.06$) in richness (Table 3). In my plots, richness was the lowest in unburned plots (mean = 19 ± 2 s.e.), peaked in moderate severity plots (mean = 32 ± 3 s.e.), and fell in high severity plots (mean = 24 ± 3 s.e.). Reburns did not significantly differ in richness from unburned plots, but single burns had 65% higher richness than unburned plots ($p < 0.01$). Evenness increased as

plots experienced successively higher fire severity. However, evenness varied more across reburned plots than in single burns, and at high severity reburns had somewhat lower evenness than single burns. Diversity was almost 70% greater in high and moderate severity plots than in unburned plots. Low severity plots (mean = 1.77 ± 0.14 s.e.) also had somewhat higher diversity than unburned plots (mean = 1.48 ± 0.11 s.e.). Reburns showed evidence of having slightly more homogenized species composition, with lower diversity in reburns (mean = 2.12 ± 0.14 s.e.) than in single burns (mean = 2.42 ± 0.12 s.e.), especially between high severity plots.

DISCUSSION

Fire severity and fire frequency interacted with repeat burning, at least at the temporal scale of this study. Single burns and reburns exhibited different post-fire responses for certain forest characteristics, such as tree regeneration and species composition. Additionally, forest structure and composition were very different between unburned and burned plots. My study supports the idea that variations in disturbance severity and frequency influence ecosystem structure and function (Bond and van Wilgen, 1996; Agee, 2005; Donato et al., 2009b), though not always in ways that are likely to reinstate a self-regulating mixed-conifer forest that eventually exhibit reduced tree density and fuel loading, more heterogeneous fuel continuity, diverse native plant species composition, and dominant shade in-tolerant/fire-tolerant vegetation without additional pre- or post-fire management.

The effects of reintroducing wildfire on forest landscapes and the magnitude or directionality of post-fire response can be evaluated in part based on how forest structure and composition approximate qualities similar to historic conditions. In general, evidence from primary sources (e.g., Muir, 1911; McKelvey and Johnston, 1992; Gruell, 2001), presumed reference conditions like those existing in northern Baja California, Mexico (Dunbar-Irwin and Safford, 2016), fire history reconstructions of forests elsewhere in the Sierra Nevada (e.g., Skinner and Chang, 1996; Beaty and Taylor 2008, Baker 2014), and a review paper by Safford and Stevens (*in press*) suggest that conditions in Sierra Nevada forests consisted of substantially fewer, but larger, trees dominated by sun-tolerant (fire-

adapted) species, with open or patchy overstories, and light surface fuel loadings. Fire severity was mostly low to moderate, with patches of high severity contributing to structural complexity (Sugihara et al., 2006; Mallek et al., 2013; Odion et al., 2014). Thus, this disturbance and landscape heterogeneity likely supported great vegetative diversity and abundance than today's fire-suppressed forests (Sugihara et al., 2006; Webster and Halpern, 2010).

For fire-prone ecosystems such as the Sierra Nevada, a key ecological theory is that landscape patterns and processes shape each other, thereby creating self-regulating systems (Watt 1947, Turner 1989, Agee 1999, Peterson 2002). My study corroborates the concept that fire severity affects the vegetation, fuels, and composition of a forested landscape, and that the magnitude and direction of change from a pre-existing state is largely contingent upon fire severity (Agee, 1993; Barbour et al., 1993, Turner et al., 2004; Sugihara et al., 2006; Keeley et al., 2012). Tree density and fuel loading in my study's unburned plots was much higher than in plots that experienced a single burn or reburn. Conversely, species richness, evenness, and diversity were lower in unburned plots than in single burns. Tree regeneration in unburned plots was at times lower than single burns, but higher than reburns. However, results from my research are mixed as to whether reintroducing just one or two wildfires onto a fire-suppressed landscape can meet land management objectives aimed at enhancing forest resilience, reducing fuel loads while increasing tree vigor, or resetting the ecological feedbacks and create biological legacies needed to restore and sustain historic self-regulating mixed-conifer ecosystems (CBFFP, 2010; USFS, 2011; USFS, 2012).

My research demonstrated that reintroducing wildfire could alter tree regeneration and tree structure in mixed-conifer Sierra Nevada forests, suggesting that self-regulating tree characteristics or historic composition may be unlikely to occur from introductions of wildfire without supplemental active restoration by land managers. Wildfire dramatically reduced live tree density (DBH >7.6 cm; Fig. 3, Table 3). Live basal area was reduced proportionately less than tree density, indicating that often, the younger, smaller-girthed trees were killed while trees with larger diameters were less impacted (Fig. 3, Table 3). However, reductions in tree density decreased seed source availability, which limited tree regeneration at high severity and in reburns.

As in previous studies of wildfire effects on regeneration in northern Sierra Nevada mixed-conifer forests (e.g., Ansley and Battles, 1998; Collins and Roller, 2013; Crotteau et al., 2013; Welch et al. *in press*), the tree regeneration observed in my plots was heavily dominated by shade-tolerant species. This could be due in part to the fact that the shade-tolerant tree species are primarily wind-dispersed and are able to travel father distances from intact seed sources than the shade-intolerant tree species which are primarily rodent-dispersed (Bonnett et al., 2005; Bohlman et al., 2016). Also, more shade-tolerant seed trees were present than shade-intolerant seed sources (Fig. 3, Table 3). Reconstructed tree densities in Sierra Nevada mixed conifer and yellow pine forests suggest historic conditions ranged from roughly 60-330 trees ha^{-1}, with an average of about 160 trees ha^{-1} (Safford and Stevens, *in press*). The post-fire suppression plots I surveyed at times exhibited double or even more than triple this tree density. However, exact historic tree composition ratios and tree regeneration abundance or survivorship are

unknown, so seedling response can be evaluated instead from an existing silvicultural perspective. Informal silvicultural guidelines suggest that mature shade-intolerant and shade-tolerant trees occur in a 70:30 ratio, respectively (Welch et al., *in press*). Of the 74 plots surveyed in my study, only six plots had shade-tolerant species constituting <30% of the trees, with only one plot of those six actually having both shade-intolerant and shade-tolerant species. The other five of those six plots were the only high severity plots with trees, though minimal in density, which were shade-intolerant species (Fig. 3). Thus, it makes sense that shade-tolerant seedling density was observed to be greater overall than shade-intolerant (fire-adapted) density despite the presence of wildfire on the landscape. However, of the seedlings that were present in my plots, the proportion of shade-intolerant tree species was greater in plots that experienced higher fire severities, especially in reburns (Fig. 2, Table 3). This indicates that reburns at high severities may create favorable conditions for shade-intolerant tree regeneration. If seed availability of shade-intolerant species is limited, reburns at high severities may be areas worthy of supplemental planting treatments that emphasize pine species.

In single burns, seedling density followed a unimodal response, with the highest regeneration occurring at low and moderate fire severities. Unburned plots representing fire-suppressed baselines had less seedlings than single burns, but reburns at any severity had much lower seedling densities at any severity than even unburned plots (Fig. 2, Table 3). Stevens-Rumann et al. (2016) also found that reburns exhibited lower tree seedling densities than single burns in montane and subalpine forests in central Idaho. These patterns may be attributed to single burns having increased available light and growing

space compared to fire-suppressed unburned stands (Fig. 5 and 6, Table 3), but variable

seed source presence and distance limiting tree regeneration. I was surprised to find a

negative correlation in my study between seedling density and bare soil (r = -0.28) and a

positive correlation between seedling density and litter cover (r = 0.27), considering

mixed-conifer tree species tend to establish preferentially on bare soil (Stark, 1965).

Perhaps litter cover provides beneficial moisture retention that aids in germination in

xeric-montane environments.

Silvicultural stocking recommendations for Sierra Nevada mixed-conifer and

yellow-pine forests are approximately 494 seedlings ha^{-1} (USFS 1989). Comparatively,

for fir forest types (forests historically dominated by shade-tolerant species), the goal is

740 seedlings ha^{-1}. Compared to these guidelines, all fire severities and fire frequencies

included in my study exhibit extreme tree seedling overstocking in plots where tree

regeneration is present (Fig. 2, Table 3). However, >75% of my plots did not meet

stocking guidelines for shade-intolerant species (Fig. 2, Table 3). Additionally, low

survivorship of all seedlings regardless of tree species is expected over the next 5-10

years, based on the paltry number of saplings, live or dead, I observed in my plots, as

well as the seedling densities of other studies in similar forests observed after a longer

time since the most recent fire (e.g., Crotteau et al., 2013; Bohlman et al. 2016; Collins

and Roller, 2013; Coppoletta et al., 2013). Indeed, conifer establishment is quite

stochastic and is influenced by numerous biotic and abiotic factors (Bonnet et al., 2005;

Welch et al., *in press*).

Regeneration and resilience of mixed-conifer forests could also be compromised by the increased competition from shrubs, especially in high fire severities and reburns where decreased overstory cover produces less shade to limit shrub growth (Smith et al., 1997; Bohlman et al., 2016). In my study, no tree seedlings were overtopped by shrubs as of two years post-fire, although seedling density and shrub cover had a negative correlation ($r = -0.21$) and the vast majority of shrubs present were <0.5 m tall. As time-since-fire increases, shrubs could grow and potentially outcompete tree seedlings and or burn before the regenerated tree cohort is mature, creating an alternative forest pathway of mixed-conifer conversion to montane-chaparral (Harvey et al., 2016).

Reintroducing wildfire had profound effects on fuel loading in my study. As severity and frequency increased, the potential for extreme fire behavior or severity in a subsequent fire decreased. Nearly every fuel characteristic we measured differed between plots that burned and unburned plots by a factor of two, at minimum. Reburns tended to have higher fuel loads, especially at moderate severity in fine fuels, and high severity in coarse woody debris (Fig. 4, Table 3). This is in contrast to what Stevens-Rumann and Morgan (2016) observed in their montane (Douglas fir-dominated) and subalpine plots (spruce-fir dominated) in central Idaho, Donato et al. observed in their mixed-conifer (Douglas fir-dominated) plots in southwestern Oregon, and Larson et al. (2013) observed in their lower-montane mixed-conifer plots (ponderosa pine-dominated) in western Montana. In these studies, reburns exhibited reduced fuel loads compared to single burns. It is possible that time-since-fire, fire interval, vegetation types, and weather or climatic variations among other variables could explain the differences between our studies. These

factors would affect productivity, decomposition, fire consumption, and snag retention, and highlight the danger of generalizing assumptions beyond the research domain of the study. In my study, it is plausible that the greater fuel loading in reburns could be driven by post-fire mortality, as trees died and fell after the initial (Storrie) fire. The reburn, the Chips Fire, could then have consumed some but not all of the fuels during the blaze, and also killed whole or parts of more trees. Between the fire and my survey two years later, dead vegetation matter once again fell and increased the surface fuel loading observed on reburn plots. Greater fuel loading in reburns is complimented by the greater areal groundcover of woody debris and fewer standing snags in reburns than single burns. Aside from coarse woody debris fuel load, reburns had lower horizontal and vertical fuel continuity: lower tree overstory cover, live tree density, and snag density, plus greater fuel strata gap than single burns or unburned plots. Where unburned plots had deep and continuous litter depth and cover, reburns exhibited comparatively lower litter cover and depth and so could promote a patchier burn mosaic or lower severity in subsequent fires. Reburns, though, also possessed more shrub and herb cover (Fig. 6, Table 3), which could potentially serve as flammable surface fuels in times of drought. Based on these conditions, it appears as though the fuel characteristics of reburns and single burns could possess latent resilience through self-regulation, and are a major contributor to future fire behavior (Sugihara et al., 2006; Stevens et al., 2014).

My study also demonstrated that forest composition can be impacted by the reintroduction of wildfire into a landscape altered by fire-suppression. Overstory tree cover and vegetation cover drastically diminished as in plots that experienced higher fire

severity (Fig. 6, Table 4), which makes sense because those forest characteristics were a primary determinant of how fire severity was classified. Additionally, the disturbance-diversity hypothesis assumes that species composition in fire-adapted landscapes homogenizes without fire (Agee 1998, Fulé et al., 2004; Hessburg et al., 2005). Indeed, my unburned plots consistently exhibited the lowest richness, evenness, and diversity of all other fire severity-frequency combinations (Fig. 7, Table 3). However, comparisons of composition between single burns and reburns revealed that reburns had a marginally-significantly lower richness than single burns (Table A6). Although evenness and diversity in reburns were not different from single burns, these species composition metrics were still lower in reburns compared to single burns. These results do not support the findings in the few other studies investigating species composition in reburns. Like my study, the work of Donato et al. (2009b) took place two years post-fire in mixed-conifer forests, but in the Klamath-Siskiyou Mountains of Oregon and only in high severity patches. Additionally, their reburn plots had 15 years between wildfires, whereas my study had a 12-year interval. Donato et al. (2009b) found that diversity and abundance of single burns were similar to that of reburns, both at the plot (alpha) level and sample-wide (gamma) level. In fact, Donato et al. (2009b) shows that richness and evenness were highest when his plots experienced reburn. Conversely, richness in my reburned plots were not significantly different from unburned plots, and even reburns at high severity had a similar range of responses to unburned plots (Fig. 7, Table A6). Meanwhile, unburned plots were significantly different from single burn plots, alluding to the potential deleterious effects of reburns on species composition. However, Webster

and Halpern's (2010) multi-decadal study of repeat prescribed fire in the southern Sierra Nevada mixed-conifer forests argues that reburns do not have detrimental effects on plant diversity, at least within the moderate and low severities they studied. Furthermore, like Donato et al., (2009b), Webster and Halpern's prescribed burns promoted significant increases in richness and cover. The caveat is that the differences in post-fire responses were not apparent for 5-20 years after burning. Therefore, the species composition observed in my study could potentially have a delayed appearance of differences between fire severities or frequencies. This is especially plausible since only about half the species found in a reburn were also found in unburned or single burned plots.

Interestingly, in my study, reburns show greater support than single burns for the intermediate disturbance hypothesis, which says that post-fire vegetation diversity is maximized at the levels of disturbance common to the fire regime with which ecosystems evolved (Connell, 1978). Species composition in single burns responded to fire severity in a positive linear manner. Reburns, though, exhibited a somewhat stronger unimodal response to fire severity, with species richness and diversity increasing at low and moderate fire severity, the predominant severities of the historic fire regime, before decreasing in high severity. These general trends and values persist even when nonnative species are excluded from my calculations. This could be an indication that the process of restoring plant communities can begin with the reintroduction of low-moderate severity fire (Peterson and Reich, 2008; Burkle et al., 2015).

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

My study contributes to a newly emerging and rapidly growing field of research regarding reburn effects on forested landscapes and offers insight into forest resilience following the reintroduction of wildfire on fire-suppressed western North American forests. Single burns and reburns exhibited vastly different forest structure and composition compared to unburned plots, with reduced live tree densities and vegetation cover, lower fuel loading and continuity, and increased richness, evenness, and diversity, reflecting paths towards forest restoration. Fuel loading and other fuel characteristics between single burns and reburns were fairly comparable, though reburns exhibited almost twice as much coarse woody debris on average. However, tree composition in plots that had burned was still dominated by shade-tolerant species, and vegetation richness, evenness, and diversity were somewhat lower in reburns than single burns. Reburns occurring within a short fire interval after the initial fire could also potentially convert mixed-conifer forests to montane-chaparral, especially after high severity fire, due to paltry levels of post-fire tree regeneration, increased shrub cover, and increased snag density and basal area.

However, this study reports observations from an early seral standpoint of two years post-fire. This temporal limitation could influence our observations and assertions about stand structure, composition, and the effects of fire frequency and fire severity on forested landscapes. Differences between fire severities and fire frequencies may become apparent as post-fire effects materialize or reach an asymptote 8-20 years post-fire, as

shown in studies introducing prescribed fire to a forest ecosystem (e.g., Stephens and Moghaddas, 2005; van Mantgem et al., 2011; Webster and Halpern, 2010; Winford et al., 2015).

The results from this study and others underscore the importance of recurring wildland fire disturbance in creating and maintaining landscapes resilience and heterogeneity (Turner, 1989; Inglalsbee, 2015; Hutto et al., 2016). More research is needed about reburns' effects on landscapes to inform management decisions under a range of scenarios before any wide-spread policies are implemented (Donato et al., 2009b; Webster and Halpern, 2010; Stevens-Rumann and Morgan, 2016). I highly encourage conducting long-term studies that monitor both uninterrupted and managed forest succession pathways. Such studies are crucial, especially since important post-fire management decisions often happen in the immediate months to few years following a wildfire.

Widespread reintroduction of wildfire has not occurred and is perhaps unlikely despite the high economic costs of suppression and impracticality of large-scale forest management and fuel treatments (Gebert et al., 2007; North et al., 2012; Houtman et al, 2013). However, forest ecosystems will continue to change and diverge from historic conditions while fire suppression remains a common practice. Additionally, little is known about how climate change can impact fire severity and fire frequency interactions on vegetation (Stevens-Rumann and Morgan, 2016). Therefore, land managers may want to adjust their approach to forest management that emphasizes the development of mature tree stands by allowing for heterogeneity in areas of the landscape where economics and

public safety is not an issue (DellaSala et al., 2014). Permitting early seral patches to

recover unassisted and naturally regenerate could increase the biodiversity, adaptability,

and resilience of western US forests (Swanson et al., 2011; Howell et al., 2012; DellaSala

et al., 2014).

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Table 1. Rubric for ground-truthing wildfire severity in 74 observed plots in and
surrounding the Chips Fire (Plumas and Lassen National Forests, CA). Fire severity was
initially determined though the Composite Burn Index (CBI) derived from remote
sensing (Key and Benson, 2006; Miller and Thode, 2007). In the field, fire severity was
ground-truthed using ocular estimates of vegetation burned following a condensed
version of severity classes from the National Park Service (NPS, 2003).

This study's fire severity	CBI	NPS fire severity	Description
Unburned	0 – <0.10	5	Unburned
Low	0.10 – <1.25	4,3	Lightly burned, very little or isolated overstory mortality, some - most saplings/shrubs dead
Moderate	1.25 – <2.25	2, 1	Moderately burned, understory mostly burned to ground, significant proportion of overstory killed
High	2.25 – 3.00	1, 0	High severity burn, total/near total mortality of overstory, some dead needles or no needles remaining on trees

Table 2. Contingency table of sample sizes within fire severity and fire frequency categories for 74 observed plots in and surrounding the Chips and Storrie Fires (Plumas and Lassen National Forests, CA). Fire severity was the observed fire severity at the time of the Chips Fire (2012). "Unburned" plots did not experienced wildfire or prescribed fire within the past century. "Single burn" plots only experienced the Chips Fire but no other fire within the past century. "Reburn" plots experienced the Storrie Fire (2000) followed by the Chips Fire (2012), but no other fire within the past century. All plots contained no evidence of previous management that would have altered forest structure, such as salvage logging.

Fire Severity	Fire Frequency		
	Unburned	Single burn	Reburn
Unburned	24		
Low		9	8
Moderate		8	8
High		8	9

Table 3. Means (± 1 standard error) of measured forest characteristics from a total of 74 plots in northern Sierra Nevada mixed-conifer stands. The data shown in each fire frequency column (unburned, single burn, reburn) are means for all plots of the same fire frequency, pooling observed fire severity. Conversely, data shown in each fire severity column (unburned, low, moderate, high) are means for all plots of the same fire severity, pooling fire frequency. Fire severity is the observed fire severity from the Chips Fire (2012). * indicates median = 0. (*Continued on next page*)

	Sample size	Reburn $n = 25$	Single burn $n = 25$	Unburned $n = 24$	Low $n = 17$	Mod $n = 16$	High $n = 17$
Trees	Shade-tolerant seedling density (ha^{-1})	3634 (1645)	17596 (5297)	9797 (3591)	16335 (5453)	11960 (6353)	3630 (2557) *
	Shade-intolerant seedling density (ha^{-1})	249 (96)	1803 (549)	107 (48)	547 (217)	1080 (386)	1454 (768) *
	Total seedling density (ha^{-1})	3884 (1644)	19456 (5404)	10173 (3594)	16929 (5517)	13080 (6447)	5084 (3141)
	Shade-tolerant tree density (ha^{-1})	124 (28)	147 (33)	720 (73)	287 (36)	120 (18)	0 (0)
	Shade-intolerant tree density (ha^{-1})	5 (3) *	43 (17) *	147 (43)	47 (24) *	22 (7) *	3 (2) *
	Total snag density (ha^{-1})	244 (40)	759 (93)	156 (27)	375 (85)	550 (86)	583 (139)
	Shade-tolerant basal area ($m^2 ha^{-1}$)	41 (9)	25 (6)	62 (6)	60 (10)	40 (9)	0 (0)
	Shade-intolerant basal area ($m^2 ha^{-1}$)	2 (1) *	11 (4)	23 (5)	10 (4) *	8 (3) *	1 (1) *
	Total snag basal area ($m^2 ha^{-1}$)	35 (5)	38 (7)	13 (3)	14 (3)	39 (5)	57 (8)
Fuels	1hr ($mg ha^{-1}$)	1.94 (0.31)	1.90 (0.20)	4.30 (0.51)	2.40 (0.20)	2.06 (0.37)	1.31 (0.31)
	10 hr ($mg ha^{-1}$)	6.33 (0.82)	7.05 (6.26)	24.75 (2.36)	7.49 (0.88)	5.33 (0.85)	7.18 (1.49)
	100 hr ($mg ha^{-1}$)	8.43 (2.17)	4.86 (1.09)	27.71 (3.72)	10.94 (2.88)	3.41 (1.06)	5.40 (1.57)
	Coarse woody debris ($mg ha^{-1}$)	29.98 (7.57)	16.97 (6.05)	53.87 (10.66)	19.69 (8.51)	30.94 (10.54)	20.23 (6.23)
	Litter depth (cm)	1.9 (.03)	2.9 (0.6)	6.2 (1.1)	2.4 (0.3)	3.3 (0.9)	1.5 (0.4)
	Duff depth (cm)	0.2 (0.1) *	0.0 (0.0) *	4.1 (0.5)	0.2 (0.1) *	0.1 (0.0) *	0 (0.0) *
	Fuel strata gap (m)	16.1 (1.7)	12.5 (1.4)	6.2 (0.5)	12.5 (1.6)	16.1 (1.5)	0 (0.0) *
Ground Cover	Bare soil (%)	8 (3)	4 (2)	0 (0)	1 (0)	2 (1)	15 (4)
	Rock (%)	25 (4)	11 (3)	3 (1)	9 (2)	10 (3)	34 (6)
	Litter (%)	65 (6)	84 (5)	91 (2)	87 (3)	88 (4)	48 (8)
	CWD (%)	3 (1)	2 (0)	6(1)	2 (0)	3 (1)	3 (1)
Vegetation Cover	Overstory trees (%)	20 (4)	35 (7)	75 (3)	58 (6)	25 (3)	0 (0)
	Shrubs (%)	12 (3)	6 (2)	10 (3)	3 (1)	2 (1)	20 (5)
	Herbs (%)	12 (4)	6 (2)	2 (0)	11 (5)	7 (3)	8 (3)
	Total vegetation cover (%)	42 (5)	43 (6)	79 (3)	67 (5)	32 (4)	29 (5)
Species Composition	Richness	24 (2)	31 (2)	19 (2)	26 (2)	32 (3)	24 (3)
	Pielou's evenness	0.68 (0.04)	0.73 (0.03)	0.51 (0.03)	0.55 (0.04)	0.74 (0.02)	0.83 (0.04)
	Shannon-Wiener diversity index	2.12 (0.14)	2.42 (0.12)	1.48 (0.11)	1.77 (0.14)	2.52 (0.14)	2.54 (0.15)

Table 4. Results (adjusted *p*-values) of frequentist tests determining if characteristics for trees, fuels, and composition among 74 observed plots in and around the Chips and Storrie Fires (Plumas and Lassen National Forest, CA) significantly differed by the severity of the last fire (Chips Fire), fire frequency, or their interaction. Method acronyms: ANOVA= Two-sample analysis of variance; MANOVA= Two-sample multivariate analysis of variance; perMANOVA= permutational analysis of variance; S-H-R= Two-sample Scheirer-Ray-Hare test. **Bold** indicates significance at alpha = 0.05. **Bold **** indicates marginal significance at alpha ≤ 0.10.

|		Method	Severity df = 3	Frequency df = 1	Sev x Freq df = 2
Trees	Proportion shade-intolerant seedlings	S-H-R	**<0.001**	0.39	0.65
	Total seedling density	ANOVA	**<0.001**	**<0.01**	0.56
	Shade-tolerant tree density	S-H-R	**<0.001**	0.97	0.96
	Shade-intolerant tree density	S-H-R	**<0.001**	**<0.05**	0.89
	Total snag density	S-H-R	**<0.001**	**<0.001**	0.39
	Shade-tolerant basal area	S-H-R	**<0.001**	0.16	0.59
	Shade-intolerant basal area	S-H-R	**<0.001**	**<0.05**	0.84
	Total snag basal area	S-H-R	**<0.001**	0.92	0.19
Fuels	1-Hour fuels	MANOVA	**<0.01**	0.83	**0.07 ****
	10-Hour fuels		**<0.01**	0.65	**0.07 ****
	100-Hour fuels		**<0.01**	0.16	0.25
	Coarse woody debris		**<0.05**	**0.07 ****	0.94
	Litter depth	ANOVA	**<0.001**	0.17	0.66
	Duff depth	S-H-R	**<0.001**	0.26	0.85
	Fuel strata gap	ANOVA	**<0.001**	**<0.05**	**<0.05**
Ground Cover	Ground cover	perMANOVA	**0.001**	**0.001**	**0.10 ****
Vegetation Cover	Vegetation cover	perMANOVA	**0.001**	0.25	0.21
Species Composition	Richness	ANOVA	**<0.01**	**<0.05**	0.75
	Shannon-Wiener Diversity	ANOVA	**<0.001**	**<0.05**	0.42
	Pielou's evenness	ANOVA	**<0.001**	**0.10 ****	0.23
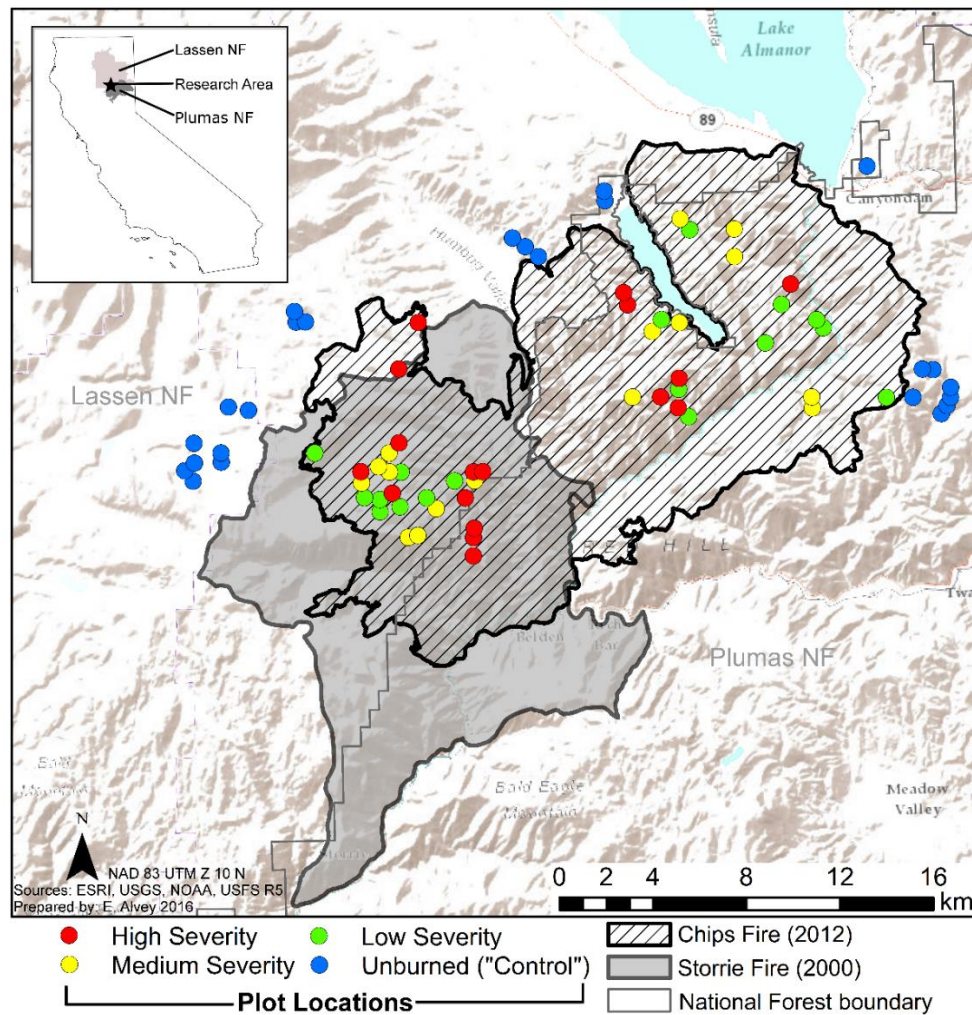
Figure 1. Map of study area, consisting of two wildfires in the Plumas and Lassen National Forests. The locations of 74 survey plots are represented by circles, and color-coded according to the fire severity they experienced in 2012. The 2012 Chips Fire in northern California reburned a large portion of the 2000 Storrie Fire. Plots were selected and surveyed based on the fire severity of the Chips Fire, the fire frequency, a compatible range of topographic attributes, and lack of previous fires and management activities by the USDA Forest Service that would convolute post-fire effects, such as salvage logging.
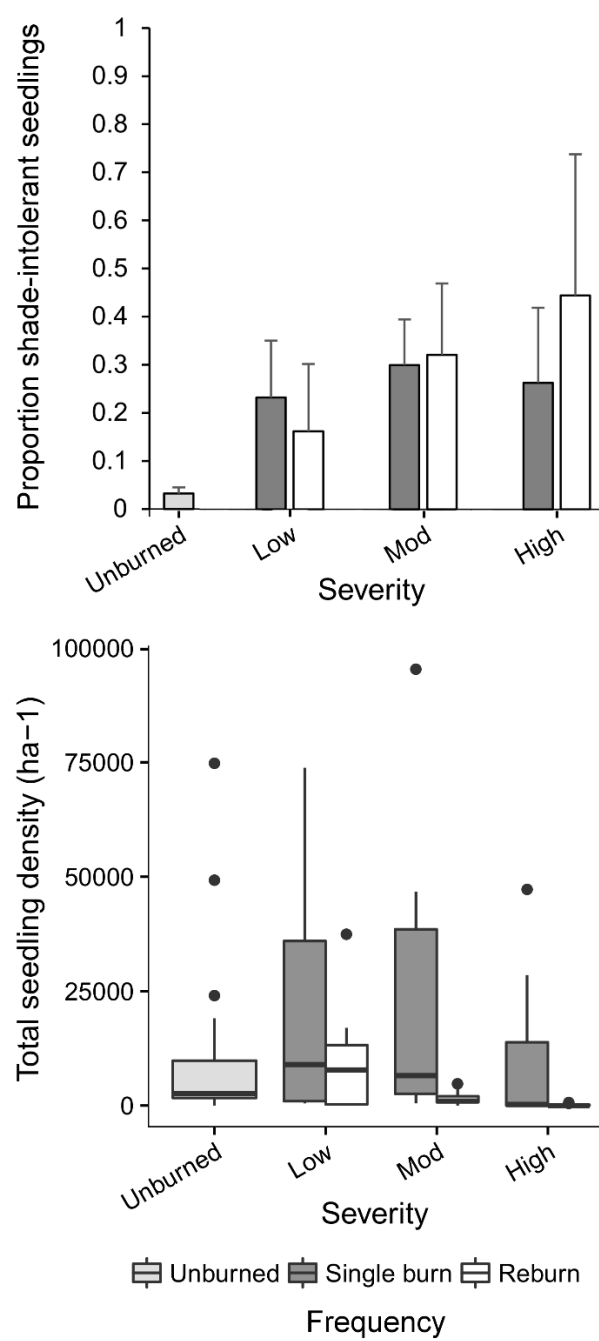
Figure 2. Proportion of shade-intolerant seedlings found in 74 observed plots in mixed-conifer forests in the Sierra Nevada (Plumas and Lassen National Forests, CA) compared to the total stem density per hectare of all seedlings in those plots. Samples are separated by the severity of the last fire (Chips Fire) and fire frequency. The proportion barchart represents mean proportion (whiskers are ± 1 standard error) of shade-intolerant seedlings for each fire severity by fire frequency combination. In the density boxplot, middle lines indicate medians of seedling density, while the top and bottom of the boxes represent upper & lower quantiles of data. Whiskers indicate maximum and minimum values. While dots signify extreme values, data inspections determined them to be valid measured values. Note the different y-axis scales.
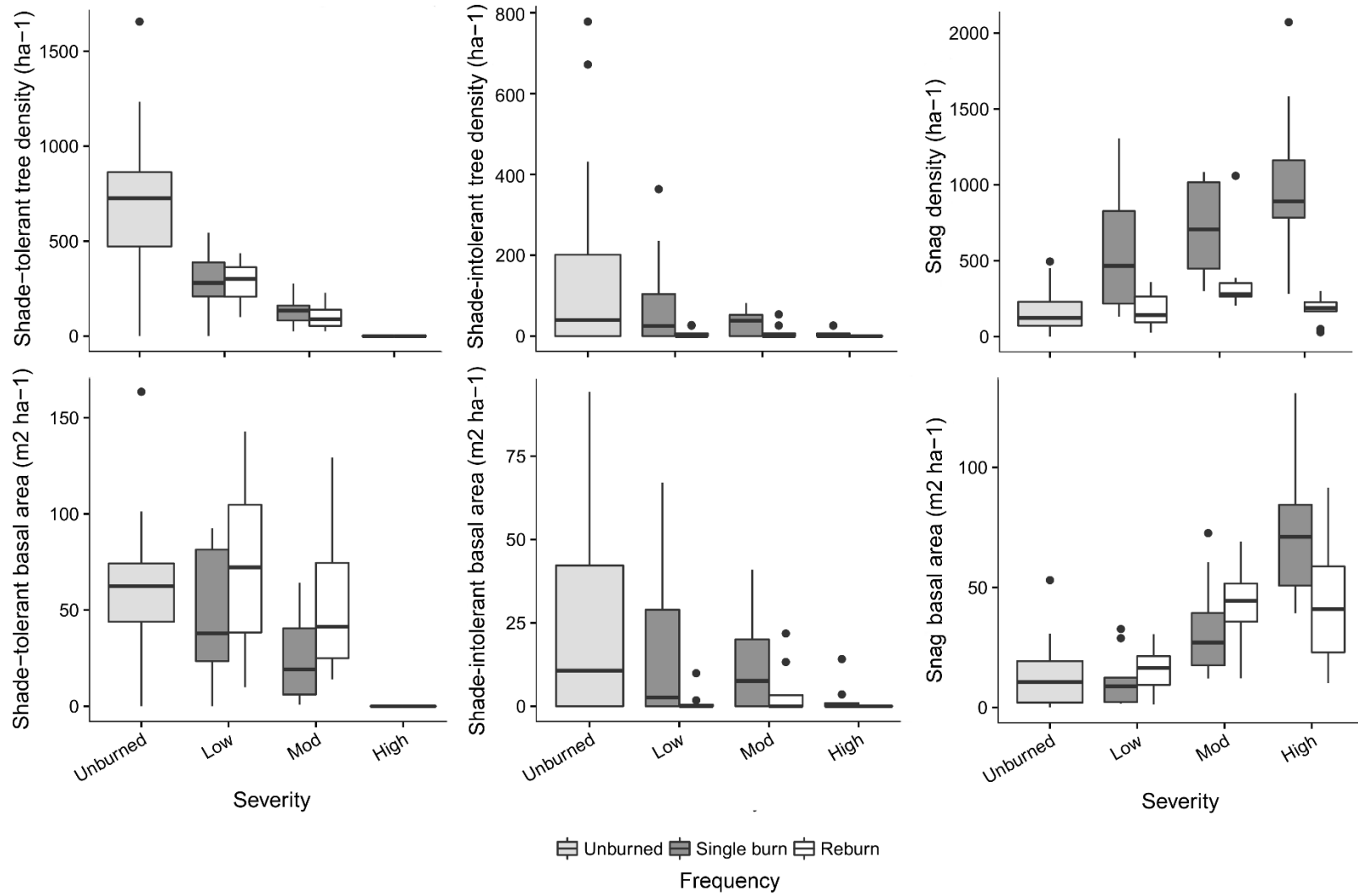
Figure 3. Per-hectare density and basal area of live shade-tolerant or shade-intolerant tree species, or snags, in 74 observed plots, separated by the severity of the last fire (Chips Fire) and fire frequency. Boxes represent the interquartile range of each category, with the line representing the sample's median. Data were collected in and immediately outside of the Chips Fire (2012) in northern Sierra Nevada, California (Plumas and Lassen National Forests, CA). Reburn plots were a result of the Chips Fire burning over part of the Storrie Fire (2000). Note the different y-axis scales.

Figure 4. Medians, interquartile ranges, and spread of post-fire responses in fuel

characteristics of 74 observed plots in northern Sierra Nevada separated by the severity of

the last fire and fire frequency. Data were collected in and immediately outside of the

Chips Fire (2012) in northern Sierra Nevada, California (Plumas and Lassen National

Forests, CA). Reburn plots were a result of the Chips Fire burning over part of the Storrie

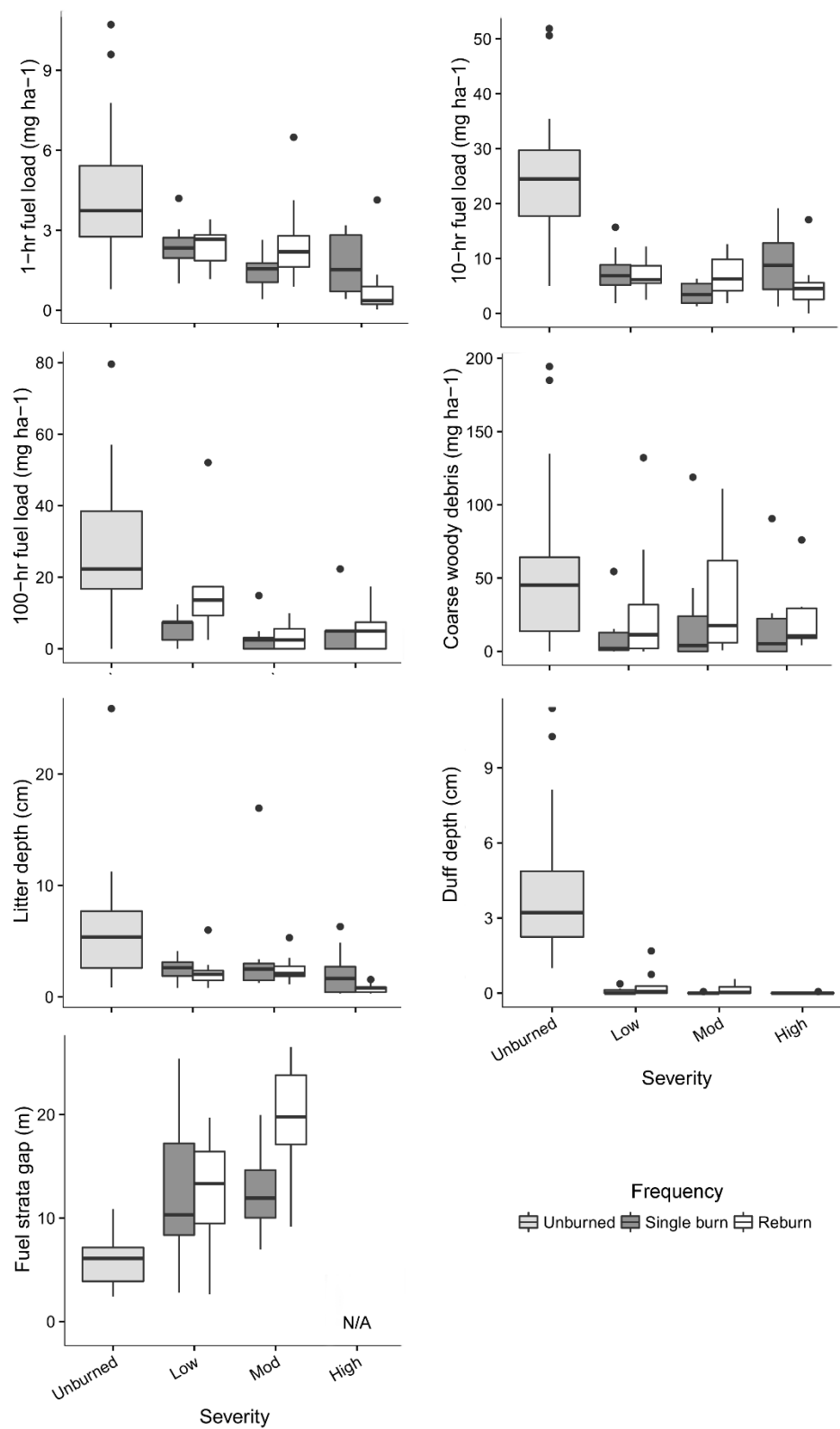Fire (2000). Note the different y-axis scales.

Figure 5. Areal ground cover composition of 74 observed plots in northern Sierra Nevada (Plumas and Lassen National Forests, CA) separated by the severity of the last fire and fire frequency. Covers were estimated by substrate, and all substrates within a plot sum to 100%. Y-axes are the same for all substrates.
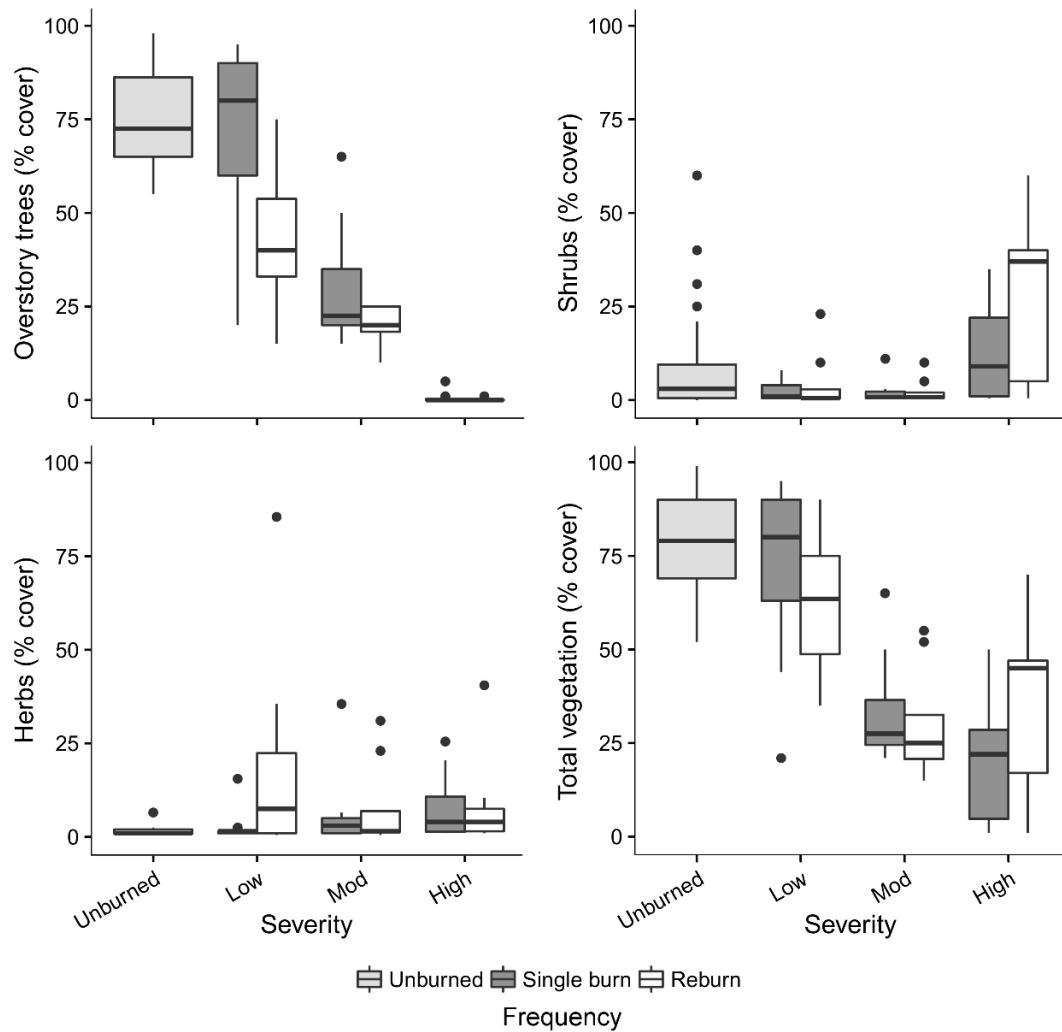
Figure 6. Medians, interquartile ranges, and spread of post-fire responses in areal vegetation cover of 74 observed plots separated by the severity of the last fire and fire frequency. Covers were estimated by lifeform, and all lifeforms in a plot may sum to >100%. Data were collected in and immediately outside of the Chips Fire (2012) in northern Sierra Nevada, California (Plumas and Lassen National Forests, CA). Reburn plots were a result of the Chips Fire burning over part of the Storrie Fire (2000). Y-axes are the same for all lifeforms.
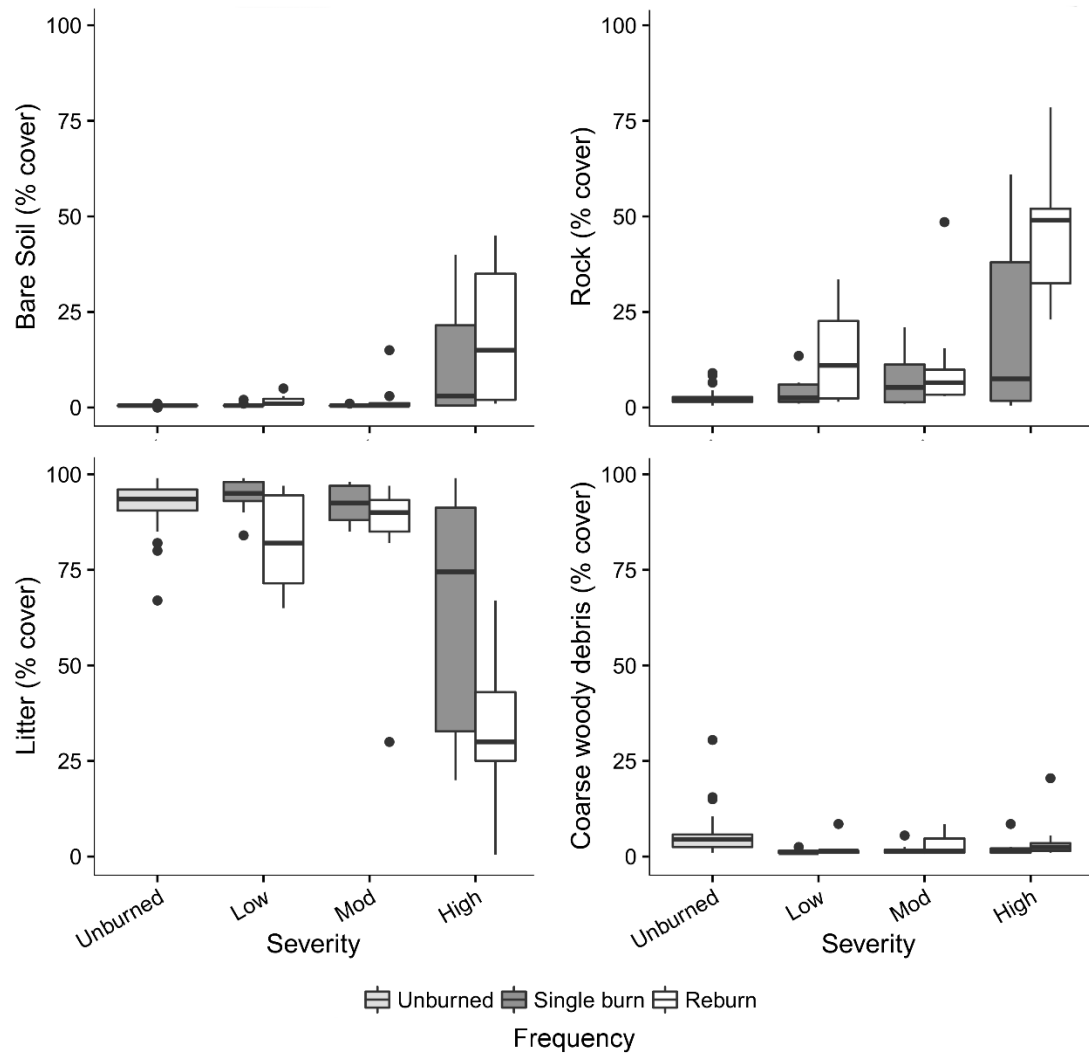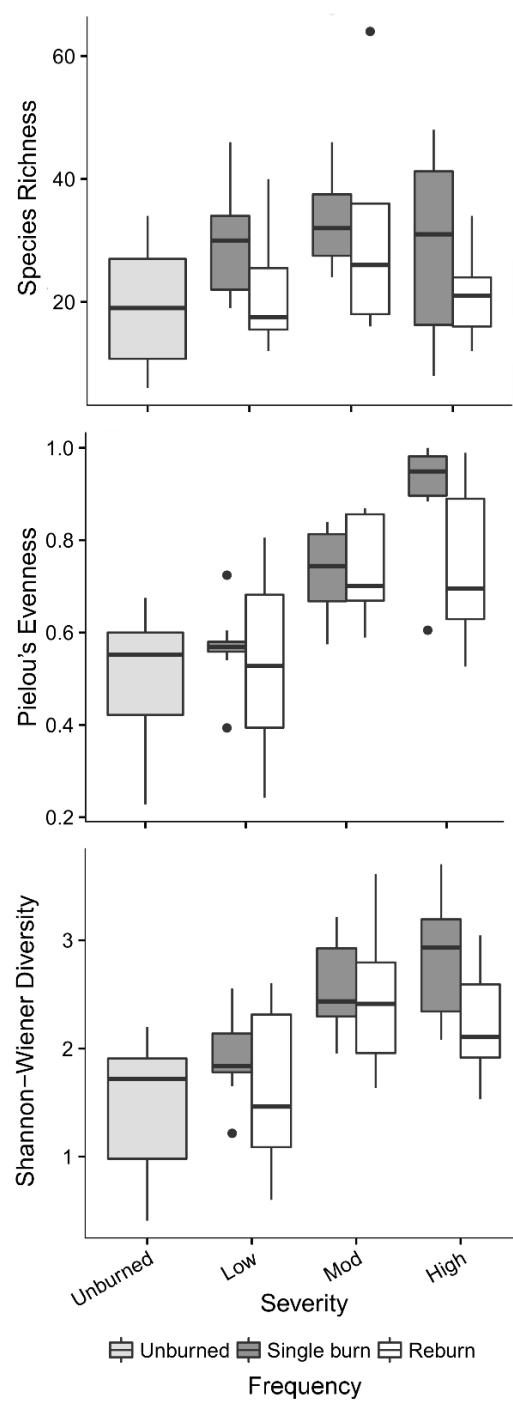
Figure 7. Species composition metrics for 74 observed plots in northern Sierra Nevada mixed-conifer forests (Plumas and Lassen National Forests, CA), separated by the severity of the last fire and fire frequency. Note the different y-axis scales.

APPENDICES

APPENDIX 1. Contingency table of sample sizes for each previous fire severity (Storrie Fire, 2000) x observed fire severity (Chips Fire, 2012) combination in this study. This study surveyed a total of 74 plots in and around two overlapping wildfires in the northern Sierra Nevada mixed-conifer forests. Previous severity is only greater than "unburned" for plots that reburned in the Storrie Fire. Observed severity was sampled following the Chips Fire. Light grey = unburned plots; dark grey = single burn plots; white = reburn plots.

Observed Severity	Previous Severity			
	Unburned	Single burn	Reburn	High
Unburned	24			
Low	9	8	0	0
Moderate	8	7	1	0
High	8	4	2	3

APPENDIX 2. Stem density per hectare of shade-tolerant and shade-intolerant seedlings in 74 observed plots, separated by the severity of the last fire (Chips Fire) and fire frequency. Boxes represent the interquartile range of each category, with the encased line representing the sample's median. Data were collected in and immediately outside of the Chips Fire (2012) in northern Sierra Nevada, California (Plumas and Lassen National Forests, CA). Reburn plots were a result of the Chips Fire burning over part of the Storrie Fire (2000). Note the different y-axis scales.
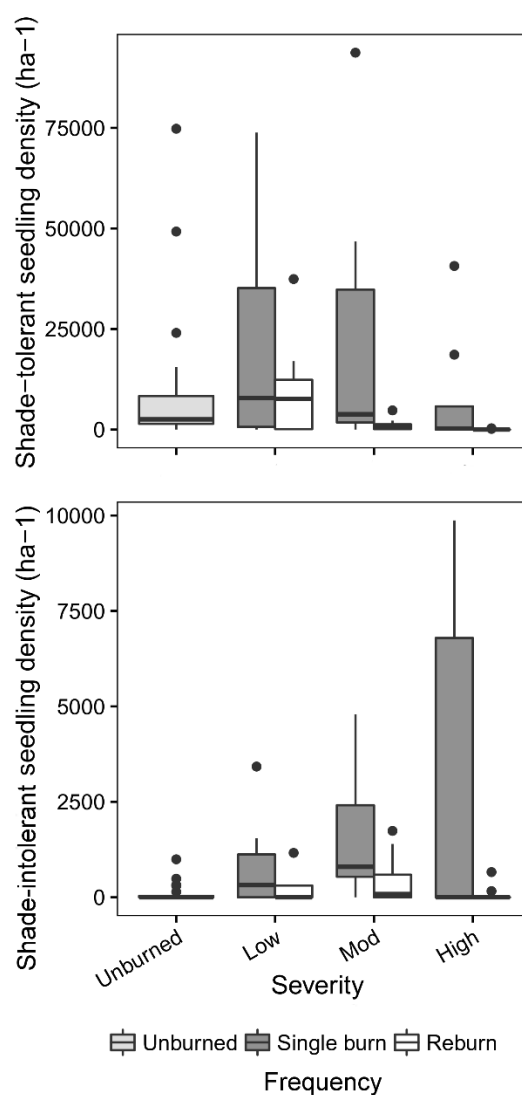
APPENDIX 3. Total tree density and total basal area per hectare of all trees, regardless of shade-tolerance, in 74 observed plots separated by the severity of the last fire and fire frequency. Data were collected in and immediately outside of the Chips Fire (2012) in northern Sierra Nevada mixed-conifer forests (Plumas and Lassen National Forests, CA). Reburn plots were a result of the Chips Fire burning over part of the Storrie Fire (2000). Note the different y-axis scales.

APPENDIX 4: Total fuel load per hectare for 74 observed plots in northern Sierra

Nevada mixed-conifer forests (Plumas and Lassen National Forests, CA), separated by

the severity of the last fire and fire frequency.

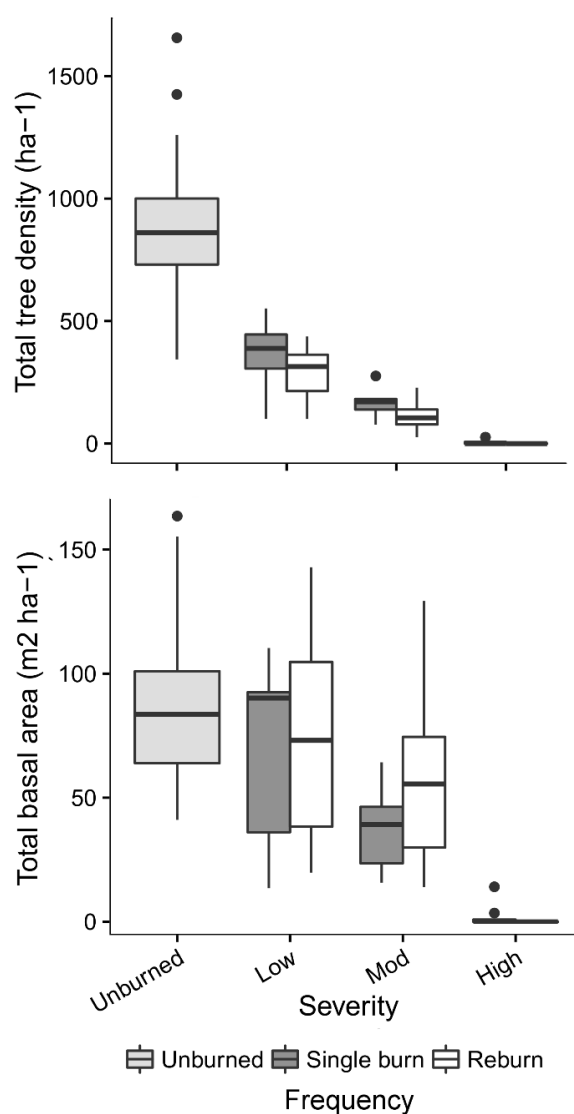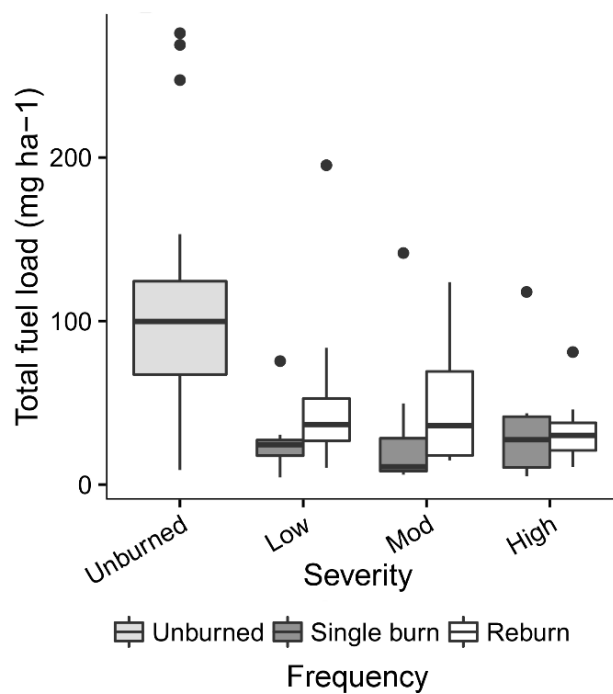APPENDIX 5. Species list of the 58 taxa out of a total 215 that were present in $\geq$5% of 74 observed plots. Data were collected in 2014, in and immediately outside of the Chips Fire (2012) in northern Sierra Nevada, California (Plumas and Lassen National Forests, CA). *(Continued on next page)*

Species name	Species code	Lifeform	Origin
Abies concolor	ABCO	Tree	Native
Abies magnifica	ABMA	Tree	Native
Allium campanulatum	ALLCAM	Forb	Native
Amelanchier alnifolia	AMEALN	Shrub	Native
Antennaria rosea	ANTROS	Forb	Native
Apocynum androsaemifolium	APOAND	Forb	Native
Arctostaphylos patula	ARCPAT	Shrub	Native
Bromus orcuttianus	BROORC	Graminoid	Native
Calocedrus decurrens	CADE	Tree	Native
Campanula prenanthoides	CAMPRE	Forb	Native
Carex multicaulis	CARMUL	Graminoid	Native
Carex rossii	CARROS	Graminoid	Native
Ceanothus cordulatus	CEACOR	Shrub	Native
Ceanothus integerrimus	CEAINT	Shrub	Native
Ceanothus prostratus	CEAPRO	Shrub	Native
Ceanothus velutinus	CEAVEL	Shrub	Native
Chimaphila menziesii	CHIMEN	Forb	Native
Chimaphila umbellata	CHIUMB	Forb	Native
Chrysolepis chrysophylla	CHRCHR	Shrub	Native
Cirsium vulgare	CIRVUL	Forb	Non-native
Claytonia perfoliata	CLAPER	Forb	Native
Claytonia rubra	CLARUB	Forb	Native
Cornus nuttallii	CORNUT	Shrub	Native
Cryptantha affinis	CRYAFF	Forb	Native
Draperia systyla	DRASYS	Forb	Native
Elymus elymoides	ELYELY	Graminoid	Native
Epilobium brachycarpum	EPIBRA	Forb	Native
Epilobium ciliatum	EPICIL	Forb	Native
Epilobium minutum	EPIMIN	Forb	Native
Festuca spp. - Unknown #001	UNKNOWN	Graminoid	Unknown
Galium bolanderi	GALBOL	Forb	Native

Species name	Species code	Lifeform	Origin
Gayophytum diffusum var. parviflorum	GAYDIF	Forb	Native
Hieracium albiflorum	HIEALB	Forb	Native
Kelloggia galioides	KELGAL	Forb	Native
Lactuca serriola	LACSER	Forb	Non-native
Lilium washingtonianum	LILWAS	Forb	Native
Maianthemum stellatum	MAISTE	Forb	Native
Malacothrix floccifera	MALFLO	Forb	Native
Monardella odoratissima	MONODO	Forb	Native
Nama lobbii	NAMLOB	Shrub	Native
Pedicularis semibarbata	PEDSEM	Forb	Native
Penstemon gracilentus	PENGRA	Forb	Native
Pinus jeffreyi	PIJE	Tree	Native
Pinus lambertiana	PILA	Tree	Native
Pinus ponderosa	PIPO	Tree	Native
Prunus emarginata	PRUEMA	Shrub	Native
Pseudotsuga menziesii	PSME	Tree	Native
Pteridium aquilinum	PTEAQU	Forb	Native
Pyrola picta	PYRPIC	Forb	Native
Quercus vaccinifolia	QUEVAC	Shrub	Native
Ribes roezlii	RIBROE	Shrub	Native
Rosa bridgesii	ROSBRI	Shrub	Native
Rubus parviflorus	RUBPAR	Shrub	Native
Salix scouleriana	SALSCO	Shrub	Native
Senecio sylvaticus	SENSYL	Forb	Non-native
Stephanomeria lactucina	STELAC	Forb	Native
Symphoricarpos mollis	SYMMOL	Shrub	Native
Viola purpurea	VIOPUR	Forb	Native

APPENDIX 6. Results (adjusted *p*-values) of post hoc tests determining the levels of fire severity (Chips Fire), fire frequency, or the interaction between severity and frequency at which characteristics for trees, fuels, and composition among 74 observed plots in and around the Chips and Storrie Fires (Plumas and Lassen National Forest, CA) significantly differ. Holmes or Bonferroni corrections were applied to post-hoc tests to reduce Type I error. Method acronyms: Tukey's HSD = Tukey's honest significant difference test; pairwise perMANOVA= pairwise permutational analysis of variance. U = Unburned; L = Low fire severity; M = Moderate fire severity; H = High fire severity. 1x = Single burn (Chips Fire only); 2x = Reburn (overlap of Storrie and Chips fires). **Bold** indicates significance at alpha = 0.05; **Bold **** indicates marginal significance at alpha $\leq$ 0.10; [+] indicates result not significant at Bonferroni-corrected alpha = 0.017. *(Continued on next page)*

		Method	Chips Fire Severity						Fire Frequency		
			U-L	U-M	U-H	L-M	L-H	M-H	U-1x	U-2x	1x-2x
Trees	Proportion shade-intolerant seedlings	Tukey's HSD (ranks)	0.23	**<0.01**	**0.05**	0.43	0.77	0.99	**<0.01**	**0.05**	0.64
	Total seedling density	Tukey's HSD	0.96	0.99	**<0.01**	0.9	**<0.01**	**0.03**	0.95	**0.03**	**0.01**
	Shade-tolerant tree density	Tukey's HSD (ranks)	**<0.001**	**<0.001**	**<0.001**	**<0.01**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.93
	Shade-intolerant tree density	Tukey's HSD (ranks)	**0.06****	**0.08****	**<0.001**	0.99	0.26	0.25	**0.04**	**<0.001**	**0.06**
	Total snag density	Tukey's HSD (ranks)	**0.05**	**<0.001**	**<0.01**	0.12	0.77	0.55	**<0.001**	0.09	**<0.001**
	Shade-tolerant basal area	Tukey's HSD (ranks)	0.94	**0.09**	**<0.001**	0.34	**<0.001**	**<0.001**	**<0.001**	**0.03**	0.41
	Shade-intolerant basal area	Tukey's HSD (ranks)	**0.1**	0.15	**<0.001**	0.99	0.28	0.23	**0.1**	**<0.001**	**0.04**
	Total snag basal area	Tukey's HSD (ranks)	0.98	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.52	**<0.01**	**<0.001**	0.94
Fuels	1-Hour fuels										
	10-Hour fuels	Hotelling's T^2	**<0.001**	**<0.001**	**<0.001**	**<0.01**	**<0.001**	0.04$^+$	**<0.001**	**<0.001**	0.39
	100-Hour fuels										
	Coarse woody debris										
	Litter depth	Tukey's HSD	**<0.01**	**0.03**	**<0.001**	0.94	0.11	**0.03**	**<0.001**	**<0.001**	0.33
	Duff depth	Tukey's HSD (ranks)	**<0.001**	**<0.001**	**<0.001**	0.58	**<0.01**	0.23	**<0.001**	**<0.001**	**0.08****
	Fuel strata gap	Tukey's HSD	**<0.001**	**<0.001**	NA	0.12	NA	NA	**<0.001**	**<0.001**	0.12
Ground Cover	Ground cover	pairwise perMANOVA	**0.01**	**<0.01**	**<0.01**	0.86	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**0.01**
Vegetation Cover	Vegetation cover	pairwise perMANOVA	**0.05**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	0.64
Species Composition	Richness	Tukey's HSD	0.22	**<0.01**	0.39	0.33	0.99	0.2	**<0.001**	0.26	**0.06****
	Shannon-Wiener Diversity	Tukey's HSD	0.36	**<0.001**	**<0.001**	**<0.01**	**<0.01**	0.99	**<0.001**	**<0.01**	0.22
	Pielou's evenness	Tukey's HSD	0.74	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.22	**<0.001**	**<0.01**	0.52