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Fire Effects on Seed banks and Vegetation in the Eastern Mojave Desert: Implications for Post-fire Management

Matthew L. Brooks
U.S. Geological Survey, mlbrooks@usgs.gov

Steven Ostoja
U.S. Geological Survey

Robert Klinger
U.S. Geological Survey

Fire Effects on Seed banks and Vegetation in the Eastern Mojave Desert: Implications for Post-fire Management

By Matthew Brooks[1], Steven Ostoja[1] and Robert Klinger[1]

[1] U.S. Geological Survey
Western Ecological Research Center
Yosemite Field Station
El Portal, California

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U.S. Geological Survey
Marcia K. McNutt, Director

Contents

Abstract

Area burned has increased during the past few decades in the Mojave Desert due in part to increased dominance of highly flammable invasive non-native annual grasses. Management responses such as post-fire seedings have been implemented during the first 3 post-fire years to suppress the growth of the invasive annual grasses, promote recovery of native species, and facilitate the restoration of plant species diversity and abundance. Although there is a fair amount of information available on the effects of fire on plant diversity, density, and cover, there is very little information available regarding effects on soil seed banks to help guide the development of management prescriptions. This project was designed to evaluate the short-term effects of fire on soil seed bank diversity and density, and vegetation diversity and cover, following the Hackberry Fire Complex of summer 2005 in the eastern Mojave Desert. A secondary objective was to evaluate the correlations between measures of burn severity and seed bank and vegetation abundance to evaluate the utility of burn severity metrics in evaluating fire effects. The study region encompasses upper elevation blackbrush and lower elevation sagebrush ecotones of the Mojave Desert.

Fire reduced soil seed bank diversity during the first two post-fire fall seasons, although evenness was slightly higher in burned areas during all three post-fire years, possibly due to loss of annual plant microhabitats previously created by shrub canopies. Fire also reduced seed bank density by 81%, but only during the first post-fire spring. Seed bank reductions were greater for non-natives, *Bromus rubens* in particular, than for natives. Aboveground vegetation diversity was reduced in burned areas during all three post-fire years due to declines in species richness of perennials, as native species richness was not affected. Fire reduced cover of perennials and increased cover of annuals during all three years, but fire did not affect cover of non-native annual grasses (*Bromus rubens*, *Bromus tectorum*, and *Schismus* spp.). Virtually all of the seed bank and annual plant vegetation metrics evaluated in this study returned to unburned condition by the second or third post-fire years, and varied more among years than due to burning. In addition, the effects of fire on seed bank density during the first year were over an order of magnitude higher than what typically seeding prescriptions would have replaced if they had been implemented. These results call into question the need to seed annual plant species after fires in the Mojave Desert. In contrast, persistent reductions in cover of perennials means that their seed sources were limited and post-fire seedings may have help to overcome this establishment limitation for those species, although further studies are needed to evaluate this dynamic.

Both dNBR and CBI burn severity metrics were negatively correlated with total vegetation cover, annual cover in particular, during the first post-fire spring, which appeared to carry over to the seed bank during following fall which was also negatively correlated with dNBR. It therefore appears that dNBR may be a potentially useful tool in estimating reduced cover of annuals during the first post-fire spring, and reduced seed bank density during the following fall.

Background and Purpose

Fires can be stand replacing, and plant communities may take over a century to return to pre-fire perennial species composition in the Mojave Desert (Brooks and Minnich 2006; Abella 2009; Engel and Abella 2011). Mojave Desert fires can also reduce the dominance of native plants and increase the dominance of non-native annuals for at least the first few post-fire decades (Brooks and Minnich 2006), especially following repeated burning (Brooks and Chambers 2011; Brooks 2012). Robust native plant communities can resist invasion by non-natives, and reductions of their dominance after fires can make control of non-natives more difficult (Brooks and Chambers 2011). These potential changes have obvious implications for managing plant communities, but they also may affect animals (Woodbury and Hardy 1948; Duck *et al.* 1997; Esque *et al.* 2003; Shaffer and Laudenslayer 2006; Horn *et al.* 2012), watersheds (Wohlgemuth *et al.* 2006), and future fire regimes (D'Antonio and Vitousek 1992; Brooks *et al.* 2004).

Historically, post-fire landscapes have been left to recover on their own in most of the Mojave Desert. Although actions such as restricting access by livestock or humans for a few years have been implemented in limited areas to promote quicker recovery of plant cover, significant efforts to control invasive plants or promote the re-establishment of native species have been rare (Brooks *et al.* 2007). This general lack of active management in the Mojave Desert is due partly to the observation that fires in desert shrublands were historically uncommon (Humphrey 1974; Brooks *et al.* 2013) and the perception at a national scale that fire management problems were greater in other regions. This perception, coupled with poor establishment rates of seeding treatments that have occurred in the past (Brooks and Klinger 2011), has led to post-fire resources being primarily directed to other ecoregions.

Area burned has increased during the past few decades due in part to increased dominance of invasive non-native annual grasses which provide supplemental fuels that promote the spread of fire (Brooks and Esque 2002, Brooks and Minnich 2006; Brooks *et al.* 2013). Due to this increased fire activity, more emphasis is being placed on managing post-fire landscapes in this region. Objectives of these management actions are typically to promote recovery of native plant species and reduce dominance of non-native annual grasses. Of all the potential management tools, aerial seeding is potentially the most cost-effective over large areas. There are clearly many questions associated with aerial seeding, not the least of which is the potentially low establishment rate of seeding treatments in an environment of generally low rainfall, high seed predation, and significant competition from non-native annuals plants (Brooks and Klinger 2011; Klinger *et al.* 2011b). However, the more proximate question is whether seeding treatments are necessary in the first place. This question hinges on understanding the short-term effects of fire on soil seed bank densities and composition, and to some degree on plant cover and diversity during the first few years following Mojave Desert fires. This information is especially needed during the first 3 post-fire years, a time period that corresponds with the availability of federal funding to manage post-fire landscapes in the United States of America. Emergency Stabilization and Rehabilitation (ES&R) and Burned Area Emergency Response (BAER) plans often prescribe post-fire seeding during the first 3 post-fire years to mitigate various negative effects of fire in the Mojave Desert, even though it is still unclear if these treatments are beneficial or even necessary in this ecosystem.

Although there is a fair amount of information available on the effects of fire on plant diversity, density, and cover in the Mojave Desert (e.g. Callison et al. 1985; Brooks and Matchett 2003; Brooks and Minnich 2006; Abella 2009; Engel and Abella 2011; Brooks 2012), there is very little information available on responses of soil seed banks. Only four soil seed bank studies exist from the Mojave Desert which report: seed bank density, species composition, and species richness one year after experimental fires (20 m× 20 m) at a creosotebush scrub site (Esque et al. 2010); seed bank density of the invasive

annual grass *Bromus rubens* 2 years after a fire at an ecotone between blackbrush and creosotebush scrub (Abella *et al.* 2009); seed bank density of *Bromus rubens* 5 to 31 years post-fire in a blackbrush community (Jurand 2012; Jurand and Abella 2013); and seed bank density of woody species 10 years after a fire at a blackbrush site (Lei 2001). Collectively, these vegetation and seed bank studies suggest that annuals and non-native plant species are more resilient to fire than are perennials and native plant species. These general patterns form the foundations of the hypotheses that were evaluated in the current study.

There is also a need to evaluate the utility of burn severity (BARC) maps that are typically created to help inform the development of ES&R and BAER plans. Although these maps most directly estimate absolute or relative vegetation consumption, they are often used to estimate where seed bank and/or vegetation abundance has been most negatively affected and post-fire seeding projects are then prioritized to those areas. The problem is that there has been no systematic effort to evaluate how closely these burn severity estimates correlate with post-fire seed bank and vegetation abundance. As a result, seeding treatments may be applied where they are not needed.

Objectives and Hypotheses

This project was designed to evaluate the short-term effects of fire on soil seed bank diversity and density, and associated vegetation diversity and cover, following the Hackberry Fire Complex of summer 2005. A secondary objective was to evaluate the correlations between measures of burn severity and seed bank and vegetation abundance. Our focus was on the first 3 post-fire years, which correspond directly to the timeframe of ES&R and BAER projects. We focused on middle elevation sites that span the blackbrush and sagebrush/pinyon-juniper woodland vegetation zones, two Mojave Desert vegetation types that are susceptible to burning (Brooks and Matchett 2006) and are often the focus of post-fire seeding efforts (e.g. Brooks and Klinger 2011; Klinger *et al.* 2011b). The vegetation plots established in this study were also integrated into the NPS fire effects database, creating a permanent record that will facilitate revisiting them in the future. We also used ground-based burn severity data to evaluate the ecological relevancy of the burn severity (BARC) map produced for the Hackberry Fire Complex BAER team.

The seven hypotheses that were tested are:

- Hypothesis 1: Soil seed bank diversity will be <u>lower</u> in burned than unburned areas.
- Hypothesis 2: Soil seed bank density will be <u>lower</u> in burned than unburned areas.
- Hypothesis 3: Vegetation diversity will be <u>lower</u> in burned than unburned areas.
- Hypothesis 4: Perennial plant cover will be <u>lower</u> in burned than unburned areas.
- Hypothesis 5: Annual plant cover will be <u>higher</u> in burned than unburned areas.
- Hypothesis 6: Non-native plant cover will be <u>higher</u> in burned than unburned areas.
- Hypothesis 7: Native plant cover will be <u>lower</u> in burned than unburned areas.

Study Description and Location

Study area

This study was conducted in the eastern Mojave Desert, at the Mid Hills region within the Mojave National Preserve (MOJA), San Bernardino Country, California, USA (NAD 83 UTM Zone 11 643436 E, 3887857 N, general location) within and adjacent to the Hackberry Fire Complex of 2005. The topography of the region is gently rolling degenerate granite hills, monzo-granite rock piles and volcanic mesas between 1400-1700 meters with soils composed of a course granitic type low in organic matter. The region receives approximately 16 cm of rainfall annually, 2/3 in the winter and 1/3 in the summer, supporting both a winter and a summer flora (Rowlands *et al.* 1982). Vegetation in the study area is typical of the middle elevation ecological zone and lower parts of the high elevation ecological zone of the Mojave Desert (Brooks and Minnich 2006). Vegetation was dominated by blackbrush (*Coleogyne ramossissma*) and big sagebrush (*Artemisia tridentata*) and lower and upper elevations respectively, and co-dominant species included banana yucca (*Yucca baccata*), bitterbrush (*Purshia tridentata*), goldenbush (*Ericameria* spp.), purple sage (*Salvia dorii*), and Utah Juniper (*Juniperus osterosperma*).

The Hackberry Fire Complex started on June 22, 2005 from dry lightning strikes which ignited numerous fires across the MOJA. These fires followed a period of record rainfall during the 2004-2005 winter producing high amounts of fine fuels from herbaceous perennial and annual plants. The combination of low relative humidity, high temperatures, wind gusting at 10-20 mph, steep topography and ample fine fuels allowed for the fires to spread rapidly. The Hackberry Complex Fire BAER team reported that thunderstorms moving through the area caused downburst winds with little or no precipitation in the area during the burning event. Fire intensity was variable, but generally moderate to low over the entire area based on the heterogeneity of the burn pattern and amount of shrub skeletons that were not completely consumed by fire. (ML Brooks personal observation). The complex burned for 6 days until it was finally contained on June 28, 2005, with a total of the 28,697 hectares (70, 912 acres) burned (National Interagency Burned Area Emergency Response Team 2005).

Experimental design and sampling

Using fire perimeter and burn severity maps generated by the Hackberry Fire Complex BAER team, and digital elevation and surficial geology maps, we identified burned and unburned areas located in proximity to each other on similar slope, aspect, elevation, and geologic strata. These sampling strata were further constrained within GIS to contain only Federal land that was relatively undisturbed prior to burning, using maps identifying land use history, historical fires, and transportation routes. Undisturbed areas were defined as those > 100 m from livestock infrastructure (e.g. watering tanks, corrals), home sites or other buildings, mines, utility corridors (e.g. pipelines, transmission lines, etc.), past fires, and transportation corridors (e.g. open and closed vehicle routes). We also screened for sites 100-500 m from a vehicular access point (i.e. an open vehicle route) to facilitate access by foot within wilderness areas. After ground-truthing and eliminating a number of sites which were misrepresented by the spatial data, we identified 6 sites that matched our criteria which were then used as replicate sampling blocks, each containing one burned and one unburned experimental unit. Within each experimental unit, we randomly established 5 non-overlapping sampling units resulting in the following randomized blocks study design: 6 blocks (groups) × 2 fire treatments (burned/unburned) × 5 sampling units = 60 total

sampling units. Each sampling unit consisted of a 5 m x 30 m FMH brush belt transect (USDI National Park Service 2001) centered within a 20 m x 50 m modified Whittaker plot (Stohlgren *et al.* 1995). The corners of the belt transect were permanently marked with 3/8 inch rebar and georeferenced using a GPS unit.

Seed bank diversity and density were derived using data associated with ten 1 m² subplots, five each located at random points along the 30 m sides of the belt transect. All soils were collected within four 5.0 cm diameter (19.6 cm^2) x 5 cm deep (volume = 98.2 cm³) circular cores located just outside the corner of each subplot and these cores were combined to create a single pooled soil sample for each subplot (392.7 cm³ combined sample volume). Soil seed banks were assayed by removing a 59.0 cm^3 subsample from each soil sample and then growing it out in a greenhouse and counting the number of seedlings of each species that emerged after being treated with various wetting and drying and chemical treatments . The specific treatments and procedures were adapted from standard seed bank assay methods (Brenchley and Warington 1939; Young and Evans 1975; Belnap *et al.* 2008). A subsample of each soil sample was assayed rather than using the total soil sample to allow more samples to be analyzed due to limited resources to perform the assays and to retain archived samples that could be analyzed during subsequent years in the event that any samples had to be discarded due to mold, decay, or other confounding factors. Because each soil sample was mixed to homogenize it prior to collecting the 59.0 cm^3 subsample, each subsample was assumed to contain representative seeds of all species present in the total soil sample. Thus, diversity values were based on the full soil sample volume of 392.7 cm³ and a 5.0 cm deep soil area of 78.5 cm^2. The resulting seed bank density values were based on the soil subsample volume of 59.0 cm^3 and the associated 5.0 cm deep soil area of 11.8 cm^2, and scaled to seeds per 1 m^2 to facilitate comparison with other published seed bank data.

Cover of woody perennial and herbaceous plants, litter and soil was measured by the point-intercept method, using a single side of the 5 m x 30 m belt transect. Starting at the end of each transect and repeated every 30 cm, a 0.25 inch diameter sampling rod, graduated in decimeters, was lowered gently so that the sampling rod is plumb to the ground. Since the transect length was 30 m, there were 100 points from 30 to 3,000 cm. The height at which each species touches the sampling rod was recorded, tallest to shortest. If the rod failed to intercept any vegetation, the substrate was recorded (e.g., bare soil, rock, litter) (USDI National Park Service 2001). Plant species numbers were measured in spatially nested modified-Whittaker plots at 1 m², 10 m², 100 m² and 1,000 m² scales within the 20 m x 50 m mod-whit plot (Stohlgren *et al.* 1995).

Burn severity maps were obtained from the Hackberry Fire Complex BAER team. These maps are derived from Landsat satellite imagery and are typically created for post-fire characterization of "soil burn severity" or for research and as a proxy for vegetation consumption, vegetation mortality, and other fire effects (Eidenshink *et al.* 2007). The Normalized Burn Ratio (NBR) is a remote sensing image derivative that exploits the characteristics of the near-infrared and short-wave infrared portions of the electromagnetic spectrum as they have proven to be good discriminators of burn scars and the mosaic of severities that typically occur within a fire perimeter. The dNBR compares NBR imagery acquired before the fire with imagery of the same area acquired after the fire to identify the location and magnitude of changes in vegetation. The NBR is computed using Landsat Enhanced Thematic Mapper (ETM) or Thematic Mapper (TM) near-infrared (NIR) and short-wave infrared (SWIR) spectral bands (4 and 7) respectively. For burn severity mapping purposes, the NBR is generally calculated for both a pre- and post-fire image and then used to derive a differenced NBR (dNBR) as follows:

$dNBR = NBR_{prefire} - NBR_{postfire}$. A relativized dNBR (RdNBR) is also calculated to evaluate potential limitations of dNBR to characterize fire severity on low biomass sites and potentially enhance inter-fire comparability of the results at larger scales. The RdNBR data have been shown to have stronger

correlations to Composite Burn Index plot data in some western ecosystems (Randy McKinley, pers. comm.). Burn severity maps are typically validated with ground-based Composite Burn Index (CBI) measurements comparing burned with remaining unburned vegetation using the density and cover methods described above for woody perennial vegetation (USDI National Park Service 2001). One CBI plot was established at the center of each of the belt transects within burned vegetation in this study.

Field sampling was conducted within the 60 sampling units (20 m x 50 m modified Whittaker plots) during 2005 through 2007 follows. Soil seed bank samples were collected in late summer in September 2005 (3 months after the fire) before the first fall rains to characterize the immediate effects of fire before the first post fire germination event. This initial time was referred to as year post-fire 0 (YPF 0). Similar soils seed bank sampling was done in September 2006 (YPF 1) and 2007 (YPF 2). Aboveground vegetation measurements were done during peak annual plant productivity in spring 2006 (YPF 1), 2007 (YPF 2), and 2008 (YPF 3). CBI data were collected during September 2005, but only from the 30 burned sampling units.

Data analysis

Seed bank and Vegetation

Multilevel models were used to analyze patterns of seed bank diversity and density, and vegetation diversity and cover. Seed bank density and vegetation cover were each evaluated at multiple hierarchical levels including total values, evolutionary origin inside or outside of North America (natives, non-natives), life history (annual, perennial), and life or growth form (grass, forb, shrub, tree). Multilevel models are a very flexible and robust set of methods where parameter estimates are derived with maximum-likelihood and variance is partitioned into fixed and random effects (Gelman and Hill 2007). Fixed effects in the models included burn condition (burned and unburned), the linear and quadratic effects of time (year post-fire; year and year2), and the interaction between burning and time. Because plots were located in a hierarchical spatial arrangement, groups of plots were considered a level-2 random effect (N = 5 plots per group; N = 12 groups). Model building proceeded in a two-step procedure. First, the bias-corrected Akaike Information Criteria (AICc) was used to determine the model with the greatest support from a pool of 6 possible fixed effects models (Table 1). After the fixed-effect model with the greatest support was selected, three additional models with random effects were added to the model pool (the best-supported model with random intercepts, random slopes, and random intercepts and slopes). AICc was then used to compare the fixed and random effects models and select the one with the greatest level of support.

We derived four diversity indices for aboveground vegetation and seed banks. Three of these indices comprised Hill's series (Hill 1973 , Magurran 2004); N0, the overall species richness in a sample; N1, which equals expH', where H' is Shannon's index of diversity; and N2, the reciprocal of Simpson's index. Hill's series is considered one of the most useful measures of diversity because the units are species numbers (more specifically, the "effective" number of species in a sample) (Routledge 1979, Tóthmérész 1995, Legendre and Legendre 1998). The fourth index we derived was Simpson's index of evenness:

$E1/d = (D-1/S)$

where D = Simpson's index of concentration (Magurran 2004) and S the total number of species in a sample. E1/d has what are generally considered to be the most desirable properties among evenness

indices, especially because it is not sensitive to differences in species richness among samples (Magurran 2004, Smith and Wilson 1996). It is particularly useful when a community is dominated by a few species (see Results; Smith and Wilson 1996). The diversity indices for the aboveground vegetation data were derived from absolute cover values while the indices for seed banks were derived from mean seed bank density (59 cm3 per sampling unit). Because diversity indices vary in their sensitivity to rare species (and hence, interpretation of diversity patterns), we displayed values for Hill's series as diversity profiles (Tóthmérész 1995). If a profile in one condition (e.g. unburned) is greater than that of all three indices in another condition (e.g. burned), then the diversity patterns can be unambiguously interpreted. However, if the profiles in different conditions cross then diversity must be interpreted differently for each index .

Table 1. Models that were evaluated and reported in the results listed in Appendices 1-5.
The first set of models were used for analyses reported in appendices 1 (seed bank diversity), 2 (seed bank density, 3 (vegetation species diversity), and 5 (vegetation species cover), and the second set of models were used in Appendix 4 (multiple scale vegetation species richness).

Model #	Variables	

Models used for analyses reported in Appendices 1, 2, 3, and 5

1	Null – fixed intercept	
2	Model 1 + year	(fixed intercept + year)
3	Model 2 + year^2	(fixed intercept + year + year^2)
4	Model 3 + burn	(fixed intercept + year + year^2+ burn)
5	Model 4 + year×burn	(fixed intercept + year + year^2+ burn + year×burn)
6	Model 5 + year^2×burn	(fixed intercept + year + year^2+ burn + year×burn + year^2×burn)
7	One of the previous models with the greatest support + random intercept (group)	
8	One of the previous models with the greatest support + random slope (group)	
9	One of the previous models with the greatest support + random intercept + random slope	

Models used for analyses reported in Appendix 4

1	Null – fixed intercept	
2	Model 1 + year	(fixed intercept + year)
3	Model 2 + year^2	(fixed intercept + year + year^2)
4	Model 3 + area	(fixed intercept + year + year^2 + area)
5	Model 4 + burn	(fixed intercept + year + year^2+ area + burn)
6	Model 5 + year x area	(fixed intercept + year + year^2+ area + burn + year×area)
7	Model 6 + year^2×area	(fixed intercept + year + year^2+ area + burn + year×area + year^2×area)
8	Model 7 + area×burn	(fixed intercept + year + year^2+ area + burn + year×area + year^2×area + area x burn)
9	Model 8 + year×area×burn	(fixed intercept + year + year^2+ area + burn + year x area + year^2×area + area×burn + year×area×burn)
10	Model 9 + year^2×area×burn	(fixed intercept + year + year^2 + area + burn + year×area + year^2×area + area×burn + year×area×burn + year^2×area×burn)
11	One of the previous models with the greatest support + random intercept (group)	
12	One of the previous models with the greatest support + random slope (group)	
13	One of the previous models with the greatest support + random intercept + random slope	

Multilevel models were used to analyze patterns of species richness across the four plot sizes (1 m^2, 10 m^2, 100 m^2, and 1,000 m^2). Fixed effects in the models included plot size, burn condition, the linear and quadratic effects of time (year and $year^2$), three two-way interactions (area×burn, area×year, area×year2), the three-way interaction between plot size, burning and year, and the three-way interaction between plot size, burning and $year^2$ (Table 1). Groups of plots (within each of 6 blocks) were considered a level-2 random effect. Model building was conducted with the same approach described above. The analyses were based on the mean number of species per plot for the 1 m^2 and 10 m^2 sizes and the total number per plot for the 100 m^2 and 1,000 m^2 sizes. Annual and perennial species were analyzed separately.

Differences in species composition among plot sizes across time and burning conditions were analyzed with Analysis of Similarity (ANOSIM) followed by a similarity percentage analysis (SIMPER) when the ANOSIM indicated significant differences in composition. ANOSIM is a non-parametric multivariate analysis of variance that uses a distance matrix to determine if species composition differs between two or more conditions (Clarke 1993). A test statistic R is calculated that measures the mean rank dissimilarities between groups relative to within groups. R can range between 1 and -1; as R approaches 1 species composition is becomes increasingly greater between groups than within groups, R values near 0 indicate no differences in species composition between groups, and R values that approach -1 indicate species composition is more different within groups than between them. We used the Sorenson dissimilarity measure (Legendre and Legendre 1998) calculated from the incidence of species per plot and 999 bootstrap samples to determine the significance of R. SIMPER is conducted after an ANOSIM to compute the percentage contribution of each species to the dissimilarity between all pairs of sampling units between groups and within groups (Clarke and Warwick 1994). Species with a large average dissimilarity/standard deviation ratio are those that discriminate most between groups.

Burn Severity

The correspondence between the ground-based CBI data from the 30 burned sampling units and the burn severity map were evaluated quantitatively using regression methods (Bobbe *et al.* 2004). CBI scores and burn severity values (dNBR, RdNBR) were extracted from GIS maps based upon a bilinear (nearest 2x2 pixel) weighting option then input to a linear regression. Two separate analyses were performed for CBI vs. dNBR and CBI vs. RdNBR. Linear regression analyses were then used to evaluate relationships between each of the three measures of burn severity (CBI, dNBR, and RdNBR) and seed bank density and aboveground vegetation cover variables.

Results

Seed bank diversity

Species richness (N0) was lower in burned than unburned areas during YPF 0 and 1, then converged to no difference in YPF 2 (Fig. 1A). The three models with the greatest relative support for richness (99% cumulative relativized AIC weights) each included Model 6 (fixed intercept + year + $year^2$ + burn + year×burn + $year^2$×burn) (Table 1) and individually included random slope, random intercept, and slope plus intercept in ascending order of importance (Appendix 1). The diversity metrics N1 and N2 displayed similar patterns across YPF, with the most pronounced decreases in burned areas during YPF 1, followed by a convergence in YPF 2 (Fig. 1C and D). The three models with the greatest

relative support for N1 (96% cumulative relativized AIC weights) each included Model 6 and individually included random slope, random intercept, and slope plus intercept in ascending order (Appendix 1). The three models with the greatest relative support for N2 (94% cumulative relativized AIC weights) each included Model 6 as well, and individually included random intercept, random slope, and slope plus intercept in ascending order (Appendix 1). In contrast, species evenness (E1/d) was slightly increased by burning (Fig. 1B). The two models with the greatest relative support for evenness (82% relativized AIC weights) Model 4 (fixed intercept + year + year^2 + burn) (Table 1) and individually included random intercept and random intercept plus slope in ascending order of importance (Appendix 1).
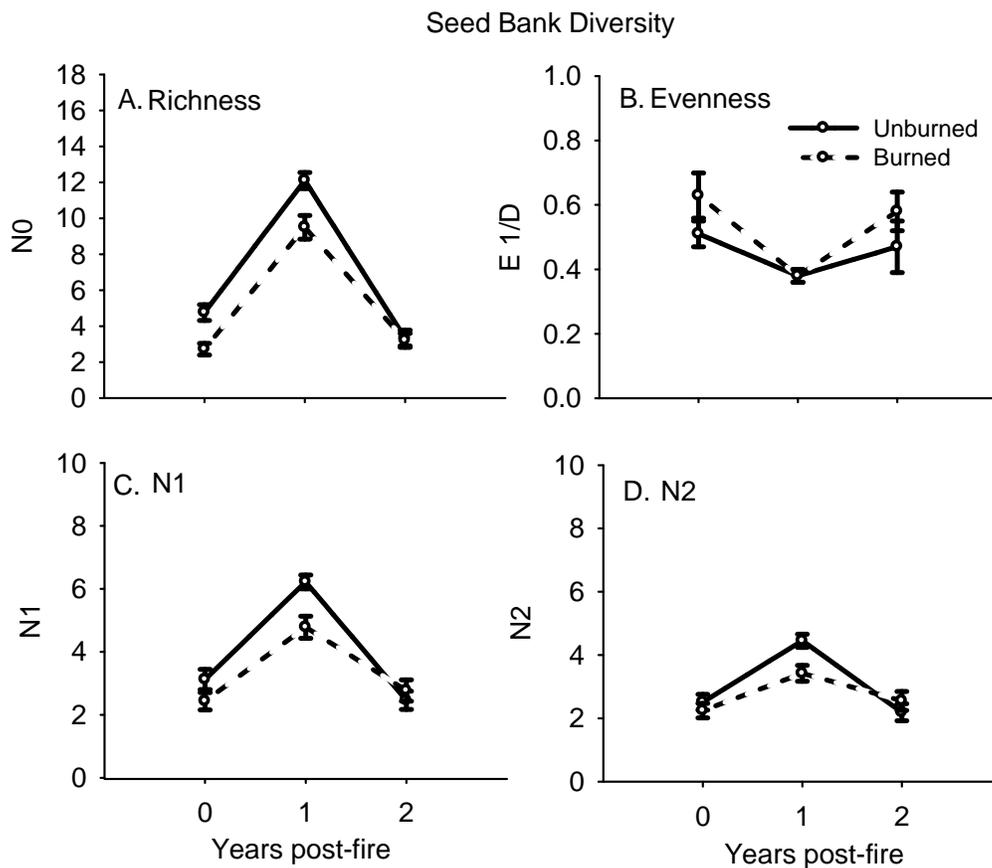

Fig. 1. Seed bank species richness (A), evenness (B), N1 Shannon's diversity (C) and N2 Simpson's diversity (D) for each of in burned and unburned plots during the first September post-fire (YPF 0) and two subsequent Septembers (YPF 1 and 2). Data are means (±SE) based on a soil volume of 392.7 cm³ (5.0 cm deep soil area of 78.5 cm^2) and n=6 replicate blocks.

These seed bank diversity results indicate significant effects of burning, year, and a burn x year interaction for species richness, N1, and N2 (Appendix 1), reflecting decreased values in burned areas during YPF 0 and 1, but not 2 (Fig 1). Only effects of burning and year were significant for species evenness (Appendix 1), reflecting slightly higher values in burned areas during all three years (Fig. 1B). The effect of year was generally greater than the effect of burning for all four seed bank diversity metrics (Fig. 1).

Seed bank density

Total seed bank density was lower by 81% in burned (974 seeds/m^2) than unburned (5,094 seeds/m^2) areas during YFP 0, but this difference was not significant during the subsequent two years (Fig. 2). This difference was due to annual plant density which was reduced by over half in burned compared to unburned areas during YPF 0 and by about one quarter during YBP 1, before it converged to no difference during YPF 2 (Fig. 3A). The two models with the greatest relative support for annual density (99% relativized AIC weights) each included Model 5 (fixed intercept + year + year2 + burn + year2 × burn + year × burn (Table 1) and individually included random intercept and random intercept plus random slope in ascending order of importance (Appendix 2).

Fig. 2. Total seed bank density in burned and unburned plots during the first September post-fire (YPF 0) and two subsequent Septembers (YPF 1 and 2). Data are means (±SE) based on a soil volume of 59.0 cm**3** (5.0 cm deep soil area of 11.8 cm²), also scaled to a soil area of 1 m², and n=6 replicate blocks.

Perennial seed bank density was exceedingly low overall (Fig. 3 B), comprising 0%, 1%, and 1% of the total seed bank in burned areas, and 1%, 3%, and 2% in unburned areas, during YPF 1, 1, and 2 respectively. However, burning did lead to decreased seed banks of native perennial grasses during YPF 1 (Table 2), due to *Elymus elymoides* which 37 seeds/m^2 in burned areas and 212 seeds/m^2 unburned areas during that year. The two models with the greatest relative support for perennial density (80% relativized AIC weights) in ascending order of importance included Model 6 (fixed intercept + year + year2 + burn + year×burn + year2×burn) (Table 1) plus random intercept and random slope, and Model 5 plus year^2×burn.

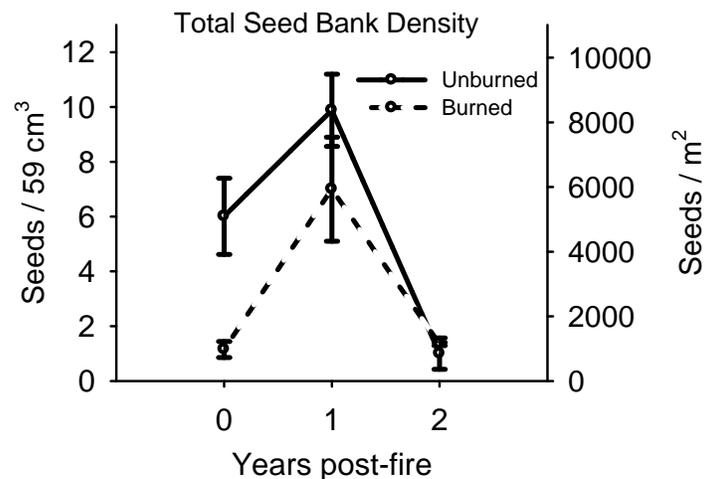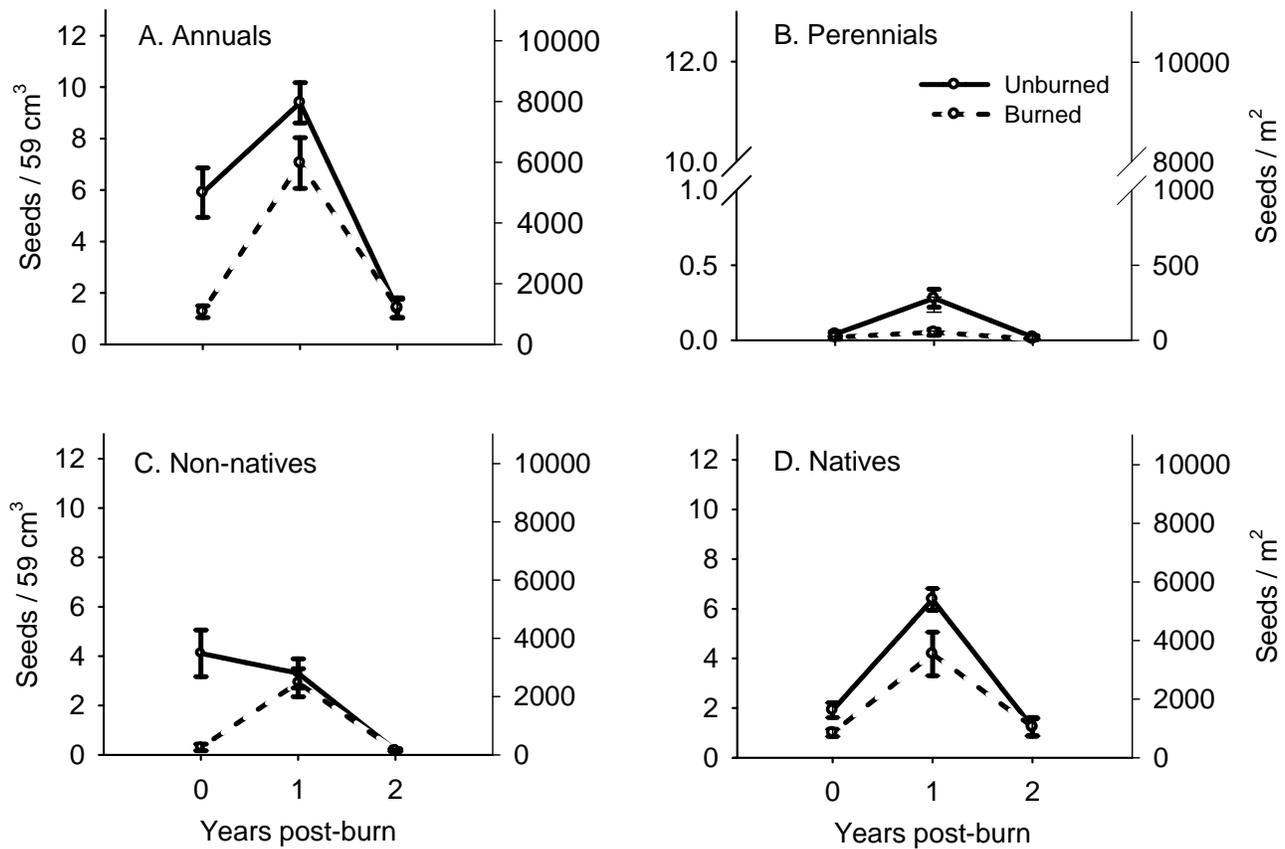**Fig. 3.** Seed bank density of annual (A), perennial (B), non-native annual (C) and native (D) species in burned and unburned plots during the first September post-fire (YPF 0) and two subsequent Septembers (YPF 1 and 2). Data are means (±SE) based on a soil volume of 59.0 cm^3 (5.0 cm deep soil area of 11.8 cm^2), also scaled to a soil area of 1 m^2, and n=6 replicate blocks.

Non-natives seed bank density was 94% lower in burned than unburned areas, but only during YPF 0 (Fig. 3C). Densities were the same in burned and unburned areas during YPF 1 and 2. The two models with the greatest relative support for non-native density (100% relativized AIC weights) each included Model 6, and individually included random intercept and random intercept plus random slope (Appendix 2). Among non-native species guilds, non-native annual grasses were significantly affected during YPF 0 and 1 (Table 2). This difference was due to *Bromus* spp. which had seed densities in burned compared to unburned areas of 34 versus 1316 seeds/m^2 during YPF 0, and 164 versus 1398 seeds/m^2 YPF 1. The other non-native annual grass, *Schismus barbatus*, was not detected in the seed bank in YPF 0 or 2, and in YPF 1 had similar seed bank densities in burned and unburned areas of 422 and 525 seeds/m^2 respectively.

Native seed bank density was decreased by 54% and 34%, but only during YPF 0 and YBP 1 respectively (Figure 3D). The two models with the greatest relative support for native annual density (100% relativized AIC weights) each included Model 6 and individually included random slope and random intercept plus random slope (Appendix 2). Burning also led to decreased seed banks of native annual forbs during YPF 0 (Table 2), during which seed bank densities were lower in burned compared

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to unburned areas for *Lepidium lasiocarpum* var. *lasiocarpum* (34 versus 73 seeds/m^2), *Cryptantha pterocarya* (25 versus 116 seeds/m^2), and *Pectocarya setosa* (31 versus 116 seeds/m^2). Native annual grass seed bank density was also lower in burned areas during YPF 1 (Table 2), due to *Vulpia octoflora* which had densities in burned compared to unburned areas of 1048 versus 2715 seeds/m^2.

These seed bank density results indicate significant effects of burning, year, and a burn x year interaction for all metrics evaluated (Appendix 2), reflecting general decreased values in burned areas during YPF 0 and 1, but not 2 (Figs. 2 and 3). The effect of year was also greater than the effect of burning, except for perennials which had low overall values.

Table 2. Seed bank density.

Eight native/non-native life history/life form species guilds in burned and unburned plots during the first September post-fire (YPF 0) and two subsequent Septembers (YPF 1 and 2). Data are means (±SE) scaled to 1 m^2 from a soil assay volume of 59.0 cm^3 (5.0 cm deep soil area of 11.8 cm^2) and n=6 replicate blocks. Notable within-year decreases due to fire are highlighted in bold font.

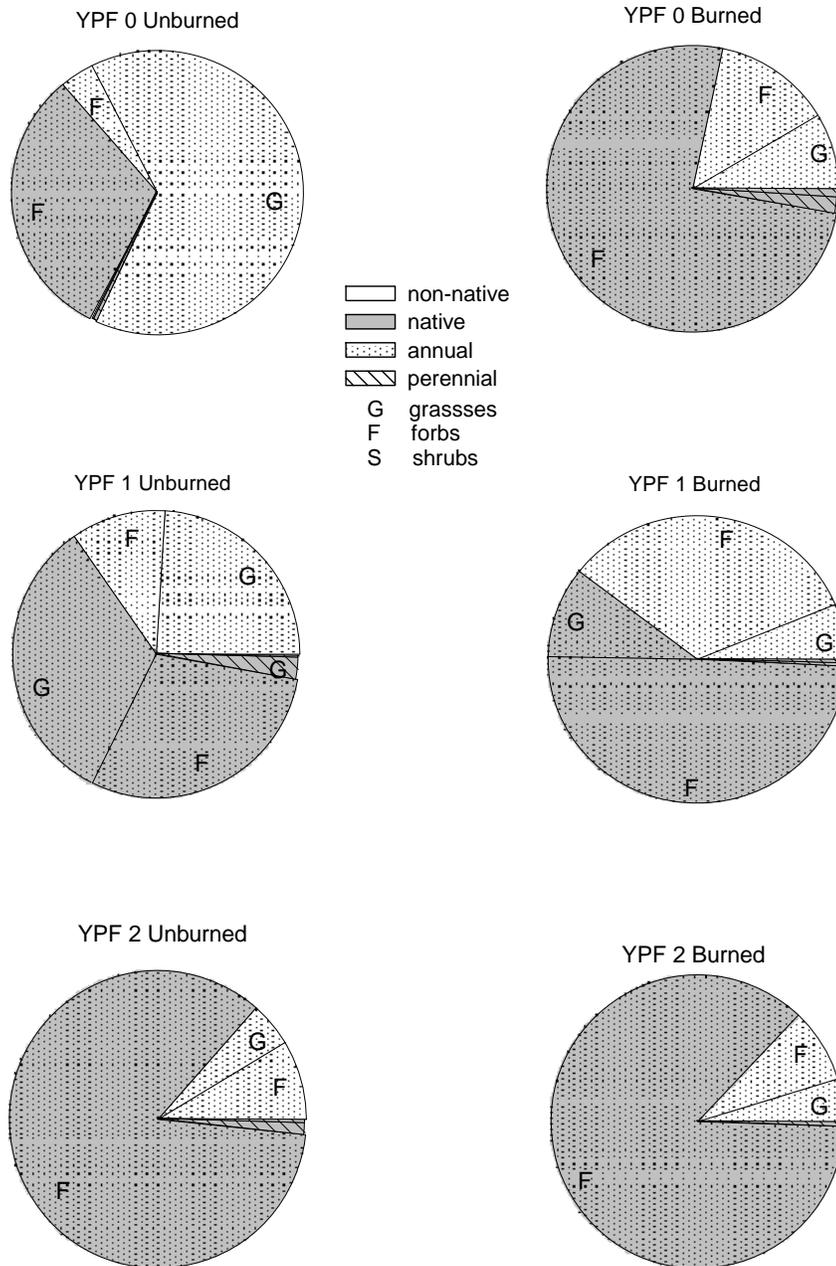| Native/non-native	Life history/life form	Burned/unburned	Years post-fire (YPF)		
			0	1	2
Non-native	Annual grass				
		Burned	**85 ±42**	**383 ±153**	54 ±47
		Unburned	**3259 ±969**	**2010 ±588**	73 ±38
Non-native	Annual forb				
		Burned	127 ±62	1944 ±757	94 ±39
		Unburned	194 ±125	896 ±385	41 ±16
Native	Annual grass				
		Burned	0 ±0	**622 ±223**	0 ±0
		Unburned	0 ±0	**2762 ±507**	0 ±0
Native	Annual forb				
		Burned	**736 ±221**	2939 ±1359	992 ±498
		Unburned	**1605 ±399**	2470 ±262	716 ±444
Native	Perennial grass				
		Burned	0 ±0	**23 ±19**	0 ±0
		Unburned	9 ±9	**210 ±74**	0 ±0
Native	Perennial forb				
		Burned	18 ±18	23 ±6	6 ±6
		Unburned	20 ±9	16 ±8	11 ±8
Native	Shrub				
		Burned	9 ±9	0 ±0	0 ±0
		Unburned	7 ±7	11 ±6	3 ±3
Native	Tree				
		Burned	0 ±0	0 ±0	0 ±0
		Unburned	0 ±0	0 ±0	0 ±0

Fig. 4. Proportion of seed bank density origin (non-native, native), life history (annual, perennial), and growth form (grass, forb, shrub) in burned and unburned plots during the first September post-fire (YPF 0) and two subsequent Septembers (YPF 1 and 2). Note that there were no tree species detected in the seed bank.

By far the greatest proportion of the seed bank was comprised of annual species, ranging from 0.97-1.00 of total seeds during any given combination of year and burn condition (Fig. 4). The relative proportions within the other two species guilds (non-native, native origins; grass, forb, shrub life forms) differed somewhat between burned and unburned areas, but also varied widely among years.

Non-natives comprised a much lower proportion of the seed bank in burned (0.22) than unburned (0.68) areas during YPF 0, but proportions were similar during YPB 1 and 2 (Fig. 4). The proportion of non-natives also varied as much among years as they did between burned and unburned areas, ranging 0.13 (YPF 2) - 0.39 (YPF 1) in burned areas and 0.14 (YPF 2) – 0.68 (YPF 0) in unburned areas (Fig. 4).

The proportion of grasses was lower in burned than unburned areas during YPF 0 (0.09 and 0.64 respectively) and YPF 1 (0.17 and 0.60), but then was similar during YPF 2 (0.05 and 0.09) (Fig. 4). In contrast, the proportion of forbs was higher in burned than unburned areas during YPF 0 (0.90 and 0.36) and YPF 1 (0.83 and 0.40), and was similar during YPF 2 (0.95 and 0.91). Thus, burning decreased the proportion of grasses but increased the proportion of forbs during the first two post-fire years, but that effect was no longer present during YPF 2.

Vegetation diversity

Three of the four measures of vegetation diversity were consistently lower in burned than unburned areas across all years, although the magnitude of the difference was less pronounced in YPF 2 than in YPF 1 and YPF 3 (Fig. 5A, C & D). The two models with the greatest relative support for richness, N1, and N2 (100% cumulative relativized AIC weights) each included the following variables Model 4 (fixed intercept + year + year^2 + burn) and individually included random intercept plus random slope and random intercept (Appendix 3). In contrast, evenness was not different in burned and unburned areas during all three years (Fig. 5B). The model with the greatest relative support for evenness (100% cumulative relativized AIC weights) included Model 3 (fixed intercept + year + year^2) (Table 1) and individually included random intercept plus random slope and random intercept (Appendix 3). These results suggest primarily main effects of year on species evenness.

Aboveground Diversity
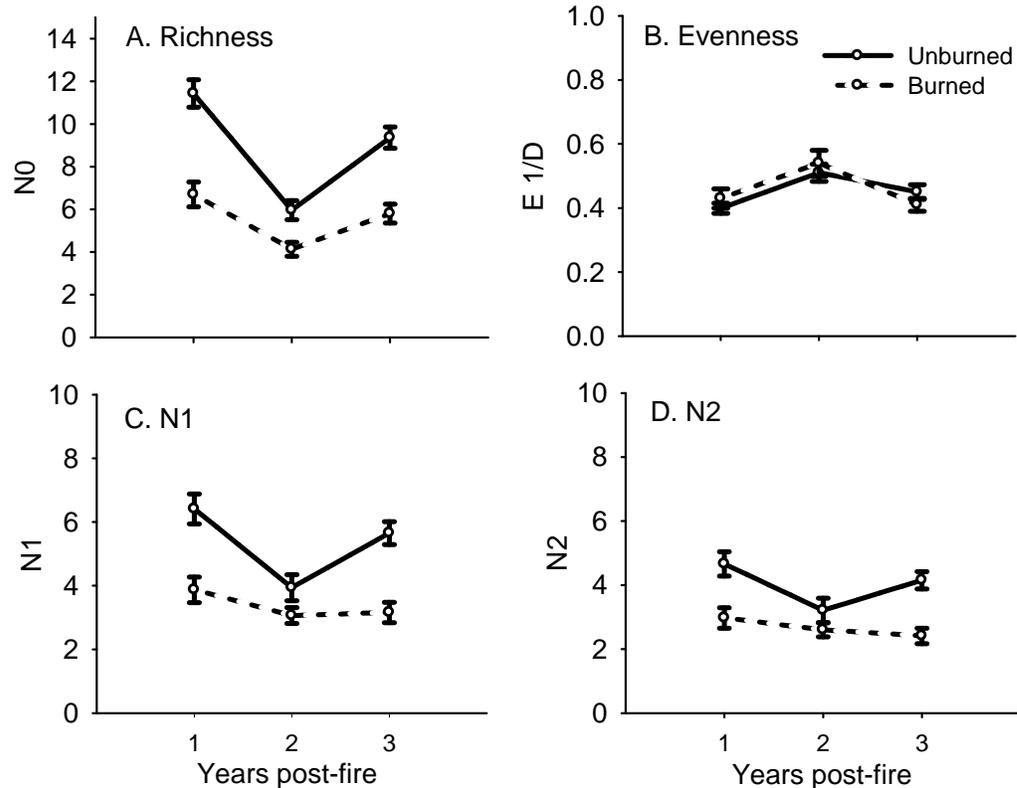
Fig. 5. Vegetation species richness (1m^2) (A), evenness (B), N1 Shannon's diversity (C) and N2 Simpson's diversity (D) in burned and unburned plots at peak annual plant productivity during the first three post-fire springs (YPF 1, 2, and 3). Data are means (±SE) of n=6 replicate blocks.

Species richness of annuals was only negligibly affected by burning at spatial scales from 1 to 1,000 m^2 across all three years (Fig. 6). This minimal effect was reflected in high similarity in annual species composition between burned and unburned conditions. Sorenson's index ranged from 79.7 (± 1.9 SE) to 89.4 (± 1.7 SE), and for any given plot size there was complete overlap of 95% confidence intervals across years. ANOSIM indicated that YPF 1 was the only year that composition varied between burned and unburned conditions, and this was only in 1 m^2 and 10 m^2 plots. *Bromus rubens*, *Pectocarya setosa*, and *Vulpia octoflora* occurred in 3x the number of 1 m^2 plots in unburned as burned conditions, which accounted for 17.3% of the cumulative difference in composition. *Descurainia pinnata*, *Lepidium lasiocarpum* var. *lasiocarpum,* and *Phacelia fremontii* occurred in 3-8x the number of 10 m^2 plots in burned as unburned conditions, which accounted for 12% of the cumulative difference in composition. The two models with the greatest relative support for annual species richness (100% cumulative relativized AIC weights) each included Model 10 (fixed intercept + year + year^2 + year×area + burn + area + year×area×burn + area×burn + year^2×area + year^2×area×burn (Table 1) and individually included random intercept plus random intercept and slope (Appendix 4).

Fig. 6. Annual plant species richness at each of four spatial scales within the 20 m x 50 m modified Whittaker plots in burned and unburned plots at peak annual plant productivity during the first three post-fire springs (YPF 1, 2, and 3). Data are means (±SE) of n=6 replicate blocks.

In contrast, species richness of perennials was consistently lower in burned than unburned areas during all three years and the difference became greater with increasing sampling area from 1 to 1,000 m2 (Fig. 7). The two models with the greatest relative support for perennial species richness (100% cumulative relativized AIC weights) each included Model 8 (fixed intercept + year^2 + year + area + burn + year^2×area + year×area + year^2×area×burn + year×area×burn + area×burn) (Table 1) and individually included random intercept and slope plus random intercept (Appendix 4).

These vegetation diversity results indicate significant effects of burning and year for richness, N1, and N2 (Appendix 3), reflecting lower levels in burned areas during all three post-fire years (Figs. 5A, C, D). They also suggest no effect of burning, but an effect of year for species evenness (Fig. 5B). The effect of burning and year had their greatest effects on species richness, which was driven by declines in perennial species that increased with increasing area, but was consistent in the burn effect among years (Fig 7). In contrast, annual species richness was not affected by burning, but was highly variable among years. Variability was so high among years that during the year when annual plant

productivity was lowest (YPF2), values at higher spatial scales (especially 10 and 100 m^2) approached those recorded at the lowest spatial scale (1m^2) during years of higher productivity.
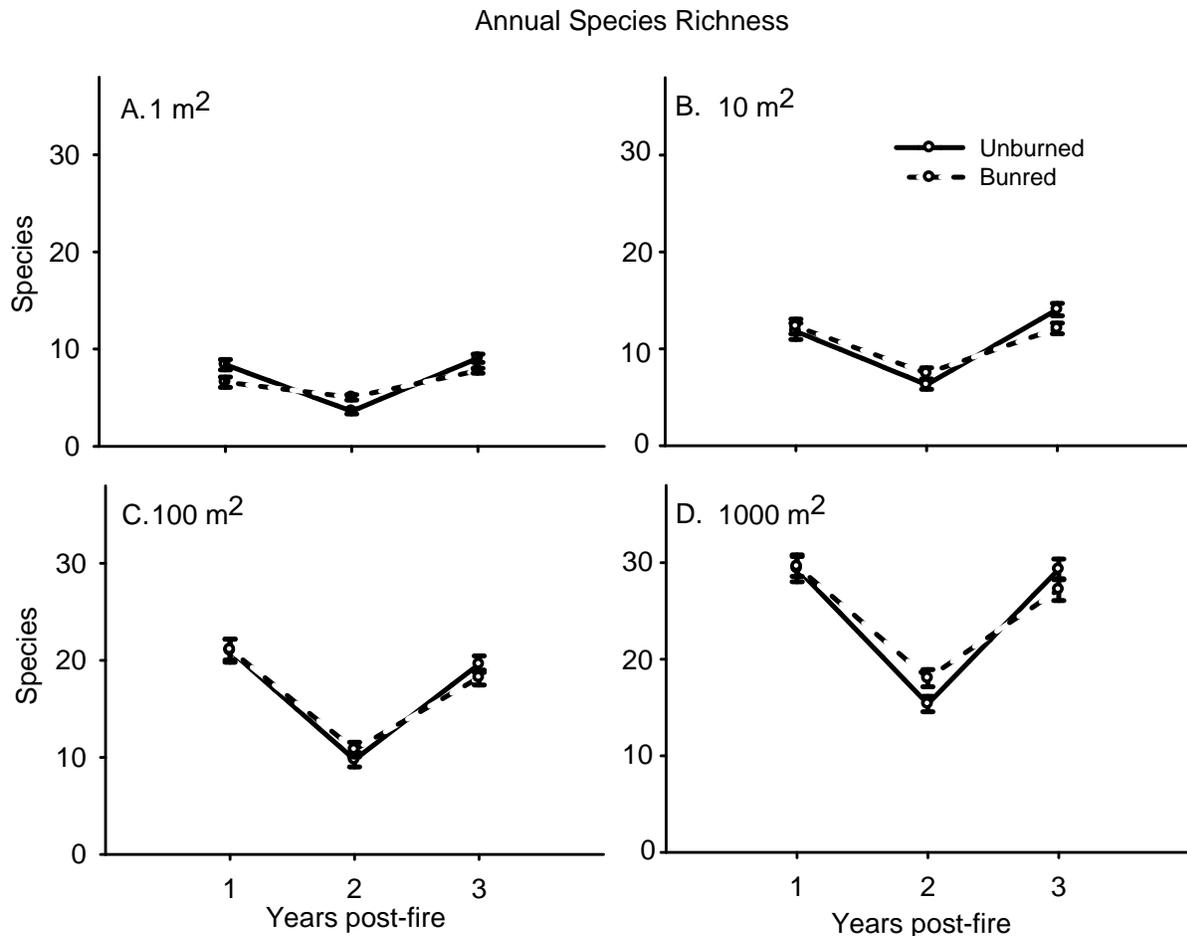
Perennial Species Richness
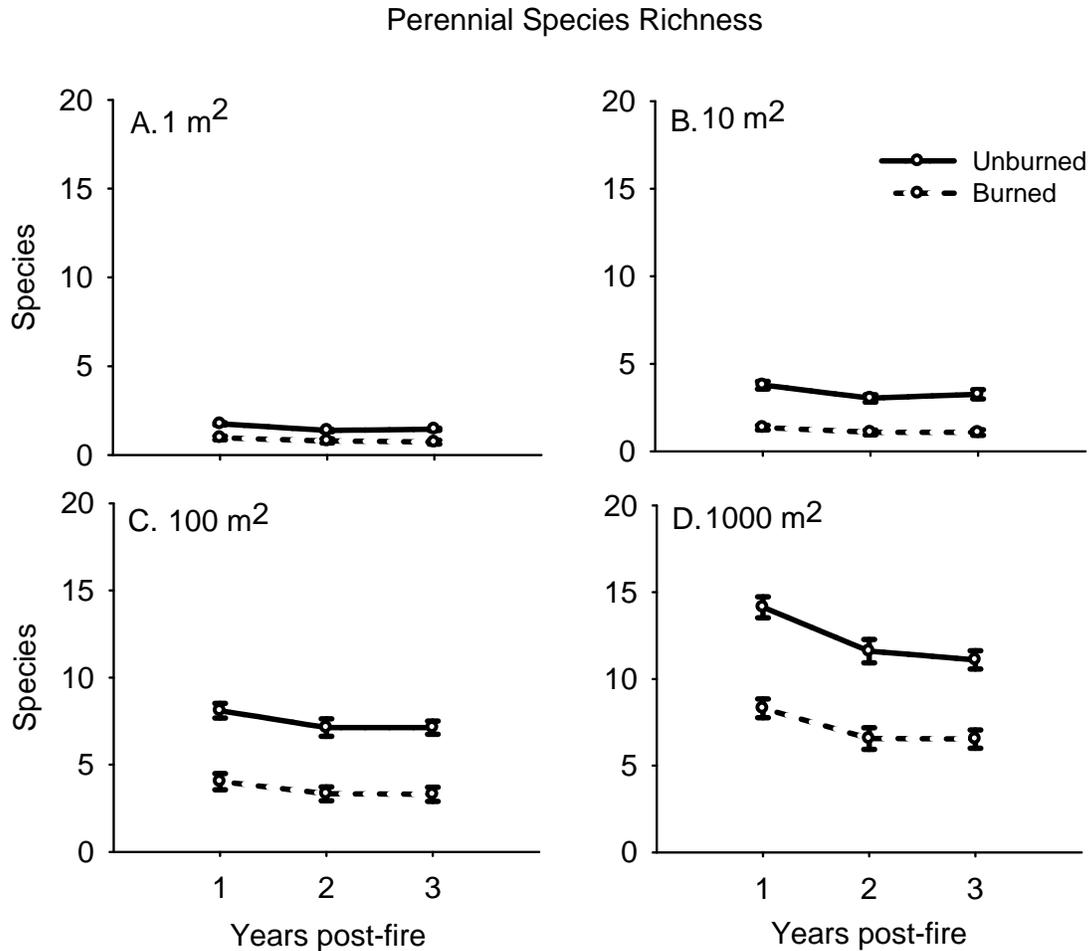
Fig. 7. Perennial plant species richness at each of four spatial scales within the 20 m x 50 m modified Whittaker plots in burned and unburned plots at peak annual plant productivity during the first three post-fire springs (YPF 1, 2, and 3). Data are means (±SE) of n=6 replicate blocks.

Vegetation cover

Total vegetation cover was lower in burned than unburned areas during all three post-fire years (Fig. 8). Percent declines in cover were 52% and 54% in YPF 1 and 2, and 23% in YPF 3. These differences were due to perennial cover and native cover which were consistently lower in burned than unburned areas during YPF 1-3 (Fig. 9 B and D). This pattern was primarily driven by cover of shrubs which was 10 times to 20 times lower burned than unburned areas (Table 3). Notable native shrubs with lower absolute cover in burned than unburned areas (burned YPF 1, 2, 3 versus unburned YPF 1, 2,3) included *Coleogyne ramossissima* (1%, 1%, 1% versus 14%, 12%, 11%) and *Artemisia tridentata* spp. *tridentata* (0%, 0%, 0% versus 10%, 8%, 6%). The two models with the greatest relative support for perennial cover (100% cumulative relativized AIC weights) each included Model 6 (fixed intercept +

year + year^2 + burn + year×burn + year^2×burn (Table 1) and individually included random intercept plus random slope random intercept (Appendix 5). The model with the greatest relative support for native cover (100% cumulative relativized AIC weights) was Model 4 (fixed intercept + year + year^2 + year×burn + burn) plus random intercept and random slope (Appendix 5).

Fig. 8. Total vegetation percent cover in burned and unburned plots at peak annual plant productivity during the first three post-fire springs (YPF 1, 2, and 3). Data are means (±SE) of n=6 replicate blocks

Absolute cover of annuals and non-natives were consistently higher in burned than unburned areas during YPF 1, 2, and 3 (Fig. 9 A and C). These patterns were driven primarily by non-native forbs which were 2 times to 10 times higher in burned than unburned areas (Table 3). Specifically, *Erodium cicutarium* absolute cover was much higher in burned (17%, 6%, 22%) than unburned (8%, 1%, 10%) areas during YBP 1, 2, and 3 respectively. Native forbs also contributed to higher annual cover during YPF 2 and 3 (Table 3). Notable native forbs with higher absolute cover in burned than unburned areas (burned YPF 2, 3 versus unburned YPF 2, 3) included *Pectocarya setosa* (2%, 1% versus 0%, 0%), *Amsinckia tessellat*a (1%, 1% versus 0%, 0%), *Cryptantha circumscissa* (1%, 1% versus 0%, 0%), *Cryptantha barbigera* (1%, 5% versus 0%, 3%), and *Descurania pinnata* (0%, 3% versus 0%, 0%). Non-native annual grasses had low overall cover (<1%) in burned and unburned areas and was comprised mostly of *Schismus barbatus* with minimal amounts of *Bromus tectorum* and *Bromus rubens*. The two models with the greatest relative support for annual cover (100% cumulative relativized AIC weights) each included Model 5 (fixed intercept + year + year^2 + burn + year^2×burn + year×burn (Table 1) and individually included random intercept plus random slope random intercept (Appendix 5). The two models with the greatest relative support for non-native cover (100% cumulative relativized AIC weights) each included Model 4 (fixed intercept + year + year^2 + year×burn + burn) (Table 1) and individually included random intercept and random intercept plus random slope (Appendix 5).
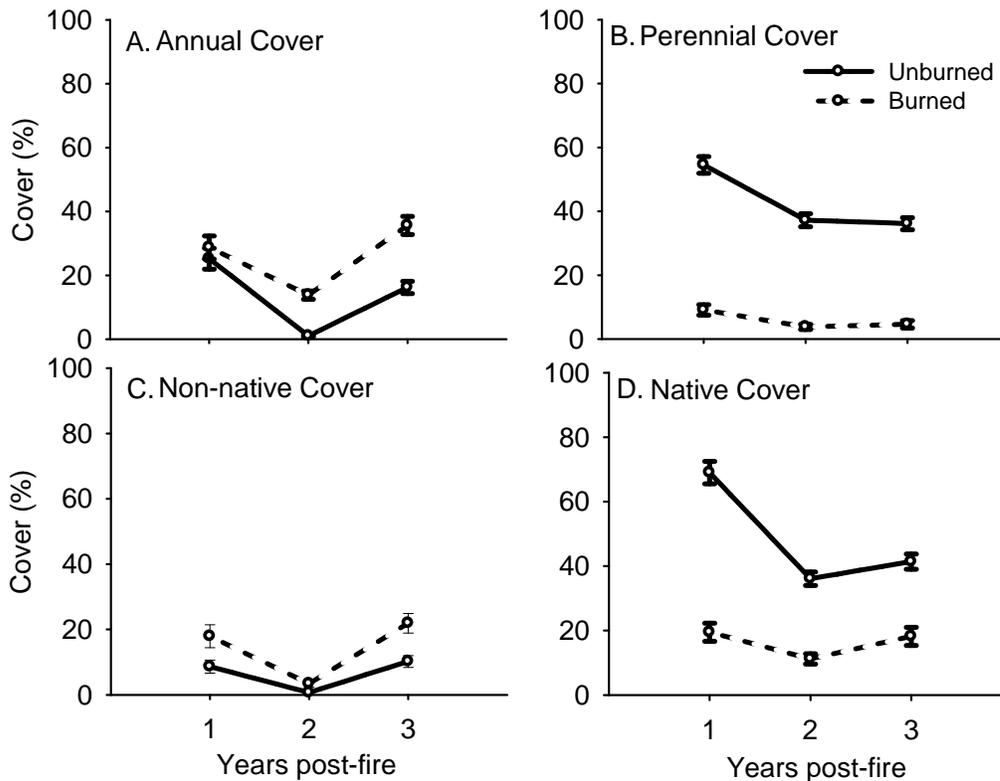
Fig. 9. Percent cover for annual (A) perennial (B), non-native annual (C) and native annual (D) species in burned and unburned plots at peak annual plant productivity during the first three post-fire springs (YPF 1, 2, and 3). Data are means (±SE) of n=6 replicate blocks.

These vegetation cover results suggest linear and non-linear effect of year on burn effects for annual cover, and a main effect of burning, and some variation the burn effect among years, for non-native cover. They also suggest a non-linear and linear effect of year on burn effects for both perennial and native annual cover. In general, annual cover was more affected by year than by burning (Fig. 8), and was primarily influenced by increases in non-native and native annual forbs in burned areas (Table 3). In contrast, perennial cover was more affected by burning than by year, driven entirely by decreased cover of shrubs in burned areas.

The relative proportion of annual cover was consistently higher in burned than unburned areas during all 3 post-fire years (0.76 vs 0.32; 0.78 vs. 0.03; 0.89 vs. 0.31) (Fig. 10). Similarly, the relative proportion of non-native cover was also higher in burned than unburned areas during all 3 years (0.48 vs. 0.11; 0.36 vs. 0.02; 0.55 vs. 0.20). These patterns were mirrored by proportional forb cover which was higher in burned areas during each year as well (0.85 vs. 0.30; 0.85 vs. 0.03; 0.95 vs. 0.31). In contrast, proportional cover in burned compared to unburned areas was lower during all 3 post-fire years for shrubs (0.10 vs. 0.52; 0.15 vs. 0.87; 0.04 vs. 0.60) and to a lesser degree for grasses (0.03 vs. 0.14; 0.00 vs. 0.07; 0.01 vs. 0.07). Thus, burning increased the proportion of annuals, non-natives and forbs, while decreasing the proportion of perennials, natives and shrubs.
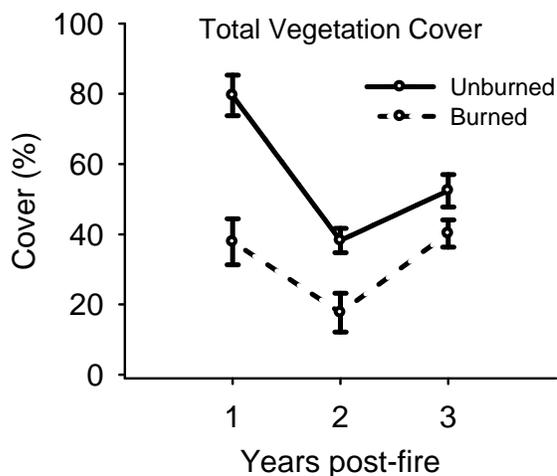
Table 3. Vegetation cover (%).
Ten native/non-native life history/life form species guilds in burned and unburned plots at peak annual plant productivity during the first three post-fire springs (YPF 1, 2, and 3). Data are means (±SE) based n=6 replicate blocks. Notable within-year decreases due to fire are highlighted in bold font, whereas increases are highlighted in bold underlined font.

Native/non-native	Life history/life form	Burned/unburned	Years post-fire (YPF)		
			1	2	3
Non-native	Annual grass				
		Burned	0.6 ±0.4	0.0 ±0.0	0.1±0.1
		Unburned	0.3 ±0.1	0.0 ±0.0	0.1±0.1
Non-native	Annual forb				
		Burned	17.4 ±7.6	**6.4 ±2.2**	**21.8 ±6.6**
		Unburned	8.3 ±4.4	**0.7 ±0.3**	**10.1 ±3.6**
Native	Annual Grass				
		Burned	**0.4 ±0.3**	0.0 ±0.0	0.1 ±0.1
		Unburned	**1.4 ±0.5**	0.0 ±0.0	0.2 ±0.1
Native	Annual Forb				
		Burned	10.4 ±5.7	**7.4 ±3.3**	**13.6 ±5.7**
		Unburned	15.2 ±5.0	**0.3 ±.0.1**	**5.9 ±1.0**
Native	Perennial Grass				
		Burned	0.4 ±0.2	0.0 ±0.0	0.1 ±0.1
		Unburned	10.7 ±4.7	2.5 ±1.1	3.6 ±1.5
Native	Perennial Forb				
		Burned	4.2 ±3.0	1.1 ±1.1	2.7 ±2.2
		Unburned	0.6 ±0.3	0.1 ±0.1	0.3 ±0.2
Native	Shrub				
		Burned	**4.2 ±1.2**	**2.6 ±1.0**	**1.8 ±0.5**
		Unburned	**41.3 ±4.0**	**33.1 ±4.5**	**31.4 ±4.5**
Native	Tree				
		Burned	0.3 ±0.3	0.1 ±0.1	0.1 ±0.1
		Unburned	1.7 ±1.3	1.5 ±1.2	0.8 ±0.4
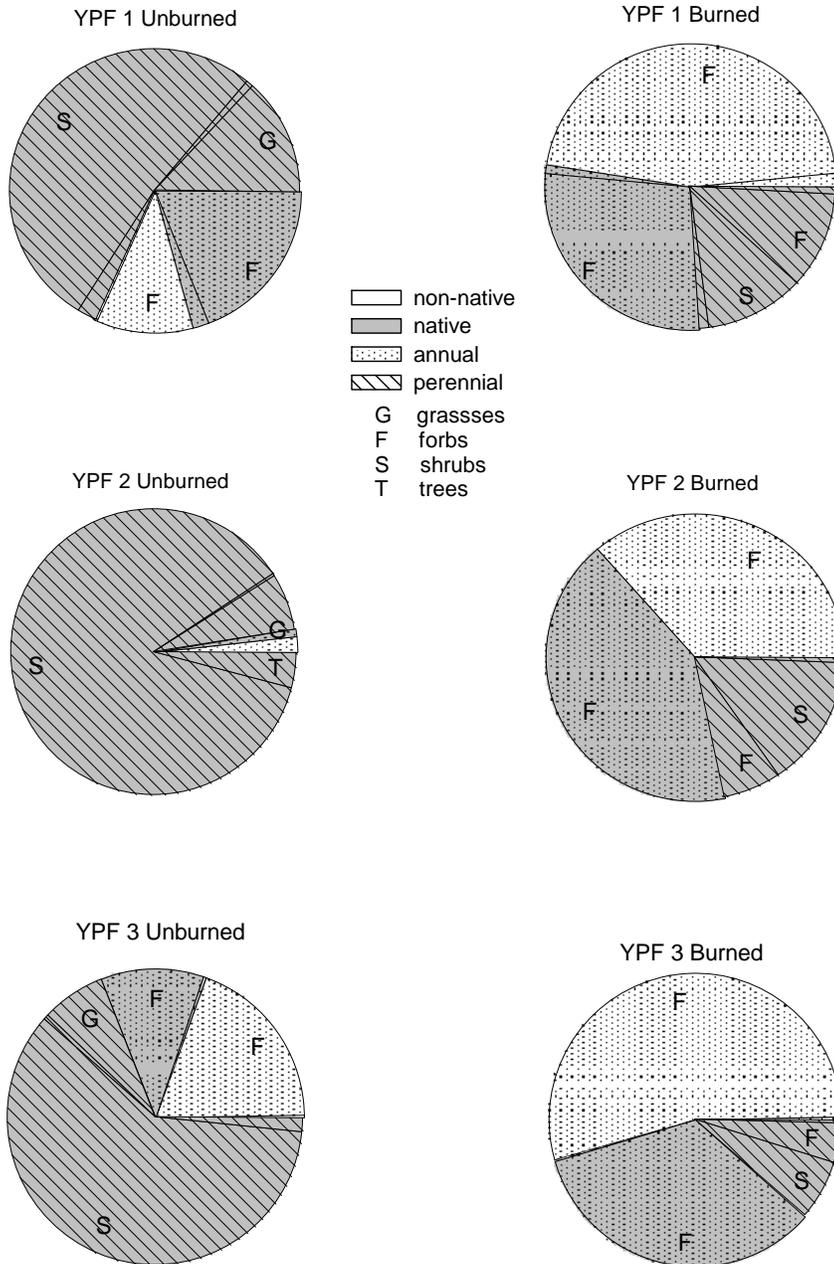
Fig. 10. Proportion of vegetation cover origin (non-native, native), life history (annual, perennial), and growth form (grass, forb, shrub) in burned and unburned plots during the first three post-fire springs (YPF 1, 2, and 3).

Burn Severity Correlations

The relationship between CBI data and dNBR values was linear and moderately strong (Fig. 11, $R^2=0.6012$). The relationship between CBI and RdNBR was also linear but not nearly as strong as for dNBR (Fig. 11, $R^2=0.2741$). Our correlations may have been stronger if our samples included the full range of dNBR and RdNBR on the landscape, since most CBI plots fell within low to moderate severity areas in this study.
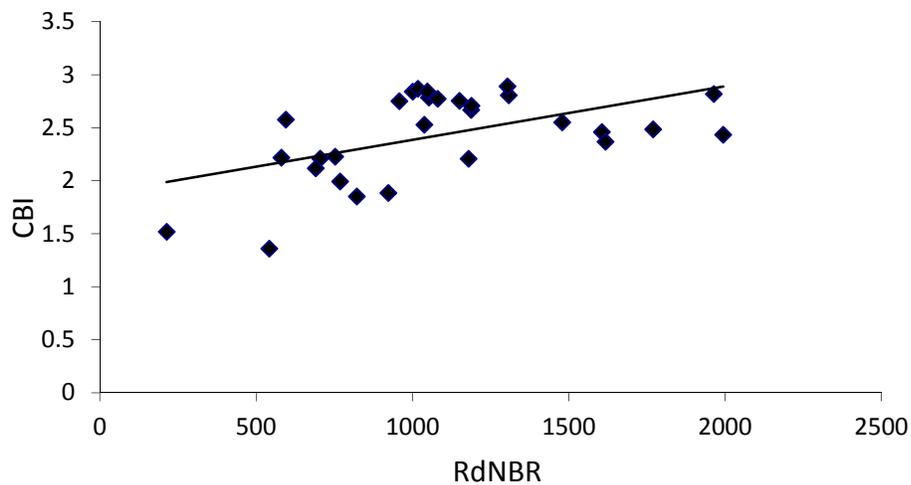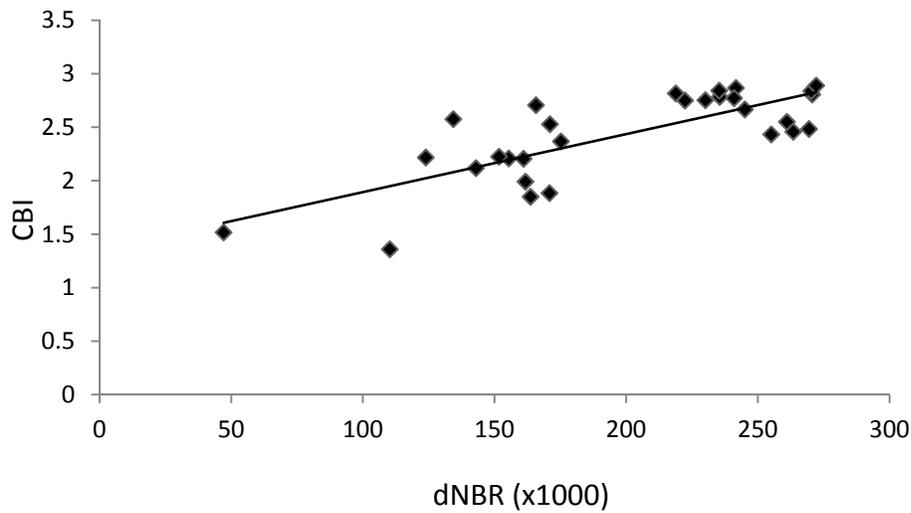
Fig. 11. Relationships between ground-based CBI data and satellite-based burn severity indices (dNBR and RdNBR) within the 30 burned vegetation sampling units. Linear regression equations are as follows: dNBR y=0.0054x + 1.3516, $R^2=0.6012$; RdNBR y=0.0005x = 1.8794, $R^2=0.2741$.

Seed bank density displayed weak negative correlations with CBI and dNBR, but only during YPF 2 (Table 4). Vegetation cover displayed the strongest negative correlations with measures of burn severity, specifically CBI and dNBR, but only during YPF 1 (Table 4). This negative correlation carried over into YPF 2 only for non-native annual cover. RdNBR did not display any significant correlations with measures of seed bank density or vegetation cover.

Table 4. Correlations between measures of burn severity and seed bank density and vegetation cover within the 30 burned vegetation sampling units during the first 3 years post-fire (YPF).
Linear regression significance (p≥0.05 bold font), directionality (+, - or none for no detectable trend), and correlation strength (R^2) are listed within each cell.

	Measures of Burn Severity								
	CBI			dNBR			RdNBR		
Seed bank Density YPF	0	1	2	0	1	2	0	1	2
Total	6.9e-6	-0.10	-0.02	-0.04	**-0.28**	-0.06	-0.09	-0.05	+0.06
Perennial	+0.10	**-0.19**	+0.13	+0.09	**-0.19**	+0.07	+8.1e-3	-0.16	-0.02
Annual	-3.2e-4	-0.09	-0.03	-0.05	**-0.27**	-0.07	-0.09	-0.04	+0.06
Vegetation Cover YPF	1	2	3	1	2	3	1	2	3
Total	**-0.24**	-0.03	+0.05	**-0.43**	-0.15	-0.02	**-0.15**	-0.05	-0.01
Perennial	+0.16	-0.08	+0.07	+0.06	-0.07	+0.06	+0.01	-0.07	+0.01
Annual	**-0.38**	-.8.4e-4	+3.4e-3	**-0.47**	-0.06	-0.04	-0.14	-7.6e-3	-0.02

Key Findings and Relationship to Other Recent Studies

Seed bank diversity findings

Hypothesis 1: Soil seed bank diversity will be <u>lower</u> in burned than unburned areas.

- Supporting results
    - Seed bank diversity as measured by species richness (N0) and two integrated measures (N1 and N2) was <u>lower</u> in burned than unburned areas during the YPF 0 and 1, but not YPF 2.
- Non-supporting results
    - Seed bank diversity as measured by evenness (El/d) was slightly <u>higher</u> in burned than unburned areas during YPF 0, 1, and 2.

The hypothesis that seed bank diversity would be lower in burned than unburned areas was generally supported in this study (with the exception of evenness). Reduced seed bank richness and composite diversity measures during YPF 0 and 1 were likely due to differential seed bank mortality

rates among species during the fire. Soil temperatures can exceed lethal levels beneath burning shrubs, but not within interspace microhabitats, exposing seeds to differential mortality rates across the landscape (Brooks 2002). Abella *et al.* (2009) found that seed bank density of *Bromus rubens* 2 years post-fire was 28% of the density in unburned areas due to large declines beneath the canopies of *Larrea tridentata* and *Yucca* spp. Additionally, Esque *et al.* (2010) found that seed bank species richness beneath creosotebush canopies 1 month post-fire was 66% of that found beneath unburned canopies, but that there was no effect of fire within interspaces, suggesting that there may be differential mortality rates among the beneath-canopy species as well. Thus, species with affinities for the beneath-shrub microhabitat may have greater mortality rates than those which frequent interspaces and there may be differential mortality rates among beneath-shrub species. Differing mortality beneath shrubs may be due to differing seed characteristics among species which confer greater or lower susceptibility to mortality during fire (e.g. moisture content, burial depth, dispersal mechanism, insulating tissue, etc.). The convergence of burned and unburned diversity levels by YPF 2 suggests that the effect of fire on species richness can be temporary and surviving or dispersed seeds of beneath-shrub species germinate and lead to reproduction that replenishes the seed bank for those species within a few years following fire.

Fire also slightly increased seed bank evenness during YPF 0, 1, and 2, which did not support the hypothesis of decreased diversity following fire, but in retrospect made sense ecologically. Increased evenness was likely due to reduced shrub/intershrub microhabitat heterogeneity following the reduction in shrub cover due to fire. This effect persisted all three post-fire years in this study, but trends beyond this timeframe are unknown. A meta-analysis of multiple studies suggests that it may take 40 years for shrub cover to return to unburned conditions in the Mojave Desert (Abella 2009). If loss of shrub cover is the cause of increased seed bank evenness, then evenness patterns may follow the same recovery patterns as shrub cover and possibly return to unburned levels within approximately 40 years.

Seed bank density findings

Hypothesis 2: Soil seed bank density will be <u>lower</u> in burned than unburned areas.

- Supporting results
    - Total seed bank density was <u>lower</u> in burned than unburned areas during YPF 0.
    - Annual seed bank density was <u>lower</u> in burned than unburned areas during YPF 0 and 1.
    - Non-native seed bank density was <u>lower</u> in burned than unburned areas during YPF 0.
    - Native seed bank density was <u>lower</u> in burned than unburned areas during YPF 0 and 1.
    - Non-native annual grass seed bank density was <u>lower</u> in burned than unburned areas during YPF 0 and 1.
    - Native annual grass seed bank density was <u>lower</u> in burned than unburned areas only during YPF 1.
    - Native annual forb seed bank density was <u>lower</u> in burned than unburned areas during YPF 0.
    - Perennial seed bank density was <u>lower</u> in burned than unburned areas during YPF 1.
    - Native perennial grass seed bank density was <u>lower</u> in burned than unburned areas during YPF 1.
- Non-supporting results
    - Perennial seed bank density <u>did not differ</u> in burned and unburned areas during any of the post-fire years.

- Native perennial seed bank density <u>did not differ</u> between burned and unburned areas during any of the post-fire years.

The 81% reduction in seed bank density during YPF 0 (3 months post-fire) can clearly be attributed to direct mortality during the fire. Fires in the Mojave Desert can produce temperatures high enough to kill seeds, especially beneath the canopies of perennial shrubs (Brooks 2002; Abella *et al.* 2009; Esque *et al.* 2010). These beneath-canopy microhabitats are also where the highest densities of annual plants occur in desert shrublands (Tielbörger and Kadmon 2000), and ≥97% of seeds detected in the current study during any given year or burn condition were annuals. Esque *et al.* (2010) found similar reductions in seed bank densities ranging from 55 to 80% 1 month following experimental fires in a creosotebush shrubland. However, the reduction in total seed bank density in the current study was only detected immediately post-fire, and for annuals alone only through one subsequent year (YPF 1). By YPF 2, seed bank densities in burned and unburned areas were virtually identical.

Non-native seed bank densities were reduced 94% in burned areas during YPF 0, primarily due to declines in *Bromus rubens*. Declines of approximately 60% Similar declines of 4x (~94%) in *Bromus rubens* density were reported 2 years post-fire in a blackbrush shrubland, and 3x (~87%) after heating soils from that site to 100°C for 1 minute (Abella *et al.* 2009). A post-fire chronosquence study of 12 fires ranging 5 to 31 years post-fire within blackbrush shrublands suggests that seed bank densities of *Bromus rubens* may return to unburned levels at least within 5 years (Jurand 2012, Jurand and Abella 2013).

Native seed bank densities were reduced 54% and 34% during YPF 0 and 1 respectively in this study. Similar declines in natives of approximately 35% (interspace) and 60% (beneath-canopy) were reported 1 month post-fire in a creosotebush shrubland (Esque *et al.* 2010). No differences were reported among 12 fires ranging 5 to 31 years post-fire in blackbrush shrublands (Jurand 2013, Jurand and Abella 2013). Although seed bank densities of native shrubs were reported to be lower in burned than unburned areas 10 years after a blackbrush shrubland fire (Lei 2001), the seed bank community studied in the current study, and desert seed banks in general (Leck *et al.* 1989), are typically dominated by annual species. Thus, density of native annual plant seed banks seem to return to unburned levels within 5 years post-fire.

The relative proportion of non-natives to natives in the soil seed bank was dramatically higher in burned areas during YPF 0, but not during the other two post-fire years. This pattern was driven by the greater reduction in non-natives compared to natives during YPF 0. The relative proportions of grasses and forbs were also affected by fire in this study. Specifically, fire decreased proportion of grasses and increased proportion of forbs, but only during YPF 0 and 1. Only one other study mentions proportional composition of common species in the soil seed bank, indicating that burned and unburned areas were similar 1 month post-fire (Esque *et al.* 2010).

Vegetation diversity findings

Hypothesis 3: plant diversity will be <u>lower</u> in burned than unburned areas.

- Supporting results
  - Vegetation diversity as measured by species richness (N0) and two integrated measures (N1 and N2) was <u>lower</u> in burned than unburned areas during the YPF 1, 2, and 3.

- o Vegetation richness of perennial species was <u>lower</u> in burned than unburned areas and the difference became increasingly larger at increasing spatial scales from 1, 10, 100, to 1,000 m^2 and the difference was similar during YPF 1, 2, and 3.
- Non-supporting results
  - o Vegetation diversity as measured by evenness (El/d) <u>did not differ</u> in burned than unburned areas during any of the 3 post-fire years.
  - o Vegetation richness of annual species <u>did not differ</u> between burned and unburned areas at spatial scales from 1, 10, 100, to 1,000 m^2 during any of the 3 post-fire years

Reductions in diversity due to fire were largely driven by reductions in species richness, especially richness of perennial species. Effects of fire on perennial richness increased from 1, 10, 100, to 1,000 m^2 spatial scales, due to the increasing proportion of perennial species along this same spatial gradient. For example, the proportion of perennials in burned areas averaged over the 3 post-fire years increased from 0.12 at the 1m^2 scale to 0.23 at the 1,000 m^2 scale, and in burned areas increased from 0.20 at the 1m^2 scale to 0.34 at the 1,000 m^2 scale. These proportions were somewhat lower than those reported from 3 blackbrush sites in the Mojave Desert where the averages among sites in burned areas were 0.18 at 1m^2 and 0.47 at 1,000 m^2, and in unburned areas were 0.24 and 0.50 (Brooks and Matchett 2003). This difference is likely due to the previous study reporting values which varied from 6 to 14 years post-fire among sites, compared to the current study which focused only on the first 3 post-fire years.

The lack of fire effects on annual species evenness in the current study was not reflected in the Brooks and Matchett (2003) study which found that fire increased evenness by decreasing cover of the dominant *Coloegyne ramossissima* and increasing the equitability of cover among other species. As discussed above, this previous study focused on the 6 to 14 year post-fire timeframe which seems to have allowed various early successional species to increase in cover within burned areas, thus increasing evenness.

No studies have documented complete recovery of species diversity following fire in blackbrush or big sagebrush communities within the Mojave Desert. Various studies have determined that species composition of burned blackbrush communities do not return to unburned composition after 14 years (Brooks and Matchett 2003), 29 years (Engel and Abella 2011), and 37 years (Callison *et al.* 1885). If one considers cover of the type species, *Coleogyne ramossissima*, to be a major factor affecting diversity patterns in the blackbrush vegetation type, then recovery of diversity may take many decades to centuries based on reports of cover responses (Bowns 1973; Webb and others 1987; Minnich 1995; Minnich 2003; Brooks and Minnich 2006; Brooks *et al.* 2007). The post-fire succession of species guild dominance is generally thought to be annuals in the short-term and early successional perennials during the first few decades (Jenson *et al.* 1960; Bates 1984; Callison *et al.* 1985; Brooks and Matchett 2003), but beyond that the time for *Coleogyne ramossisima* to recover is largely unknown. Analyses of historical photographs from Joshua Tree National Park and southern Nevada suggest that *Coleogyne ramossisima* cover can recover after as little as 50 to 75 years (Minnich 2003; M. Brooks, unpublished data), but these photographs provide no direct evidence of species diversity.

Vegetation cover findings

Hypothesis 4: Perennial plant cover will be <u>lower</u> in burned than unburned areas.

- Supporting results
  - o Perennial plant cover was <u>lower</u> in burned than unburned areas during YPF 1, 2, and 3.
  - o Shrub cover was <u>lower</u> in burned than unburned areas during YPF 1, 2, and 3.
  - o Proportional cover of perennials was <u>lower</u> in burned than unburned areas during YPF 1, 2, and 3.
- Non-supporting results
  - o Perennial grass, forb, and tree cover <u>did not differ</u> between burned than unburned areas during any of the post-fire years.

Hypothesis 5: Annual plant cover will be <u>higher</u> in burned than unburned areas.

- Supporting results
  - o Annual plant cover was <u>higher</u> in burned than unburned areas during YPF 1, 2, and 3.
  - o Proportional cover of annuals was <u>higher</u> in burned than unburned areas during YPF 1, 2, and 3.
- Non-supporting results
  - o None

Hypothesis 6: Non-native plant cover will be <u>higher</u> in burned than unburned areas.

- Supporting results
  - o Non-native annual plant cover was <u>higher</u> in burned than unburned areas during YPF 2 and 3.
  - o Non-native annual forbs were <u>higher</u> in burned than unburned areas during YPF 2 and 3, due to increases in non-native forb cover, *Erodium cicutarium* in particular.
  - o Proportional cover of non-natives was <u>higher</u> in burned than unburned areas during YPF 1, 2, and 3.
  - o
- Non-supporting results
  - o Non-native annual grasses <u>did not differ</u> between burned and unburned areas during any of the 3 post-fire years.

Hypothesis 7: Native plant cover will be <u>lower</u> in burned than unburned areas.

- Supporting results
  - o Native plant cover was <u>lower</u> in burned than unburned areas during YPF 1, 2, and 3, primarily due to declines in perennial cover.
  - o Native annual grass cover was <u>lower</u> in burned than unburned areas only during YPF 1.
  - o Proportional cover of natives was <u>lower</u> in burned than unburned areas during YPF 1, 2, and 3.
- Non-supporting results
  - o Native annual forb cover was <u>higher</u> in burned than unburned areas during YPF 2 and 3.

The hypotheses of decreased perennial and native cover and increased annual and non-native cover following fire were generally supported in this study, as they were in numerous past studies (Jenson *et al.* 1960; Bowns 1973; Beatley 1976; Bates 1984; Callison *et al.* 1985; Minnich 1995; Lei

1999; Webb *et al*; 1987; Brooks and Matchett 2003; Brooks and Minnich 2006; Abella 2009; Abella *et al.* 2009; Engel and Abella 2011; Brooks 2012; Brooks *et al.* 2013). Most of these previous studies focused on lower and middle elevation creosotebush and blackbrush communities, but very few reported fire effects in higher elevation sagebrush, interior chaparral, pinyon-juniper, or mixed conifer stands (only Brooks and Minnich 2006; Brooks *et al.* 2007; and Brooks *et al.* 2013). However, none of these latter studies are primary research, rather they are reviews which rely on citations from other adjacent desert and mountain regions. Thus, the results of the current study which span blackbrush and sagebrush elevational zones provide the first direct evidence of fire effects in the sagebrush vegetation type within the Mojave Desert.

There were a few interesting exceptions which did not follow the hypothesized patterns of vegetation cover responses to fire. Most notably, cover of non-native annual grasses (*Bromus rubens*, *Bromus tectorum*, and *Schismus* spp.) did not significantly differ between burned and unburned areas in the current study. The lack of a difference may have been due to cover of these species being very low overall in both burned and unburned areas (<1%), which is somewhat surprising since seed bank densities (dominated by *Bromus* spp.) were relatively high, peaking at 3,259/m^2 in unburned areas during YPF 0 (Table 2). It is likely that cover and seed production of non-native annual grasses was very high during winter 2004-2005 when rainfall was extremely high immediately before the Hackberry Complex fires, and those seed banks carried over to the following few years. Previous studies suggest that *Bromus rubens* cover/biomass can be reduced during the first few (up to 4) post-fire years (Brooks 2002; Abella *et al.* 2009), but that biomass of *Schismus* spp can increase during this same time period (Brooks 2002). Other studies from the Sonoran Desert report also report biomass of *Bromus rubens* lower in burned than unburned areas 1 year post-fire (Cave and Patten 1984), and cover/biomass of *Schismus* spp being higher in burned than unburned areas 1 year post-fire (Cave and Patten 1984) and 3 years post-fire (Steers and Allen 2011). However, all of these previous studies were conducted at more arid lower elevation sites than the upper blackbrush/lower sagebrush ecotones in the current study. It appears that non-native annual grasses may be less of a factor in plant community and fire regime dynamics in the upper blackbrush and higher elevation vegetation types than at lower elevations in the Mojave Desert (Brooks and Matchett 2002; Brooks and Mininch 2006).

Native annual forb cover was also higher in burned than unburned areas in the current study, which supports the hypothesis that annuals will increase in cover following fire, but does not support the hypothesis that natives will increase. Similar increases in native annual plant biomasss were reported during post-fire years 1 and 2 (Brooks 2002). Interestingly, cover of natives was lower in burned than unburned areas 3 years post-fire at a Sonoran desert site where cover of invasive annual grasses (mostly *Schismus* spp.) in burned areas was extremely high (28-42%) (Steers and Allen 2011, Fig. 2). That study suggested that high abundance of non-native grasses may have exerted a strong competitive effect that suppressed growth of native annuals. Competition between non-native an native annuals has been documented in the Mojave Desert (Brooks 2000; DeFalco *et al.* 2003), and it is likely that the increase in native forb cover following fire in the current study was at least partially due to the low abundance of non-native annual grasses.

Burn severity correlation findings

- CBI values were more strongly correlated with dNBR than RdNBR values.
- Vegetation cover was negatively correlated with CBI and dNBR, but only during the YPF 1.
- Seed bank density was negatively correlated with CBI and dNBR, but only during the YPF 2.

The correlations between dNBR and CBI were moderately strong and within the range typical of 0.5 to 0.7 R^2 range typical of other shrublands and grasslands in the western United States (R. McKlinley, unpublished data). Values of 0.6 to 0.8 might be considered typical of good results for forested ecosystems. Interestingly, RdNBR displayed lower correlations with CBI, even though it may be more useful in quantifying burn severity in sparse vegetation types like those found in desert regions (Miller and Thode 2007).

Both dNBR and CBI were negatively correlated with total vegetation cover and annual cover in particular, but only during YPF 1. This result is interesting because comparisons between burned and unburned areas indicated a much large effect of fire on perennial cover than annual cover (Fig. 9). Apparently, fire of any severity compared to unburned areas leads to reduced total perennial cover. This may be because post-fire cover of some perennial species are highest at one severity level, whereas cover of other perennial species are higher at other severity levels. For example, relationships between plant cover RdNBR are negative for density of the shrubs *Coleogyne ramosissima*, *Encelia virginensis*, and *Thamnosma montana*, and positive for the shrubs *Ericameria nauseosa* and *Ephedra viridis* (Klinger *et al.* 2011a). In contrast, increased severity within burned areas leads to increased reductions in annual plant cover, indicating a more universal effect of severity on annuals, probably mediated through effects on physical and/or chemical soil properties. These negative fire effects on annual cover during the first post-fire spring (YPF1) appear have carried over to the seed bank during following fall (YPF1), which was also negatively correlated with dNBR. It therefore appears that dNBR may be a potentially useful tool in estimating reduced cover of annuals during the first post-fire spring, and reduced seed bank density during the following fall, in the upper blackbrush and lower sagebrush ecotones of the Mojave Desert.

Management Implications

The results of this study call into question the need to seed annual plant species after fires in the Mojave Desert. Although seed bank diversity and density declined due to fire, and this effect was mostly due to annuals, values in burned and unburned areas converged by the third post-fire year. In addition, despite having lower seed bank densities during the first two post-fire years, annual cover was higher in burned areas during all three years, although mostly comprised of the non-native forb *Erodium cicutarium*. Seed bank density and vegetation cover of annual species also varied about as much or possibly more among years than between burned and unburned areas within years. Thus, it could be argued that that these results provide more support for seeding after years of low seed productivity than for seeding after fires in the Mojave Desert.

In addition, the depletion rate of 81% of the seed bank during YPF 0 (burned areas 974 seeds/m^2, unburned 5,094 seeds/m^2), representing a net loss of 4,120 seeds/m^2 (383 seeds/ft^2), is much larger than typical seeding treatments would have replaced if they had been implemented. For example, recent aerial seedings of post-fire landscapes in the Mojave Desert range from 140 seeds/m^2 (13 seeds/ft^2)(Christiana Lund, BLM, pers. comm.) to 646 seeds/m^2 (60 seeds/ft^2) (Karen Prentice, BLM, pers. comm.), and post-fire drill seedings are typically applied at a rate of 323 seeds/m^2 (30 seeds/ft^2)(Karen Prentice pers. comm.). If these seeding rates had been applied after the Hackberry Fire Complex, they would have only reduced the depletion rate of total seed bank density by 3 percentage points (81 to 78%) if 140 seeds/m^2 were added, or 13 percentage points (from 81 to 68%) if 646 seeds/m^2. Even if seed mixes could match the species composition and genetic characteristics of the Hackberry Complex landscape (which of course they can't), a few percentage point changes in seed bank densities are probably ecologically negligible. This is especially true considering that both native

and non-native seed banks returned to densities found in unburned areas by YPF 2, the third post-fire fall.

Although there was little evidence that fire decreased seed bank densities of perennials species, it should be noted that the methods used were most suited for assaying annual rather than perennial seed banks. Much larger sampling area than that used in the current study (78.5 cm^2 circular area for each 1 m^2 subplot) do a better job of characterizing perennial seed banks which are spatially very heterogeneous (e.g. 100 to 625 cm^2 or more for perennials, Belnap *et al.* 2008). However, fire did clearly reduce cover of perennial plants and persistent reductions in cover of these species means that seed sources are limited and post-fire seedings may help to overcome this establishment limitation. Further studies of perennial seed banks are clearly warranted.

This study was conducted in blackbrush and sagebrush shrublands within the Mojave National Preserve in the eastern Mojave Desert. This vegetation zone is situated at the middle and higher elevations within the Mojave Desert and is characterized by some of the highest plant cover in the region. This relatively high cover supports fires that spread in contiguous flaming fronts leaving few unburned islands. In contrast, the vegetation types situated at lower elevations such as creosotebush scrub have less contiguous fuels and leave more unburned islands resulting in higher post-fire heterogeneity of burned, lightly burned, and unburned patches. Although the results of this study should not be directly applied to those lower elevations, some general inferences can be made. For example, unburned islands and potentially lower fire intensities at lower elevations should lead to even lower average seed bank mortality rates than at higher elevations. Accordingly, the conclusion in the current study that seeding annual plant species is not warranted to restore overall seed bank diversity and density after fires should also be valid at lower elevations where average effects on seed banks are likely even less.

On-the-ground CBI measurements were more strongly correlated with satellite-based dNBR than they were with RdNBR measurements. In addition, CBI and dNBR data were most strongly correlated with seed bank density and vegetation cover. Burn severity, as measured by these two metrics, was negatively correlated with vegetation cover during YBP 1 and with seed bank density during YPF 1. Thus, there was an initial effect of burn severity on vegetation cover (primarily annuals) during YPF 1 (late Spring approximately 11 months post-fire), followed by a lag effect which may be the result of lowered seed production by annuals during that first post-fire growing season carrying over to affect seed bank density during YPF 1 (early Fall approximately 15 months post-fire). These results suggest that within burned areas measures of burn severity may not be useful indicators of immediate effects on the soil seed bank since there were no significant correlations with seed bank density during YPF 0 (early Fall approximately 3 months post-fire), although they may indicate lag effects that emerge during YPF 1. However, because all correlations with seed bank density and vegetation cover disappear by YPF 3, it seems that these results do not support the idea of using measures of burn severity to target areas for post-fire seedings.

Future Studies Needed

Modified with permission from Brooks *et al.* 2013

Understanding Fire Histories
A better understanding of fire histories of major Mojave Desert ecosystem types can be used to develop more effective management plans for these areas. Specific studies targeting key ecosystem types and locations are needed to test current hypotheses regarding assumed historic fire frequencies. These include dendrochronology studies of the mixed conifer zone in the Spring Mountains, and soil stratigraphy studies using charcoal lenses as proxies for fire events within watersheds dominated by single ecosystem types.

Climate and Fire Size and Frequency
Routine evaluations of the relationship of climate to fire size and frequency and how this relationship might change with climate warming are needed to develop effective fire management strategies. Precise descriptions of spatial and temporal patterns of burning only span a few decades of comprehensive records (e.g., agency reports and satellite imagery). Conclusions about fire trends can vary widely depending upon which time interval one evaluates within the current record. Re-evaluation of these data should be done at regular intervals (e.g., 5 year) to test the robustness of the current hypotheses regarding short-term ENSO and longer-term PDO effects on fire regimes.

Fire Effects on Plant Species and Vegetation Types
The effects of fire on plant species and vegetation types must be more thoroughly understood before predictive models can be useful to management. Within each ecosystem type the various effects of fire, fire regime, and local site characteristics need to be investigated further. This will require intensive data from numerous fires, and possibly the use of experimental fires. Even less information is available regarding the effects of fire on animals, but because so many sensitive species are associated with particular ecosystem types, a full understanding of fire effects on animals can only be realized after a more complete understanding of vegetation responses.

Post-Fire Management
Additional information is needed regarding appropriate management actions after fire. It is well established that aerial seedings of post-fire landscapes have very low establishment rates. However, much less is understood about other management actions designed to reestablish native vegetation. Also, little is known about the effects of postfire grazing. For example, how does the duration and intensity of post-fire grazing by livestock affect vegetation resilience to fire and expansion of invasive annual grasses? How effective is livestock grazing at managing fuels created by invasive annual plants?

Fire Suppression Impacts
Considering that fire suppression may be the most effective fire management tool in low to mid elevation ecosystem types, there is a need to better understand the relative impact, both negative and positive, of aggressive fire suppression tactics (e.g. retardant drops and off-road travel) versus allowing fires to spread and burn more area.

Semi-Arid Ecosystem Response to Wildfire
Because tree infilling and growth are ongoing processes in higher elevation conifer and piñon and juniper ecosystems, information is needed on the response of these semiarid ecosystems to wildfire and fire and fuels treatments. Information also is needed on how fire and fuels treatments can be used for restoring and maintaining landscape heterogeneity of these diverse ecosystems.

Deliverables by Category Listed in the Project Proposal

Website
http://cafiresci.org/desert

Progress reports
Progress report #1 – September 2006
Progress report #2 – September 2007
Progress report #3 – December 2010

Final report
Final report – November 2013

Manuscripts
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Brooks, M.L, S.M. Ostoja, and R.C. Klinger. In review. Short-term effects of fire on seed banks and vegetation response in an upper elevation Mojave Desert shrubland. International Journal of Wildland Fire.

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Field workshop and other tech transfer
1 field workshop – for federal agency staff
7 agency training sessions – for federal agency staff
14 invited papers – for researchers, students, and agency staff

Acknowledgments

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Appendices

Appendix 1. Seed bank diversity model selection statistics for burn (burned, unburned) and year (2006-2008) factors in the Hackberry Complex fire of 2005.
Models are listed in decreasing order of relative support, and those with clearly the greatest support are highlighted using bold/italics font. Within each response variable category, each sequential model includes the variables from the previous models. YPF = years post-fire. N0 (species richness), N1 (exp of Shannon's index), and N2 (reciprocal of Simpson's index) are Hill's series of diversity indices, and E1/d is Simpson's index of evenness. Group is a random factor accounting for the hierarchical spatial arrangement of sampling plots within each of 6 blocks. The diversity indices were derived from absolute density values. ΔAICc is the difference in the bias-corrected Akaike Information Criterion (AICc) between a given model and the best supported model, wAICc is the absolute support for a given model (= exp(-ΔAICc/2)), and rwAICc is the support relative to the other models.

Model	Variables	ΔAICc	wAICc	rwAICc
Species Richness (N0)				
8	*Model 6 + random slope (group)*	*0.0000*	*1.0000*	*0.4329*
7	*Model 6 + random intercept (group)*	*0.6620*	*0.7182*	*0.3109*
9	*Model 6 + random intercept + random slope*	*1.0656*	*0.5870*	*0.2541*
6	Model 5 + year^2*burn	11.6843	0.0029	0.0013
5	Model 4 + year*burn	13.1431	0.0014	0.0006
4	Model 3 + burn	14.5837	0.0007	0.0003
3	Model 2 + year^2	29.4777	0.0000	0.0000
1	Null - fixed intercept	191.3531	0.0000	0.0000
2	Model 1 + year	193.2477	0.0000	0.0000
Species Evenness (E1/D)				
9	*Model 4 + random intercept + random slope*	*0.0000*	*1.0000*	*0.4140*
7	*Model 4 + random intercept (group)*	*0.0520*	*0.9743*	*0.4034*
8	Model 4 + random slope (group)	3.9650	0.1377	0.0570
4	Model 3 + burn	4.0456	0.1323	0.0548
3	Model 2 + year^2	4.7477	0.0931	0.0386
5	Model 4 + year*burn	6.1790	0.0455	0.0188
6	Model 5 + year^2*burn	6.9593	0.0308	0.0128
1	Null - fixed intercept	13.4960	0.0012	0.0005
2	Model 1 + year	15.2266	0.0005	0.0002
N1				
8	*Model 6 + random slope (group)*	*0.0000*	*1.0000*	*0.4172*
7	*Model 6 + random intercept (group)*	*0.3510*	*0.8390*	*0.3500*
9	*Model 6 + random intercept + random slope*	*1.5336*	*0.4645*	*0.1938*
6	Model 5 + year^2*burn	5.3393	0.0693	0.0289
5	Model 4 + year*burn	8.8731	0.0118	0.0049
4	Model 3 + burn	9.0007	0.0111	0.0046
3	Model 2 + year^2	13.3837	0.0012	0.0005
1	Null - fixed intercept	91.8431	0.0000	0.0000
2	Model 1 + year	93.8567	0.0000	0.0000
N2				

7	*Model 6 + random intercept (group)*	*0.0000*	*1.0000*	*0.4926*
8	*Model 6 + random slope (group)*	*1.2930*	*0.5239*	*0.2581*
9	*Model 6 + random intercept + random slope*	*1.8296*	*0.4006*	*0.1973*
6	Model 5 + year^2*burn	5.3153	0.0701	0.0345
4	Model 3 + burn	8.3857	0.0151	0.0074
3	Model 2 + year^2	9.1187	0.0105	0.0052
5	Model 4 + year*burn	9.2411	0.0098	0.0049
1	Null - fixed intercept	47.7521	0.0000	0.0000
2	Model 1 + year	49.8057	0.0000	0.0000

Appendix 2. Seed bank density model selection statistics for burn (burned, unburned) and year (2006-2008) factors in the Hackberry Complex fire of 2005.

Models are listed in decreasing order of relative support, and those with clearly the greatest support are highlighted using bold/italics font. Within each response variable category, each sequential model includes the variables from the previous models. YPF = years post-fire. Group is a random factor accounting for the hierarchical spatial arrangement of sampling plots within each of 6 blocks. ΔAICc is the difference in the bias-corrected Akaike Information Criterion (AICc) between a given model and the best supported model, wAICc is the absolute support for a given model (= exp(-ΔAICc/2)), and rwAICc is the support relative to the other models.

Model	Variables	ΔAICc	wAICc	rwAICc
Annual seed bank density				
7	*Model 5 + random intercept (group)*	*0.0000*	*1.0000*	*0.8970*
9	*Model 5 + random intercept + random slope*	*4.3792*	*0.1120*	*0.1004*
8	Model 5 + random slope (group)	11.9490	0.0025	0.0023
5	Model 4 + year*burn	16.4837	0.0003	0.0002
6	Model 5 + year^2*burn	18.6620	0.0001	0.0001
4	Model 3 + burn	24.2154	0.0000	0.0000
3	Model 2 + year^2	36.7664	0.0000	0.0000
2	Model 1 + year	93.8353	0.0000	0.0000
1	Null - fixed intercept	97.3477	0.0000	0.0000
Perennial seed bank density				
9	*Model 6 + random intercept + random slope*	*0.0000*	*1.0000*	*0.5393*
6	*Model 5 + year^2*burn*	*1.4498*	*0.4844*	*0.2612*
7	Model 6 + random intercept (group)	3.1494	0.2071	0.1117
8	Model 6 + random slope (group)	3.6554	0.1608	0.0867
4	Model 3 + burn	12.8501	0.0016	0.0009
5	Model 4 + year*burn	15.0015	0.0006	0.0003
3	Model 2 + year^2	23.3462	0.0000	0.0000
1	Null - fixed intercept	43.7755	0.0000	0.0000
2	Model 1 + year	45.7011	0.0000	0.0000
Non-native seed bank density				
9	*Model 6 + random intercept + random slope*	*0.0000*	*1.0000*	*0.6466*
7	*Model 6 + random intercept (group)*	*1.2104*	*0.5460*	*0.3530*
6	Model 5 + year^2*burn	16.3138	0.0003	0.0002
5	Model 4 + year*burn	16.7845	0.0002	0.0001
8	Model 6 + random slope (group)	18.4134	0.0001	0.0001
4	Model 3 + burn	25.8621	0.0000	0.0000

3	Model 2 + year^2	32.3452	0.0000	0.0000
2	Model 1 + year	43.2131	0.0000	0.0000
1	Null - fixed intercept	52.5075	0.0000	0.0000

Native seed bank density

8	*Model 6 + random slope (group)*	*0.0000*	*1.0000*	*0.6911*
9	*Model 6 + random intercept + random slope*	*2.2006*	*0.3328*	*0.2300*
7	Model 6 + random intercept (group)	4.3480	0.1137	0.0786
6	Model 5 + year^2*burn	17.2473	0.0002	0.0001
4	Model 3 + burn	17.9377	0.0001	0.0001
5	Model 4 + year*burn	19.3351	0.0001	0.0000
3	Model 2 + year^2	22.9087	0.0000	0.0000
1	Null - fixed intercept	84.9521	0.0000	0.0000
2	Model 1 + year	86.9697	0.0000	0.0000

Appendix 3. Above-ground plant species diversity model selection statistics for burn (burned, unburned) and year (2006-2008) factors in the Hackberry Complex fire of 2005.
Models are listed in decreasing order of relative support, and those with clearly the greatest support are highlighted using bold/italics font. Within each response variable category, each sequential model includes the variables from the previous models. YPF = years post-fire. N0 (species richness), N1 (exp of Shannon's index), and N2 (reciprocal of Simpson's index) are Hill's series of diversity indices, and E1/d is Simpson's index of evenness. Group is a random factor accounting for the hierarchical spatial arrangement of sampling plots within each of 6 blocks. The diversity indices were derived from absolute cover (%) values. ΔAICc is the difference in the bias-corrected Akaike Information Criterion (AICc) between a given model and the best supported model, wAICc is the absolute support for a given model (= exp(-ΔAICc/2)), and rwAICc is the support relative to the other models.

Model	Variables	ΔAICc	wAICc	rwAICc
	Species Richness (N0)			
7	*Model 4 + random intercept (group)*	*0.0000*	*1.0000*	*0.7438*
9	*Model 4 + random intercept + random slope*	*2.1321*	*0.3444*	*0.2562*
8	Model 4 + random slope (group)	36.6670	0.0000	0.0000
6	Model 5 + year^2*burn	53.2713	0.0000	0.0000
4	Model 3 + burn	57.3025	0.0000	0.0000
5	Model 4 + year*burn	58.1356	0.0000	0.0000
3	Model 2 + year^2	111.0216	0.0000	0.0000
2	Model 1 + year	145.1435	0.0000	0.0000
1	Null - fixed intercept	148.0537	0.0000	0.0000
	Species Evenness (E1/D)			
7	*Model 3 + random intercept (group)*	*0.0000*	*1.0000*	*1.0000*
3	Model 2 + year^2	24.1851	0.0000	0.0000
4	Model 3 + burn	26.1980	0.0000	0.0000
5	Model 4 + year*burn	26.6061	0.0000	0.0000
6	Model 5 + year^2*burn	28.5648	0.0000	0.0000
1	Null - fixed intercept	34.7081	0.0000	0.0000
2	Model 1 + year	36.5219	0.0000	0.0000
	N1			
7	*Model 4 + random intercept (group)*	*0.0000*	*1.0000*	*0.7260*
9	*Model 4 + random intercept + random slope*	*1.9491*	*0.3774*	*0.2740*

Model	Variables	ΔAICc	wAICc	rwAICc
8	Model 4 + random slope (group)	63.5460	0.0000	0.0000
6	Model 5 + year^2*burn	84.5903	0.0000	0.0000
4	Model 3 + burn	86.4635	0.0000	0.0000
5	Model 4 + year*burn	88.5946	0.0000	0.0000
3	Model 2 + year^2	120.5906	0.0000	0.0000
2	Model 1 + year	130.1545	0.0000	0.0000
1	Null - fixed intercept	130.9527	0.0000	0.0000

N2

Model	Variables	ΔAICc	wAICc	rwAICc
7	*Model 4 + random intercept (group)*	*0.0000*	*1.0000*	*0.7250*
9	*Model 4 + random intercept + random slope*	*1.9391*	*0.3792*	*0.2750*
8	Model 4 + random slope (group)	64.0820	0.0000	0.0000
6	Model 5 + year^2*burn	85.0403	0.0000	0.0000
4	Model 3 + burn	85.1135	0.0000	0.0000
5	Model 4 + year*burn	87.2466	0.0000	0.0000
3	Model 2 + year^2	109.3376	0.0000	0.0000
2	Model 1 + year	112.1225	0.0000	0.0000
1	Null - fixed intercept	112.5427	0.0000	0.0000

Appendix 4. Above-ground species richness model selection statistics for burn (burned, unburned), year (2006-2008), and area (1 m^2, 10 m^2, 100 m^2, 1000 m^2) factors in the Hackberry Complex fire of 2005.

Models are listed in decreasing order of relative support, and those with clearly the greatest support are highlighted using bold/italics font. Within each response variable category, each sequential model includes the variables from the previous models. YPF = years post-fire. Group is a random factor accounting for the hierarchical spatial arrangement of sampling plots within each of 6 blocks. ΔAICc is the difference in the bias-corrected Akaike Information Criterion (AICc) between a given model and the best supported model, wAICc is the absolute support for a given model (= exp(-ΔAICc/2)), and rwAICc is the support relative to the other models.

Model	Variables	ΔAICc	wAICc	rwAICc
Annual species richness (N0)				
11	*Model 10 + random intercept*	*0.0000*	*1.0000*	*0.7359*
13	*Model 10 + random intercept & slope*	*2.0491*	*0.3590*	*0.2641*
12	Model 10 + random slope	82.5810	0.0000	0.0000
10	Model 9 + year^2*area*burn	141.0508	0.0000	0.0000
7	Model 6 + year^2*area	141.5459	0.0000	0.0000
8	Model 7 + area*burn	143.3568	0.0000	0.0000
9	Model 8 + year*area*burn	144.0984	0.0000	0.0000
4	Model 3 + area	174.6617	0.0000	0.0000
5	Model 4 + burn	176.5604	0.0000	0.0000
6	Model 5 + year*area	177.2548	0.0000	0.0000
3	Model 2 + year^2	730.2577	0.0000	0.0000
1	Null - fixed intercept	855.8216	0.0000	0.0000
2	Model 1 + year	857.6444	0.0000	0.0000
Perennial species richness (N0)				
11	*Model 8 + random intercept*	*0.0000*	*1.0000*	*0.7217*
13	*Model 8 + random intercept & slope*	*1.9054*	*0.3857*	*0.2783*

Model	Variables	ΔAICc	wAICc	rwAICc
12	Model 8 + random slope	99.4650	0.0000	0.0000
8	Model 7 + area*burn	154.2824	0.0000	0.0000
9	Model 8 + year*area*burn	154.4710	0.0000	0.0000
10	Model 9 + year^2*area*burn	156.4884	0.0000	0.0000
6	Model 5 + year*area	201.3004	0.0000	0.0000
7	Model 6 + year^2*area	201.3605	0.0000	0.0000
5	Model 4 + burn	211.7681	0.0000	0.0000
4	Model 3 + area	410.8874	0.0000	0.0000
2	Model 1 + year	914.2590	0.0000	0.0000
3	Model 2 + year^2	914.5154	0.0000	0.0000
1	Null - fixed intercept	918.5163	0.0000	0.0000

Appendix 5. Above-ground plant species cover (absolute %) model selection statistics for burn (burned, unburned) and year (2006-2008) factors in the Hackberry Complex fire of 2005.
Models are listed in decreasing order of relative support, and those with clearly the greatest support are highlighted using bold/italics font. Within each response variable category, each sequential model includes the variables from the previous models. YPF = years post-fire. Group is a random factor accounting for the hierarchical spatial arrangement of sampling plots within each of 6 blocks. ΔAICc is the difference in the bias-corrected Akaike Information Criterion (AICc) between a given model and the best supported model, wAICc is the absolute support for a given model (= exp(-ΔAICc/2)), and rwAICc is the support relative to the other models.

Model	Variables	ΔAICc	wAICc	rwAICc
Annual plant cover				
7	*Model 5 + random intercept (group)*	*0.0000*	*1.0000*	*0.6693*
9	*Model 5 + random intercept + random slope*	*1.4107*	*0.4939*	*0.3306*
8	Model 5 + random slope (group)	18.9370	0.0001	0.0001
5	Model 4 + year*burn	56.3853	0.0000	0.0000
6	Model 5 + year^2*burn	58.4520	0.0000	0.0000
4	Model 3 + burn	64.2062	0.0000	0.0000
3	Model 2 + year^2	92.4253	0.0000	0.0000
1	Null - fixed intercept	142.6564	0.0000	0.0000
2	Model 1 + year	144.6212	0.0000	0.0000
Perennial plant cover				
7	*Model 6 + random intercept (group)*	*0.0000*	*1.0000*	*0.7426*
9	*Model 6 + random intercept + random slope*	*2.1191*	*0.3466*	*0.2574*
8	Model 6 + random slope (group)	22.7670	0.0000	0.0000
6	Model 5 + year^2*burn	32.3763	0.0000	0.0000
5	Model 4 + year*burn	32.8306	0.0000	0.0000
4	Model 3 + burn	44.6505	0.0000	0.0000
3	Model 2 + year^2	300.8946	0.0000	0.0000
2	Model 1 + year	301.5335	0.0000	0.0000
1	Null - fixed intercept	307.8457	0.0000	0.0000
Non-native plant cover				
9	*Model 4 + random intercept + random slope*	*0.0000*	*1.0000*	*0.5792*
7	*Model 4 + random intercept (group)*	*0.6393*	*0.7264*	*0.4208*
8	Model 4 + random slope (group)	26.0203	0.0000	0.0000
4	Model 3 + burn	121.1362	0.0000	0.0000

5	Model 4 + year*burn	122.9723	0.0000	0.0000
6	Model 5 + year^2*burn	123.4480	0.0000	0.0000
3	Model 2 + year^2	143.1513	0.0000	0.0000
1	Null - fixed intercept	169.2154	0.0000	0.0000
2	Model 1 + year	170.0672	0.0000	0.0000

Native plant cover

9	*Model 4 + random intercept + random slope*	*0.0000*	*1.0000*	*1.0000*
7	Model 4 + random intercept (group)	52.7938	0.0000	0.0000
8	Model 4 + random slope (group)	70.6818	0.0000	0.0000
6	Model 5 + year^2*burn	114.7141	0.0000	0.0000
5	Model 4 + year*burn	115.6965	0.0000	0.0000
4	Model 3 + burn	124.3824	0.0000	0.0000
3	Model 2 + year^2	125.3844	0.0000	0.0000
2	Model 1 + year	141.2893	0.0000	0.0000
1	Null - fixed intercept	142.1615	0.0000	0.0000