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

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**Abstract**

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

# ****Introduction****

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

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

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

These communities are composed of species that are highly tolerant of severe disturbance by fire, and display varying adaptive strategies that allow for post-fire dominance through rapid recolonization and regeneration. These adaptations include vigorous sprouting after top-kill in fire, for which plants rely on below-ground carbohydrate reserves, often stored in lignotubers (Keeley and Zedler 1978, Odion and Davis 2000). Other species experience fire-stimulated germination of long-lived seeds stored in the seedbank (Wells 1969, Keeley 1991). These species have been categorized as “fire-endurers” or “fire resisters” and “fire-evaders” or “fire-recruiters”, respectively (Rowe 1983, Kauffman and Martin 1990, Keeley 1991). For analysis of post-fire impacts, chaparral species are often grouped into these two rough categories. However, many species rely on differential regeneration strategies that are dependent on fire intensity, eluding easy categorization. [more about fire-adaptive strategies? Name species?]

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

Methods Green indicates copied from cbo ms (for now)

Study Area

Our plots were randomly located within the intersection of two wildfires that occurred in the Lassen National Forest in northern California, USA. . The Storrie Fire burned 23,000 ha in 2000, and the Chips Fire burned approximately 30,000 ha, including a portion of the Storrie Fire footprint, 12 years later. The 9,900 ha reburn area that resulted was the focus of this study. Both wildfires burned at a mix of severities, allowing sampling across a spectrum of combined burn severity strata. Data collection occurred in the summer of 2015, three years after the Chips Fire, and 15 years after the Storrie Fire.

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

Field Sampling

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

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

Data analysis

**Indicator species analysis (Dufrêne and Legendre 1997) using the multipatt function of the indicspecies package in R (cite).**

Non-metric Multidimensional Scaling (**NMDS) was employed to reduce dimensionality and examine patterns present in the data in ordination space. A matrix of Bray-Curtis distance measures was created, based on relative percent cover values of more common mid-story species (present in at least 5% of plots). These values were used in order to account for differences in number of growing season following each fire event (15 years post Storrie Fire and 3 years post Chips Fire). This process was conducted in R using the metaMDS function available in the vegan package (okasen), with a maximum of 100 iterations.**

* **Vectors of predictor variables added using envfit in R (R Core Team 2015)**

**PERMANOVA of effect of continuous fire severity indice (RdNBR) for each fire on species composition**

**Results**

Indicator species analysis: ALL 16 SEVERITY COMBINATIONS

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

Multilevel pattern analysis

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Association function: IndVal.g

Significance level (alpha): 0.05

Total number of species: 12

Selected number of species: 6

Number of species associated to 1 group: 6

List of species associated to each combination:

Group high/high #sps. 1

A B stat p.value Indicator Value

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

Group high/un #sps. 1

A B stat p.value

CEVE 0.5361 0.1667 0.299 0.805

Group low/low #sps. 2

A B stat p.value

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

CEPR 0.4685 0.3333 0.395 0.603

Group mod/low #sps. 1

A B stat p.value

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

Group mod/un #sps. 2

A B stat p.value

ARPA 0.3472 0.5000 0.417 0.236

PIPO 0.7462 0.1667 0.353 0.898

Group un/low #sps. 2

A B stat p.value

RIRO 0.2853 0.6000 0.414 0.360

SYMO 0.3719 0.4000 0.386 0.241

Group un/mod #sps. 1

A B stat p.value

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

Group un/un #sps. 2

A B stat p.value

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

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

Indicator species analysis WITH 9 COMBINATIONS, incl. UN, (LOW+MOD)=LOW, HIGH

> cov.ind <- multipatt(cover2, cluster = cat, control = how(nperm = 99), duleg = T)

Multilevel pattern analysis

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Association function: IndVal.g

Significance level (alpha): 0.05

Total number of species: 12

Selected number of species: 5

Number of species associated to 1 group: 5

List of species associated to each combination:

Group high/high #sps. 1 Ind Value

A B stat p.value

**CECO 0.3661 0.8333 0.552 0.02 \* 31**

Group low/low #sps. 1

A B stat p.value

**QUKE 0.4800 0.6364 0.553 0.04 \* 31**

Group un/high #sps. 1

A B stat p.value

**CEIN 0.2462 1.0000 0.496 0.01 \*\* 25**

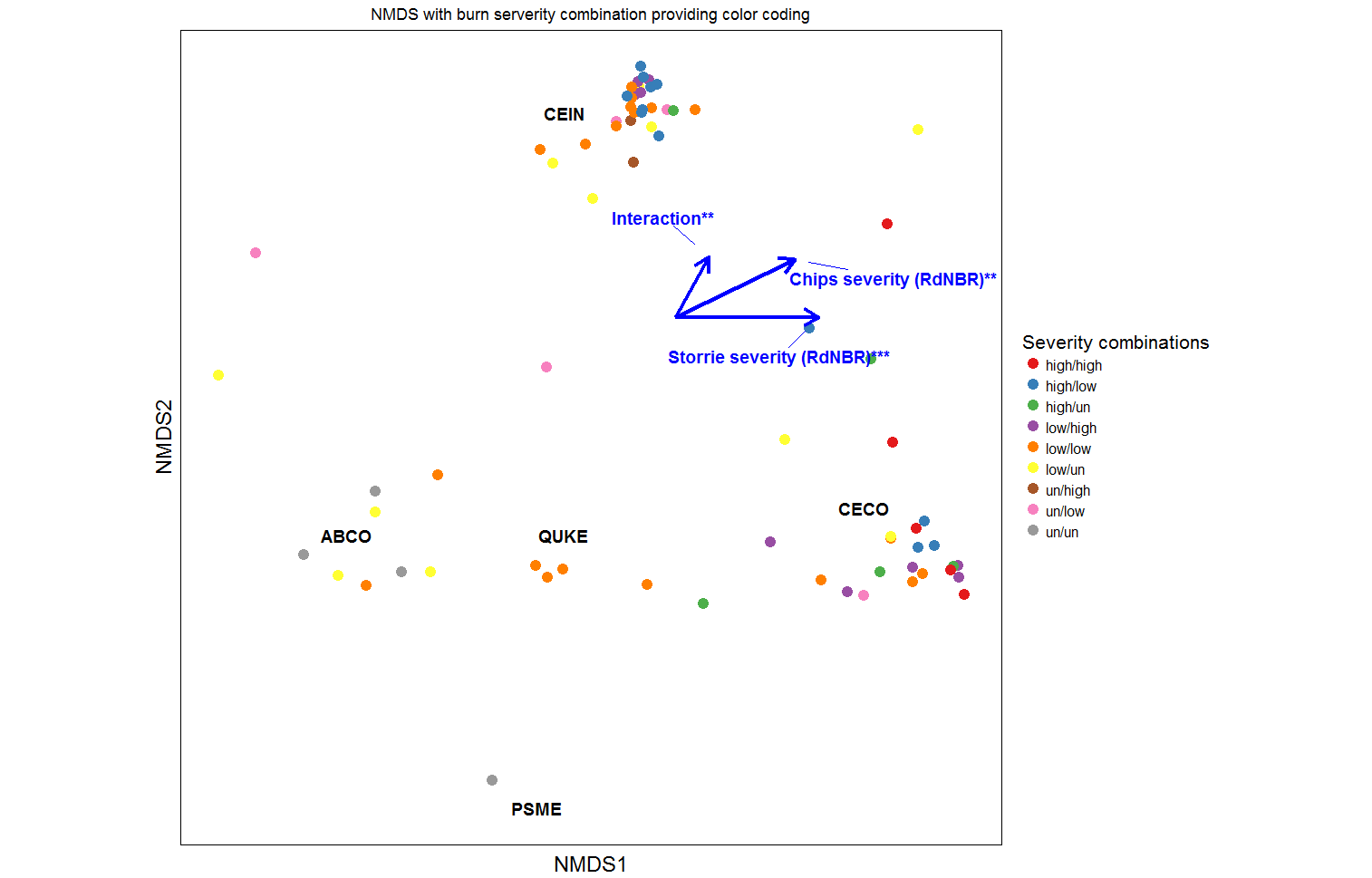
Group un/un #sps. 2

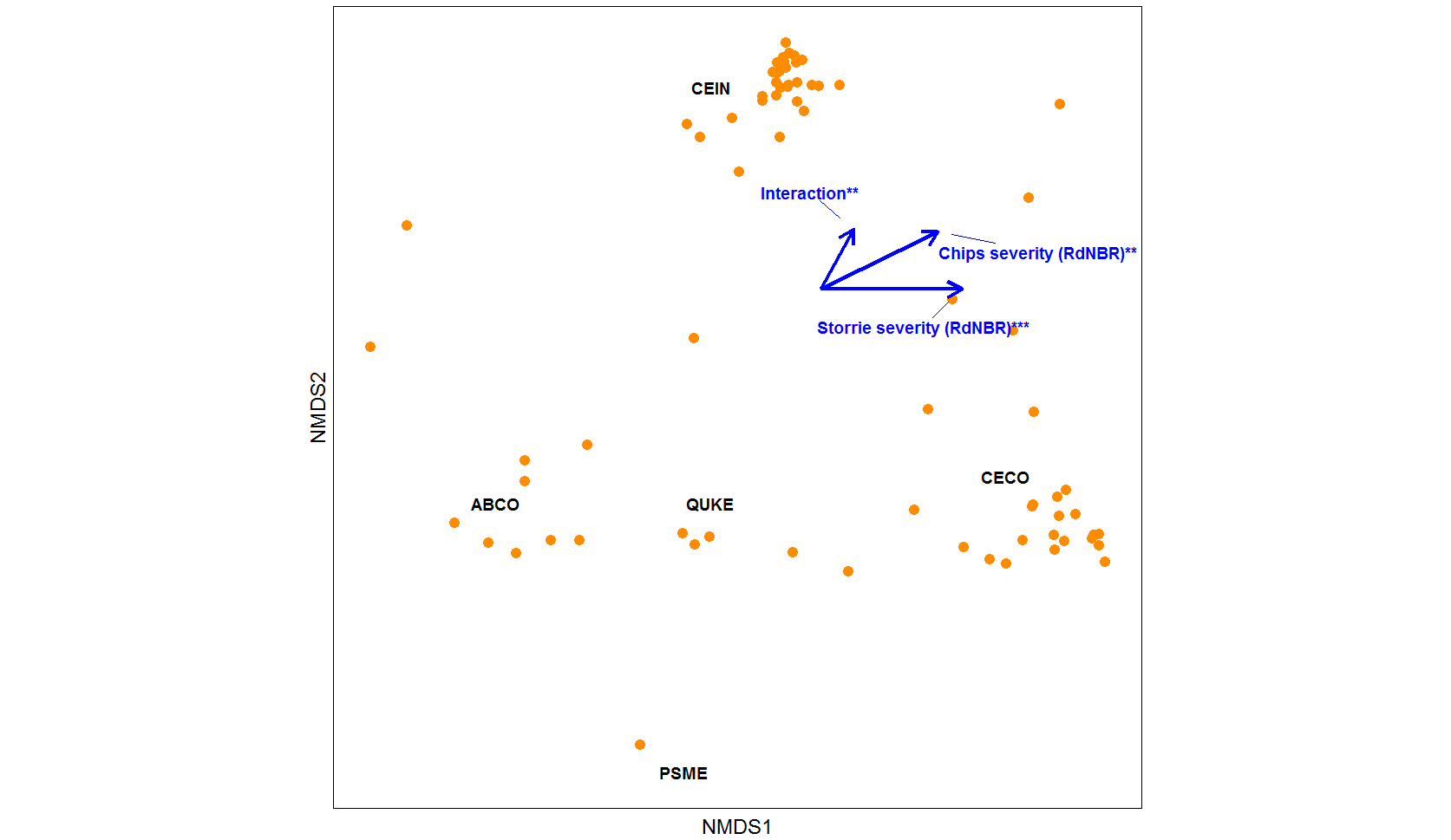
A B stat p.value

**ABCO 0.6038 0.7500 0.673 0.02 \* 45**

**PSME 0.8943 0.5000 0.669 0.01 \*\* 44**

PCA of RdNBR values for both fires yielded two orthogonal axes : PC1 is correlated with overall fire severity, PC2 is related to the differences between the fires. These, along with the original RdNBR values, were plotted as vectors onto an NMDS of the cover data. Species codes indicate dominant species of plots in distinct groupings. Colors represent 9 severity combinations.





Permanova examining influence of continuous severity on species matrix:

Call:

adonis(formula = cover2 ~ cover$storrie\_rdnbr \* cover$chips\_rdnbr)

Permutation: free

Number of permutations: 999

Terms added sequentially (first to last)

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

cover$storrie\_rdnbr 1 2.1334 2.13336 7.6264 0.07180 0.001 \*\*\*

cover$chips\_rdnbr 1 1.9175 1.91751 6.8548 0.06453 0.001 \*\*\*

cover$storrie\_rdnbr:cover$chips\_rdnbr 1 1.3260 1.32597 4.7401 0.04462 0.002 \*\*

Residuals 87 24.3368 0.27973 0.81904

Total 90 29.7136 1.00000

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

Nesting Storrie severity inside of Chips severity:

Call:

adonis(formula = cover2 ~ chip + sto %in% chip)

Permutation: free

Number of permutations: 999

Terms added sequentially (first to last)

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

chip 1 2.0786 2.07860 7.0957 0.06995 0.001 \*\*\*

chip:sto 1 1.8564 1.85642 6.3372 0.06248 0.002 \*\*

Residuals 88 25.7786 0.29294 0.86757

Total 90 29.7136 1.00000

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

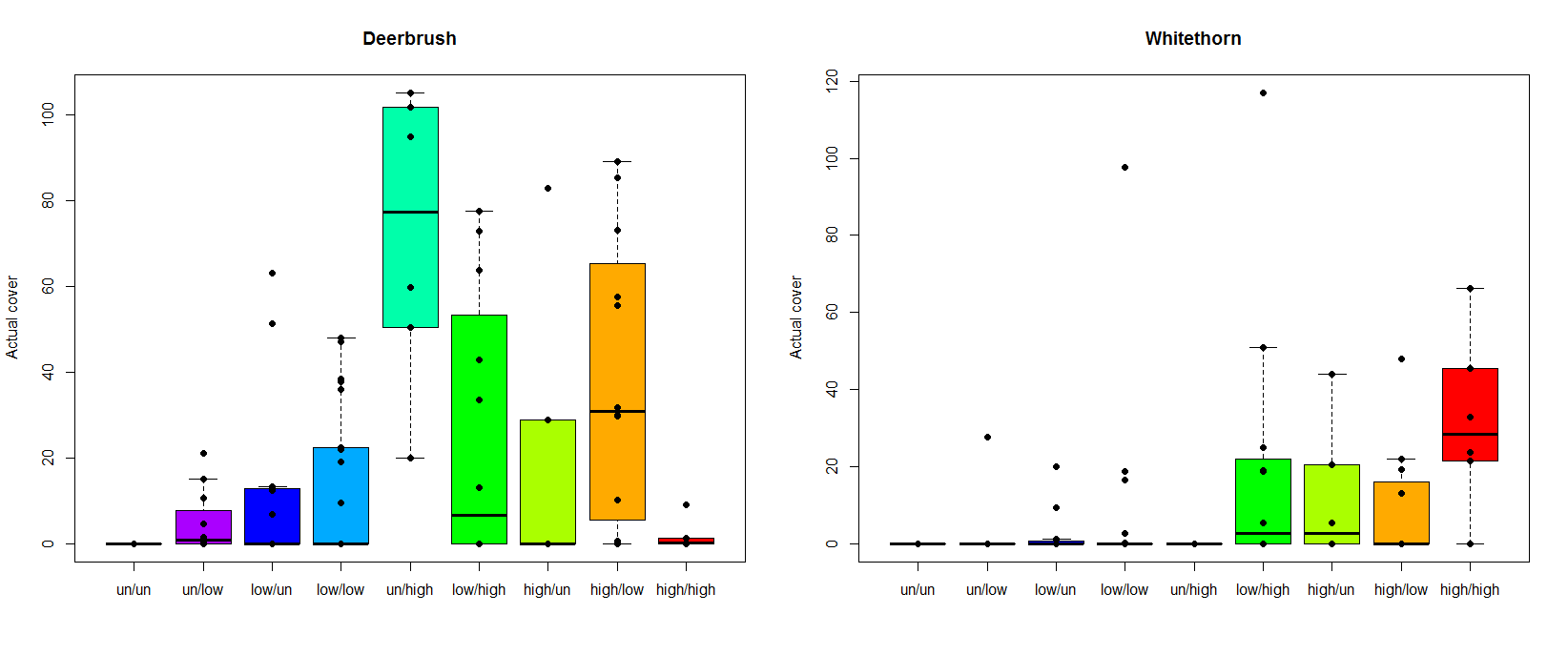
**Results - text**

Indicator species analysis (using 9 combinations) resulted in significant correlations for 5 species and 4 severity combinations (Table X). Whitethorn was associated with successive high severity burns, while deerbrush had a greater affinity for the unburned/high severity combination. While neither indicator value was very high, both species showed a high fidelity to their respective groups, occurring in most or all of plots in these categories. Higher indicator values were obtained for Douglas-fir and white fir seedlings and saplings, which had high affinity for sites unburned in either fire. Black oak seedlings were associated with successive low-severity burns. Does low/unbalanced replication per combination undermine these results?

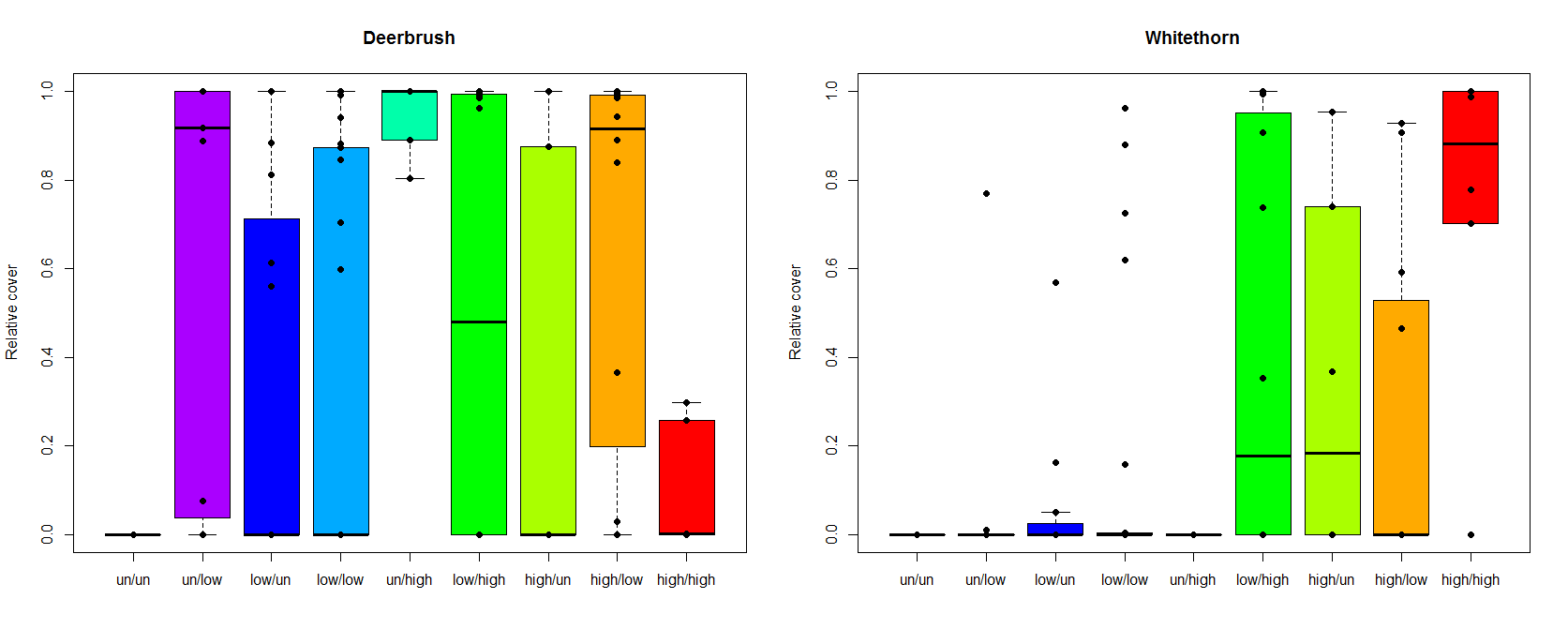
Results of a PERMANOVA testing effects of continuous burn severity indices for each fire on community composition were significant for each of the main effects as well as their interaction. Nesting of factors revealed that the effects of burn severity for the Chips Fire were dependent on levels of burn severity in the Storrie Fire. -- How should I analyze the interactive effects?

NMDS ordination of relative percent cover values for each species yielded a three-dimensional solution with a stress of 0.08 after 34 runs. Plots showed strong clustering patterns in the ordination, based largely on dominance of five species (CEIN, CECO, PSME, ABCO and QUKE) in those plots, and influenced by RdNBR values for both fires (Figure X).

Plots of CEIN and CECO actual cover (not relative % cover) for 9 combinations:



Same with relative % cover:



# Discussion

* Species composition changes relative to fire severity combination in reburns
* Likely that fire-adaptive strategy employed by each species is driving plant community outcomes – evaders (seeding) vs. endures (sprouting) vs. avoiders
* Implications for reburn severity and risk depend on flammability of resulting communities – not much work done here
* Possible that most flammable species are those that prosper under high-high scenario – self-reinforcing adaptive strategy that results in positive feedback
* Implications for tree regeneration – overstory species not resilient to high-severity reburns (avoiders psme & abco fidelity with un/un, resister pila with mod/low)
* Compositional patterns may change with time since fire, longer-term studies needed
* Initial condition (esp. seedbanks) would clearly be important to post-reburn outcomes, but were not classified in this study.
  + However, most stands were conifer-dominated (had not burned for 100 years) and likely homogenous based on post-fire assessments, aerial photography, and communication with local FS staff
  + Other authors have noted proliferation and long-term persistence of many chaparral species in seedbanks of the region (Cronemiller 1959, Quick and Quick 1961, Knapp et al. 2012)
* Natural regeneration by conifers impeded in reburns of higher severity (seed banks eliminated, seed sources, too) (Nagel and Taylor 2005)

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