Forest Ecology and Management 287 (2013) 103–112

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

# Post-fire regeneration across a fire severity gradient in the southern Cascades

Justin S. Crotteau [a,b,*], J. Morgan Varner III [b], Martin W. Ritchie [b]

[a] Department of Forestry & Wildland Resources, Humboldt State University, 1 Harpst Street, Arcata, CA 95521, USA
[b] USDA, Forest Service Pacific Southwest Research Station, 3644 Avtech Parkway, Redding, CA 96002, USA

ARTICLE INFO

*Article history:*
Received 9 March 2012
Received in revised form 7 September 2012
Accepted 13 September 2012

*Keywords:*
Regeneration
Seedlings
Vegetation dynamics
Lassen National Forest
Storrie Fire

ABSTRACT

Large scale, high-severity fires are increasing in the western United States. Despite this trend, there have been few studies investigating post-fire tree regeneration. We established a study in the footprint of the 2000 Storrie Fire, a 23,000 ha wildfire that occurred in northern California, USA. We used a stratified sampling design to quantify post-fire vegetation dynamics across four levels of burn severity and three forest types on the Lassen National Forest nine and ten years following fire. Within each sampled stand, we recorded tree seedlings, forest overstory, shrub cover, and abiotic factors hypothesized to influence growth and establishment.

Median conifer seedling densities varied substantially by burn severity: 1918 seedlings ha$^{-1}$ in the Unchanged units; 4838 seedlings ha$^{-1}$ in the Low-severity units; 6484 seedlings ha$^{-1}$ in the Medium-severity units; and 710 seedlings ha$^{-1}$ in the High-severity units. Increased burn severity was associated with greater shrub coverage: shrub cover in High-severity burns was more than three times those of lower burn severities. We calculated Shannon's Species Diversity ($H'$) and Pielou's Evenness ($E_H$) indices to examine woody shrub and tree diversity. *Abies* spp. were by far the most abundant regenerating conifer species, which may be a concern for land managers; shrub cover after High-severity burns was dominated by *Ceanothus* spp. Although fir regeneration was prolific, the Storrie Fire generated diverse vegetative responses, potentially aiding in the reintroduction of the diverse landscape mosaic homogenized by a century of landscape-scale fire exclusion.

© 2012 Published by Elsevier B.V.

## 1. Introduction

Roughly a century of fire exclusion in the western USA has led to alterations in surface and canopy fuels and increased densities of forests due to the protracted fire-return intervals (McKenzie et al., 2004). Recent evidence points to an increase in large fires (Westerling et al., 2005) and the frequency of high burn severities in large patches (Miller et al., 2009; Fried et al., 2008), resulting in structurally coarse-grained landscapes. These altered fire regimes directly affect landscape vegetation dynamics, influencing both forest structure and composition (Turner et al., 1997; Broncano et al., 2005; McIntire et al., 2005; Odion et al., 2010), yet studies examining the resultant forest legacies after mixed-severity fire are few.

Natural forest regeneration gains importance as scale of disturbance increases. High-severity burns may be less likely to naturally reforest if the scale is sufficient to preclude seed-tree adjacency (Turner et al., 1999; Sessions et al., 2004). Coniferous species rely on wind and rodents for seed dispersal, therefore spatial distribution of regeneration is limited by distance to nearest seed-bearing tree or stand (Bonnet et al., 2005; Donato et al., 2009). Current research in post-fire natural regeneration reveals desirable natural regeneration may be inhibited by dominance of woody shrubs (e.g., Gray et al., 2005; Hogg and Wein, 2005; Moghaddas et al., 2008) and suggests high spatial variability in the regenerating cohort (e.g., Turner et al., 1997; Shatford et al., 2007). Monitoring shifting trends on the landscape can provide valuable insight into post-fire vegetation dynamics (Stuart et al., 1993; Odion et al., 2010; Freeman and Kobziar, 2011) and informing forest managers about the extent and condition of mature natural regeneration.

Montane ecosystems in California have adapted to a range of historic fire frequencies and severities (Agee, 1993; Skinner and Taylor, 2006). The Mediterranean climate maintains fire-prone ecosystems, resulting in a variety of species assemblages across a topographically heterogeneous landscape (Sugihara and Barbour, 2006). Land managers in California are subject to a number of pressures in the aftermath of a wildfire event, many of which hinge on the ability of the diverse forested landscape to not only regenerate, but reestablish dominance on the landscape. Although a number of studies have examined natural regeneration immediately following fire (2–5 years; e.g., Turner et al., 1997; Donato et al., 2006, 2009; Moghaddas et al., 2008), trees may require a longer period

* Corresponding author. Address: USDA, Forest Service Pacific Southwest Research Station, 3644 Avtech Parkway, Redding, CA 96002, USA. Tel.: +1 530 226 2547; fax: +1 530 226 5091.
*E-mail address:* jscrotteau@fs.fed.gov (J.S. Crotteau).

0378-1127/$ - see front matter © 2012 Published by Elsevier B.V.
http://dx.doi.org/10.1016/j.foreco.2012.09.022

to establish, therefore a long term study of regeneration and shrub dynamics is essential for improved ecosystem understanding and long term forest management decision making.

The 2000 Storrie Fire in northern California presented an opportunity to investigate post-fire regeneration patterns across the landscape after a 9–10 year period of natural recovery. The Storrie Fire was a large (23,000 ha), mixed-severity burn, and provided occasion to study a variety of landscape conditions. The objectives of this study were to: (1) quantify post-fire tree seedling and woody shrub response; and (2) examine seedling and shrub species trends on the landscape. The latter objective addresses woody shrub and tree seedling species diversity and the relative balance between pine and fir. This study was designed to aid our understanding of tree recovery and shrub competition after mixed-severity fire in northern California. Our study presents distinct post-fire vegetation trends across a burn severity gradient that may be carefully extrapolated to a variety of fire-prone western landscapes with similar climate, fire, and management regimes.

## 2. Methods

### 2.1. Study site

The study site was a 9371 ha portion of Lassen National Forest (LNF), California, where the 2000 Storrie Fire burned. Historically, fires were observed a minimum of 9 years apart in mid-montane forests to 110 years apart in the upper montane forests of this bioregion (Skinner and Chang, 1996; Beaty and Taylor, 2001; Skinner and Taylor, 2006). USFS R5 historical burn polygons reveal that the majority of our study area (98.4%), however, had experienced approximately a century without fire preceding the 2000 event.

The Storrie Fire was characterized by high spatial complexity with varying levels of low- to high-severity burns (Table A1) on the predominantly forested landscape. The fire burned areas within the Plumas and Lassen National Forests; this study was funded by the latter and therefore focuses only on the forested portion of the LNF, ca. 41% of the total footprint of the fire. The fire was ignited on 17 August 2000 after which it rapidly spread north and then slowly fanned outward and created a burned region of approximately 24 km from north to south in Plumas County. After a period of slow fire growth in the northwestern quarter, the fire was fully contained by 27 September 2000. The most northerly edge of the burn was located at approximately 121.32°W and 40.17°N, just over 16 km southwest of Lake Almanor (Fig. 1). The 4 days prior to the fire were characterized by low minimum relative humidity (5–15%), high maximum daily temperatures (greater than 30 °C), and low mean wind speeds with gusts no greater than 32 km/h (PRISM Climate Group, 2011). Following ignition, temperatures became slightly cooler and relative humidity increased.

Elevation of the study area ranged from ca. 900 m to 2100 m above MSL. Climate for the study site is typified as Mediterranean with warm, dry summers (mean max. temperature, June–September: 21–26 °C) with precipitation less than 42 mm each summer month and wet, cool winters (mean max. temperature, November–March: 6–9 °C) with precipitation greater than 248 mm each winter month; the area receives less than 5% of annual precipitation in summer months (PRISM Climate Group, 2011). Palmer Drought Severity Index (PDSI) for the year 2000 in the encompassing Sacramento Drainage region was 0.15, a neutral year after one neutral and four very wet to extremely wet years since 1995 (National Climatic Data Center, 2011). This region is in close proximity (ca. 45 km) to Mount Lassen, the southernmost volcanic peak in the Cascades, abutting the northern edge of the Sierra Nevada. The soil-vegetation map of the area reports both volcanic and granitic parent material, a product of the two adjacent mountain ranges (Soil Survey Staff, 2011). The soils are therefore highly variable, ranging from rocky outcroppings with little or no topsoil to deep (1.5 m) loams overlying bedrock. Overstory characteristics, slope, aspect, and vegetative cover were variable across the study area, as is typical of the region (Skinner and Taylor, 2006). The Lassen NF burned area was dominated by forests of white fir (*Abies concolor* (Gordon & Glend.) Lindley), California red fir (*A. magnifica* var. *magnifica* Andr. Murray), incense-cedar (*Calocedrus decurrens* (Torrey) Florin), Sierra lodgepole pine (*Pinus contorta* Louden var. *murrayana* (Grev. & Balf.) Critchf.), Jeffrey pine (*P. jeffreyi* Grev. & Balf.), sugar pine (*P. lambertiana* Douglas), western white pine (*P. monticola* Douglas), ponderosa pine (*P. ponderosa* Laws.), Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), and California black oak (*Quercus kelloggii* Newb.). The most prevalent shrub species included deer brush (*Ceanothus integerrimus* Hook. & Arn.), snowbrush (*C. velutinus* Dougl.), huckleberry oak (*Q. vaccinifolia* Kellogg), pinemat manzanita (*Arctostaphylos nevadensis* A. Gray), greenleaf manzanita (*A. patula* E. Greene), mountain whitethorn (*C. cordulatus* Kellogg), and bush chinquapin (*Chrysolepis sempervirens* (Kellogg) Hjelmq.).

Dominant forest types were Sierra Nevada Mixed Conifer, White fir, and Red fir, following the elevation gradient of the region (Eyre, 1980). The Mixed Conifer type of the mid-montane westside zone of the southern Cascades historically experienced frequent (every 9–42.5 years), small to medium surface fires that burned with low to moderate severity, creating open stands of large diameter trees (Beaty and Taylor, 2001; Skinner and Taylor, 2006). Although each of the coniferous species in this zone (*A. concolor*, *C. decurrens*, *Pseudotsuga menziesii*, *Pinus lambertiana*, and *P. ponderosa*) are resistant to fire when mature, the fire stimulated germination of *P. ponderosa* and the ability to withstand fire at a young age suggests that *P. ponderosa* may most suitably interact with the historic fire regime. Yet, twentieth century fire suppression has resulted in a drastic inflation in fire rotation for the mid-montane westside zone, resulting in uncharacteristically high densities of the shade-tolerant *A. concolor* (Beaty and Taylor, 2001). At slightly higher elevations, the White fir forest type in this region is situated such that it occupies both mid-montane westside and the upper-montane ecological zones, while the Red fir type is most commonly associated with the upper-montane zone. These forest types often form nearly pure stands of true fir (*A. concolor* and *A. magnifica*), particularly as elevation increases. Historically, the fire regime for the White and Red fir types ranged from frequent to infrequent fire (25–110 years) that burned small to medium patches in a variety of severities, resulting in relatively high spatial stand complexities (Skinner and Taylor, 2006). Fire suppression has allowed for denser forests in these forest types as well, yet current fire return intervals may not be outside of natural variation.

### 2.2. Sampling methods

The Lassen NF landscape within the perimeter of the Storrie Fire was divided into 12 strata: four levels of fire-severity across three levels of forest type. Fire severity was determined remotely by using the Relative differenced Normalized Burn Ratio (RdNBR), which has been reported to approximate the Composite Burn Index (CBI; Miller et al., 2008), a field-based assessment of burn severity. The RdNBR is created from bands 4 and 7 from two LANDSAT Thematic Mapper images (pre-fire and 1 year post-fire) and is subsequently transformed to four nominal CBI categories: (1) Unchanged (minimal or no visible effect of fire), (2) Low-severity, (2) Medium-severity, and (4) High-severity (Table 1). Forest type was determined according to Eyre (1980) in conjunction with a digital elevation model (DEM) to guide elevation thresholds. The forested landscape was segregated into "Mixed Conifer" (dominant type: Sierra Nevada Mixed Conifer), "Low-elevation Fir" (dominant

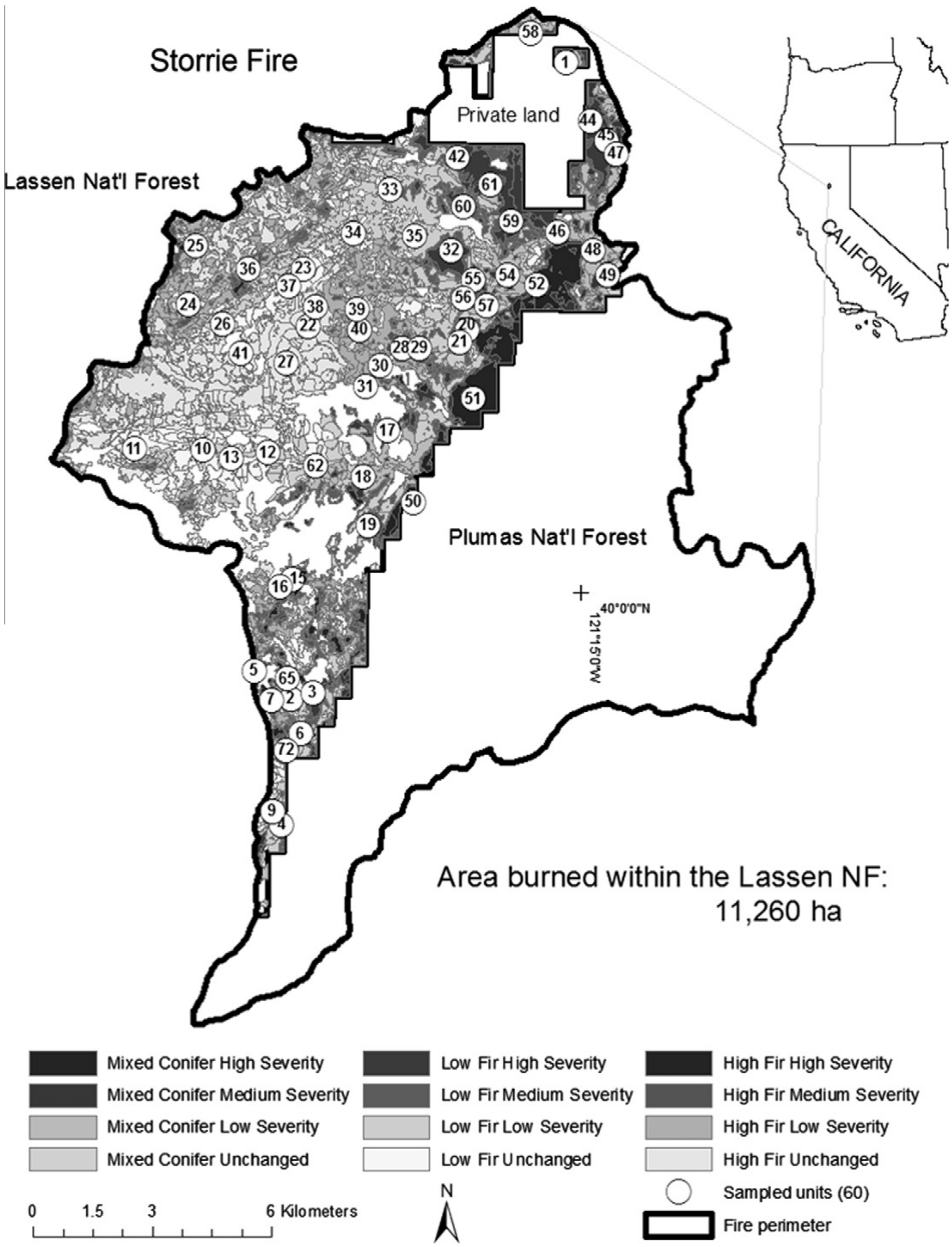


**Fig. 1.** 2000 Storrie Fire boundary in northern California, stratified by four levels of Composite Burn Index (CBI) values and three levels of forest types (12 strata). Sixty observational units were selected across the 12 strata with probability proportional to size.

type: White Fir; secondary type: Red Fir) and "High-elevation Fir" (dominant type: Red Fir; secondary type: White Fir) forests (Table 2). The 12 strata abbreviations refer to the interaction between forest type and burn severity and are as follows: MCU =

**Table 1**
Composite Burn Index (CBI) thresholds (approximated via Relative differenced Normalized Burn Ratio [RdNBR]) used to create four burn severity classes within the Storrie Fire perimeter, Lassen National Forest.

| Fire severity level | CBI values | |
|---|---|---|
| | Lower bound | Upper bound |
| Unchanged | 0.00 | 0.10 |
| Low-severity | 0.10 | 1.25 |
| Medium-severity | 1.25 | 2.25 |
| High-severity | 2.25 | 3.00 |

**Table 2**
Society of American Foresters (SAF) cover type and elevation thresholds used to delineate three forest types within the Storrie Fire perimeter, Lassen National Forest.

| Forest cover type | SAF type | Elevation (m) | |
|---|---|---|---|
| | | Minimum | Maximum |
| Mixed conifer | 243 | 0 | 1463 |
| Low-elevation Fir | 207, 211 | 1463 | 1774 |
| High-elevation Fir | 207, 211 | 1774 | 2188 |

Mixed Conifer Unchanged, MCLS = Mixed Conifer Low-severity, MCMS = Mixed Conifer Medium-severity, MCHS = Mixed Conifer High-severity, LFU = Low-elevation Fir Unchanged, LFLS = Low-elevation Fir Low-severity, LFMS = Low-elevation Fir Medium-severity, LFHS = Low-elevation Fir High-severity, HFU = High-elevation Fir Unchanged, HFLS = High-elevation Fir Low-severity, HFMS = High-elevation Fir Medium-severity, HFHS = High-elevation Fir High-severity.

Sixty observational units were randomly selected (five units per stratum) with probability proportional to unit area from a population of 2292 strata polygons that ranged in size from less than 0.4 ha to 195 ha. Due to the size and inaccessibility of the study area, field data were collected over the course of two summers (half in each 2009 and 2010), nine and ten years following the Storrie Fire. A randomly located and oriented cluster of 19 0.004 ha (3.59 m radius) circular plots 20 m apart was assigned to each of the 60 selected units to effectively capture variability (Fig. B1).

Live "mature" seedlings (here defined as seedlings that we deemed to be "well-established," i.e., taller than 15.24 cm up to any stem with diameter at breast height (dbh) <10.16 cm) were counted on each of the plots. Seedlings were classified by species, height, dbh and categorized as either overtopped by shrubs or not overtopped. Due to *Q. kelloggii*'s prolific resprouting method of regeneration (Cocking et al., 2011), all *Q. kelloggii* analysis in this study was approached with the presence/absence method, thereby avoiding miscalculating genet densities.

Additional site data recorded at the plot-level included slope, aspect, percent woody shrub cover, and surrounding overstory. Woody shrub cover was visually assessed within plot quadrants: shrub vegetation was recorded by species, height (nearest 0.3 m) and cover (%). Herbaceous species were not addressed in this study. Overstory trees were tallied via concurrent point, or variable radius, sample (from plot center of seven equidistant plots; see Fig. B1) using a basal area factor (BAF) 4.592 $m^2$ $ha^{-1}$ prism; species, diameter, and mortality were also recorded.

### 2.3. Data analysis

Plot aspect was transformed for analysis: in the manner of Stage (1976) the cosine of aspect, which was recorded in degrees, was multiplied by slope percent to create a topographic index (TI). An aggregate Stand Density Index (SDI; sensu Reineke (1933)) was calculated for each unit using overstory density and quadratic mean diameter observed, as SDI is a robust measure of stand overstory crowding. To address non-normality of data recorded in percentages, data recorded as a percentage were transformed using the arcsine transform. Non-normal seedling density data were transformed with the square-root transformation to approach normality.

Species diversity was quantified for inter-strata comparison using the Shannon's Diversity (H′) and Pielou's Evenness ($E_H$) indices. Diversity is defined as:

$$H' = -\Sigma p_i \ln p_i$$

where $H'$ is the Shannon Diversity index and $p_i$ is the relative abundance of a species within a unit. Evenness is defined as:

$$E_H = \frac{H'}{\ln S}$$

where $E_H$ is the Pielou (1966) species evenness index, $H'$ is the Shannon Diversity index, and $S$ is total species richness, or count, in the unit. Two indices, "fir index" and "pine index," were created for the examination of conifer seedling species trends, where fir index in a unit refers to the *Abies* spp. (*A. concolor* and *A. magnifica*) proportion and pine index refers to the combined *Pinus* spp. (*P. jeffreyi*, *P. lambertiana*, and *P. ponderosa*) proportion of total regeneration observed. Three additional indices were created for shrub genera *Ceanothus* (*C. cordulatus*, *C. integerrimus*, *C. prostratus*, and *C. velutinus*), *Arctostaphylos* (*A. patula* and *A. nevadensis*), and *Quercus* (*Q. chrysolepis* and *Q. vaccinifolia*) proportions of total shrub cover within a unit to better address shrub species trends.

Given that there are 60 experimental units, plot values were averaged for each unit to avoid issues with pseudoreplication. Data were subsequently summarized by strata and examined using descriptive statistics including mean and standard error. Where applicable, data were first inspected for homoscedasticity using Levene's test and then for burn severity × forest type effects via ANOVA ($\alpha = 0.05$) and independent sample *t*-tests. Although results from a MANOVA may have aided a similar analysis of burn severity × forest type effects across a matrix of species data, individual species densities were highly non-normal (right-skewed with high frequency of zeroes), thus precluding a MANOVA test.

We used Kruskal's Non-metric Multidimensional Scaling (NMS) algorithm , which does not require data normality, to inspect inter-strata community patterns within our data. Kruskal's NMS uses a non-metric algorithm to reduce the dimensionality of a dataset from *p*-dimensional (i.e., *p* groups; in our case, $p = 12$ strata) space to a two-dimensional space which has the benefit of easier interpretation (Venables and Ripley, 2002). A single 12 × 12 distance matrix was created from raw plot-level species data of tree seedlings and most prevalent shrubs. Mahalanobis distance was employed, instead of Euclidean distance, as its metric incorporates population variance. The procedure (after Manly, 2005) was conducted in R (The R Foundation, 2011) using the `isoMDS` NMS function to project the 12-dimensional dataset onto a two-dimensional plane with a maximum of 50 iterations. The output was subsequently evaluated by the "stress" instability criterion, a metric that estimates the level of impact that the projection had on the distance relationships. "Stress" ranges from 0% to 100%, where high values suggest that projected (two-dimensional) relationships compromise *p*-dimensional relationships.

## 3. Results

### 3.1. Tree and woody shrub regeneration across the landscape

Burn severity had a substantial effect on conifer seedling densities across the Storrie Fire footprint (Fig. 2; Table 3). Mean (±1 SE) conifer seedling densities along the burn severity gradient were: 1845 (530) seedlings $ha^{-1}$ in the Unchanged units; 4818 (2851) seedlings $ha^{-1}$ in the Low-severity units; 6497 (3172) seedlings $ha^{-1}$ in the Medium-severity units; and 715 (492) seedlings $ha^{-1}$ in the High-severity units. The Stagean transform of slope and aspect (TI) also had an effect on seedling densities, confirming that densities were greatest on northeastern aspects (Table 3). The proportion of overtopped tree seedlings varied by burn severity (Table 3). Mean (±1 SE) overtopped conifer seedlings were: 2.3% (0.9) of seedlings in the Unchanged units; 9.3% (3.0) in Low-severity; 15.1% (4.7) in Medium-severity; and 48.4% (8.0) in High-severity units. Observed overtopped conifer seedlings within the High-severity strata were approximately three times more common than the less severely burned sites (Table 4).

California black oak regeneration was present in the Mixed Conifer and Low-elevation Fir forests, but was absent in the High-elevation Fir type, resulting in a significant forest type effect (Table 3). Mean (±1 SE) *Q. kelloggii* presence across forest type was: 23.1% (10.7) in Mixed Conifer, 13.0% (10.0) in Low-elevation Fir, and 0% (0.0) in High-elevation Fir. The magnitude (count and size) of sprouting stems per genet was great after severe fire (Medium- and High-severity), whereas observed stems in the Unchanged and Low-severity strata largely appeared to be remnant individuals and acorn regeneration (personal observation).

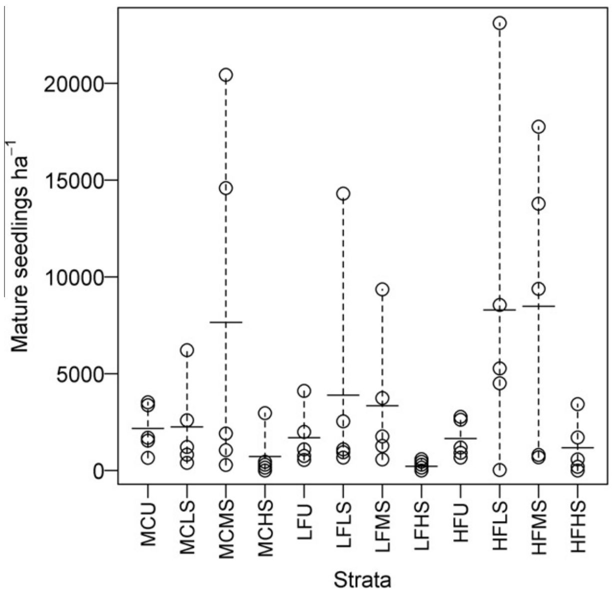


**Fig. 2.** Mean (bars) and unit-level (dots) mature conifer seedling densities (ha$^{-1}$) across three forest types and four burn-severities a decade after the 2000 Storrie Fire in Lassen National Forest. Mature seedlings were greater than 15.24 cm tall and less than 10.2 cm at DBH.

Mean shrub cover varied by severity, increasing sharply as burn-severity increased (Table 3). On average, shrubs covered 6.7% (2.8) of the Unchanged units; 8.4% (3.6) of the Low-severity; 17.2% (6.1) of the Medium-severity; and 53.0% (10.3) of the High-severity. Shrub cover in MCHS and LFHS strata was four times greater than respective Medium-severity strata, whereas HFHS shrub cover was only 1.5 times greater than cover in the HFMS stratum.

### *3.2. Post-fire conifer seedling and woody shrub species trends across the landscape*

Conifer regeneration diversity ($H'$) and evenness ($E_H$) in the Mixed Conifer forest was greater than $H'$ and $E_H$ in the High-elevation Fir forest (Fig. 3; Table 3), though differences in the $E_H$ indices were marginally significant. The effect of burn severity and the interaction between forest type and burn severity were not statistically significant for both regeneration $H'$ and $E_H$ (Table 3).

The relationships between pines and fir differed across the burned landscape (Table 3; Fig. 4). Inspection of the fir index revealed that *Abies* spp. comprised greater than 50% ($H_0$: index > 0.5) of total conifer regeneration in the Low-elevation Fir (one-sided *t*-test: $t = 4.96$, $df = 19$, $p < 0.001$) and the High-elevation Fir (one-sided *t*-test: $t = 10.69$, $df = 19$, $p < 0.001$) forest types, while there was insufficient evidence to support that the fir index in the Mixed Conifer forest type was greater than 0.5 (one-sided *t*-test: $t = 0.65$, $df = 19$, $p = 0.261$). We observed that combined *Pinus* spp. were overall less abundant than *Abies* spp. (Table 4). A heteroscedastic pine index precluded a dependable ANOVA result, yet suggested that both burn severity and forest type may have a significant effect on the proportion of pine (Table 3; Fig. 4). Pine index was lower in the Unchanged strata than Low-, Medium-, and High-severities (one-sided *t* -test: $t = -3.45$, $df = 49.75$, $p < 0.001$) and greater in the Mixed Conifer forest type (one-sided *t* -test: $t = 2.12$, $df = 37.56$, $p = 0.020$). The remaining species of conifer seedlings further reflect variation across the landscape (Table 4).

Shrub diversity ($H'$) was relatively homogeneous across the levels of burn severity and forest type (Fig. 3; Table 3). High-severity burns produced lower mean shrub $E_H$ values (35% less than Unchanged shrub $E_H$ mean), suggesting that burn severity had some effect on shrub evenness, but this result was only marginally significant. Neither was the effect of forest type on shrub species $E_H$ or the interaction between forest type and burn severity statistically significant (Table 3).

Dominant shrubs (by percent cover) within each stratum were generally *Arctostaphylos*, *Ceanothus* and *Quercus* species (Table 5), except for *Alnus incana* (dominant shrub in LFLS). We observed twice as much *Ceanothus* spp. cover in the Mixed Conifer and Low-elevation Fir than the High-elevation Fir forest type; *Ceanothus* cover also increased with burn severity (Table 3). *Arctostaphylos* cover was more than four times greater in the High-elevation Fir than the Mixed Conifer and Low-elevation Fir types (Table 3). Burn severity × forest type had a significant effect on *Quercus* cover (Table 3): the greatest cover was in LFU, HFMS, and HFHS. Although other shrub species were present, magnitude of response was marginal (Table 5).

Kruskal's NMS yielded a two-dimensional plane from high-dimensional community-level species (both tree seedling and shrub) data that facilitated the visualization of Mahalanobis distance among the 12 strata (Fig. 5). A stress value of 5.13% was reached after less than twenty iterations, thus maintaining the 12-dimensional relationship-integrity among strata. As expected, the NMS layout clustered the Unchanged and Low-severity strata together. The Medium-severity strata were also centered on this cluster, though exhibiting more variation along dimension 2. There was a disparity between the High-severity strata, both within and across the three forest types. Together, dimensions 1 and 2 segregated burn severities, though dimension 2 appeared to primarily distinguish forest types. The burn severity pathway lines that connect the four levels of burn severity to each other within the three forest types illustrate a greater difference in Mahalanobis distance between strata species abundance and composition with increased burn severity (Fig. 5). The distance between HFMS and HFHS (1.06) is slightly greater than the distance between the HFLS and HFMS strata (0.62). In contrast, the distance from Medium- to High-severity is more than eight times as great the distance from Low- to Medium-severity in Low-elevation Fir (4.11 > 0.49) and nearly four times as great in Mixed Conifer (4.42 > 1.14). Although different themselves, the MCHS and LFHS strata seem to diverge from the central mass of the remnant strata in a similar direction and magnitude.

## 4. Discussion

### *4.1. Effect of fire on the magnitude of tree and shrub response*

Although post-fire seedling establishment is driven by a series of factors (e.g., available moisture, soil insolation, rodent herbivory, damping-off fungi) the foremost requirement for most natural conifer regeneration is a seed source (e.g., Bonnet et al., 2005). It is likely that we observed greatest conifer regeneration densities in the Low- and Medium-severity burns due to nearby remnant mature, seed-bearing trees. In the case of the Storrie Fire, the Low- and Medium-severity burns resulted in such high densities of conifer regeneration (as in Turner et al. (1997)) as to merit a pre-commercial thin, were the study area a managed plantation. In addition to seed production, the remnant overstory in Low- and Medium-severity burns produced high shade, a factor which may have limited shrub competition, further permitting high densities of seedlings to establish (Smith et al., 1997). High-severity burns, on the other hand, have such poor overstory survival that distance to seed source becomes a limiting factor (Bonnet et al., 2005; Donato et al., 2009). Although our study did not measure distance to the nearest seed-bearing trees, seed trees within the High-severity

**Table 3**
ANOVA p-values for density, species diversity, and species evenness among 60 observed units a decade after the 2000 Storrie Fire, Lassen National Forest.

| Source | *df* | Regeneration | | | | Species diversity, $H'$[a] | | Species Evenness, $E_H$[b] | | Regeneration Species Indices[c] | | Shrub Species Indices[d] | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Conifer density | Oak presence | Overtopped Conifers | Shrub Cover | Regeneration | Shrubs | Regeneration | Shrubs | *Abies*[e] | *Pinus*[f] | *Ceanothus*[g] | *Arctostaphylos*[h] | *Quercus*[i] |
| Burn severity | 3 | <0.001 | 0.278 | <0.001 | <0.001 | 0.821 | 0.614 | 0.822 | 0.053 | 0.922 | 0.011 | <0.001 | 0.276 | <0.001 |
| Forest type | 2 | 0.194 | <0.001 | 0.255 | 0.212 | <0.001 | 0.412 | 0.105 | 0.245 | <0.001 | <0.001 | 0.014 | <0.001 | 0.021 |
| Topographic Index | 1 | 0.016 | 0.181 | 0.096 | 0.561 | 0.273 | 0.696 | 0.559 | 0.202 | 0.001 | 0.004 | 0.814 | 0.163 | 0.705 |
| Burn:Forest | 6 | 0.614 | 0.707 | 0.543 | 0.203 | 0.525 | 0.558 | 0.277 | 0.211 | 0.510 | 0.554 | 0.687 | 0.748 | <0.001 |
| Error | 47 | | | | | | | | | | | | | |

[a] Shannon's Diversity Index.
[b] Pielou's Evenness Index.
[c] Proportion of total conifer regeneration density.
[d] Proportion of total shrub cover.
[e] *Abies concolor* and *A. magnifica*.
[f] *Pinus jeffreyi*, *P. lambertiana*, and *P. ponderosa*.
[g] *Ceanothus cordulatus*, *C. integerrimus*, *C. prostratus*, and *C. velutinus*.
[h] *Arctostaphylos patula* and *A. nevadensis*.
[i] *Quercus chrysolepis* and *Q. vaccinifolia*.

stratum were few and far between. Inconsistent presence of a seed source was likely the cause of low seedling densities after High-severity burns in the study area; even though mean density within this burn severity was 715 seedlings ha$^{-1}$, eight of the fifteen observational units had fewer than 247 seedlings ha$^{-1}$. The stark contrast between the prolific Low- and Medium-severity burns and the sometimes sparsely regenerating High-severity burns (as in Chappell and Agee (1996) and Turner et al. (1997)) highlights the landscape structural heterogeneity created by the Storrie Fire. Although distinct landscape heterogeneity is often valuable for wildlife habitat and beta-level biodiversity, it is perhaps at the expense of optimal timber production, traditionally one of the LNF's primary concerns.

In contrast to the conifer seedling analysis, the presence/absence method by which we analyzed *Q. kelloggii* revealed dependence on elevation (forest type). We expected the significant effect of elevation, as the High-elevation Fir forest type is above the hardwood's apparent elevational band (McDonald, 1990). ANOVA showed that there was no significant difference, however, in *Q. kelloggii* presence among burn severities. Interestingly, this result may suggest that the distribution of resprouting individuals top-killed by Low-, Medium- and High-severity fire is matched by a corresponding distribution of acorn regeneration within the Unchanged strata. Therefore, although the magnitude of *Q. kelloggii* stems (ramets) may dominate vegetation after some High-severity burns (personal observation; also, McDonald and Tappeiner (1996), Cocking et al. (2011)) the distribution of genets in the study area did not depend on the impact of fire. As a caveat, this analysis takes into account only the presence of *Q. kelloggii*, not size, dominance, nor probability of individual survival. Oak resprouting was widespread across MCHS and LFHS, and although *Q. kelloggii* presence was not different among burn severities, fire-induced sprouting formed tall and vigorous thickets that were unlike the growth habit in Unchanged units.

As is common to the southern Cascades and northern Sierra Nevada ranges, we observed greatest shrub response after High-severity fire; a number of studies have observed a similar dynamic (McDonald, 1983; Kauffmann and Martin, 1990; Nagel and Taylor, 2005). The shrub response phenomenon was likely due to the multiple regenerative mechanisms common to shrubs in this bioregion (Skinner and Taylor, 2006). The ability to resprout as well as germinate from *in situ* soil seed banks enabled woody shrubs to effectively colonize High-severity patches (Keeley and Davis, 2000). Pioneering shrub species also benefit from the open growing conditions that characterize High-severity patches. Remnant overstory trees in High-severity units were sparse if not null, thus permitting shrubs unshaded access to solar energy. On the contrary, shrub cover after Medium-severity burns in the study was one third of the High-severity cover, suggesting that even a sparse tree overstory inhibits shrubs from establishing site dominance (Smith et al., 1997). Low shrub cover in the stands not burned with High-severity may also be a result of incomplete heat scarification of in-soil seed (Conard et al., 1985).

### 4.2. Landscape dominants

As two of the three forest types are defined by dominant *Abies* spp. overstories, and *Pinus* spp. are expected to comprise a significant portion of the Mixed Conifer forest type (Tappeiner, 1980), we were naturally most interested in pine and fir composition. Additionally, pine's superior fire-adaptations and timber qualities are highly valued by land managers, thus fueling the inspection of species proportions. We expected that regenerating conifer species would vary by disturbance severity (McDonald, 1976a) and forest type. Analysis of the proportion of fir regeneration (fir index; Fig. 4) clearly revealed that *Abies* spp. dominated regenerating seedling densities in the High-elevation (more than 70% of which was *A. magnifica*) and Low-elevation Fir (up to 40% *A. magnifica*). Roughly half of all regeneration in the Mixed Conifer forest type were *Abies* seedlings (mean fir index = 0.55, SE = 0.062); in fact, a more detailed species breakdown (Table 4) revealed that *A. concolor* was more than 1.2 times abundant than any of the six other Mixed Conifer species present. *Abies* spp. are known to be prolific seeders (Zald et al., 2008), therefore it was not completely unexpected that densities were so great, even in the Mixed Conifer forest type.

We did expect, however, that presence of remnant overstory *Pinus* spp. would spawn high *P. jeffreyi*, *P. lambertiana*, and *P. ponderosa* seedling densities after Medium- and High-severity burns, which are associated with increased direct sunlight and bare mineral soil (Harrington and Kelsey, 1979). Although we did not observe *Pinus* spp. densities in the same magnitude as those of *Abies* spp. (Fig. 4; as in Shatford et al. (2007) and Zald et al. (2008)) analysis of the pine index confirmed that Low-, Medium-, and High-severity burns had more positive effects on the proportion of pine regeneration than the Unchanged strata in the Low-elevation Fir and Mixed Conifer forest types. Excluding the Unchanged sites, each level of disturbance severity yielded approximately the same proportion of *Pinus* spp. regeneration. Yet proportion values mask actual densities. A regional seedling

**Table 4**
Mature conifer seedling composition and overtopped status among strata a decade after the 2000 Storrie Fire, Lassen National Forest.

| Forest type | Burn severity | Species[a] | | | | | | | | | Overtopped[b] (%) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | ABCO | ABMA | CADE | PICO | PIJE | PILA | PIMO | PIPO | PSME | |
| *Seedlings ha$^{-1}$* | | | | | | | | | | | |
| Mixed conifer | | | | | | | | | | | |
| | Unchanged | 1124 | 0 | 807 | 0 | 16 | 97 | 0 | 67 | 124 | 5.3 |
| | Low | 881 | 0 | 718 | 0 | 0 | 237 | 0 | 198 | 218 | 17.8 |
| | Medium | 6539 | 0 | 104 | 0 | 0 | 619 | 0 | 312 | 294 | 10.2 |
| | High | 500 | 0 | 10 | 0 | 0 | 101 | 0 | 88 | 34 | 60.2 |
| Low-elevation fir | | | | | | | | | | | |
| | Unchanged | 1042 | 335 | 259 | 0 | 3 | 27 | 0 | 0 | 36 | 5.3 |
| | Low | 3432 | 203 | 22 | 13 | 25 | 184 | 0 | 8 | 12 | 4.5 |
| | Medium | 1603 | 1275 | 94 | 0 | 8 | 250 | 0 | 40 | 75 | 9.9 |
| | High | 122 | 0 | 18 | 0 | 5 | 33 | 0 | 31 | 15 | 60.2 |
| High-elevation fir | | | | | | | | | | | |
| | Unchanged | 398 | 1249 | 0 | 0 | 0 | 0 | 44 | 0 | 0 | 2.3 |
| | Low | 666 | 7582 | 0 | 44 | 5 | 0 | 0 | 0 | 0 | 1.0 |
| | Medium | 179 | 8213 | 0 | 83 | 0 | 5 | 3 | 0 | 0 | 4.5 |
| | High | 185 | 957 | 0 | 36 | 3 | 5 | 0 | 0 | 0 | 19.1 |

[a] key to species codes: ABCO, *Abies concolor*; ABMA, *A. magnifica*; CADE, *Calocedrus decurrens*; PICO, *Pinus contorta*; PIJE, *P. jeffreyi*; PILA, *P. lambertiana*; PIMO, *P. monticola*; PIPO, *P. ponderosa*; PSME, *Pseudotsuga menziesii*.
[b] Percent of all mature conifer seedlings with leaders overtopped by woody shrub cover.

stocking guide suggests that minimum seedling densities exceed 247 trees ha$^{-1}$ (USDA, 1987). Only three strata (MCLS, MCMS, and LFMS) had mean *Pinus* spp. densities satisfying the stocking density requirement. The lack of sufficient *Pinus* spp. densities after High-severity fire in the Mixed Conifer and Low-elevation Fir forest types is alarming as the reduction in pine may result in an ecosystem type shift coupled with the degradation of a valued timberland. The concern is exacerbated given the large number of recent fires that burned with similar or greater proportions of high severity fire (Miller et al., 2009).

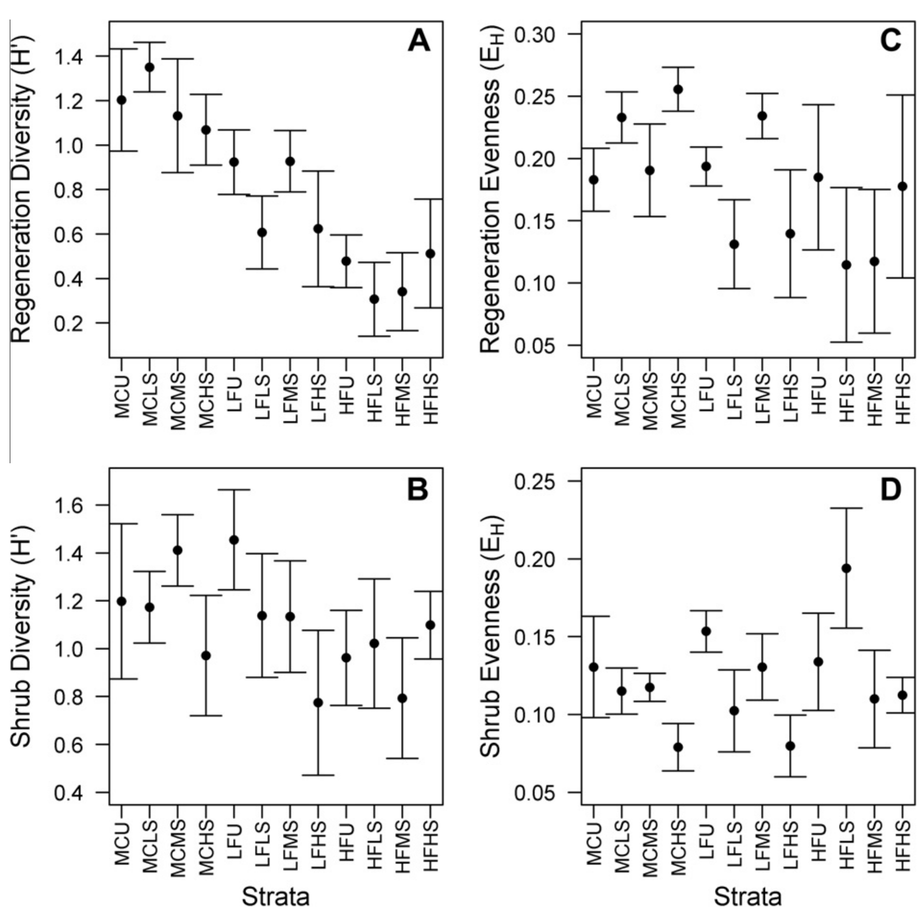


**Fig. 3.** Mean (±1 S.E.) Shannon's Diversity ($H'$; A and B) and Pielou's Evenness ($E_H$; C and D) indices as calculated a decade after the 2000 Storrie Fire in Lassen National Forest. Indices were calculated on two levels: natural tree regeneration (A and C), and woody shrubs (B and D).

Dominant shrub trends after the Storrie Fire are best emphasized by contrasting extremes, i.e., Unchanged and High-severity burns within each forest type. Where fire was severe in the Low-elevation Fir and Mixed Conifer forests, *C. integerrimus* and *C. cordulatus* dominated shrub cover (as in Kauffmann and Martin (1990)). The abundance of *Ceanothus* across our study area is likely due to the fire-stimulated adaptations of the genus, that is, the ability to resprout after disturbance and the heat-scarified germination of long-lived seedbeds (Conard et al., 1985). As pioneers, *Ceanothus* spp. site dominance is maintained by fire; lack of returning fire may result in conifer encroachment (Conard et al., 1985; Nagel and Taylor, 2005). The LFU and MCU strata were dominated by *Q. vaccinifolia* and *A. patula*. Although playing a lesser role, *Ceanothus* was also present in the High-elevation Fir forest; in the HFHS, *Q. vaccinifolia* and *C. velutinus* were the dominant shrub species in contrast to *A. nevadensis* and *Q. vaccinifolia* in HFU. Our results regarding *Arctostaphylos* and *Quercus* species in the study's Unchanged units were in line with those found by a study within the Lake Tahoe Basin, some 150 km away (Nagel and Taylor, 2005), in which these two genera were the principal resprouting shrubs in the absence of fire in montane chaparral.

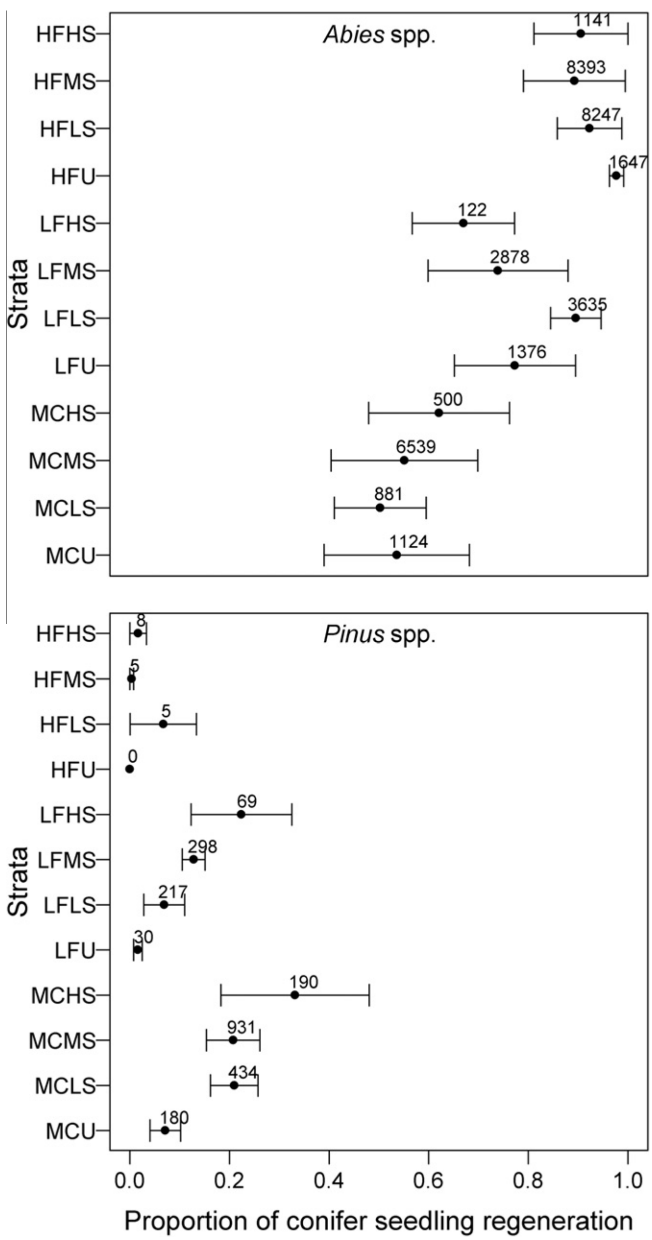


**Fig. 4.** Mean (±1 S.E.) *Abies* spp. and *Pinus* spp. proportions of mature conifer regeneration across three forest types and four burn-severities a decade after the 2000 Storrie Fire in Lassen National Forest. *Abies* spp. include *A. concolor* and *A. magnifica*. *Pinus* spp. include *P. jeffreyi*, *P. lambertiana*, and *P. ponderosa*. Mean seedling densities are concurrently provided for scale reference.

Despite the wide array of conifer seedling and woody shrub species, relative species abundance responses were fairly homogeneous across the stratified landscape. Correspondingly, there was insufficient evidence that diversity ($H'$) and evenness ($E_H$) for conifer seedlings and woody shrubs varied by burn severity. Although observed species mixes changed among strata, similar diversity values indicate that the mosaicked landscape offers an abundance of niches to support a well-balanced biota, whether or not we observe the desired species evenness. Yet, more replications within a forest type may better distinguish the effect of burn severity on species diversity. Our study would suggest that fire severity alone is not sufficient to explain post-fire species diversity. Regardless, fire severity seems as plausible a predictor of post-disturbance species diversity as a fire frequency predictor (as in Schwilk, 1997; Beckage and Stout, 2000), particularly in ecosystems prone to mixed-severity fire.

### 4.3. Impact of High-severity fire on low elevation forest types

USFS Region 5 historic fire perimeters revealed that less than 1.4% of the area within the Storrie Fire perimeter burned in the 20th century. Whereas the high proportion of *A. magnifica* in the High-elevation Fir forest type suggests a low historical fire frequency (mean composite FRI = 33.8 years), *Pinus* spp. presence in the Low-elevation Fir and Mixed Conifer forest types imply that historic fire frequency below the *A. magnifica* line may have been more frequent in pre-suppression periods (mean composite FRI = 11.5 years), as reported in a local fire regime study (Beaty and Taylor, 2001). Increase in fire-return interval as a result of suppression may have decreased overstory diversity (from a mixture of conifers to fewer conifer species) in a species shift towards shade-tolerant trees (Bock and Bock, 1977), away from historically more common pine forests, black oak woodlands, and open shrub fields (Nagel and Taylor, 2005). Thus, stand-replacing fire in the Mixed Conifer and Low-elevation Fir forest types reflects the legacy of forest densification and simultaneous shift in species composition. Similar increases in shade-tolerant species composition have been observed across western forests, contributing to landscape homogeneity and scale of stand-replacing fire (Miller et al., 2009).

Inspection of the NMS output further links the Mixed Conifer to the Low-elevation Fir forest type. NMS visually illustrates the multivariate shrub and seedling community relationships among the landscape's 12 strata (Fig. 5). Although species data appears to be better manifested on the vertical dimension, apparently ranked by proportion of *Abies* spp., greatest distinction between burn severities is evident as a result of woody shrub abundance as exemplified by dimension 2. The most salient observation is that the distances between Medium- and High-severity strata in both the Low-elevation Fir and the Mixed Conifer forests are the largest differences within each forest type pathway. The obvious trend demonstrates the marked shift in community-level shrub and conifer relationships. A similar trend was found in a post-fire Florida pine scrub community (Freeman and Kobziar, 2011), though the study suggested that vegetation communities in Medium- and High-severity strata become more similar over time. In another time-series study, five-year composition shifts in *Darlingtonia* fens in the Klamath Mountains were observed to vary more without fire and stabilize with burning (Jules et al., 2011). Although we did not conduct a time-series study, the normalizing

**Table 5**
Woody shrub vegetation observed a decade after the 2000 Storrie Fire, Lassen National Forest. Dominant species listed with percent composition of total shrub cover observed within strata (species covering < 1% of all strata omitted).

| Forest type | Burn severity | Mean cover (%) | Mean height (m) | Species[a] | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | ALIN | ARNE | ARPA | CECO | CEIN | CEPR | CEVE | CHSE | CONU | NODE | PREM | QUCH | QUVA | SASP |
| *Mean percent cover* | | | | | | | | | | | | | | | | | |
| Mixed | Unchanged | 7.8 | 0.43 | 0.0 | 0.0 | 2.5 | 0.0 | 0.0 | 0.1 | 0.0 | 0.7 | 2.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| conifer | Low | 13.1 | 0.49 | 0.0 | 0.0 | 0.2 | 3.3 | 3.6 | 0.1 | 0.0 | 2.6 | 0.6 | 0.9 | 0.0 | 0.0 | 0.5 | 0.0 |
| | Medium | 14.9 | 0.70 | 0.0 | 0.0 | 1.1 | 2.7 | 4.4 | 0.2 | 0.0 | 1.3 | 0.4 | 0.0 | 0.0 | 1.6 | 0.3 | 0.0 |
| | High | 59.0 | 1.34 | 0.0 | 0.0 | 3.3 | 9.3 | 27.0 | 0.6 | 9.5 | 0.1 | 1.3 | 3.9 | 0.9 | 0.0 | 2.2 | 0.2 |
| Low- | Unchanged | 2.9 | 0.27 | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.3 | 0.0 |
| elevation | Low | 8.5 | 0.43 | 2.5 | 0.0 | 0.1 | 2.1 | 0.1 | 0.0 | 0.1 | 1.2 | 0.1 | 0.0 | 0.0 | 0.0 | 0.4 | 0.2 |
| fir | Medium | 15.9 | 0.55 | 0.0 | 0.0 | 3.0 | 4.8 | 2.9 | 0.0 | 2.0 | 1.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.6 | 0.0 |
| | High | 62.5 | 1.01 | 0.0 | 0.0 | 3.6 | 30.3 | 11.5 | 1.8 | 7.5 | 2.8 | 0.0 | 0.0 | 1.1 | 0.0 | 3.0 | 0.1 |
| High- | Unchanged | 9.9 | 0.15 | 0.0 | 6.1 | 0.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 2.2 | 0.0 |
| elevation | Low | 4.2 | 0.15 | 0.0 | 2.8 | 0.0 | 0.3 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.6 | 0.0 |
| fir | Medium | 20.1 | 0.52 | 0.1 | 4.2 | 0.2 | 0.2 | 0.0 | 0.0 | 4.0 | 0.4 | 0.0 | 0.0 | 0.0 | 0.0 | 6.6 | 1.3 |
| | High | 36.0 | 0.70 | 0.0 | 4.3 | 2.7 | 1.9 | 0.0 | 0.0 | 8.8 | 0.8 | 0.0 | 0.2 | 0.4 | 0.0 | 15.8 | 0.1 |

[a] Key to species codes: ALIN, *Alnus incana*; ARNE, *Arctostaphylos nevadensis*; ARPA, *A. patula*; CECO, *Ceanothus cordulatus*; CEIN, *C. integerrimus*; CEPR, *C. prostratus*; CEVE, *C. velutinus*; CHSE, *Chrysolepis sempervirens*; CONU, *Cornus nuttallii*; NODE, *Notholithocarpus densiflorus*; QUCH, *Quercus chyrsolepis*; QUVA, *Q. vaccinifolia*; SASP, *Salix* spp.

effect of fire in these two studies may support the trend evident in the NMS analysis of the Storrie Fire data. Although NMS is most commonly used as a data exploration method, this analysis notably confirms analogous vegetation responses after stand-replacing fire in the Mixed Conifer and Low-elevation Fir forests, affirming the stabilizing effect of severe fire in California's forested ecosystems, which is primarily a curtailing of conifer seedling regeneration and a drastic increase of woody shrub cover. The overwhelming effect of fire severity on vegetation type conversion emphasizes the legacy that a High-severity disturbance can leave on the landscape.

Currently, *A. concolor* is dominating conifer regeneration in our study area's Mixed Conifer and Low-elevation Fir forests. *Abies concolor* was observed to be the most abundant seedling species even on sites that we believed to be the most conducive to *Pinus* spp. regeneration, i.e., MCHS and LFHS. It appears that large-scale High-severity burns in the wake of fire exclusion have the potential to further shift landscape dominance away from *Pinus* spp. toward shrubs or shade-tolerant conifers capable of growing through overtopping hardwood and shrub cover (Gray et al., 2005; Cocking et al., 2011). Given continued fire exclusion and management inactivity in low elevation forest types, the shade-tolerant and fire-intolerant *A. concolor* may have the competitive advantage and will likely emerge dominant as it is the Clementsian climax vegetation (Moghaddas et al., 2008). Alternatively, large pines, oaks or shrub fields at the lower elevation sites within the Storrie Fire are the "alternative community state" to the Clementsian climax (Odion et al., 2010), steady-state communities maintained by fire. Increase of fire-tolerant pine (i.e., *P. jeffreyi*, *P. lambertiana*, and *P. ponderosa*) and fire-facilitated *Q. kelloggii* would shift forest composition towards a more fire-resilient community, yet this process may be confounded by abundant *A. concolor* regeneration observed in our study area after the Storrie Fire (similarly, Beaty and Taylor (2008) and Zald et al. (2008)). Mosaics of artificial regeneration with shrub control may allow fire-resilient species to reclaim such sites.

While fire-vegetation and succession models have been developed for many western ecosystems, the complexity caused by decades of fire exclusion and subsequent large wildfires may confound our comprehension of tolerant–intolerant vegetation dynamics. In an era of warmer temperatures and longer drought periods with an increase of large fires (Westerling et al., 2005; Miller et al., 2009) further research in pine-fir successional relationships can guide action to promote more resilient forests, per management objective. Community shifts observed after the Storrie Fire may be commonplace to post-fire southern Cascades and northern Sierra Nevada montane ecosystems while the broader patterns observed may be relevant to many other fire-excluded temperate forests that burn with mixed-severities.

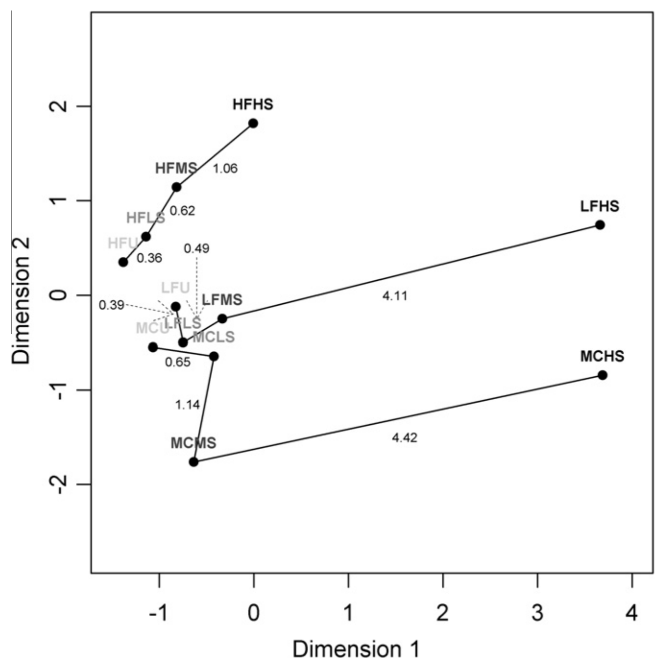


**Fig. 5.** Non-metric Multidimensional Scaling (NMS) of community-level species data across 12 strata, i.e. four burn severities by three forest types, a decade after the Storrie Fire in Lassen National Forest. Axis and distance units are in Mahalanobis distance. Lines drawn into visualize burn severity pathways within a forest type. The first two letters of each symbol represent forest type (HF = High-elevation Fir; LF = Low-elevation Fir; MC = Mixed Conifer) while the last letters represent burn severity (U = Unchanged; LS = Low-severity; MS = Medium-severity; HS = High-severity).

## Acknowledgements

Support for this paper was provided by the Lassen National Forest, Almanor Ranger District. Data collection was performed by USDA PSW-Redding's Vegetation Dynamics team. C. Edgar, P. Berrill, and two anonymous reviewers provided thoughtful comments in the formulation of the final manuscript.

## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2012.09.022.

## References


Agee, J.K., 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington, DC.

Beaty, R.M., Taylor, A.H., 2001. Spatial and temporal variation of fire regimes in a mixed conifer forest landscape, Southern Cascades, California. USA J. Biogeog. 28, 955–966.

Beaty, R.M., Taylor, A.H., 2008. Fire history and the structure and dynamics of a mixed conifer forest landscape in the northern Sierra Nevada, Lake Tahoe Basin, California. USA For. Ecol. Manage. 225, 707–719.

Beckage, B., Stout, I.J., 2000. Effects of repeated burning on species richness in a Florida pine savanna: a test of the intermediate disturbance hypothesis. J. Veg. Sci. 11, 113–122.

Bock, C.E., Bock, J.H., 1977. Patterns of post-fire succession on the Donner Ridge burn, Sierra Nevada. In: Mooney H.A., Conrad, C.E. (Tech. Coords.), Proceedings of the Symposium on the Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems. USDA For. Serv. Gen. Tech. Rep. WO-3, pp. 464–469.

Bonnet, V.H., Schoettle, A.W., Shepperd, W.D., 2005. Postfire environmental conditions influence the spatial pattern of regeneration for *Pinus ponderosa*. Can. J. For. Res. 35, 37–47.

Broncano, M.J., Retana, J., Rodrigo, A., 2005. Predicting the recovery of *Pinus halepensis* and *Quercus ilex* forests after a large wildfire in northeastern Spain. Plant Ecol. 180, 47–56.

Chappell, C.B., Agee, J.K., 1996. Fire severity and tree seedling establishment in *Abies magnifica* forests, southern Cascades. Oregon. Ecol. Appl. 6, 628–640.

Cocking, M.I., Varner, J.M., Sherriff, R.L., 2011. California black oak responses to fire severity and native conifer encroachment in the Klamath Mountains. For. Ecol. Manage. 270, 25–34.

Conard, S.G., Jaramillo, A.E., Cromack, K.J., Rose, S., 1985. The Role of the Genus *Ceanothus* in Western Forest Ecosystems. USDA Forest Service, General Technical Report PNW-GTR-182, Washington, DC.

Donato, D.C., Fontaine, J.B., Campbell, J.L., Robinson, W.D., Kauffman, J.B., Law, B.E., 2006. Post-wildfire logging hinders regeneration and increases fire risk. Science 311, 351.

Donato, D.C., Fontaine, J.B., Campbell, J.L., Robinson, W.D., Kauffman, J.B., Law, B.E., 2009. Conifer regeneration in stand-replacement portions of a large mixed-severity wildfire in the Klamath-Siskiyou Mountains. Can. J. For. Res. 39, 823–838.

Eyre, F.H, 1980. Forest Cover Types. Society of American Foresters, Washington, DC.

Freeman, J.E., Kobziar, L.N., 2011. Tracking postfire successional trajectories in a plant community adapted to high-severity fire. Ecol. Appl. 21, 61–74.

Fried, J.S., Gilless, J.K., Riley, W.J., Moody, T.J., Simon de Blas, C., Hayhoe, K., Moritz, M., Stephens, S., Torn, M., 2008. Predicting the effect of climate change on wildfire behavior and initial attack success. Climatic Change 87 (Suppl. 1), 251–264.

Gray, A.N., Zald, H.S.J., Kern, R.A., North, M., 2005. Stand conditions associated with tree regeneration in Sierran mixed-conifer forests. For. Sci. 51, 198–210.

Harrington, M.G., Kelsey, R.G., 1979. Influence of Some Environmental Factors on Initial Establishment and Growth of Ponderosa Pine Seedlings. USDA Forest Service, Research Paper INT-230, Ogden, UT.

Hogg, E.H., Wein, R.W., 2005. Impacts of drought on forest growth and regeneration following fire in southwestern Yukon, Canada. Can. J. For. Res. 35, 2141–2150.

Jules, E.S., Ellison, A.M., Gotelli, N.J., Lillie, S., Meindl, G.A., Sanders, N.J., Young, A.N., 2011. Influence of fire on a rare serpentine plant assemblage: a 5 year study of *Darlingtonia* fens. Am. J. Bot. 98, 801–811.

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

Keeley, J.E., Davis, F.W., 2000. Chaparral. In: Barbour, M.G., Keeler-Volf, T., Schoenherr, A.A. (Eds.), Terrestrial Vegetation of California. University of California Press, Berkeley, CA, pp. 339–366.

Manly, B.F.J., 2005. Multivariate Statistical Methods: A Primer. Chapman & Hall, New York, NY.

McDonald, P.M., 1976a. Forest Regeneration and Seedling Growth from Five Major Cutting Methods in North-Central California. USDA Forest Service, Research Paper PSW-115, Berkeley, CA.

McDonald, P.M., 1983. Clearcutting and Natural Regeneration Management Implications for the Northern Sierra Nevada. USDA Forest Service, General Technical Report PSW-70, Berkeley, CA.

McDonald, P.M., 1990. Quercus kelloggii Newb. In: Burns, R.M., Honkala, B.H. (Eds.), Silvics of North America: Hardwoods, vol. 2. USDA For. Ser. Agric. Handb. No. 654.

McDonald, P.M., Tappeiner, J.C., 1996. Silviculture-ecology of forest-zone hardwoods in the Sierra Nevada. In: Sierra Nevada Ecosystem Project: Final Report to Congress: Assessments and Scientific Basis for Management Options. Water Resources Center Rep. 37, Centers for Water and Wildland Resources, vol. II. University of California, Davis, CA, pp. 621–636.

McIntire, E.J., Duchesneau, R., Kimmins, J.P., 2005. Seed and bud legacies interact with varying fire regimes to drive long-term dynamics of boreal forest communities. Can. J. For. Res. 35, 2765–2773.

McKenzie, D., Gedalof, Z., Peterson, D.L., Mote, P., 2004. Climatic change, wildfire and conservation. Conserv. Biol. 18, 890–902.

Miller, J.D., Knapp, E.E., Key, C.H., Skinner, C.N., Isbell, C.J., Creasy, R.M., Sherlock, J.W., 2008. Calibration and validation of the relative differenced normalized burn ratio (RdNBR) to three measures of fire severity in the Sierra Nevada and Klamath Mountains, California. USA Remote Sens. Environ. 113, 645–656.

Miller, J.D., Safford, H.D., Crimmins, M., Thode, A.E., 2009. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and Southern Cascade Mountains, California and Nevada. USA Ecosystems 12, 16–32.

Moghaddas, J.J., York, R.A., Stephens, S.L., 2008. Initial response of conifer and California black oak seedlings following fuel reduction activities in a Sierra Nevada mixed conifer forest. For. Ecol. Manage. 255, 3141–3150.

Nagel, T.A., Taylor, A.H., 2005. Fire and persistence of montane chaparral in mixed conifer forest landscapes in the northern Sierra Nevada, Lake Tahoe Basin, California. USA J. Torrey Bot. Soc. 132, 442–457.

National Climatic Data Center. 2011. Climate Indices: Palmer Drought Severity Index. <http://ncdc.noaa.gov> (accessed 03.06.11).

Odion, D.C., Moritz, M.A., DellaSala, D.A., 2010. Alternative community states maintained by fire in the Klamath Mountains. USA J. Ecol. 98, 96–105.

Pielou, E.C., 1966. Species-diversity and pattern-diversity in the study of ecological succession. J. Theor. Biol. 13, 131–144.

PRISM Climate Group. 2011. Time Series Analysis. <http://www.prism.oregonstate.edu> (accessed 03.06.11).

Reineke, L.H., 1933. Perfecting a stand density index for even-aged forests. J. Agric. Res. 46, 627–638.

Schwilk, D.W., Keeley, J.E., Bond, W.J., 1997. The intermediate disturbance hypothesis does not explain fire and diversity pattern in fynbos. Plant Ecol. 132, 77–84.

Sessions, J.P., Bettinger, R., Buckman, M.Newton., Hamann, J., 2004. Hastening the return of complex forests following fire: the consequences of delay. J. Forest. 102, 38–45.

Shatford, J.P.A., Hibbs, D.E., Puettmann, K.J., 2007. Conifer regeneration after forest fire in the Klamath-Siskiyous: how much, how soon? J. Forest. 105, 139–146.

Skinner, C.N., Chang, C., 1996. Fire regimes, past and present. In: Sierra Nevada Ecosystem Project: Final report to Congress: Assessments and scientific basis for management options. Water Resources Center Rep. 37, Centers for Water and Wildland Resources, vol. II. University of California, Davis, CA, pp. 1041–1069.

Skinner, C.N., Taylor, A.H., 2006. Southern Cascades bioregion. In: Sugihara, N.G., van Wagtendonk, J.W., Shaffer, K.E., Fites-Kaufman, J., Thode, A.E. (Eds.), Fire in California's Ecosystems. University of California Press, Berkeley, CA, pp. 195–224.

Smith, D.M., Larson, B.C., Kelty, M.J., Ashton, P.M.S., 1997. The Practice of Silviculture. John Wiley and Sons, New York, NY.

Soil Survey Staff, 2011. USDA NRCS. Soil Survey Geographic (SSURGO) database for Lassen National Forest, CA. <http://soildatamart.nrcs.usda.gov> (accessed 03.06.11).

Stage, A.R., 1976. An expression for the effect of aspect, slope and habitat type on tree growth. For. Sci. 22, 457–460.

Stuart, J.D., Grifantini, M.C., Fox III, L., 1993. Early successional pathways following wildfire and subsequent silvicultural treatment in Douglas-fir/hardwood forests, NW California. For. Sci. 39, 561–572.

Sugihara, N.G., Barbour, M.G., 2006. Fire and California vegetation. In: Sugihara, N.G., van Wagtendonk, J.W., Shaffer, K.E., Fites-Kaufman, J., Thode, A.E. (Eds.), Fire in California's Ecosystems. University of California Press, Berkeley, CA, pp. 195–224.

Tappeiner, J.C., 1980. Sierra Nevada mixed conifer. In: Eyre, F.H. (Ed.), Forest Cover Types. Society of American Foresters, Washington, DC.

The R Foundation, 2011. R version 2.11.0. <http://www.r-project.org/index.html> (accessed 06.06.11).

Turner, M.G., Romme, W.H., Gardner, R.H., Hargrove, W.W., 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecol. Monogr. 67, 411–433.

Turner, M.G., Romme, W.H., Gardner, R.H., 1999. Prefire heterogeneity, fire severity, and early postfire plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. Int. J. Wildl. Fire 9, 21–36.

USDA, 1987. Forest Service Handbook: Silvicultural Practices Handbook, R-5 FSH 9/87. USDA Forest Service, Washington, DC (Chapter 40).

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S. Springer Science+Business Media, New York, NY.

Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2005. Warming and earlier spring increase western US forest wildfire activity. Science 313, 940–943.

Zald, H.S.J., Gray, A.N., North, M., Kern, R.A., 2008. Initial tree regeneration responses to fire and thinning treatments in a Sierra Nevada mixed-conifer forest. USA For. Ecol. Manage. 256, 168–179.