Post-Cedar Fire Mixed Conifer-Hardwood Monitoring at Cuyamaca Rancho State Park, San Diego, California

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Final Report

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Executive Summary – Findings and Recommendations

The 2003 Cedar Fire burned extensive forested areas of the Cuyamaca Mountains in the Peninsula Ranges of San Diego County, CA, USA. This large fire severely affected these forests. The purpose of this study was to examine the effect of the heterogeneity of both the landscape and disturbance on patterns of post-fire vegetation dynamics. An earlier project (Agreement C0443021) reported that conifer mortality in Cuyamaca Rancho State Park (CRSP) was extremely high and positively related to fire severity, and that early post-fire vegetation dynamics during the first two growing seasons were dominated by the establishment of abundant and diverse native herbs (including fire-obligates) as well as shrub seedlings, and resprouting by shrubs and oak trees. This project reports on the analysis of data from 38 vegetation monitoring plots in West and East Mesas resurveyed in May-June 2007, the fourth post-fire growing season. Vegetation changes in the first four years following a large, severe crown fire in Coulter pine and mixed conifer forests are described.

1.   Areas with high cover of *Ceanothus* shrubs

Dense shrub cover, primarily *Ceanothus palmeri*, has established on about 40% of the area surveyed, especially in stands with higher former forest cover and fire severity. About half of these stands had lower shrub cover, averaging 32%, and half had high cover, averaging 70%.

On a landscape scale I recommend no vegetation management of *C. palmeri* dominated stands. *Ceanothus* is a nitrogen fixing genus of California shrubs that serves an important ecosystem function, especially following fire on low-nutrient soils in California's montane forests. These shrub stands will naturally thin over time, resulting in lower, patchier cover, and allowing establishment of conifers.

Site-specific removal of shrubs over small areas may be required for tree planting projects, but the disadvantage of *Ceanothus* removal, again, is that it may affect the availability of nutrients for successful tree establishment. *Ceanothus* is also known to be an intermediate host for mycorrhyzal fungi associated with conifer species and necessary for their survival.

In the stands examined that fell at lower elevations in the forested zone (1300-1400 m), shrub cover averaged around 60% and chaparral species dominated vegetation recovery, especially *Ceanothus leucodermis*. Again, *Ceanothus* plays an important nutrient cycling role post-fire in California ecosystems. These sites appear to be following a normal trajectory of succession for chaparral-dominated sites. There is no indication that vegetation management is required.

2.   Areas with high cover of invasive, exotic annual grasses and forbs

By 2007, 4 years after the Cedar Fire, exotic annual brome grasses (*Bromus* spp.) and a mustard, *Sisymbrium altissimum*, were the most abundant herbaceous species in the areas surveyed. Forested areas of CRSP are interspersed with dry meadows (grasslands) with a history of grazing, and the most abundant brome species have been established there for at least a century. *Bromus tectorum*, in particular, has been observed to invade following fire in low elevation pine forest. Therefore, it is not surprising that these species were found in abundance following a stand-replacing crown fire. Concerns that are raised, however, are: what is the impact of high exotic herbaceous cover on 1) native herbs, and 2) conifer regeneration? In other words, is there a negative impact on native biodiversity and natural patterns of succession?

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Although it is disheartening to see plant diversity dominated by exotic species, I think it is unlikely for these exotic Eurasian grasses to lead to altered fire regimes or type conversion, as has been found elsewhere in sagebrush ecosystems. These grasses are dependent on dispersal in order to establish in forested areas following disturbance because they do not have persistent seed banks. They did not reach potential establishment sites in abundance during the first post-disturbance year, when most resources are available, owing to dispersal limitation. Because of this, they had little impact on the post-fire annuals and bulbs that are a significant component of biodiversity in this forest community. They are shade-intolerant, and therefore I predict that they will not persist in such great abundance in these sites after 5-10 years as the woody canopy closes. Given their temporal and spatial patterns of establishment, they have the greatest potential impact native perennials and opportunistic annuals. They are also likely to re-invade, but only during the same time window (2-10 years after fire), given the proximity of propagule pools, the dry meadows found in the mountains where non-native grasses have long been established. If *Sisymbrium altissimum* forms a persistent seed bank it could have a greater impact on native plant communities.

I do not know of any practical means to remove these exotic annuals on a landscape scale. Fire has shown to be a particularly ineffective tool for controlling these species, because it tends to promote their establishment (especially low intensity prescribed fire that does not kill seed banks). It fact, one of the biggest challenges to re-establishing fire in western forests is the threat of invasive species. They are likely to persist in these forests, given their establishment in the grasslands (dry meadows) that are interspersed with forest at CRSP, but occur primarily in a short temporal window following fire, after the native post-fire flora has flourished, and before woody cover has re-established. It is not known to what extent exotic annuals interferes with conifer establishment. This will be discussed in the next report (C0643016). Anecdotally, pines are establishing in grass-dominated areas. But it is not known if the amount of conifer establishment would be greater in the absence of competition from exotic annuals.

3. Conifer Regeneration

Conifer seedlings or saplings (established post fire) are so sparse in the study area that even 40 stands, comprising 160 314-m2 circular plots that were thoroughly searched, turned up very few seedlings (five in 2004 and 36 in 2007). We felt that this was not adequate to estimate their density. A more thorough, park-wide survey of pine regeneration is ongoing under Interagency Agreement C0643016, and by 2008, it was evident that some conifer establishment has occurred, almost all of it Coulter Pine. About 700 pine juveniles were recorded in 1250 2000-m^2 quadrats (a total of about 25 ha searched), for an average density of about 28 juvenile pines per ha. Given that most of the forest in CRSP was Coulter Pine-dominated, this indicates that there is some natural forest regeneration occurring, albeit slowly.

Further, as previously reported, incense cedar was observed to regenerate in dense patches of small seedlings in 2005 in one out of 40 stands that experienced low burn severity and retained living adult incense cedar (Franklin et al. 2006). This was also observed elsewhere in the Park in 2007, for example in the Azalea Glen area, and on Middle Peak. Additionally, sugar pine seedlings were found in 16 (1.3%) of the quadrats in 2007. This suggests that to claim that mixed conifer forest has been "extirpated" in CRSP (Goforth and Minnich 2008) may be overstated. However, the potential reestablishment of mixed conifer forest on the highest peaks of CRSP is likely to be very slow, limited in extent, and compromised by future fires and climate change. This will be discussed more thoroughly in a future report (C0643016).

4. Monitoring Recommendations

The established monitoring stands are an excellent framework for long term monitoring of post-fire vegetation succession. I recommend that the stands be resurveyed at 3-5 year intervals in the absence of fire. After the first five post-fire years, vegetation change is likely to occur more slowly, and annual monitoring is not necessary in the absence of fire. These stands provide detailed baseline data on fire effects and species establishment following fire.

It will probably also be necessary to establish additional monitoring locations in order to track conifer establishment because conifer regeneration is so sparse on the landscape that it is not adequately captured in this set of vegetation stands whose locations were based on a random stratified sample. A future report (C0643016) will provide recommendations for monitoring conifer recovery throughout CRSP.

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Vegetation dynamics and exotic plant invasion following high severity crown fire

Introduction

Vegetation dynamics following large, often severe wildfires have been studied in a variety of plant communities in western North America in recent decades, revealing the effects of spatial heterogeneity of both vegetation and disturbance on patterns of succession (Turner et al. 1994, Turner et al. 1997, Keeley 1998, Crawford et al. 2001, Keeley et al. 2005, Jayen et al. 2006, Haire and McGarigal 2008).   The 113,000-ha Cedar Fire in 2003 (Keeley et al. 2004, Moritz et al. 2004) was the largest recorded fire in California since fire perimeter maps have been routinely made (early 1900s).

Large, severe fires have long been a feature of the chaparral shrublands (Keeley and Davis 2007) that dominate the foothills of the California Floristic Province and burn in stand-replacing crown fires (Mensing et al. 1999, Keeley and Fotheringham 2001, Keeley and Zedler in press). However, large chaparral fires that ignite during severe fire weather (extremely strong winds and low humidity) occurring in the fall often burn for days or weeks and affect forested areas in the southern California mountains after strong, easterly down slope (Santa Ana) winds subside and synoptic westerly winds return (Keeley et al. submitted-a, Keeley et al. submitted-b). This was the case with the Cedar Fire that burned extensive forested areas of the Cuyamaca Mountains in the Peninsula Ranges of San Diego County, CA, USA (Franklin et al. 2006, Goforth and Minnich 2008). This large fire severely affected these forests (M. Wells, unpubl. data, Oberbauer 2007). .

An earlier study (Interagency Agreement C0443021) reported that conifer mortality in the Cuyamaca Mountains was extremely high and positively related to fire severity, and that early post-fire vegetation dynamics during the first two growing seasons were dominated by the establishment of abundant and diverse native herbs (including fire-obligates) as well as shrub seedlings and resprouting by shrubs and oak trees (Franklin et al. 2006). This study extends the previous investigation by reporting on the analysis of vegetation data from monitoring plots resurveyed in 2007, the fourth post-fire growing season. Vegetation changes in the first four years following a large, severe crown fire in Coulter pine and mixed conifer forests are described.

The purpose of this study was to examine the effect of the heterogeneity of both the landscape and disturbance on patterns of post-fire vegetation dynamics. The study area encompasses an ecotone located at the altitudinal transition from lower-elevation chaparral and oak woodland to higher-elevation Coulter pine and mixed conifer forest. Ecotones (or ecoclines) tend to be species rich because they support species at the edges of their range whose distributions are centered towards the extremes of an environmental gradient (van der Maarel 1990, Holland et al. 1991). I expected that, because this forest-shrubland ecotone would also have experienced a heterogenous disturbance regime (Agee 1998, Schoennagel et al. 2004), both in terms of fire history and historical land use, it would support a diversity of pathways of post-fire vegetation recovery (sensu Crawford et al. 2001), in other words, succession (Glenn-Lewin and van der Maarel 1992). I also expected this ecotone landscape to be heterogeneous with respect to its susceptibility to invasion by nonnative species (Stohlgren et al. 2002).

Methods

The Study Area and Data

Vegetation in 38 forest stands has been repeatedly surveyed following the 2003 Cedar Fire, a severe crown fire throughout much of the forested landscape affected by the fire (Goforth and Minnich 2008). Stands were surveyed in the 2004 and 2005 growing seasons, reported in Franklin et al. (2006). The stands were revisited during May-June 2007, the fourth growing season following the Cedar Fire. This paper reports on the post-fire vegetation changes that were observed in the 2007 survey.

The details of the sample design and survey methods were reported in Franklin et al. (2006) and are summarized briefly here. Stands were located between 1310 and 1650 m elevation in the West and East Mesa areas of Cuyamaca Rancho State Park (CRSP), Cuyamaca Mountains, San Diego County (approximately 32° 56' N; 116° 34' W). Forty West Mesa stand locations were originally allocated by stratified random sampling in a study of forest structure conducted in 1992 (Krofta 1995). Stands were located in the elevation range that constitutes the transition zone between foothills Coulter pine forest, dominated by Coulter pine-canyon live oak (in some sources referred to as a form of mixed evergreen forest, and in others as a closed cone pine type), and mid-montane forest (mixed conifer forest, Jeffrey pine forest) (Barbour and Minnich 2000, Minnich and Everett 2001, Barbour 2007, Minnich 2007). Conifer woodland and forest (together 32% of the area of CRSP) occurs in a mosaic along with oak woodland (8%), montane chaparral (49%) and montane dry meadows (grassland; 10%). Area estimates are from statewide vegetation type maps (California Department of Forestry and Fire Protection; frap.cdf.ca.gov) developed in the 1990s (Franklin et al. 2000).

These generalized vegetation maps are not sufficiently precise to accurately distinguish species dominance patterns within CRSP (Franklin et al. 2001), but local patterns of species composition on the elevation gradient were documented by Krofta (1995). The dominant conifers in the forested portions of the study area are *Pinus jeffreyi* Grev. & Balf. (Jeffrey pine) below about 1500 m, and *Pinus coulteri* D. Don (Coulter pine) between 1250-1700 m. Mixed conifer forest, characterized by the occurrence of *Calocedrus decurrens* (Torrey) Florin (incense cedar) and *Abies concolor* (Gordon & Glend.) Lindley (white fir) with occasional *Pinus ponderosa* Laws. (ponderosa pine, which reaches its southern range limit in CRSP (Griffin and Critchfield 1972)) and *P. lambertiana* Douglas (sugar pine), occurs above about 1600 m (the highest elevation found in the study area is 1985 m at Cuyamaca Peak). The dominant oaks are *Q. agrifolia* Nee var. *oxyadenia* (Torrey) J. Howell (coast live oak) below about 1500 m, *Q. kelloggii* Newb. (black oak) above about 1400 m, and *Quercus chrysolepis* Liebm. (canyon live oak) found throughout the elevation range observed in this study.

The original stands could only be approximately but not exactly located, and so new plot locations were established in 2004 using a modern global position system (GPS; Trimble Geo XM 2003, Trimble Navigation, Sunnyvale, CA), and revisited in 2005 and 2007. Some 2004 plots were dropped in 2005 because of lack of forest cover. Eight additional stands were established on East Mesa by stratified random sampling in 2005 in order to observe a greater range of fire severity. Trees in each stand were sampled in 1992 (Krofta 1995) and 2004 within four 10-m radius circular sublots, 36 m from the stand center, at 45°, 135°, 225° and 315° aspect. The four subplots were intended to describe forest structure in a stand of approximately 1 ha. Adult tree sampling was discontinued after 2004/2005 because of almost complete tree mortality resulting from the Cedar Fire. All other vegetation, including herbaceous annuals and perennials, resprouting shrubs and (oak) trees, and shrub and tree seedlings, was measured in five 1-m^2 quadrats placed 4 m apart on the east-west axis of each subplot, yielding 20 quadrats per stand. In this paper, cover (projected ground cover) by plant species and by life form was

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averaged for stands as the basis of the analyses. Exotic versus native herbaceous annuals and perennials were analyzed separately. In this study, exotic refers to alien species, non-native to the study area.

Data Analysis

Overall changes in plant cover by life form were examined for each year, distinguishing native from non-native plant cover. The relationship between the abundance of native and exotic herbaceous species was examined at the quadrat and at the stand level using linear models (regression). Then, in order to describe the growing divergence in the species composition of the stands with time, vegetation data from the 38 stands visited in 2007 were organized into a stand by species abundance (cover) matrix and subjected to hierarchical multivariate clustering based on Ward's linkage method and relative Euclidean distance. The significance of the resulting groups was evaluated using a Multi-Response Permutation Procedures (MRPP) (Mielke 1984).

The stand by species matrix was then subjected to multivariate ordination analysis using Non-metric Multidimensional Scaling (NMS) (Minchin 1987, Clarke 1993) in order to describe continuous variation in species composition among stands. Detrended Correspondence Analysis (DCA), another ordination method (ter Braak 1995), was also used in order to examine the results for congruence with NMS (Økland 1996). Classification and ordination were carried out using the PC-Ord software (McCune and Mefford 1999). All other statistical analyses used the R statistical programming environment (R Development Core Team 2007).

The correlation of environmental variables with NMS axes (describing variation in stand composition) was estimated using a non-parametric correlation coefficient, Kendall's τ, in an indirect ordination approach (Jongman et al. 1995). Environmental covariates examined included elevation, slope, aspect (sine- and cosine-transformed to linear northness and eastness indices respectively, Beers et al. 1966), stand age (years prior to 2003 since previous fire), the Composite Burn Index estimated in 2004 as a measure of fire severity (van Wagtendonk et al. 2004, Cocke et al. 2005, as described in Franklin et al. 2006), and conifer and oak basal area prior to the 2003 fire (estimated as the sum of killed and living trees measured in 2004, Franklin et al. 2006).

Results

The greatest changes resulting from four years of post-fire vegetation dynamics in these formerly-forested stands were an overall increase in shrub cover, especially in sites dominated by *Ceanothus palmeri*, from 3% to 31%, and the dramatic increase in the cover of exotic herbaceous species, primarily annual grasses, from 3% to 40% (Figure 1). Cover of native annuals increased from an average of 17% in 2004 to 33% in 2005, but then dropped to 15% in 2007. It is interesting to note that annual precipitation in rain year 2004 (Nov 2003 – Oct 2004) was below average, 2005 was above average, and 2007 was, like 2004, very dry (Figure 2). Therefore, native annual cover mirrored precipitation variation.

Cover of native and exotic annuals in 2007 was positively correlated at the stand level (R^2 = 0.21, P = 0.0039; N = 38), and also at the individual 1-m^2 quadrat level, although at this scale very little variance was explained (R^2 = 0.03; P << 0.001; N = 744; Figure 3). Native perennial cover increased over the three sampling periods, from 6% to 14%, and oak resprout cover increased from near zero to 5%.

These general trends observed in the formerly forested areas of CRSP mask spatial variation in successional pathways found among the stands. Hierarchical clustering revealed five groups of plots that are distinct based on MRPP (P << 0.0001) showing within-group homogeneity typical of plant community data (A = 0.34). Groups 1 and 2 (both strongly dominated by *Ceanothus palmeri*) were most similar, separating at 70% information remaining, groups 3 and 4 (both dominated by exotic grasses) at 50%, and groups 4 and 5 at 30%. Groups 1 and 2 together were most dissimilar from 3, 4 and 5. These groups differ in their life form composition and relative abundance of native and exotic species (Figure 4), and capture the main patterns of variation in early post-fire succession.

Groups of stands identified by clustering separated reasonably well on NMS axes 1 and 2 (Figure 5), and environmental variables were correlated with these transformed axes that represent composite species composition (Table 2). Results from DCA ordination were concordant with NMS, but DCA groups were not as well separated, nor were environmental correlations with axes as strong, and so only NMS results are presented. NMS axis 1 describes a gradient from higher elevation conifer-dominated stands to lower elevation stands with a greater chaparral component, while axis 2 describes a gradient of high to low burn severity (Figure 5). The groups are described in the following paragraphs.

Group 1 (comprising 7 stands), "*Ceanothus palmeri* and *Bromus* spp. with native annuals," is a group whose indicator species includes the native shrub *Quercus berberidifolia* (scrub oak) and the native annuals *Camissonia hirtella* and *Allophyllum glutinosum*, but note that this group is dominated by *Ceanothus palmeri* (average cover 32%), *Bromus tectorum* (17%) and *B. diandrus* (8%; Table 1). This group has relatively high cover of native annuals and perennials complementing moderate cover of exotic annuals and native shrubs (Figure 4). These stands, with low values on NMS axis 1 and intermediate to low values on NMS axis 2 (Figure 5), are found at somewhat higher elevations (in contrast with Group 5, below), on east facing exposures, in older stands (longer time since previous fire) with higher pre-fire conifer basal area (Table 2).

Group 2 (8 stands), "*Ceanothus palmeri*," comprises dense shrub stands dominated by *C. palmeri* (Table 1) with *B. tectorum* (5%) and the resprouting oak, *Quercus chrysolepis* (4%). This group of sites had very high shrub cover in 2007, and low cover of all other life forms (Figure 4). Group 2, with low values on NMS axes 1 and 2 (Figure 5), and high values on axis 3 (not shown), is found on steeper slopes and more severely burned sites, that were older prior to the 2003 fire, and, like Group 1, also found at higher elevations on east facing exposures with higher pre-fire conifer basal area (Table 4).

Group 3 (10 stands), "*Bromus tectorum* and *Sisymbrium altissimum*," is a large group of stands dominated by a non-native grass and forb, the two most common herbaceous species in the 2007 survey (Table 3). The third and fourth most abundant species in this group are also non-native grasses, *B. diandrus* (11%) and *Vulpia myuros* var. *hirsuta* (4%). This group of plots has the highest exotic annual cover, and relatively low cover of other life forms (Figure 4). With low values on NMS axis 1, intermediate values on axes 2 (Figure 5), and low values on axis 3 (not shown), this group is associated with intermediate within the study area, higher conifer basal area, and is found on less steep slopes (Table 2).

Group 4 (9 stands), "*Bromus diandrus*, *B. tectorum* and native perennial herbs," consists of stands dominated by non-native *B. diandrus* (an indicator species for this group), but also with significant cover of *B. tectorum*, and low cover of *C. palmeri* (7%; Table 1). In addition to the exotic brome grasses, non-natives *Vulpia myuros* var. *hirsuta* (6%) and *Sisymbrium altissimum* (5%) are also dominant. Several native herbaceous perennials, *Achillea millefolium*, *Ambrosia psilostachya*, *Leptosiphon floribundus* ssp. *glaber* , and *Calystegia macrostegia* (a

vine), are indicator species for this group (Table 1). This group of stands, like group 3, is found at low values of NMS axis 1, but also at high values of axis 2 (Figure 5), and is therefore associated with somewhat higher elevations and higher conifer basal area, but with lower burn severity (Table 2).

Group 5 (4 stands), "chaparral," is dominated by *Ceanothus leucodermis*, and indicator species also include other woody perennial shrubs and subshrubs associated with lower-elevation chaparral in the study area including *C. greggii*, *Ericameria linearifolia*, *Hazardia squarrosa* and *Lotus scoparius* (Table 1). The resprouting oak, *Quercus agrifolia* var. *oxyadenia*, is also found in this group (3%). Even this group has significant cover of a non-native brome (*B. diandrus*; 5%). Group 5 stands have extremely high values on NMS axis 1 (Figure 5) and low values on axis 3 (not shown), and are therefore associated with steep slopes, west-facing exposures, low conifer basal area, and lower elevations in the study area (Table 2).

Stands within groups tend to cluster on the landscape to some extent (Figure 6), and this is primarily due to the topographic gradient or pattern of elevation in the study area. Group 5 stands are found in the low-elevation southwestern area of West Mesa, and groups 1 and 2 in the higher-elevation northwest section. Groups 3 and 4, dominated by exotic herbs, are found on both West and East Mesas at middle elevations.

A total of 175 species were recorded in the stands in at least one of the three sample years. Of 136 species recorded in 2007, only 12 (9%) were non-native. However, four of the six most abundant plants were exotic species in 2007, the most abundant being the brome grasses *Bromus tectorum* and *B. diandrus* and the mustard (Brassicaceae) *Sisymbrium altissimum* (Table 3).

Conifer recruitment was generally low, and patchy and rare on the landscape such that it is not captured adequately in the stand sampling (Franklin et al. 2006). However, ongoing, systematic surveys suggest that pines, especially *Pinus coulteri* (which is partially cone serotinous), are establishing and surviving in about 25% of the formerly forested area – that is, 318 out of 1231 (2000-m^2) quadrats that were searched contained at least one conifer seedling or that has established since the fire (unpubl. data).

Discussion

Plant community dynamics following a major disturbance (secondary succession) are shaped by multiple interacting factors including propagule availability, species' life history differences, competition, herbivory, climate cycles and environmental factors that change over time (Pickett et al. 1987, Glenn-Lewin and van der Maarel 1992). The vital attributes approach developed to predict multiple pathways of succession following fire focuses on life history traits, specifically the timing of key events (e.g., maturity) relative to the fire interval (Cattelino et al. 1979, Noble and Slatyer 1980). However, in this study the focus was on early vegetation dynamics following one particularly large, severe and unusual fire, with limited ability to examine fire interval effects (Franklin et al. 2006).

In the gradient-in-time conceptual model of succession, species traits predict their distribution in time following disturbance, as environmental conditions, such as light, moisture and nutrient availability, change with this temporal "gradient" (Pickett 1976, Peet 1992). Life history traits are expected to change with succession in a predictable way. The patterns found in this study (see also Franklin et al. 2006) that are consistent with the gradient-in-time model are: a) high abundance and diversity of obligate post-fire herbaceous species throughout the study area in the first year; b) establishment of perennial shrubs and tree species with stored seed banks in the first year, and thinning in the second year; c) continually increasing

abundance (cover) of resprouting species from the first to fourth year; and d) establishment and increasing abundance of species dependent on dispersal to reach a site in the second through fourth year, including exotic and native annuals and perennials.

The gradient-in-time model described the association of plants with certain life history and functional traits to particular regeneration niches in time. In addition, four years following extensive, high-severity crown fire, the prediction that these ecotonal communities would support diverse pathways of succession was supported by the divergence of species composition among groups of stands, and their association with topographic and fire severity gradients.

Dramatic increases in shrub cover were documented, especially in the most severely burned sites, and those with the longest time since previous fire. Shrub cover also increased in sites that were found on steeper slopes with lower pre-fire conifer basal area and at somewhat lower elevations within the study area, at the chaparral-forest ecotone. A baseline survey of forest structure conducted in 1992, although it provided less detail, did record shrub cover of greater than 25% in half of the West Mesa forest stands examined (average cover for all stands 32%) (Krofta 1995). Tree cover in the same stands ranged from 20-140% (average 59%) in 1992, describing a patchy mosaic of oak, Coulter pine and conifer woodland and forest, interspersed with the chaparral and grasslands that together comprise more than half of the vegetation cover at CRSP. Therefore, following almost complete forest canopy mortality (Franklin et al. 2006, Goforth and Minnich 2008), large increases in shrub cover are not unexpected (Keeley et al. 2003). Given that almost half of CRSP was chaparral shrubland (spanning the entire elevational range of the Park), it is unsurprising that, even in formerly forested stands, post-fire vegetation dynamics shared similarities with chaparral succession (Keeley et al. 2005, Keeley et al. 2006), including residual species (obligate resprouters and obligate seeders) dominating early succession, and species with specific life-history adaptations to fire (fire cued seed germination or vegetative reproduction) adding significantly to early plant diversity (Franklin et al. 2006).

Shrub cover, dominated by *Ceanothus palmeri*, was 30% or greater in 40% of the stands surveyed in 2007 (groups 1 and 2). *C. palmeri* is found from central to southern California at elevations of 100-1800 m, but is most abundant in the Peninsular and Transverse Ranges (www.calflora.org). It can reproduce following fire both by resprouting and seedling establishment, and did so in profusion following the Cedar Fire (Franklin et al. 2006, Goforth and Minnich 2008). Montane species of *Ceanothus* often dominate post-fire succession in pine and mixed-conifer forest in North America (Conard and Radosevich 1982) because extremely large soil seed banks can remain dormant and viable for a century or more and are induced to germinate by fire scarification (Kauffman and Martin 1991). *Ceanothus* species are nitrogen fixers, important to ecosystem recovery following nitrogen volatilization by fires (Binkley et al. 1982). While dense *Ceanothus* stands also established following a 1986 fire in the Cuyamaca Mountains (Airplane Ridge), within 15 years *Ceanothus* was overtopped by young *P. coulteri* (M. Wells, pers. obs.).

I expect that these dense, almost monospecific *Ceanothus* stands will undergo self-thinning in the coming years (e.g, Conard and Radosevich 1982), as was already observed at the seedling stage (Franklin et al. 2006). Cover is likely to decrease as stands are increasingly dominated by fewer, larger individuals. Resprouting oaks are likely to continue to increase in importance, given their high post-fire survival and the trend observed in the first four years (see also Goforth and Minnich 2008).

I also predicted that this ecotone landscape would be spatially heterogeneous in its susceptibility to invasion by exotic species. This was also supported. There was a large

increase in the abundance of exotic herbaceous annuals, namely the hyper-abundant brome grasses (*Bromus tectorum*, *B. diandrus*) and the mustard *Sisymbrium altissimum*, but primarily in those stands that experienced slightly lower fire severity, and were found on less steep slopes, than those stands where shrub cover has become very high. Most non-native species that are invasive in California are of Mediterranean or Eurasian origin (Baker 1989, Fox 1990), and they are especially well-established in valley grasslands and foothills. The abundance and richness of exotic plant species generally decreases with elevation in montane southern California, as well as elsewhere (Stohlgren et al. 2002), presumably because the Eurasian grasses and forbs that are well established in California are poorly adapted for high-elevation forested environments (Pierson and Mack 1990b, Keeley et al. 2003). Soil seed banks of these species do not survive high-severity fire (Keeley 2001), and therefore they must colonize from a source area (D'Antonio et al. 2001, Haire and McGarigal 2008). Proximity of seed sources is an important factor affecting invasion of exotic species following disturbance (Wiser et al. 1998).

However, several factors contribute to the susceptibility of the forested areas of CRSP to the increased abundance of these exotic annuals observed over four years following the Cedar Fire. First, the fire was large and severe, leading to the conditions of increased light and nutrients that favor their establishment (Tilman 1982, Rejmánek 1989), and exposing the area to post-fire plant colonization for a longer period (Keeley 2006). Secondly, the study area is situated at an ecotonal elevation range that supports a complex mosaic of chaparral, valley grasslands (dry meadows), oak and pine woodlands and conifer forest. Those grasslands appeared to have burned at lower severity in the Cedar Fire (pers. obs.), e.g. on East Mesa (Franklin et al. 2006). This suggests that seed sources for these exotic herbaceous species were not far from formerly forested areas whose tree canopy was removed by the fire. When exotic species must colonize from source areas, landscape patterns of vegetation, we well as disturbance severity, affect patterns of invasion (Keeley et al. 2003). Given the history of grazing, logging and mining at Cuyamaca Rancho State Park (a Spanish land grant) prior to Park establishment in 1933 (California Department of Parks and Recreation 1986), by 2003 these species were probably well established in grasslands and woodlands within the landscape matrix.

Although the history of exotic species establishment in CRSP is not known in detail, following the approach of Keeley and McGinnis (2007) herbarium records were consulted (Consortium of California Herbaria) to determine the earliest collections from the mountains of San Diego County. *Bromus tectorum* was collected in 1937 at 1500 m elevation in the Laguna Mountains (La Posta Creek), 25 km from the Cuyamaca Mountains. *Bromus diandrus* was recorded from 1100 m in the Cuyamaca Mountains in 1899. Therefore, both species have been well-established in these mountains for at least a century and probably much longer.

Bromus tectorum (cheatgrass) is an invasive exotic grass species in North America whose impacts have been most extensively studies in the sagebrush steppe plant communities of the intermountain West (Young and Evans 1978, Mack 1981). A number of studies have also studied the invasion of *B. tectorum* into montane conifer forests of western North America, in particular low-elevation ponderosa pine forest (Crawford et al. 2001, Keeley and McGinnis 2007), typically found adjacent to shrub steppe, grasslands or oaks woodlands on an elevation gradient. Cheatgrass invasion in lower elevation dry forest is more likely to occur following disturbance such as logging and fire (Pierson and Mack 1990a), and this species responds positively to post-fire nutrient availability (Gundale et al. 2008). In the southern Sierra Nevada, California, post-fire cheatgrass dominance in ponderosa pine forest was positively related to growing season precipitation and soil nitrogen, and negatively to fire intensity (Keeley and McGinnis 2007).

In CRSP, I found that the stands dominated by *Bromus* species also tended to have experienced lower fire severity than those dominated by *Ceanothus* (especially *C. palmeri*). It is not known whether this is cause or effect. It seems unlikely that a *Bromus* seed bank survived the Cedar Fire throughout much of CRSP, especially in light of the low cover of this species observed in the stands in 2004, the first post-fire growing season. It is more likely that *Bromus* species seeded in from nearby source areas, including less severely burned grassland areas of CRSP and surrounding areas, established in abundance in wet 2005, and were well established by 2007 (in spite of the dry conditions).

Although other studies have found the overall abundance of exotic annuals to generally be positively related to forest fire severity, that seemed to be because of canopy removal and light availability (Crawford et al. 2001, Keeley et al. 2003). Keeley and McGinnis (2007) found that cheatgrass cover was negatively associated with other understory species cover, but we only observed that pattern in a wet year, 2005 (Franklin et al. 2006). While exotic annual cover in CRSP increased dramatically from 2004 to 2005 to 2007, the cover of native annuals tracked rainfall patterns, and was higher in wetter 2005 than in either 2004 or 2007. Our previous study (Franklin et al. 2006) found that exotic and native annual cover were positively correlated within stands in the dry, first post-fire growing season (2004), when plant cover was generally low. In the wetter, second post-fire year (2005), exotic and native annual cover both increased two- to five-fold but were negatively correlated. In 2007, native and exotic annual cover were once again positively, although weakly, correlated, suggesting that in the dry years both native and exotic species were abundant in moister sites on the landscape. In dry 2007, native annual cover returned to 2004 levels, although species composition changed as fire-following annuals were replaced by more opportunistic native annuals, and in addition native perennial cover and diversity increased. However, exotic herbaceous cover almost doubled from 2005 to 2007. High seed output, the buildup of large seed banks and early germination by exotic species (D'Antonio and Vitousek 1992) may account for their increasing abundance, once established, that is seemingly independent of precipitation.

Cheatgrass has been implicated in altering fire cycles and nutrient availability with positive feedbacks, e.g., tending to increase in abundance, leading to irreversible changes in community life form composition ("type conversion") (Agee 1998, Mack and D'Antonio 1998, Brooks et al. 2004). In contrast, at the chaparral-conifer ecotone studied, it is unlikely for exotic Eurasian grasses to lead to altered fire regimes or type conversion, in spite of their alarming increase in the fourth year. These grasses are dependent on dispersal in order to establish in forested areas following disturbance because they do not have persistent seed banks. They did not reach potential establishment sites in abundance during the first post-disturbance year (e.g., Franklin et al. 2006), when most resources are available, owing to dispersal limitation. Because of this, they had little interaction with the post-fire annuals and bulbs that are a significant component of biodiversity in this community (Keeley and Davis 2007).

Given their shade-intolerance, I predict that exotic annuals will not persist in these sites after 5-10 years as the woody canopy closes, both at the chaparral and forest end of the elevation gradient. Given their temporal and spatial patterns of establishment, they have the greatest potential interaction with native perennials and opportunistic annuals. Their impact on these functional groups is unknown. They are likely to re-invade during the same time window (2-10 years) after severe disturbance given the proximity of propagule pools, the dry meadows where non-native grasses have long been established.

Conifer regeneration is the subject of an ongoing contract (Interagency Agreement C0643016). Preliminarily, it appears that the dominant conifer species throughout much of CRSP (Krofta 1995), *Pinus coulteri*, is the one that is regenerating, albeit sparsely, throughout its elevational range in the Park, 1182-1930 m. Limited regeneration of incense cedar and

sugar pine have been observed in small patches of forest where fire severity was low. However, the extent of mixed conifer forest in CRSP was limited to forested areas above 1500 m, comprising about 1400 ha (14%) of the Park, and including a significant component of *P. coulteri* (Krofta 1995). *P. coulteri* is partially cone serotinous, (Borchert 1985, Borchert et al. 2002, Borchert et al. 2003), and therefore expected to respond to fire with some degree of seedling establishment.

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Table 1. Mean cover of indicator species for groups of stands defined by clustering (standard deviation given in parentheses). Monte Carlo test of significance of observed maximum indicator value for species, 1000 permutations: * -- P < 0.05; ** -- P < 0.01; *** -- P < 0.001. † -- non-native (exotic) species.

Species	Group1		Group2		Group3		Group4		Group5	
Group 1: *Ceanothus palmeri* and *Bromus* spp. with native annuals										
*Allophyllum glutinosum**	0.02	(0.026)	0.00	(0.000)	0.00	0.0000	0.00	(0.000)	0.00	(0.000)
*Camissonia hirtella****	0.39	(0.697)	0.04	(0.124)	0.011	0.0222	0.00	(0.000)	0.00	(0.000)
*Quercus berberidifolia***	1.25	(3.092)	0.00	(0.000)	0.00	(0.000)	0.00	(0.000)	0.00	(0.000)
Group 2: *Ceanothus palmeri*										
*Ceanothus palmeri****	32.80	(4.891)	57.06	(23.187)	1.98	(3.272)	7.14	(10.745)	2.75	(5.500)
Group 3: *Bromus tectorum* and *Sisymbrium altissimum*										
*Bromus tectorum*** †	17.10	(6.659)	5.13	(5.746)	28.56	(14.916)	10.11	(3.761)	1.94	(3.2490
*Sisymbrium altissimum** †	2.16	(1.370)	2.18	(3.466)	12.30	(9.130)	5.41	(3.820)	0.04	(0.075)
Group 4: *Bromus diandrus, B. tectorum* and native perennial herbs										
*Achillea millefolium**	0.39	(0.454)	0.04	(0.106)	0.42	(0.607)	1.57	(1.928)	0.00	(0.000)
*Ambrosia psilostachya***	0.02	(0.057)	0.00	(0.000)	0.12	(0.347)	1.16	(1.403)	0.00	(0.000)
*Bromus diandrus** †	8.01	(7.966)	3.18	(3.631)	10.55	(10.576)	23.71	(17.487)	4.56	(8.959)
*Calystegia macrostegia**	1.14	(1.691)	0.08	(0.212)	0.60	(1.029)	1.53	(1.713)	0.00	(0.000)
Leptosiphon floribundus ssp. glaber***	0.00	(0.000)	0.00	(0.000)	0.00	(0.000)	0.82	(1.144)	0.00	(0.000)
*Trifolium willdenovii**	0.46	(0.587)	0.42	(0.729)	0.78	(1.585)	2.06	(1.947)	0.00	(0.000)
Group 5: Chaparral										
Ceanothus greggii var. perplexans***	0.00	(0.000)	0.00	(0.000)	0.00	(0.000)	0.00	(0.000)	0.99	(1.041)
*Ceanothus leucodermis****	0.54	(0.984)	2.66	(7.513)	0.08	(0.237)	0.06	(0.167)	38.71	(18.124)
*Ericameria linearifolia***	0.00	(0.000)	0.00	(0.000)	0.00	(0.000)	0.08	(0.250)	1.40	(2.258)
Galium angustifolium ssp. angustifolium***	0.24	(0.624)	0.03	(0.071)	0.08	(0.237)	0.22	(0.384)	1.29	(1.726)
*Hazardia squarrosa****	0.00	(0.000)	0.00	(0.000)	0.00	(0.000)	0.00	(0.000)	4.85	(5.112)
*Hirschfeldia incana*** †	0.00	(0.000)	0.00	(0.000)	0.00	(0.000)	0.00	(0.000)	0.88	(1.439)
Lotus nevadensis var. nevadensis***	0.00	(0.000)	0.00	(0.000)	0.11	(0.348)	0.04	(0.133)	0.30	(0.367)
Lotus scoparius var. *scoparius****	0.00	(0.000)	0.00	(0.000)	0.00	(0.000)	0.00	(0.000)	0.53	(0.466)
*Turricula parryi***	0.00	(0.000)	0.00	(0.000)	0.20	(0.633)	0.00	(0.000)	0.50	(0.456)

Table 2. Kendall's τ, non-parametric linear correlations of environmental covariates with NMS ordination axes 1-3. Correlations greater than 0.2 are highlighted using bold. BA = Basal Area.

Variable	Axis 1	Axis 2	Axis 3
Stand Age	**-0.223**	-0.170	-0.057
Elevation	**-0.542**	0.029	-0.073
Slope	0.003	-0.038	**0.233**
Northness	-0.124	-0.080	0.066
Eastness	**-0.251**	-0.012	-0.061
Composite Burn Index	0.056	**-0.429**	0.105
Conifer BA	**-0.214**	-0.006	**-0.233**
Oak BA	-0.189	-0.036	-0.033

Table 3. The 40 most abundant species in the 2007 survey (average cover > 0.4%), shown in rank order, separated by life form.

Life form	Species	Average Cover
Exotic annual	*Bromus tectorum*	14.35
	Bromus diandrus	11.01
	Sisymbrium altissimum	5.38
	Vulpia myuros var. *hirsuta*	3.18
	Avena barbata	1.27
	Bromus hordeaceus	0.85
	Bromus madritensis ssp. *rubens*	0.42
	Erodium cicutarium	0.41
Native annual	*Bromus arenarius*	2.21
	Madia gracilis	1.55
	Galium aparine	1.40
	Trifolium albopurpureum var. *albopurpureum*	1.12
	Clarkia rhomboidea	1.02
	Trifolium ciliolatum	0.94
	Trifolium willdenovii	0.87
	Claytonia parviflora ssp. *parviflora*	0.82
	Erigeron foliosus var. *foliosus*	0.79
	Cryptantha sp.	0.71
	Trifolium microcephalum	0.69
	Lupinus bicolor	0.62
	Cryptantha intermedia	0.62
	Bromus carinatus var. *carinatus*	0.55
Native perennial	*Solidago californica*	2.40
	Lessingia sp.	1.31
	Calystegia macrostegia	0.75
	Achillea millefolium	0.56
	Lupinus excubitus	0.55
	Vicia americana var. *americana*	0.53
Oak	*Quercus agrifolia* var. *oxyadenia*	1.95
	Quercus chrysolepis	1.78
	Quercus kelloggii	0.74
Shrub	*Ceanothus palmeri*	20.56
	Ceanothus leucodermis	4.77
	Rhus trilobata	0.83
	Arctostaphylos pringlei	0.81
	Arctostaphylos glandulosa	0.66
	Toxicodendron diversilobum	0.63
	Symphoricarpos mollis	0.63
	Hazardia squarrosa	0.51

Figure 1. Box plots showing distribution of cover of life forms: exotic versus native annuals and native perennials, shrubs and resprouting oak trees in stands over three survey years.
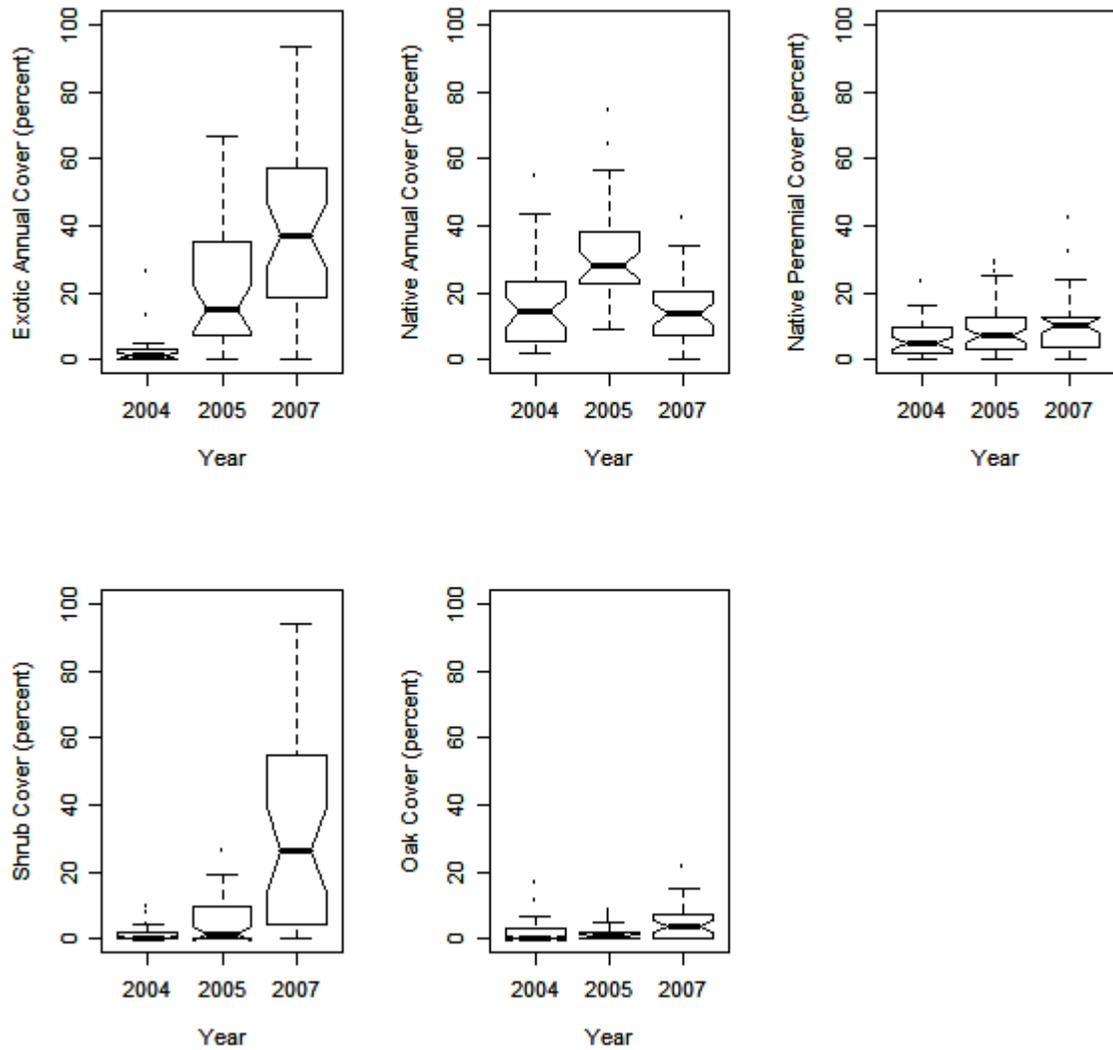
Figure 2. Total precipitation in rain years (November to October) 1997-2007, shown for the Mt. Laguna weather station, east of the study area. Long term average (344 mm) shown as solid horizontal line. Although the precipitation is higher in the study area the interannual pattern would be very similar.
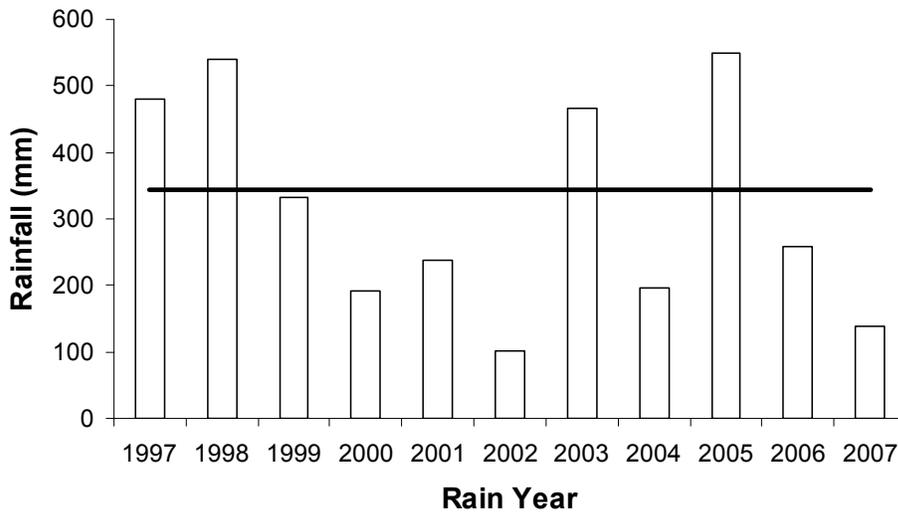
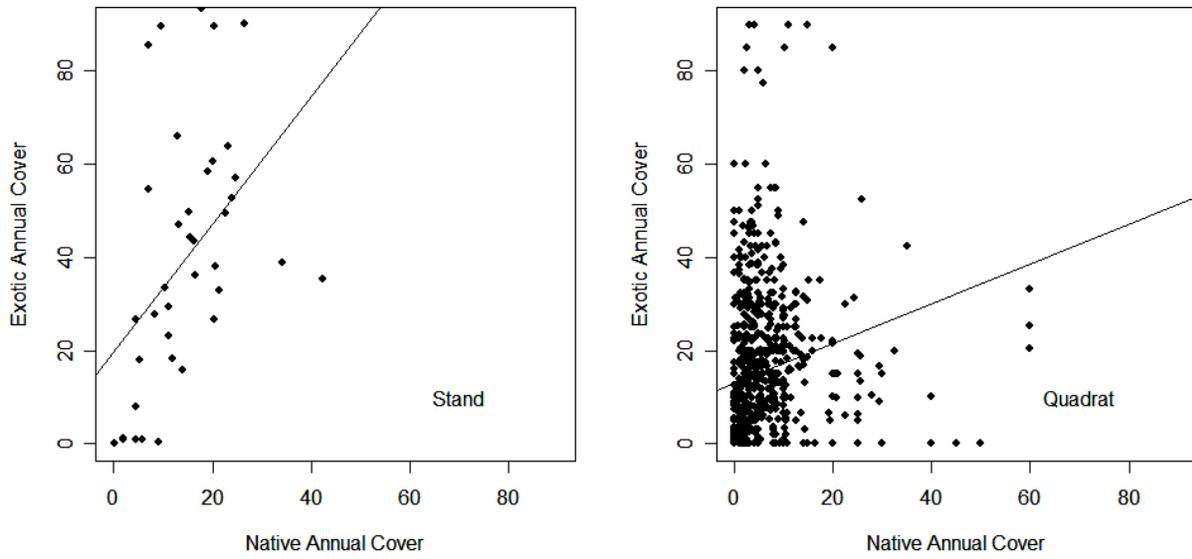Figure 3. Native versus exotic annual cover in stands (N = 37) and quadrats (N = 744).

Figure 4. . Box plots showing distribution of cover of exotic and native annuals, native perennials and shrubs in stands, shown for groups of stands defined by clustering. Average oak resprout cover (2-5%) did not vary much among groups (not shown).
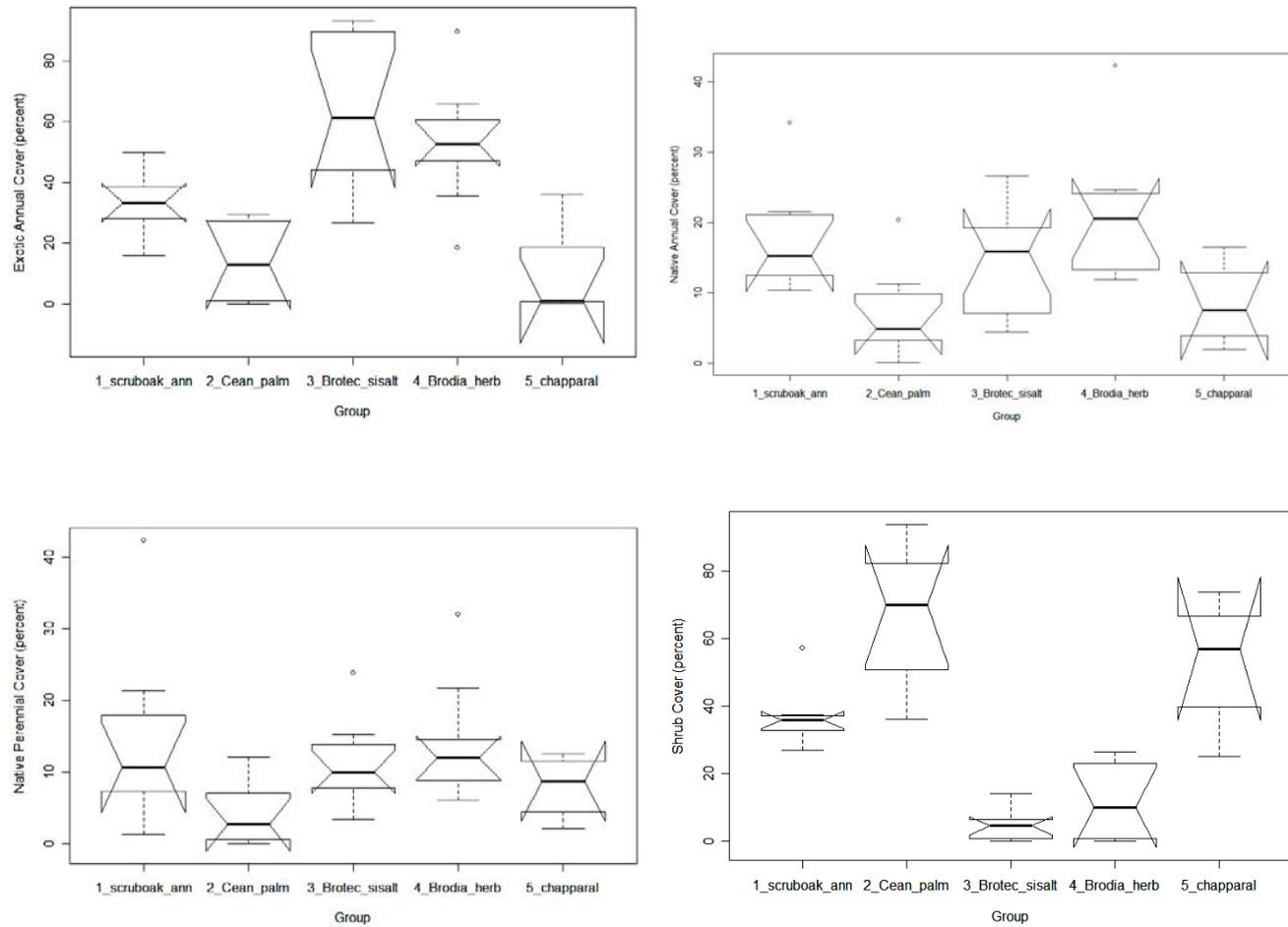
Figure 5. Variation in species composition summarized using indirect ordination (Non-metric Multidimensional Scaling; NMS). Stands identified by Group (Ward's linkage method; Table 1), displayed on first two NMS ordination axes, illustrating variation in species composition. Vectors, with length proportional to correlation of environmental variables with axes, shown for variables with correlations (Kendall's τ) > 0.4 (Table 2), elevation (Elevatio) and Composite Burn Index (CBI).
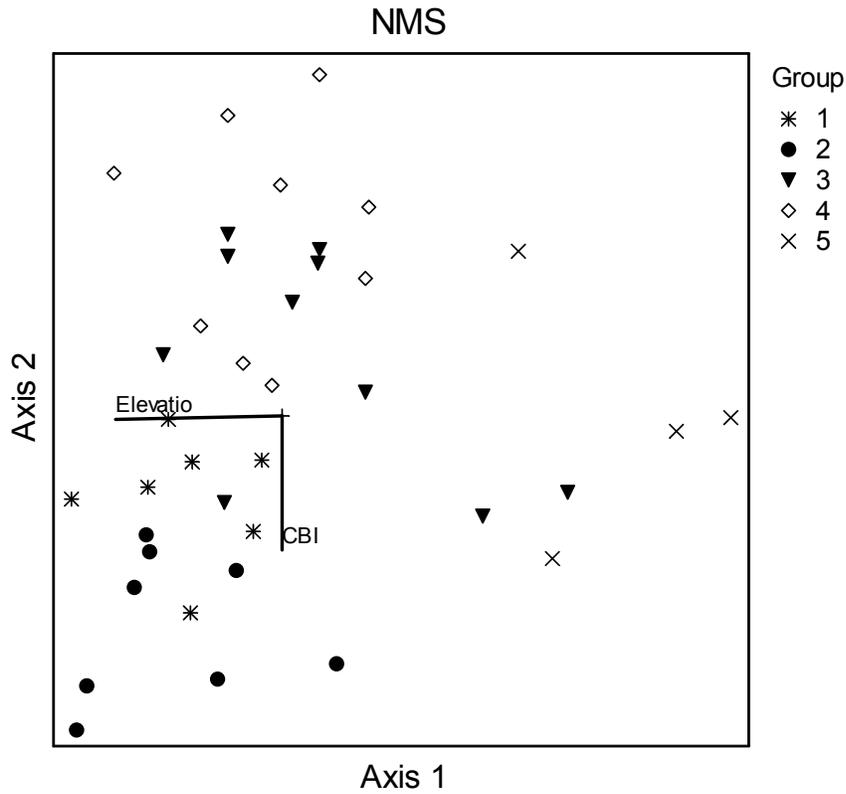
Figure 6. Shaded relief map of East and West Mesa areas of Cuyamaca Mountains, showing plot locations. Group 1: light green square with dot; Group 2: green open square; Group 3: yellow triangle with dot; Group 4: orange open triangle; Group 5: pink open circle.