FIRE EFFECTS ON PERENNIAL VEGETATION IN THE WESTERN COLORADO DESERT, USA

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ABSTRACT

The impacts of fire on creosote bush scrub vegetation have received attention recently as fire has become locally common throughout the Mojave and Sonoran deserts. One area of particular concern is western Coachella Valley, which forms the northwestern extent of the Colorado Desert. This is a major wildland-urban interface area that has been significantly impacted by atmospheric nitrogen deposition concomitant with fuel alterations from invasive annual grasses and increased ignition frequencies from human activities. Creosote bush scrub takes much longer than more mesic vegetation types to re-establish after fire, and the majority of desert species lack traits associated with resiliency to fire disturbance. Previous research in this area has only investigated once-burned stands for up to five years since fire. This study documents perennial vegetation from seven sites that represent a 2- to 28-year-old fire chronosequence. Our surveys revealed that fire significantly reduced shrub richness and diversity regardless of time since fire. Total shrub cover and density returned to or exceeded unburned levels at least 20 years after fire, although species composition was almost entirely brittlebush (*Encelia farinosa*), a short-lived shrub. Longer-lived shrubs indicative of unburned vegetation, such as creosote (*Larrea tridentata*), white bursage (*Ambrosia dumosa*), and white ratany (*Krameria grayi*), failed to recover. Shrub plus cacti richness and diversity were lower in burned stands regardless of time since fire. *Encelia* shrublands may form an alternate stable state following fire in this region.

Keywords: creosote, diversity, *Encelia farinosa*, resiliency, species richness, vegetation structure

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INTRODUCTION

Historically, fires have been relatively rare in creosote bush scrub of the Colorado and Mojave deserts, but the frequency and extent have increased significantly during the last 40 years as alien annual grasses and human ignition sources have become increasingly more

common (Brooks and Esque 2002, Brooks and Matchett 2006). Since most native shrub components of creosote bush scrub lack traits associated with fire resiliency (Brooks and Minnich 2006), fires can result in long-lasting alterations to vegetation. In addition, invasive species, such as red brome (*Bromus madritensis* L. ssp. *rubens* [L.] Durin), Mediterranean grasses (*Schismus* spp.), and redstem filaree (*Erodium cicutarium* [L.] L'Hér ex Aiton), may either be aggressive fire followers in the immediate post-fire growing season or will initially suffer set-backs, but can then regain or exceed pre-fire abundance within a few years after fire (Brown and Minnich 1986, Minnich and Dezzani 1998, Brooks 2002, Brooks and Matchett 2003, Keeley *et al.* 2005). Since these invasive annual species are competitive with the dominant shrub species in this vegetation type (Melgoza *et al.* 1990, Holzapfel and Mahall 1999, DeFalco *et al.* 2007, Steers and Allen 2010), the combination of fire and the particular suite of invasive plants is a threat to desert ecosystems.

In the part of the western Colorado Desert where this study took place, the relevant literature has only reported the effects of fire in creosote bush scrub from burns less than five years old (O'Leary and Minnich 1981, Brown and Minnich 1986). Both of these short-term fire effect studies reported decreases in long-lived shrubs like creosote (*Larrea tridentata* [DC.] Coville) and white bursage (*Ambrosia dumosa* [A.gray] Payne), and decreases in cacti (*Opuntia* spp., *Cylindropuntia* spp.). However, relatively short-lived shrubs like burrobush (*Hymenoclea salsola* Torr. & A. Gray) or brittlebush (*Encelia farinosa* A. Gray ex Torr.) showed increases following fire. Also, the impact of fire on perennial plant richness or diversity was not examined. The primary objective of this study was to build upon the short-term findings of these two previous studies in order to determine relatively longer-term impacts of fire. Specifically, we evaluated short-term (2 years) to relatively long-term (28 years) fire recovery. Our hypotheses were that: 1) plant cover, density, and diversity of perennial plants would be lower in burned than unburned creosote bush scrub, regardless of time since fire; and 2) certain functional groups, like succulents, would be disproportionately impacted by fire.

METHODS

Study Area

The study area was located in western Coachella Valley, situated on the far western edge of the Colorado Desert, a subdivision of the Sonoran Desert, at its nexus with the San Jacinto Mountains, San Bernardino Mountains, and the inland valleys of cismontane southern California, USA (Figure 1). To the east of the study area, average precipitation in the city of Palm Springs, which is in a significant rain-shadow, is 9.5 cm with 13.4 % occurring during the summer monsoonal season (July through September). At Cabazon to the west, where creosote bush scrub reaches its most western extent in the study area, average precipitation is 29.9 cm with 4.8 % occurring during the summer monsoonal season (WRCC 2008). Thus, the study area is situated in the middle of a very steep precipitation and ecotonal gradient between arid desert transmontane conditions immediately to the east and more mesic montane and cismontane conditions immediately to the west.

Since the 1970s, fire frequency in this area has increased dramatically (Brown and Minnich 1986, Brooks and Esque 2002). This increase is thought to be due to a combination of high rates of atmospheric nitrogen deposition that promote fine fuel loads (e.g., invasive annual grasses) (Rao *et al.* 2010), and increased opportunities for human ignitions since the study area is within a wildland-urban interface immediately adjacent to major southern California metropolitan areas (Brooks and Esque 2002).
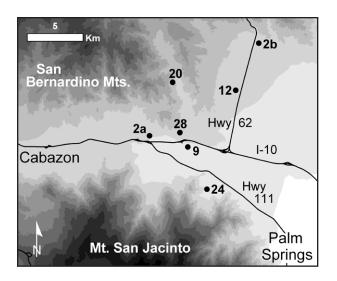
Figure 1. Western Coachella Valley study area in Riverside County, California, USA, showing the names and locations of the study sites. Study sites were named after the number of years since their fires occurred. Darker colors represent increasing elevation.

Study Site Selection Process

In the spring of 2006, potential study sites were identified based on stereoscope validation of fire perimeters of the study landscape from a series of aerial photographs that spanned from 1949 to 2005. Aerial photos were obtained from Riverside County Flood Control and Water Conservation District, Coachella Valley Water District, and University of California Riverside Science Library. We analyzed aerial photographs from 1949, 1957, 1974, 1980, 1984, 1985, 1986, 1987, 1989, 1990, 1995, 1996, 1998, 2000, and 2005 to determine dates of fires. If the year of each fire could not be determined from the aerial photographs, then historic *Los Angeles Times* articles (via ProQuest©; http://www.proquest.com), personal communication (R. Minnich, University of California, Riverside), and personal observations (i.e., for all fires that occurred in 2005) were used. At two of the study sites utilized, the year of fire was only narrowed down to a 2-year period. Since fires in desert vegetation are more common following winter sea-

sons with above average rainfall (Brooks and Matchett 2006), the wetter of the two possible burn years are reported in this experiment as the assumed burn year.

Unburned reference stands selected for comparison with each burned stand were also identified from aerial photographs in the spring of 2006. All paired unburned reference sites were adjacent to burned stands in similar areas of shrub cover based on remotely sensed pre-fire conditions visible on aerial photographs. They were also located opposite fuel breaks (bulldozer-lines, dirt roads, or paved roads) to minimize the potential for fuel differences between burned and unburned vegetation at the time of each fire. Originally, over 20 unique sites that had burned were identified in the study area from aerial photography but, after ground-truthing each site in July and August of 2006, only seven were selected for this study. Sites were dismissed from the study if they lacked suitable unburned reference vegetation (i.e., unburned vegetation adjacent to burned vegetation did not appear to be separated by a fuel break so differences in fuel between the two areas may have existed at the time of fire). Other reasons for dismissal were recent grazing history (based on sightings of livestock, the presence of trails and ruts indicative of livestock, drinking troughs, scat, and browsed vegetation within large fenced-in areas), and irregular soil type (based on NRCS soils maps or percent sand, silt, and clay analyses [Steers 2008]). Lastly, because of the strong precipitation gradient in the study area, additional sites adjacent to Cabazon and Palm Springs were removed to minimize climatic variation. All sites are assumed to be exposed to similar levels of precipitation and nitrogen deposition based on regional analyses (Rao *et al.* 2011).

Seven study sites that included burned and adjacent unburned stands of creosote bush scrub were sampled. These sites ranged in year burned from 1979 to 2005 and are named after their time since fire as of 2007 sampling: 2a, 2b, 9, 12, 20, 24, and 28. Two of the

burned sites experienced fire in the same year (two years before sampling) and were given the suffix 'a' and 'b' to distinguish them.

Vegetation Sampling

At each site, perennial plant cover and density were collected from six sampling units in both the burned and paired unburned reference vegetation. A stratified random sample design was utilized, which entailed dividing each stand into six equal subdivisions and then randomly placing one sample unit per subdivision (Barbour *et al.* 1999). Sampling units consisted of a 100 m line transect and 5 × 100 m belt transect on the right side of the line transect, facing upslope. Transects were oriented perpendicular to elevation contours. Desert wash habitat was specifically avoided since it can be more productive and can include perennials that are capable of vigorous resprouting following disturbances (Brown and Minnich 1986). The line transects were used to measure cover of live and dead perennial plants. Belt transects were used to measure density by species. Study sites were sampled in the spring of 2007. All species nomenclature follows USDA Plants database (http://plants.usda.gov).

Data Analyses

For comparing the vegetation structure between paired burned and unburned stands, total live and dead plant cover (excluding overlap), live shrub plus cacti cover (excluding overlap), dead shrub plus cacti cover (excluding overlap), live herbaceous perennial plant cover (excluding overlap), live shrub plus cacti density, dead shrub plus cacti density, and live herbaceous perennial plant density were evaluated. For comparing shrub and cacti species composition between paired burned and unburned stands, species richness, Shannon diversity (*H'*) (Shannon and Weaver 1963), and the probability of interspecific encounter (Δ_1) (Hurlbert 1971) were evaluated. To improve normality for statistical tests, arcsine transformations were performed on all cover and Δ_1 data. Also, density and richness values were square root transformed.

Vegetation between unburned and burned stands were compared three ways: 1) for each of the seven study sites, vegetation parameters from paired unburned and burned stands were compared using one-way ANOVA (*n* = 6, based on number of sample units per stand) with a Bonferroni corrected significance level (0.05 n^{-1}) equal to 0.0083; 2) mean vegetation parameters for all once-burned stands were compared to respective unburned reference stands using one-way ANOVA with a time since fire interaction (*n* = 7, based on the number of study sites) with a significance level equal to 0.05; and 3) species-specific impacts from fire, based on cover and density of the most common species across the study area (*A. dumosa*, *E. farinosa*, white ratany [*Krameria grayi* Rose and Painter], and *L. tridentata*), in addition to the sum of all cacti species, were compared between paired unburned and burned stands using the Kruskal-Wallis test for nonparametric data since they were severely nonnormal even after transformations (*n* = 6, based on number of sample units per stand) with a Bonferroni corrected significance level equal to 0.0083. The programs JMP® 7.0.2 (SAS Institute, Inc. Cary, North Carolina, USA) and SYSTAT® 12 (Systat Software, Inc. Chicago, Illinois) were used for statistical analyses.

RESULTS

Across the study area, 22 shrub and cacti species were documented. In unburned vegetation, *L. tridentata* and *A. dumosa* exhibited the highest cover (Table 1) and density (Table 2), respectively, which is typical of *Larrea-Ambrosia* microphyllous scrub that is common throughout the Colorado Desert (Ezcurra *et al*. 1987). *Ambrosia dumosa*, *E. farinosa*, *K. grayi*, and *L. tridentata* occurred in every unburned stand, with the exceptions that *E. fari-*

Table 1. Mean cover (%) of live perennial species in paired unburned and burned stands per study site. Study sites are named after the years since fire. Only the four most common species, preceded by a 'K' superscript, had their cover values statistically compared between paired burned (Burn) and unburned (UB) stands within each site, based on Kruskal-Wallis tests. Significantly greater cover values in one stand versus its paired burned or unburned stand are indicated by * for *P* values < 0.0083 (Bonferroni-corrected *P* < 0.05). The '<' symbol represents cover values less than 0.1 %.

Species	2a UB	2a Burn	2b UB	2b Burn	9 UB	9 Burn	12 UB	12 Burn	20 UB	20 Burn	24 UB	24 Burn	28 UB	28 Burn
Shrubs														
Asclepias subulata[a]	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Acamptopappus sp.[b]	0.0	0.0	0.0	0.0	0.0	0.0	<	0.0	0.0	0.0	0.0	0.0	0.0	0.0
[K]*Ambrosia dumosa*	1.8*	0.0	3.9	0.8	<	0.0	1.9	0.3	6.3*	0.4	0.9	1.0	0.4	<
Bebbia juncea	0.0	0.0	0.0	0.0	0.0	0.0	0.0	<	0.0	0.0	0.0	0.0	0.0	0.0
[K]*Encelia farinosa*	0.0	0.1	0.4	<	0.0	0.0	2.5	9.8*	1.3	27.1*	1.7	6.6	0.6	12.6*
Hymenoclea salsola	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.3
Ephedra californica[c]	0.0	0.0	1.6	0.0	0.1	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	<
[K]*Krameria grayi*	0.0	0.0	1.5	0.0	2.1*	0.0	<	0.0	2.9*	0.0	0.7	0.0	0.7	0.0
Psorothamnus arborescens	0.0	0.0	0.8	0.3	0.0	0.0	0.0	0.0	0.2	0.0	0.2	1.0	0.0	0.0
Thamnosma montana[d]	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
[K]*Larrea tridentata*	11.0*	0.0	13.1*	<	9.0*	0.6	9.0*	0.6	9.0*	0.6	7.1*	0.0	11.1*	<
Cacti														
Echinocereus engelmannii[e]	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0
Ferocactus cylindraceus[f]	0.0	0.0	0.0	0.0	0.0	0.0	<	0.0	0.0	0.0	0.0	0.0	0.2	0.0
Mammillaria tetrancistra[g]	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	<	0.0
Opuntia basilaris[h]	0.0	0.0	<	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	<	0.0
Opuntia bigelovii[i]	0.0	0.0	0.0	0.0	0.0	0.0	<	0.0	0.0	0.0	0.0	0.0	<	0.0
Opuntia echinocarpa[j]	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.2	<	<	0.0	0.5	0.0
Herbaceous perennials														
Stephanomeria pauciflora	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	<
Croton californicus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0
Stillingia linearifolia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	<	0.0	0.0	0.0	0.0	0.0	0.0
Ditaxis neomexicana	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	<
Mirabilis bigelovii	0.0	0.0	0.0	0.0	0.0	0.0	<	<	<	0.0	0.0	0.0	<	<
Datura wrightii[l]	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	<	0.0	0.0

[a] *Asclepias subulata* Decne.
[b] *Acamptopappus sphaerocephalus* (Harve. &. A. Gray ex A. Gray) A. Gray
[c] *Ephedra californica* S. Watson
[d] *Thamnosma montana* Torr. & Frém.
[e] *Echinocereus engelmannii* (Parry ex Engelm) Lem
[f] *Ferocactus cylindraceus* (Engelm.) Orcutt
[g] *Mammillaria tetrancistra* Engelm.
[g] *Opuntia basilaris* Engelm. & J.M. Bigelow
[i] *Opuntia bigelovii* Engelm.
[j] *Opuntia echinocarpa* Engelm. & J.M. Bigelow
[l] *Datura wrightii* Regel

nosa was absent from site 9 and *K. grayi* was absent from site 2a (Tables 1 and 2).

Fire Effects on Vegetation Cover

Fire disturbance decreased live and dead perennial cover for stands with a time since fire of 12 years or less (Table 3). For stands with a greater time since fire, live and dead perennial cover either showed no difference compared to paired unburned stands or was reduced (Table 3). Live shrub plus cacti cover was low for at least 12 years after fire but then increased in older stands (Table 3). At the

Table 2. Mean density (500 m^{-2}) of live perennial species in paired unburned and burned stands per study site. Study sites are named after the years since fire. Only the four most common species, preceded by a 'K' superscript, had their density values statistically compared between paired burned (Burn) and unburned (UB) stands within each site, based on Kruskal-Wallis tests. Significantly greater density values in one stand versus its paired burned or unburned stand are indicated by * for *P* values < 0.0083 (Bonferroni-corrected *P* < 0.05).

	2a		2b		9		12		20		24		28	
Species	UB	Burn	UB	Burn	UB	Burn	UB	Burn	UB	Burn	UB	Burn	UB	Burn
Shrubs														
Acacia greggii[a]	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Acamptopappus sp.[b]	0.0	0.0	0.3	0.0	0.0	0.0	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
[K]*Ambrosia dumosa*	16.5*	0.2	53.3*	6.7	1.2	0.0	20.5*	3.0	62.7*	3.2	26.7	6.5	5.7	2.0
Asclepias subulata	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bebbia juncea	0.0	0.0	0.2	0.0	0.0	0.0	0.2	0.5	0.0	0.0	0.0	0.0	0.0	0.5
[K]*Encelia farinosa*	0.8	1.5	5.2	3.8	0.0	0.0	26.3	94.5*	9.8	281*	12.5	60.7*	3.5	82.5*
Ephedra californica	0.0	0.0	7.5	1.0	2.2	0.0	0.0	0.0	3.3	0.0	0.0	0.0	0.3	0.3
Eriogonum fasciculatum[c]	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hymenoclea salsola	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.2	2.0	0.0	6.0
Isomeris arborea[d]	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
[K]*Krameria grayi*	0.0	0.0	6.5*	0.7	11.5*	0.8	1.3	0.0	16.3*	0.3	4.5*	0.0	3.0*	0.0
[K]*Larrea tridentata*	16.8*	1.5	10.5*	0.7	25.0*	4.7	13.0*	0.2	10.3*	3.0	9.7*	0.3	10.0*	0.3
Psorothamnus arborescens	0.0	0.0	1.5	1.2	0.0	0.0	0.0	0.0	0.0	0.0	1.0	4.8	0.0	0.0
Thamnosma montana	0.0	0.0	0.2	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Viguiera parishii[e]	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	1.3	0.0	0.0	0.0	0.0
Yucca schidigera[f]	0.0	0.0	0.2	0.0	0.0	0.0	0.3	0.2	0.5	0.0	0.0	0.0	0.2	0.0
Cacti														
Echinocereus engelmannii	0.8	0.0	0.2	0.0	0.2	0.0	0.0	0.0	2.5	0.0	0.0	0.0	2.2	0.5
Ferocactus cylindraceus	0.2	0.0	0.2	0.0	0.0	0.0	0.7	0.0	0.2	0.0	0.0	0.0	8.8	0.2
Mammillaria tetrancistra	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0
Opuntia basilaris	0.0	0.0	0.8	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.2	0.0	2.7	0.5
Opuntia bigelovii	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.7	2.2	0.0
Opuntia echinocarpa	2.7	0.0	1.8	0.0	0.2	0.0	0.2	0.0	7.0	0.0	1.2	0.0	6.5	0.3
Herbaceous perennials														
Croton californicus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	25.5	0.0	0.0
Cucurbita palmata[g]	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Datura wrightii	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
Ditaxis neomexicana	0.0	0.0	0.0	2.3	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	2.0	4.8
Mirabilis bigelovii	0.0	0.0	0.2	0.0	0.2	0.0	0.5	0.3	0.7	0.0	0.0	0.0	2.3	6.5
Sphaeralcea ambigua	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
Stephanomeria pauciflora	0.0	0.0	0.3	0.0	0.0	1.0	0.5	1.5	0.0	0.0	0.5	3.2	0.0	0.5
Stillingia linearifolia	0.0	0.0	0.0	0.2	0.0	0.0	0.0	4.5	0.0	0.0	0.0	0.0	0.0	0.0

[a] *Acacia greggii* A. Gray
[b] *Acamptopappus sphaerocephalus*
[c] *Eriogonum fasciculatum* Benth.
[d] *Isomeris arborea* Nutt.
[e] *Viguiera parishii* Greene
[f] *Yucca schidigera* Roezl. Ex Ortgies
[g] *Cucurbita palmata* S. Watson

three oldest burned sites (20, 24, and 28), live shrub plus cacti cover was either greater than the paired unburned stand or was not different (Table 3). The reestablishment of live cover in older burns was due to *E. farinosa* (Tables 1 and 2). Lastly, unburned stands had greater dead shrub plus cacti cover than their respec-

tive paired burned stands except in the oldest burned stands (Table 3). When comparing unburned and burned stands from all sites simultaneously, there was never any significant difference between total live and dead plant cover (*F* = 0.899, *P* = 0.363), live shrub plus cacti cover (*F* = 2.063, *P* = 0.179), dead shrub plus

Table 3. Mean cover (%) and density values (500 m^{-2}) in paired unburned (UB) and burned (Burn) stands per study site. Study sites are named after the years since fire. All structural parameters shown were statistically compared between paired stands per site. *P* values < 0.0083 (Bonferroni-corrected *P* < 0.05) are indicated by *. The '<' symbol represents cover values less than 0.1 %.

Structural parameters	2a UB	2a Burn	2b UB	2b Burn	9 UB	9 Burn	12 UB	12 Burn	20 UB	20 Burn	24 UB	24 Burn	28 UB	28 Burn
Live and dead perennial cover (%)	24.3*	8.0	33.6*	15.0	18.4*	9.1	24.8*	13.6	34.3	52.0*	14.6	11.0	21.6	18.5
Live shrub & cacti cover (%)	12.8*	0.2	21.0*	1.1	11.3*	0.6	13.8	10.8	20.2	28.2	10.6	8.9	13.6	13.1
Dead shrub & cacti cover (%)	11.9	8.0	14.2	13.8	7.2	8.5	11.4*	3.0	15.1	27.4*	4.0	1.4	8.1	5.4
Live herbaceous perennial cover (%)	0.0	0.0	0.0	0.0	0.0	0.0	<	<	<	0.0	0.0	0.9*	0.2	0.2
Live shrub & cacti density (500 m^{-2})	37.8*	3.2	90.3*	14.0	40.2*	5.5	65.2	98.5	113.8	288.8*	55.8	75.2	46.3	93.2*
Dead shrub & cacti density (500 m^{-2})	86.0*	24.2	68.0*	36.7	44.8	38.2	87.5*	30	105.7	131.0	75.5*	25.0	80.0	79.0
Live herbaceous perennial density (500 m^{-2})	0.0	0.0	1.5	2.8	0.2	1.0	1.0	6.5	0.7	0.0	0.8	29.0*	4.3	11.8

cacti cover (*F* = 0.032, *P* = 0.860), or live herbaceous perennial plant cover (*F* = 0.946, *P* = 0.352), nor a time since fire interaction; although, the time since fire interaction for live herbaceous perennial plant cover was near significant (*F* = 3.529, *P* = 0.087).

Fire Effects on Vegetation Density

Most shrub species and all cacti species were severely reduced by fire, especially in regard to density (Table 2). Almost all sites exhibited a significant difference in live shrub plus cacti density between paired burned and unburned stands. However, stands that had recently burned had less live shrub plus cacti density than paired unburned stands, while relatively older burned stands had greater density than paired unburned stands (Table 3). Dead shrub plus cacti density was usually higher in unburned than paired burned stands (Table 3). Elevated herbaceous perennial plant density was found in the two oldest burned stands (Table 3). Similar to cover, when all sites were compared simultaneously, plant density did not differ significantly between burned and un-

burned stands for live shrubs plus cacti (*F* = 0.229, *P* = 0.641), dead shrubs plus cacti (*F* = 3.907, *P* = 0.074), and live herbaceous perennial plant density (*F* = 2.907, *P* = 0.116). Also, there was no time since fire interaction; however, there was a near significant interaction with herbaceous perennial plant density (*F* = 4.003, *P* = 0.071).

Fire Effects on Richness, Diversity, and Interspecific Encounter

Total shrub plus cacti richness was lower in burned compared to unburned stands at every site except for site 24, which exhibited less richness in the burned stand but not significantly so (*F* = 7.0957, *P* = 0.0237) based on the Bonferroni corrected *P* value of 0.0083 (Figure 2). Likewise, Shannon diversity was always reduced by fire except at stand 2a (*F* = 9.7010, *P* = 0.0110) (Figure 2). Measures of the probability of interspecific encounter (PIE) for the most recently burned sites, 2a, 2b, and 9, did not differ between the burned and paired unburned stands (Figure 2) due to low density of live plants (Table 3). However, PIE was
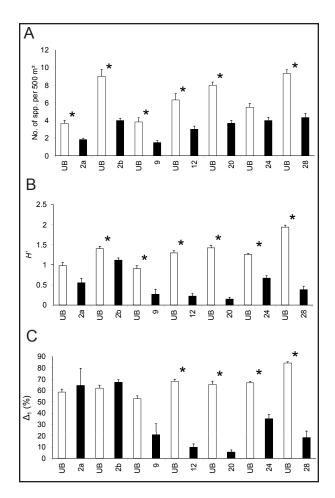
Figure 2. Average live shrub and cacti species richness (500 m^{-2}), Shannon diversity (H') (500 m^{-2}), and probability of interspecific encounter (Δ_1) (500 m^{-2}). An asterisk represents significant differences at $\alpha = 0.0083$ (Bonferroni-corrected $P < 0.05$).

lower in burned versus paired unburned stands at all other sites (Figure 2). When examining all sites simultaneously, burned stands exhibited significantly lower species richness ($F = 13.431$, $P = 0.004$), Shannon diversity ($F = 20.126$, $P = 0.001$), and PIE ($F = 10.442$, $P = 0.008$) compared to all unburned stands, with no time since fire interactions (data not shown).

Species Specific and Functional Group Responses to Fire

At all sites, dominant, long-lived shrubs like *A. dumosa*, *K. grayi*, and *L. tridentata* ex-

hibited lower cover and density in burned stands compared to unburned stands (Tables 1 and 2). Often the difference between paired stands was significant, lasting up to 28 years after fire. However, due to overall low cover and density in some stands, statistical differences were not always detectable. Relative density and cover values of long-lived perennials also exhibited similar impacts to fire disturbance (Figures 3 and 4).

Average cacti density and cover also decreased after fires. Sites 2a and 2b showed decreases in cacti density ($\chi^2_1 = 9.504$, $P = 0.0021$; $\chi^2_1 = 7.2052$, $P = 0.0073$, respectively), dropping from 3.7 (SE = 1) and 3.2 (SE = 0.9) individuals (500 m^{-2}) to zero individuals, respectively. Cacti density at site 12 decreased ($\chi^2_1 = 5.2537$, $P = 0.0219$) from 1.2 (SE = 0.5) to zero individuals (500 m^{-2}). At site 20, both cover and density of cacti decreased ($\chi^2_1 = 11.0056$, $P = 0.0041$; $\chi^2_1 = 16.1288$, $P = 0.0003$, respectively); cover dropped from 0.5 % (SE = 0.1) to near elimination (0 %, SE
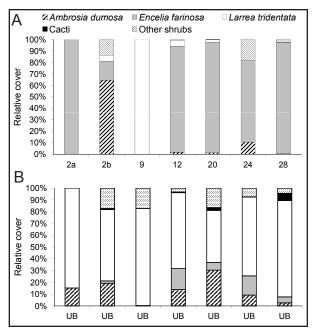

Figure 3. Relative cover of live shrubs and cacti in burned (A) and paired unburned (B) stands. Unburned stands are indicated by the letters UB and are below the burned stand they correspond to.
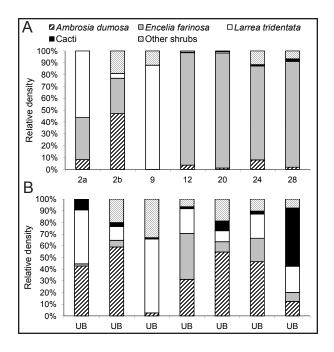
Figure 4. Relative density of live shrubs and cacti in burned (A) and paired unburned (B) stands. Unburned stands are indicated by the letters UB and are below the burned stand they correspond to.

= 0.4) and density dropped from 9.7 (SE = 1.1) individuals (500 m⁻²) to zero individuals. Site 28, which had the greatest cacti abundance of all sites, also significantly lost cover and density of cacti after fire ($\chi^2_1 = 9.4661$, $P = 0.0021$; $\chi^2_1 = 8.3958$, $P = 0.0038$, respectively), dropping from 0.9 % (SE = 0.3) to zero cover and from 22.8 (SE = 2.5) individuals to just 1.5 (SE = 0.7) individuals (500 m⁻²). Overall, sites with relatively high cover and density of cacti experienced the greatest decreases when burned (Figures 3 and 4).

The species with the greatest positive response to fire was *E. farinosa*, which was evident in 12 year old or older burned stands (Tables 1 and 2). Other shrubs, such as sweetbush (*Bebbia juncea* [Benth.] Greene), burrobrush, and indigo bush (*Psorothamnus arborescens* [Torr. Ex A. gray] Barneby var. *simplicifolius* [Parish] Barneby), appeared less impacted by fire relative to other shrubs (Table 1). However, it is difficult to draw conclusions about their individualistic responses since they were less

common and the study suffers from low sample size. The positive response by herbaceous perennial vegetation was mostly due to increases in croton (*Croton californicus* Müll. Arg) at site 24 and by common ditaxis (*Ditaxis neomexicana* [Muell. Arg.] A. Heller) and wishbone bush (*Mirabilis bigelovii* A. Gray) at site 28. The herbaceous perennials, wire lettuce (*Stephanomeria pauciflora* [Torr.] A. Nelson) and linear leaved stillingia (*Stillingia linearifolia* S. Watson), also responded positively where they occurred (Table 1).

DISCUSSION

The impact of fire on the shrub and cacti species in the study area is consistent with findings from other fires in the American Southwest (Abella 2009). In our study area, *Encelia farinosa* is an especially important colonizer of burned sites. The positive or advantageous response of *E. farinosa* to disturbance has also been documented in other deserts, such as Upland Sonoran vegetation of Arizona (Cave and Patten 1984); desert scrub of Sonora, Mexico (Turner 1990); and desert scrub of the southeastern Mojave Desert (Abella *et al*. 2007). Abella (2009) has also listed other perennials (such as desert globe mallow [*Sphaeralcea ambigua* A. Gray], desert stipa [*Achnatherum speciosum* {Trin. & Rupr.} Barkworth], and desert marigold [*Baileya multiradiata* Harv. & A. Gray ex A. Gray], among others) that react opportunistically in post-fire environments elsewhere.

Fire Effects in the Western Colorado Desert

The short-term impact of single burns on creosote bush scrub vegetation of the study area has been previously investigated up to five years since fire, at five separate sites in two separate studies (O'Leary and Minnich 1981, Brown and Minnich 1986). Like our findings from recently burned stands, Brown and Minnich (1986) observed increased *E. fa-*

rinosa cover and density relative to other shrubs. They also documented *E. farinosa* seedling densities that were orders of magnitude greater than other shrub species and concluded that burned stands would convert to *Encelia*-dominated shrublands capable of persisting for decades.

Our observations in relatively older stands (12 yr to 28 yr since fire) confirm the predictions of Brown and Minnich (1986). However, if *E. farinosa* is not a component of the pre-fire community, then type conversion to an *Encelia* shrubland does not seem to occur. For example, *E. farinosa* was absent from the unburned vegetation at study site 9, and the only shrub components in the post-fire community were several *L. tridentata* resprouts. Alternatively, O'Leary and Minnich (1981) have shown that where *H. salsola* is abundant in prefire stands, it becomes dominant following fire. *Hymenoclea salsola* was also absent in both burned and unburned areas at site 9.

The observations from site 9 are important because they suggest that where shrublands lack propagules of early colonizers (Vasek 1983), the potential for type conversion to invasive annual grassland might be higher (see Steers and Allen 2011). Also, our results suggest that whether the post-fire community is dominated by *E. farinosa* or invasive annuals, the reestablishment of other shrubs typical of creosote bush scrub can be virtually non-existent. However, even though shrub plus cacti diversity is significantly reduced compared to unburned stands for at least 30 years after fire and likely to be reduced for many decades into the future, this outcome should be expected considering the slow population dynamics (Cody 2000), and the long time periods required for desert shrubland development (McAuliffe 1988) and recovery from disturbances (Lovich and Bainbridge 1999, Abella 2010).

It is also very unlikely that all of our study sites experienced the same fire intensity when they burned, which can affect post-fire recovery (Bazzell 1988, Brooks 2002). Furthermore, based on unburned reference stands, initial species composition was not the same among all burned stands. Despite this variation, all sites experienced major alterations to vegetation structure, species richness, or diversity. Alternatively, in creosote bush scrub of the eastern Mojave Desert, diversity never differed between burned and unburned sites, and richness recovered ≥10 years post fire; although, these measures included all perennials, even herbaceous species, and were recorded from smaller, 100 m² plots (Engel and Abella 2011).

Alterations to Fuel Properties

The replacement of *L. tridentata* and other evergreen desert shrubs and cacti with *E. farinosa*, a short-lived (Goldberg and Turner 1986) and shallow rooted (Nobel and Jordan 1983), drought to semi-drought deciduous shrub (Cunningham and Strain 1969), may alter the fire regime. *Encelia farinosa* plants are relatively short, hemi-spherical shrubs with relatively large leaves. They are highly sensitive to water stress and rapidly alter their phenology at the onset of drought (Smith and Nobel 1977). They produce their largest leaves during the winter wet season, which desiccate from lower portions of the branches up to the tips as summer drought progresses (Cunningham and Strain 1969). Moisture content of *E. farinosa* might be very low early in the dry season (although, see Sandquist and Ehleringer 1998). Because of these traits, shrublands dominated by this species may be more prone to combustion earlier in the dry season than other species typical of unburned creosote bush scrub, and thus facilitate the spread of fire earlier in the calendar year. Also, the spatial distribution of *E. farinosa* in burned shrublands is more dense and regularly spaced than shrubs in unburned creosote bush scrub (Steers 2008), resulting in altered horizontal fuel properties that may lessen the importance of herbaceous fuel loads necessary to carry fire and allow fires to become larger.

Although changes due to dominance by *E. farinosa* may promote fire, fire intensity might be reduced since *E. farinosa* does not accumulate organic matter (Muller 1953) or support high amounts of herbaceous species in their understories as does *L. tridentata* (Went 1942, Muller 1953). Thus, while type conversion to exotic annual grassland is generally not occurring (although, see site 9 in this study), the fire regime of the study area may still be altered due to post-fire formation of *E. farinosa* shrublands.

Areas for Future Research

The relatively long-term impact of fire on shrub plus cacti diversity was one of the most striking findings from this study. Several hypotheses may explain the lack of shrub and cacti reestablishment observed in burned stands. First, seeds may be eliminated by fire (propagule limitation) (Brooks 2002). Second, past fires that were not visible on the aerial photographs used to select study sites may have depleted the density, cover, or species richness of these plants (e.g., Brooks in press); however, we feel that this is highly unlikely. Third, competition with invasive annual plants could prevent shrub seedling recruitment and reduce the survival rate of resprouts (competitive exclusion) as observed in an exotic grass removal study (Steers and Allen 2010). Fourth, establishment of long-lived shrubs is a rare phenomenon in general (Barbour 1969, Boyd and Brum 1983) and inadequate time may have passed to observe a recruitment event. Fifth, the removal of nurse plants or alterations to "fertile islands" by fire may result in safe-site limitation, preventing successional processes from advancing. For example, *E. farinosa* understories do not accumulate understory debris like *L. tridentata* and *A. dumosa* (Muller 1953). Sixth, allelopathic exudates from *E. farinosa* leaves have been shown to cause mortality to plants (Gray and Bonner 1948) and could also explain why a lack of shrub reestablishment has been observed. However, these allelopathic chemicals are inactive under field conditions typical of the study area (Muller 1953). Evaluating the importance of each of these hypotheses will provide essential information for understanding the future of creosote bush scrub in invaded and fire prone regions of the western Colorado Desert.

A mechanistic understanding of woody and succulent plant establishment for multiple species may be necessary for reinstating the diversity and structure that characterize unburned vegetation. For example, the potential for *E. farinosa* that occur in post-fire stands to act as nurse plants (Sherbrooke 1989, Flores and Jurado 2003) for recruiting long-lived desert shrubs and cacti should be investigated. The role of other ecologically important structural characteristics, like fertile islands (Dean *et al*. 1999, Carrillo-Garcia *et al*. 2000, Bolling and Walker 2002, El-Bana *et al*. 2003), horizontal shrub distribution (Barbour 1969, Phillips and MacMahon 1981, Huenneke *et al*. 2001, Schenk and Mahall 2002, Schenk *et al* 2003), vertical heterogeneity of the canopy (Steers 2008), or belowground structure of roots (Mahall and Callaway 1991, Wilcox *et al*. 2004, Schenk 2005) may be 'keystone structures' (*sensu* Tews *et al*. 2004) that are critical for biodiversity. The loss of *L. tridentata* and substitution by *E. farinosa* is a major shift in structure, but it is still unclear what key structural features, if any, are associated with high biodiversity in creosote bush scrub vegetation; or what restoration actions can be employed to recreate those features or speed recovery (although, see Abella *et al*. 2007, Bainbridge 2007).

Management Implications

Preventing fire is critical for preserving arid shrublands. The most ecologically beneficial way to accomplish this would be through the removal of invasive annual plants from the study area (Brooks 1999). Because invasive plants can competitively inhibit native perennials (DeFalco *et al*. 2007, Steers and Allen

2010), control of these invaders is important regardless of their fire-promoting traits. Thus, invasive plant removal could decrease overall fire frequency and release native plants from competition—a double benefit. Similar recommendations have also been made for fire prone areas of the eastern Mojave Desert (Brooks *et al*. 2007). However, invasive annual plant control at large scales is a daunting if not impossible task. Poaceae- and Geraniaceae-specific herbicides show promise for success at large scales (Steers and Allen 2010), but are also capable of producing non-target impacts. Lastly, recent studies have shown that the high nitrogen deposition in this region of the Colorado Desert is increasing invasive annual productivity (Rao and Allen 2010, Rao *et al*. 2010), so reducing air pollution could be an indirect mechanism to control invasive species.

The maximum life span of *E. farinosa* has been reported at 32 years (Goldberg and Turner 1986). In the next decade, many *E. farinosa* individuals in the older burned stands will likely die off. Once dead, if *E. farinosa* shrub skeletons break up and begin accumulating windblown debris, then microsites more suitable to shrub establishment for longer-lived species may occur. For example, Went (1942) found higher annual species richness, composed of 'understory obligates,' under dead *E. farinosa* compared to live *E. farinosa*. Utilizing dead *E. farinosa* shrubs in combination with other shrub planting techniques may be a successful restoration approach.

CONCLUSIONS

Our hypothesis that native perennial live plant cover and density would be lower in burned than unburned creosote bush scrub, regardless of time since fire, was rejected because we did not find a significant overall effect of fire on these response variables. However, the three sites with the longest time since fire (20 yr, 24 yr, and 28 yr) displayed higher or similar total cover and density in burned than unburned areas, almost entirely attributed to one species, *E. farinosa*. Besides *E. farinosa*, we found that almost all other shrub species decreased in abundance as a result of fire regardless of time since fire. We also found that certain functional groups, like succulents, were severely impacted by fire, similar to other studies in desert shrublands (O'Leary and Minnich 1981, McLaughlin and Bowers 1982, Cave and Patten 1984, Brown and Minnich 1986, Alford *et al*. 2005). In this study, herbaceous perennials showed a positive, yet delayed, response to fire. In contrast, other desert studies have observed increased herbaceous perennial abundance within one to three years post fire (Cave and Patten 1984, Abella *et al*. 2009).

Our hypothesis that shrub plus cacti diversity would be lower in burned than unburned creosote bush scrub regardless of time since fire, was not rejected. Return of pre-fire plant richness and diversity appears to take much longer than two to three decades after fire. In conclusion, fire is a major threat to creosote bush scrub in the western Colorado Desert. Active management and restoration that target vegetation structure and species diversity appear essential for the conservation of this vegetation type in fire prone regions.

ACKNOWLEDGMENTS

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