

Effects of fire on vegetation and small mammal communities in a Mojave Desert Joshua tree woodland

M.S. Vamstad^{a,*}, J.T. Rotenberry^b

^a United States Department of the Interior, National Park Service, Joshua Tree National Park, 74485 National Park Drive, Twentynine Palms, CA 92277, USA

^b Department of Biology and Center for Conservation Biology, University of California, Riverside, CA 92521, USA

ARTICLE INFO

Article history:

Received 9 June 2009

Received in revised form

30 March 2010

Accepted 5 April 2010

Available online 20 May 2010

Keywords:

Chronosequence

Fire

Rodents

Succession

Vegetation

Mojave Desert

Joshua tree Woodland

ABSTRACT

Wildfire size and frequency are increasing in Mojave Desert Joshua tree woodlands principally due to anthropogenic factors. These habitats are generally considered to be fire intolerant and the effects from fire are a major concern for land managers. This study investigated trends of ecosystem response to fire by looking at a chronosequence of historic burns. Plots were chosen at 2, 9, 13, 15, 19, and 65 years since burn in which to sample vegetation and rodent communities. Rodent diversity was lower in burned plots and increased over time. The abundance of rodents however, was not significantly different between the burned and unburned plots. Vegetation showed a directional change in species composition with time since fire. However, reestablished vegetation assemblages did not converge to the assumed pre-burn condition. It is probable that this difference relates to the slow rates of establishment of certain vegetation components that make up the pre-burn condition of the plots. There is a concern that invasion by exotic plant species, nitrogen deposition, and global climate change may initiate a fire cycle in this ecosystem that will arrest succession before the Joshua tree woodland is allowed to reestablish.

Published by Elsevier Ltd.

1. Introduction

Natural disturbances are recurring components of the vast majority of ecosystems, and numerous ecological theories have been developed in an attempt to predict biotic responses to them (Lindenmayer et al., 2008). In arid environments, surface soil disturbance severely disrupts an ecosystem that is especially slow to recover (Lovich and Bainbridge, 1999). Evidence of this slow recovery comes from study of debris flow terraces (Bowers et al., 1997) and well-documented human developments in deserts (military camps, ghost towns and mines) that were long abandoned from human use (Abella, 2009, 2010; Belnap and Warren, 2002; Knapp, 1992; Prose et al., 1987; Webb and Wilshire, 1980; Webb et al., 1987). Soil compaction from these types of disturbances appears to be a significant factor in retarding the establishment of desert plants (Prose et al., 1987; Webb and Wilshire, 1980). However, fire, as a natural vegetative denudation event, avoids substrate disturbance and soil compaction and may lead to a different trajectory of ecosystem response. Recovery of plant cover after fire (within 10% cover value of unburned plots) in the Mojave and Sonoran Deserts has shown to occur within 40 years;

however, species composition of these sites did not converge within a 47-year timeframe sampled (Abella, 2009).

Large fires have been historically infrequent in Joshua tree woodlands (see Appendix A for scientific names of plants) found within the Mojave Desert of the American Southwest, and the recent increase in fire size and frequency is partially due to invasion of exotic grasses, principally *Bromus tectorum*, *Bromus rubens* and *Schismus barbatus* (Brooks, 2000). Winter seasons with relatively high amounts of precipitation produce an increase in biomass of native and especially non-native annual plants sufficient to carry fire in invaded habitats. The most dramatic impacts have occurred in middle elevation shrublands dominated by *Larrea tridentata*, *Yucca brevifolia*, and/or *Coleogyne ramosissima*, where most of the fires occurred between 1980 and 2004 (Brooks and Matchett, 2006). The increase in fine, flashy fuel biomass from exotic plant species has increased the fire potential of these habitats sufficiently to allow for more frequent large fires than were carried by native vegetation alone (Brooks and Matchett, 2006). The impact of vegetation denudation and the role of exotic grasses in this increased fire size and frequency is a major concern for land managers in the Mojave Desert. The proper management of this desert ecosystem depends on improved understanding of how the ecosystem responds to wildfire.

The vegetation in Joshua tree woodlands is generally not adapted to fire, in part due to its lack of a previously documented

* Corresponding author. Tel.: +1 760 367 5562.

E-mail address: michael_vamstad@nps.gov (M.S. Vamstad).

fire regime and in part due to its slow recovery from fire (Steers, 2008). Many species of long-lived perennial plants (e.g., *Y. brevifolia*, *C. ramosissima*, *Juniperus californicus*) in these habitats tend to have low recruitment and long life spans. Over time, these species attain dominance over other perennial species that have higher recruitment and mortality rates (e.g., *Hymenoclea salsola*, *Salazaria mexicana*, *Sphaeralcea ambigua*). Understanding changes to the cover of vegetation during reestablishment over time since fire may show secondary succession trends important to the management as well as the restoration of burned habitats.

Rodents are a key component of desert ecosystems (Brown et al., 2000). They are important consumers of plant materials (Price and Joyner, 1997) and are a significant portion of the prey base for a variety of carnivores. As rodents also have small home ranges and are sensitive to habitat change, they make likely candidates as biological indicators of environmental quality (Haim and Izhaki, 1994). Furthermore, seed predation by desert rodents has shown to significantly influence ecosystem structure and dynamics (Brown and Heske, 1990; Guo et al., 1995; Hoffmann et al., 1995; Longland, 2007; Montiel and Montana, 2003).

Results of studies of rodent response to fire in arid environments have been inconsistent (Fitzgerald et al., 2001; Fox, 1982; Letnic, 2003; Letnic et al., 2004; Letnic and Dickman, 2005; Price and Waser, 1984; Valone et al., 2002). However, in a study of the rodents in the Sonoran Desert, it was found that species from the genus *Dipodomys* were associated with sparser vegetative cover while species of the genera *Peromyscus* and *Perognathus* required a more complex shrub cover (Rosenzweig and Winakur, 1969; Simons, 1991). This concept is further demonstrated in the Sonoran Desert as well as in semi-arid California Coastal Sage Scrub habitats where species composition responded to the availability of structural microhabitats (Price and Reichman, 1987; Price and Waser, 1984). As fire removes much of the vegetation structure, we predicted a reduction of rodent diversity in response to this type of disturbance. By exploring sites across a relatively long gradient of time-since-burned, the rodent community should provide an additional metric with which to sample the level of ecosystem response to fire.

We investigated trends in vegetation and small mammal reestablishment (secondary succession) following fire in a chronosequence in the Mojave Desert. Specifically, we examined the abundance and distribution of both vegetation and small mammal species along a time-since-burned gradient in a Joshua tree woodland habitat. We hypothesized that early-colonizing disturbance-adapted rodent species will be joined or replaced by species with more complex habitat structural requirements as the long-lived perennial vegetation initially removed from the system by fire increases over time.

Heightened understanding of these patterns is critical for improved biodiversity conservation, a goal of natural resource management (Abella, 2009). This work, coupled with the known increased fire frequency resulting from nitrogen deposition (Allen et al., 2009; Brooks, 2003; Fenn et al., 2003; Rao et al., 2009; Rao and Allen, 2010) and exotic grass invasion (Brooks et al., 2004) (by promoting exotic grass fuel accumulation due to greater biomass production), may provide valuable insights for better management of wildfire and recovery from wildfire in these habitats.

2. Methods

2.1. Study area

The Mojave Desert is topographically and vegetatively diverse, and is characterized by hot, dry summers and cool winters with low and variable amounts of precipitation. Mountain ranges tend to be isolated and narrow with extensive alluvial fans extending from the

base of mountains to low elevation basins. The Mojave Desert has the highest number of endemic plant species of the American southwestern deserts (McLaughlin, 1986).

The northwestern half of Joshua Tree National Park (JOTR), where this work was performed, is part of the Mojave desertscrub biome (Brown, 1994). Average July maximum and minimum temperatures are 41 °C and 22 °C, while average January maxima and minima are 17 °C and 0 °C. Using data from the Black Rock weather station (6 km west from study area), average annual rainfall is 17.7 cm (National Park Service Air Resources Division). Located entirely within the boundary of JOTR, the area we sampled is characterized by long-lived perennial species such as California juniper, Joshua tree, and blackbrush. The areas sampled are considered part of the *Y. brevifolia* Wooded Shrubland Alliance (Sawyer et al., 2009). In this alliance, trees are generally <14 m, the shrub layer is open to intermittent, and the herbaceous layer is open to intermittent with perennial grasses and seasonal annuals. The elevation of the sites sampled was between 1342 and 1481 m, which is considered mid-elevation for the Mojave Desert.

Study sites were chosen on the basis of the time that had passed since they last burned. Using National Park Service fire maps, which have recorded fire history in JOTR since 1943, we located six sites of 2, 9, 13, 15, 19 and 65 years since they were burned (Table 1, Fig. 1) and avoided areas that experienced repeat burns. Adjacent to each burned site we selected an unburned “control” site based on a lack of recorded fire history. Superficially, the unburned sites appeared vegetatively similar, consisting of typical juniper and Joshua tree woodland, which we assumed was the pre-burn condition of the burned sites. All of the sites are found within the Park’s boundary in a little-visited area, with little additional disturbance and no management manipulation. The majority of the burns we sampled during the 1980–2004 interval identified by Brooks and Matchett (2006) as one of relatively high fire frequency.

2.2. Survey and sampling design

Two sampling grids were placed at each burned and unburned plot to sample both the vegetation and rodents. The grid locations were chosen with an attempt to control for aspect, slope, and substrate. Using precise burn maps, we were able to avoid any large unburned islands of vegetation missed by the wildfire. Sampling grids were placed at least 100 m from any burned edge to reduce any major edge effects. Sampling was performed in May and June of 2008 after a winter of average rainfall.

2.2.1. Vegetation

We sampled vegetation at the sites using the Point Intercept (PI) method (Caratti, 2006) in June 2008. The PI method is used to assess plant species cover or ground cover for a macroplot. Sampling pins are placed at random intervals along linear transects within grids (see below), and all plant species, including annuals, that touched the pin were recorded as “hits” along the transect line. Percent cover values were calculated by dividing the number of hits

Table 1

Characteristics of burned sites studied in western Joshua Tree National Park. See Fig. 1 for locations.

Name	Year burned	Years since burned	Size (ha)	Elevation (m)
Whispering Pines fire	2006	2	401	1353
Juniper fire	1999	9	770	1412
Covington fire	1995	13	2234	1401
Nolina 3 fire	1993	15	38	1356
Nolina 2 fire	1989	19	10	1342
Unnamed fire	1943	65	372	1481

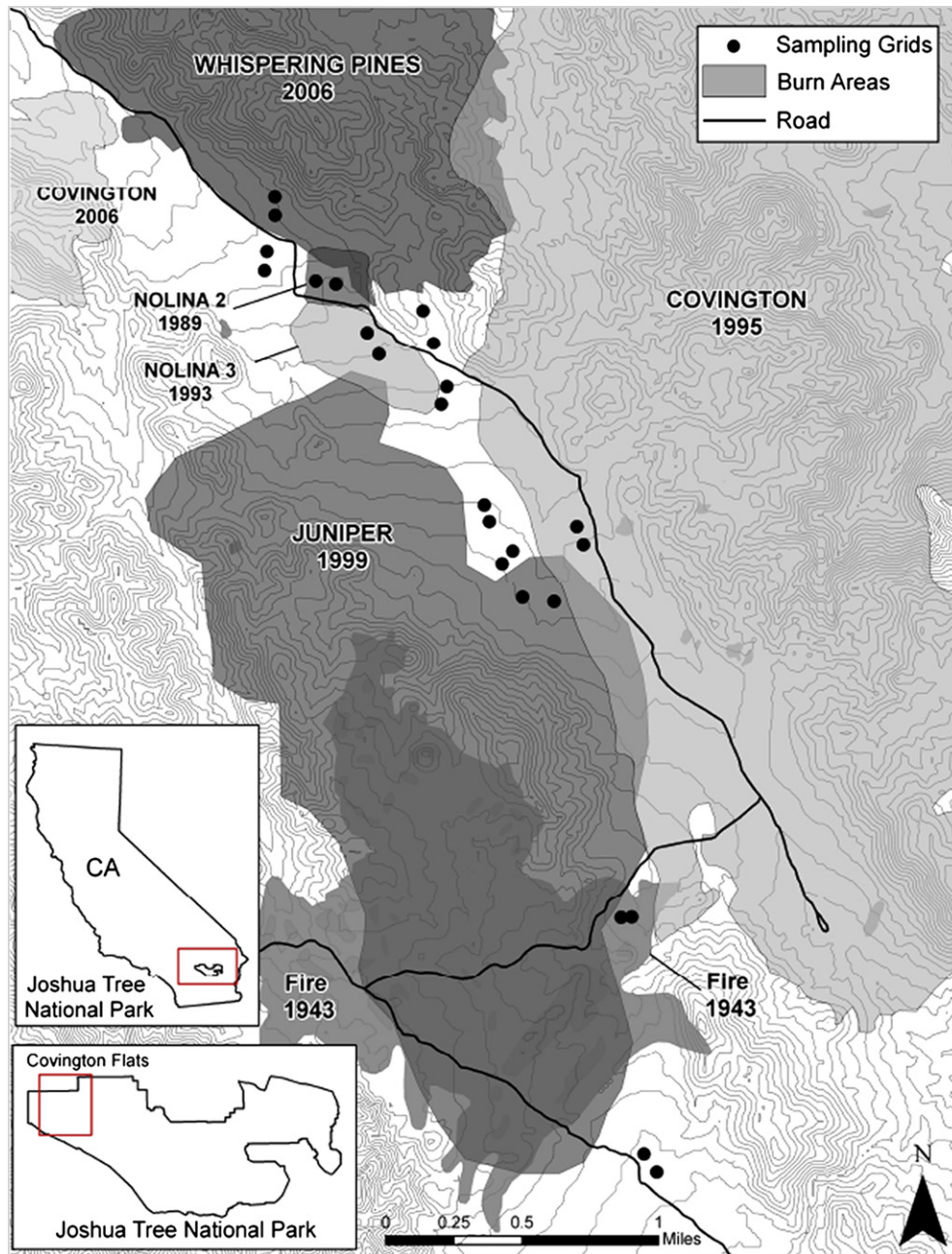


Fig. 1. Study area in Joshua Tree National Park showing approximate extent of burned areas and details of sampling grid locations.

for each plant species by the total number of points sampled. This method is primarily suited for vegetation types less than 1 m in height and is particularly useful for recording perennial shrubs, bunchgrasses, annual plants, and ground cover (Caratti, 2006).

Within each rodent sampling grid (described below) we placed twelve 50-m line transects along which we recorded PI data. Points were randomly placed and hits recorded in a stratified random manner within each 5-m interval of each transect. Thus, 120 points were recorded for each grid. As each plot contained two rodent sampling grids, a total of 240 point intercepts were recorded per site.

2.2.2. Rodents

Each burned and unburned site included two small mammal trapping grids. A grid consisted of 18 perforated Sherman live-traps (H.B. Sherman, Tallahassee, Florida, USA. model LFATDG-P 3" × 3.5" × 9" (7.6 cm × 8.9 cm × 22.9 cm)) set 10 m apart in

a 6 × 3 configuration. For three consecutive nights, traps were opened and baited, then checked and closed the following morning. Bait consisted of an easily managed mixture of rolled oats and peanut butter. Full moon effects on rodent activity (Price et al., 1984) were avoided by suspending sampling on weeks with full moons.

At the time of capture, each rodent species was identified by using a number of recorded morphologic measurements (Jameson and Peeters, 1988). Each individual was uniquely color marked with a "permanent" ink felt-tipped marker so as to distinguish new captures from recaptures across the season.

Rodents were sampled from March to June of 2008. In all, each grid was sampled four times over the duration of the field season for a total of 216 trap-nights per grid. A grand total of 5184 trap nights was recorded during the entire season among all six burned and six unburned plots.

2.3. Statistical analysis

2.3.1. Vegetation

To describe the structure of the vegetation community, we calculated species richness and diversity based on presence and percent cover values of each plant species. Richness was simply the number of species detected. Species diversity was calculated using Shannon's Diversity Index (SDI),

$$SDI = -\sum p_i \ln(p_i)$$

where p_i is the relative proportion of the i th species. The SDI is useful in this context as it takes into account both the number of species as well as the evenness of the distribution of abundances among the species.

Furthermore, we used Detrended Correspondence Analysis (DCA); (Gauch, 1982; Hill and Gauch, 1980; Pielou, 1984) to describe the composition of the vegetation community. Detrended Correspondence Analysis is an eigenvalue-based technique that is particularly suited for community data gathered along environmental gradients (ter Braak, 1995). It recovers the relationships among the species and provides an ordering of the sampling sites (ter Braak and Prentice, 1988). A sample's score on a DCA axis is a weighted combination of the abundances of the species that occur there; thus the similarity between two sample scores represents the similarity in their species composition. We ran DCA ordinations on a matrix that included all 24 sampling grids and point intercept cover values of all plant species that were detected in more than four sampling grids. Ordinations were calculated using PC-ORD (McCune and Mefford, 1999).

Next, we compared structure and composition of burned and unburned communities using the Mann–Whitney U test to test for differences in richness, SDI, and DCA scores. To assess whether community composition as indexed by DCA scores reflected any successional pattern, we examined the Spearman rank correlation between DCA scores and years since burned for the burned grids.

To better visualize the similarities between unburned and burned grids, we analyzed the data with Sørensen's distance (Abella, 2009). For each site we calculated the mean Sørensen distance between the two burned and two unburned grids; the more the grids had converged, the smaller the distance. To provide context, we also calculated the distance between each pair of burned grids and each pair of unburned grids; because each pair was intended to be replicates, we expected a relatively small distance.

2.3.2. Rodents

In general, the rodent community was subjected to the same analyses as the vegetation. However, we also used Canonical Correspondence Analysis (CCA) to describe the relationship between the small mammal community relative to the vegetation community and other environmental variables. The main matrix was constructed using the rodent captures across the sites. The

second (constraining) matrix was constructed using vegetation data grouped into life forms (Appendix A) and substrate variables. We used Monte Carlo permutations to determine if the strength of the species sorting along the environmental gradient was more than would be expected by chance (ter Braak, 1986).

3. Results

3.1. Vegetation

We detected 56 different plant species (Appendix A), which we grouped into five vegetation types based on size and life history (Table 2). The percent cover of long-lived perennial plants after fire showed an expected reduction (Table 2) followed by a return to unburned cover levels between 19 and 65 years since burned. Subshrubs established in the 9 and 13 years since burned and then declined. Annual plant cover showed a general increase through time in sites that had burned. Exotic annuals (*B. tectorum*, *B. rubens*, *Schismus barbatus* and *Erodium cicutarium*) appeared to rapidly invade the burned sites, achieving cover values similar to all other sites between 2 and 9 years since burned. Bunchgrasses showed no significant pattern through time.

There were no consistent relationships between burned and unburned grids with respect to either plant species richness or SDI (Fig. 2). The rank order correlation between species richness and time-since-burned was marginally significant ($r_s = 0.435$, $p = 0.079$). However, the relationship between the species diversity and the time since plots burned was not significant ($r_s = 0.212$, $p = 0.253$). No relationships were found by plotting the SDI values by growth form across the time-since-burned gradient, either (Fig. 3). Both annuals and perennial plants varied similarly and annuals were consistently more diverse than the other groups.

Based on DCA, the major gradient in vegetation composition ranged from grids dominated by long-lived perennials *C. ramosissima* and *J. californicus* at one end to sub-shrubs *Mentzelia albicaulis* and *S. ambigua* on the other end; the middle was dominated by *Ephedra nevadensis*, *H. salsola*, and *Linanthus aureus* (see Appendix B). The total variance (inertia) in the plant species data was 1.3219 and the eigenvalues of the first two axes were 0.315 and 0.164, respectively.

Scores from the burned and unburned sites differed significantly on DCA axis 1 ($U = 4$, $p < 0.0001$; mean of burned grids = 1.82, mean of unburned grids = 0.68), indicating a strong difference in overall plant community composition. Scores from axis 2 burned and unburned sites, however, were not significantly different ($U = 84.5$, $p = 0.245$; burned grid mean = 1.15, unburned grid mean = 1.35). The rank correlation between DCA axis 1 scores of burned plots and time-since-burned is marginally significant ($r_s = 0.533$, $p = 0.077$) and on axis 2 is not ($r_s = -0.071$, $p = 0.415$). Thus, the DCA captures turnover in plant species associated with a time-since-burned successional gradient along axis 1.

The vegetation differences (Sørensen distance) between burned and unburned grids at each plot were greater than within-grid

Table 2
Percent cover of vegetation types on burned and unburned plots. Percent cover calculated as the proportion of contacts observed over 240 pin placements. See Appendix A for list of species within each vegetation type.

Years since burned	Burned					Unburned				
	Annual	Exotic annuals	Bunch-grass	Sub-shrub	Long-lived perennial	Annual	Exotic annuals	Bunch-grass	Sub-shrub	Long-lived perennial
2	73	8	3	1	1	26	50	9	8	27
9	62	55	1	13	8	20	50	0	0	46
13	19	56	3	21	1	21	54	3	3	37
15	7	43	7	9	7	15	57	3	4	40
19	34	59	6	4	18	25	50	6	6	28
65	59	32	0	2	25	28	48	2	5	20

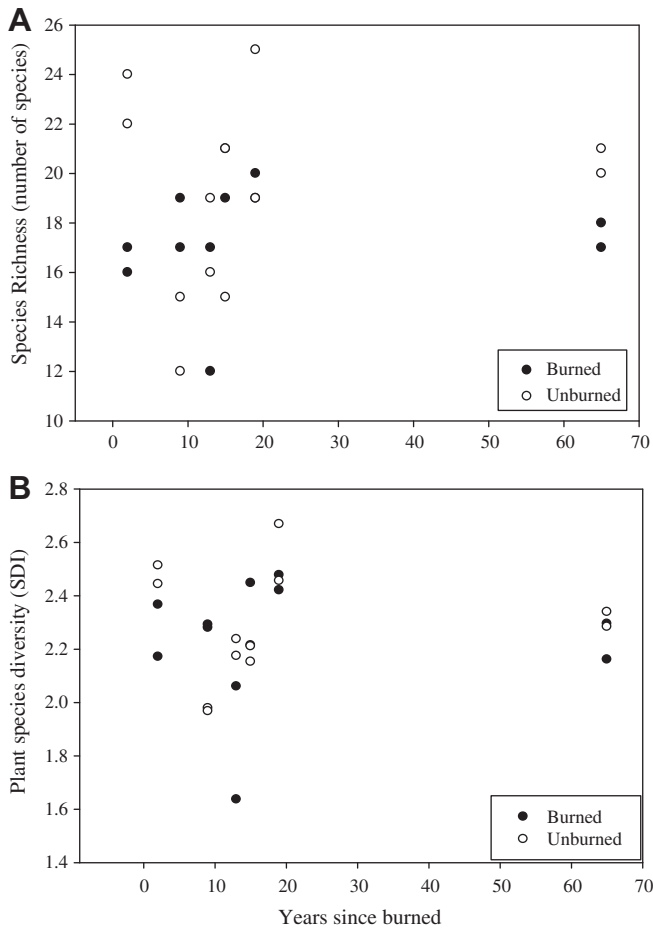


Fig. 2. Per-plot species richness (A) and Shannon Diversity Index (B) of the vegetation vs. time since fire. Richness levels and diversity index scores for the burned grids compared to the unburned grids were not significantly different (Mann–Whitney U test, $U = 90.5$, $p = 0.149$ and $U = 76$, $p = 0.421$).

differences in either burn replicates or unburned replicates in 11 of 12 cases (Fig. 4). Moreover, distances between burned and unburned did not narrow with time, implying that burned grids were not converging in their vegetation composition to those of unburned grids nearby, even after 65 years.

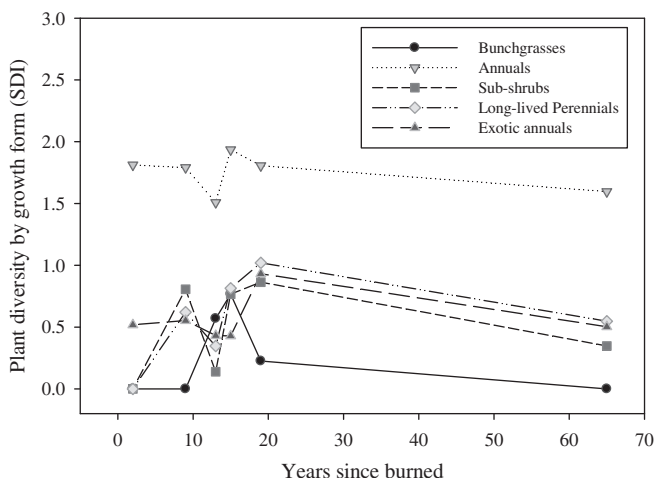


Fig. 3. SDI values by growth form across the year-since-burned gradient.

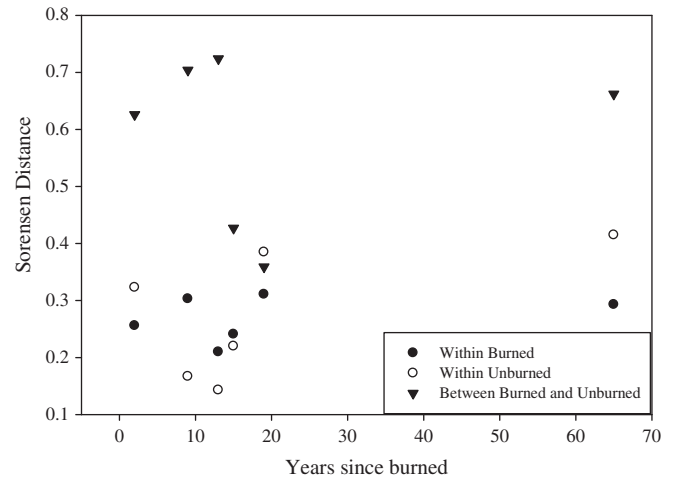


Fig. 4. Sørensen distance between grids based on vegetation composition. Within Burned denotes the distance between each pair of burned grids, Within Unburned denotes the distance between each pair of unburned grids, and Between Burned and Unburned denotes average distance between two burned and two unburned grids.

3.2. Rodents

Trapping across the entire season yielded 1886 captures (Table 3). Of these, 1202 were first captures rather than recaptures, representing unique individuals. Fifteen different species of small mammals were identified, with five species trapped two or fewer times. With 5182 total trap nights, trap success rate was 36.4% for all captures and 23.2% for unique individual captures.

Total small mammal abundance between the burned and unburned sites was not statistically different (Mann–Whitney U test, $U = 20$, $p = 0.405$) implying that the total abundance of rodents was not affected by fire. However, Shannon Diversity Index values were significantly higher in the unburned sites (Mann–Whitney U test, $U = 30$, $p = 0.033$; Fig. 5). Species richness values were not statistically different between the burned and unburned sites at the $p < 0.05$ level but, nearly so ($U = 28.5$, $p = 0.055$).

The rank correlations of rodent species richness and SDI with the time since the plots were burned were significant ($r_s = 0.806$, $p = 0.001$; $r_s = 0.721$, $p = 0.004$), showing an increase in richness and diversity over time. The total variance (inertia) in the rodent species data was 0.4967 and the eigenvalues of the first two DCA axes were 0.291 and 0.050, respectively (see Appendix C).

Scores from DCA axis 1 differed between burned and unburned sites (Mann–Whitney U test, $U = 116$, $p = 0.006$; burned grid mean = 0.88, unburned grid mean = 1.62), indicating that the rodent composition was different between the burned and unburned sites. Site scores compared on axis 2 were not significantly different ($U = 67.5$, $p = 0.409$; burned grid mean = 1.29, unburned grid mean = 1.21). Site DCA scores from both axis 1 and 2 were significantly correlated with the time since the plots were burned ($r_s = 0.679$, $p = 0.008$; $r_s = -0.049$, $p = 0.049$), implying a successional gradient in rodent community composition.

The rodent community similarities found by using Sørensen's distance coefficient between burned and unburned grids were highly variable (Fig. 6). Compositional heterogeneity within the rodent community assemblage at the grids was too great to elucidate any patterns relating to response from fire. Indeed, the greatest difference between burned and unburned grids was observed for the 65-year old plots, clearly indicating a lack of convergence in composition.

Table 3

Number of rodents captured in 432 trap-nights per plot in burned and unburned sites. Recaptured individuals and rare species not included.

Years since burned	Burned				Unburned			
	<i>Dipodomys merriamii</i>	<i>Perognathus longimembris</i>	<i>Peromyscus maniculatus</i>	<i>Peromyscus crinitus</i>	<i>Dipodomys merriamii</i>	<i>Perognathus longimembris</i>	<i>Peromyscus maniculatus</i>	<i>Peromyscus crinitus</i>
2	85	10	0	0	73	9	3	2
9	99	6	2	0	96	8	12	5
13	86	0	6	0	77	14	2	9
15	95	6	5	0	71	15	11	3
19	89	10	8	1	61	10	1	7
65	51	25	10	16	21	32	19	31

3.3. Vegetation and rodents

When we ordinated the rodent data constrained by their relationship to the vegetation data using CCA, we found that *Dipodomys merriamii* was associated with the burn sites, whereas *Peromyscus crinitus* and *Perognathus longimembris* were more likely to be found with the old burned and control sites (see Appendix D). Long-lived perennial plant species were associated more with unburned sites, and sub-shrubs and bunchgrasses were more closely associated with the burned sites (Table 4). The total inertia in the rodent dataset was 0.502, of which the first axis explained 41.8% of variance, with an additional 9.9% explained by the second for a total of 51.7%. Results of the Monte Carlo permutations indicated that the strength of the species sorting along the environmental gradient was more than would be expected by chance ($p = 0.019$).

4. Discussion

4.1. Response to fire

Wildfire caused the expected dramatic reduction of perennial plant cover. With this reduction of perennials, native annual plants responded quickly. So strong was this annual plant response that there was no significant difference in species diversity or richness between the burned and unburned sites. Consistent with other studies of post-fire changes in vegetation in Mojave and Sonoran Deserts (Abella, 2009), plant coverage values returned to pre-fire levels between 19 and 65 years and plant community composition post-fire failed to converge to that of adjacent unburned controls, even after 65 years. Fire did not increase the coverage of exotic annual plants in this system and took between two and nine years to attain levels found across all burned and unburned plots.

The removal by fire of the complex vegetation structure provided by the long-lived perennial plant cover in these habitats had a negative but apparently temporary effect on the biodiversity of the rodent community. However, it is important to note that fire did not have a similar negative effect on overall rodent abundance. This lack of an effect on abundance was due principally to the positive response of Merriam's kangaroo-rat to the denuded habitats. The overall rodent response from fire in this ecosystem coincides with previous small mammal work (Rosenzweig and Winakur, 1969; Simons, 1991) in southwest deserts in that bipedal species (e.g., *D. merriamii*) seem to prefer more open habitats (e.g., burned plots) and that quadrupedal species (e.g., *P. crinitus* and *P. longimembris*) preferred the more complex structural habitat from increased cover of long-lived perennial plants (unburned plots).

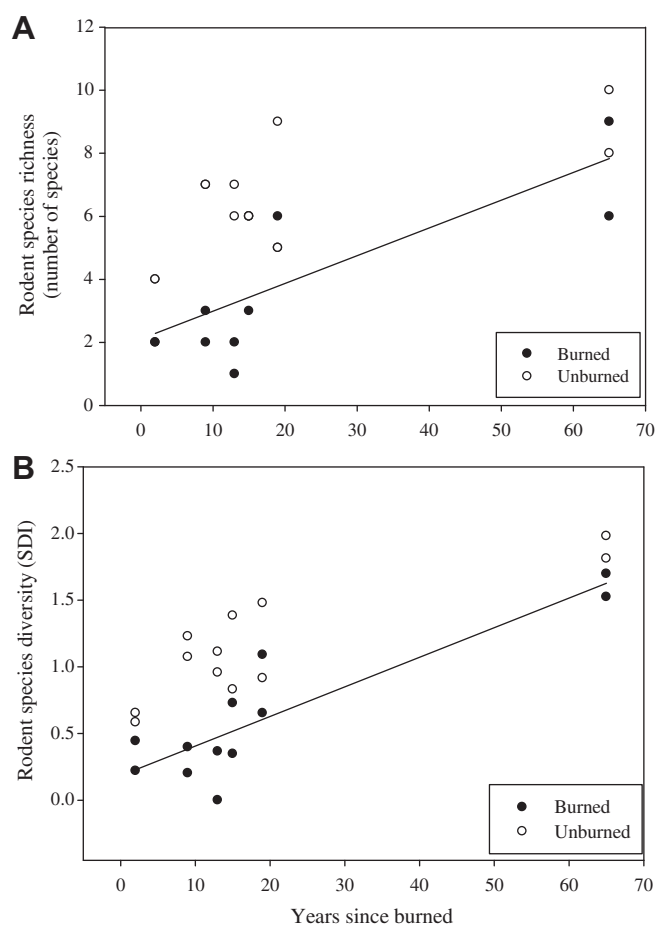


Fig. 5. Per-plot species richness (A) and Shannon Diversity Index (B) of the rodents vs. time since fire.

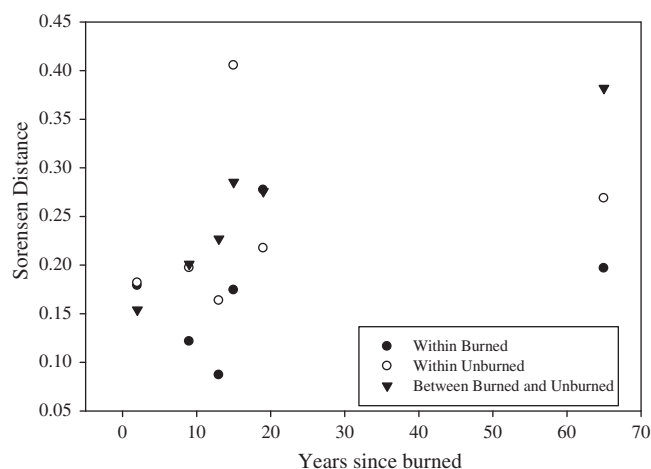


Fig. 6. Sørensen's similarity coefficient statistic on distance between grids based on rodent community composition. Within Burned denotes the distance between each pair of burned grids, Within Unburned denotes the distance between each pair of unburned grids, and Between Burned and Unburned denotes average distance between two burned and two unburned grids.

Table 4

Correlations of coverage of vegetation types with canonical correspondence axes based on rodent communities.

Vegetation type	Axis 1	Axis 2
Native annuals	0.080	−0.076
Exotic grasses	0.043	−0.101
Long-lived perennials	−0.319	0.604
Sub-shrubs	0.424	−0.410
Bunchgrasses	0.306	−0.333

4.2. Succession

The use of a chronosequence to describe patterns of succession in vegetation and rodent communities was the initial goal of this work. The successful use of these data relies on the assumption that all the sites making up the sequence have identical histories of disturbance, biotic influences, and environmental conditions so that the effects of the disturbance of interest can be isolated (Luken, 1990). Although it can be argued that these were not identical across these sites, the sites were similar enough in elevation, aspect slope and geographic location to broadly describe the patterns witnessed in this system. Replication of the burned areas that would have strengthened the dataset, however, was not logistically possible.

The vegetation in these sites appeared to follow a directional change in species composition with time since fire. Native annual plants had the largest cover values in the years immediately following fire. The native annuals were highly variable in composition among sites and so no particular species can be used as a descriptor. Sub-shrubs, especially *S. ambigua* and *M. albicaulis*, did not have appreciable cover values until nine years post-burn and then decreased in coverage starting with the 19-year old site. Long-lived perennial species coverage was appreciable at 19 years after being burned and seemed to return to pre-burn coverage values by 65 years. However, this return of pre-burn long-lived perennial coverage of the 65-year old site was largely driven by the presence of *Lycium cooperi*, a plant not frequently found outside of this particular burn. This suggests that the even though the structure of the site in terms of vegetation type has returned, the assemblage of the vegetation species is different. This notion is supported by the Sørensen distance measure between the 65-year since burned grids and the paired unburned grids (Fig. 4). Furthermore, a systematic synthesized dataset review of post-fire plant recovery in the Mojave and Sonoran Deserts describes similar results of little convergence of plant species over the 47-year time frame analyzed (Abella, 2009). It is probable that the 65-year time frame in this dataset is not long enough to witness a full reestablishment of vegetative components found in the unburned sites. *Y. brevifolia* was still rare even in the oldest site and it has been suggested that it may require a host plant before it can germinate (Brittingham and Walker, 2000; Loik et al., 1997). This host plant dynamic may further retard the reestablishment of a species that requires such a host plant to first establish. However, it has also been suggested that seed caching by rodents may form an obligate mutualistic relationship by promoting seed germination of *Y. brevifolia* (Vander Wall et al., 2006).

The diversity of rodents found in the burned sites increased over time since the site was burned (Fig. 5). As the vegetation changed over time from annuals to sub-shrubs to long-lived perennial species, the structural complexity of the ecosystem increased and therefore seemed to favor a higher diversity of rodents. These results coincide with previous studies of desert rodents where increased vegetation structure favors rodent diversity (Rosenzweig and Winakur, 1969; Simons, 1991).

Heteromyid rodents have shown to have large impacts on vegetation assemblages (Brown and Heske, 1990; Guo et al., 1995). As the recently burned sites were dominated by the Heteromyid rodent, Merriam's Kangaroo-rat (*D. merriami*), it is possible that the successional trajectory of the vegetation assemblage is influenced by the seed and foliage preference of the rodent.

Previous studies of secondary succession in deserts describe the critical period for biota regeneration after disturbance as that involving establishment (West et al., 1981). Variable rainfall events in the desert may make germination and subsequent establishment of certain species of plants an episodic event (Vasek et al., 1975). It is quite possible that such episodic events have occurred in the burned sites that we sampled. However, as only the percent cover values of the vegetation were measured, germination of long-lived species could have occurred and been missed due to their small size.

The exotic grasses in this system have become more abundant and widespread in the last two decades (Allen et al., 2009). As the 65-year old burn has been allowed to reestablish during a period largely devoid of impact from these exotic grasses, this site may follow a different trajectory when compared to more recent burn sites with significant coverage of exotic species. The specific impact that these exotic species will have on the succession of the burns is unclear. However, it has been shown that exotic species compete with native species in the Mojave Desert (Brooks, 2000; DeFalco et al., 2003; Steers, 2008). If the exotic species have a significant effect on the native species by reduction of habitat and species diversity through competition, one can expect that the native plant reestablishment of the burns will be slowed.

It is likely that increased fire risk will continue in these habitats as long as native and exotic annual vegetative cover is augmented by nitrogen deposition (Allen et al., 2009; Rao et al., 2009). The exotic grasses are of particular concern as they can form a continuous fuel bed for fire well into the hot, dry summer months and tend to not disarticulate as quickly as the native annual plants. Consequently, this increased biomass may form an established, cyclical fire regime (D'Antonio and Vitousek, 1992). If a shortened fire cycle is realized in this ecosystem where fire returns on a cycle that does not allow for reestablishment of sub-shrub and/or long-lived perennial cover, fire may have the effect of arresting succession (Niering and Goodwin, 1974). It is therefore quite possible that the long term reestablishment of plants and animals in these habitats, with a shorter fire-return interval, may never return to a pre-burned condition.

4.3. Management implications

National Park Service management of this ecosystem now exposed to an increased wildfire threat will be a challenge. With the increased risk of large fires that are significantly influenced by anthropogenic nitrogen deposition and exotic grass invasion (Allen et al., 2009; Brooks and Matchett, 2006; Rao et al., 2009), the managers will have to decide how to best mitigate these human impacts on the ecosystem. Taking into account global climate change models that predict a warming trend coupled with higher winter rainfall (Hayhoe et al., 2004), proper management will also have to address future impacts that will likely lead to increased risk from large fires. Although fire is natural in this system, it is apparent that these human based influences are disrupting natural processes by increasing fire size and frequency beyond historical natural levels (Brooks and Matchett, 2006).

The model of arrested succession and its effects on this ecosystem will be of strong interest to Joshua tree woodland land managers. If management decisions are made with biodiversity only in mind, these results show that fire does not seem to

significantly impact vegetation diversity levels. In fact, the response of this habitat to fire shows a succession of plants and animals that can be considered important to the overall biodiversity of the area. However, if the goal is to manage these habitats for specific “old growth” species like the Joshua tree, California juniper, blackbrush, little pocket mouse or canyon mouse, the rates of reestablishment of these species will have to be more closely measured and considered in the context of a much shortened fire cycle. It is likely that full fire suppression tactics and/or fire prevention measures will have to be employed to achieve this type of management. If and when these activities are utilized, it is of utmost importance that Minimum Impact Suppression Tactics (MIST) (National Park Service, 2008) are used to avoid soil disturbance and compaction to the fullest extent possible. The long term negative effects from activities that cause such soil disruption in the Mojave Desert are well documented (Belnap and Warren, 2002; Knapp, 1992; Prose et al., 1987; Webb and Wilshire, 1980; Webb et al., 1986; Webb, 2002) and should be avoided.

Acknowledgements

This work was made possible through funding provided by the National Park Service and the Community Foundation of Riverside and San Bernardino Counties. Jane Ashdown-Cipra, Erin Hailstones, Mitzi Harding, and Kristen Lalumiere deserve much recognition for many long hours in the field baiting traps as well as handling hundreds of rodents. We thank Katy Matthews, Jason Van Warmerdam, Miriam Lara-Vamstad, Tasha La Doux, James André, Lamp Truitt, and April Johnson for assistance with vegetation sampling. Further support provided by Paul DePrey, Curt Sauer, and Alice Miller of Joshua Tree National Park was invaluable to the completion of this project. We thank M. Allen, E. Allen, and an anonymous reviewer for helpful comments on an earlier version of this paper. JTR acknowledges support from the UCR Center for Conservation Biology.

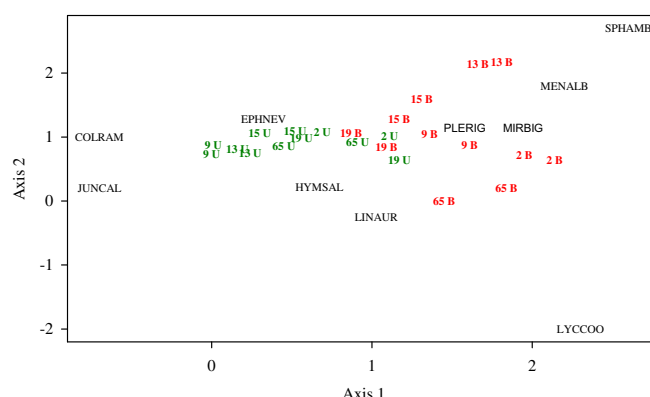
Appendix A

Plant species detected, grouped by life form. Common names of plant species mentioned in text are given in parentheses.

Annuals	Exotic annuals	Bunchgrasses	Sub-shrubs	Long-lived perennials
<i>Amsinckia tessellata</i>	<i>Bromus diandrus</i>	<i>Achnatherum hymenoides</i>	<i>Acamptopappus sphaerocephalus</i>	<i>Atriplex canescens</i>
<i>Aster</i> sp.	<i>Bromus rubens</i>	<i>Achnatherum speciosum</i>	<i>Encelia actoni</i>	<i>Coleogyne ramosissima</i> (Blackbrush)
<i>Baileya multiradiata</i>	<i>Bromus tectorum</i>	<i>Pleuraphis rigida</i>	<i>Eriogonum fasciculatum</i>	<i>Ephedra nevadensis</i>
<i>Bouteloua barbata</i>	<i>Erodium cicutarium</i>	<i>Poa secunda</i> sp. <i>juncifolia</i>	<i>Gutierrezia sarothrae</i>	<i>Juniperus californicus</i> (California Juniper)
<i>Cryptantha</i> sp.	<i>Schismus barbatus</i>		<i>Hymenoclea salsola</i>	<i>Lycium cooperi</i>
<i>Calyptidium monadrum</i>			<i>Mirabilis bigelovii</i>	<i>Opuntia echinocarpa</i>
<i>Chamaesyce albomarginata</i>			<i>Salvia dorrii</i>	<i>Prunus fasciculata</i>
<i>Chaenactis fremontii</i>			<i>Salazaria mexicana</i>	<i>Purshia tridentata</i>
<i>Erigeron breweri</i>			<i>Sphaeralcia ambigua</i>	<i>Quercus john-tuckeri</i>
<i>Eriogonum davidsonii</i>				<i>Tetradymia stenolopis</i>
<i>Eriastrum eremicum</i>				<i>Yucca brevifolia</i> (Joshua Tree)
<i>Eriogonum plumatella</i>				<i>Yucca schidigera</i>
<i>Eriophyllum pringlii</i>				
<i>Eriogonum</i> sp.				
<i>Gilia</i> sp.				
<i>Layia glandulosa</i>				
<i>Lepidium lasiocarpum</i> var. <i>las.</i>				
<i>Linanthus aureus</i>				
<i>Lotus scoparius</i>				
<i>Lupinus concinnus</i>				
<i>Mentzelia albicaulis</i>				
<i>Nama demissum</i>				
<i>Oenothera californica</i> sp. <i>cal.</i>				
<i>Phacelia distans</i>				
<i>Salvia columbariae</i>				
<i>Stephanomeria exigua</i>				

Appendix B

Detrended Correspondence Analysis of burned and unburned plots based on vegetation composition. Burned (red) and unburned (green) plots are indicated by B and U, respectively, and numbers are years since burned. Codes for plant species that describe the ordination are: COLRAM = *Coleogyne ramosissima*; JUNCAL = *Juniperus californicus*; EPHNEV = *Ephedra nevadensis*; HYMSAL = *Hymenoclea salsola*; LINAUR = *Linanthus aureus*; PLERIG = *Pleuraphis rigida*; MIRBIG = *Mirabilis bigelovii*; SPHAMB = *Sphaeralcia ambigua*; MENALB = *Mentzelia albicaulis*; LYCCOO = *Lycium cooperi*.



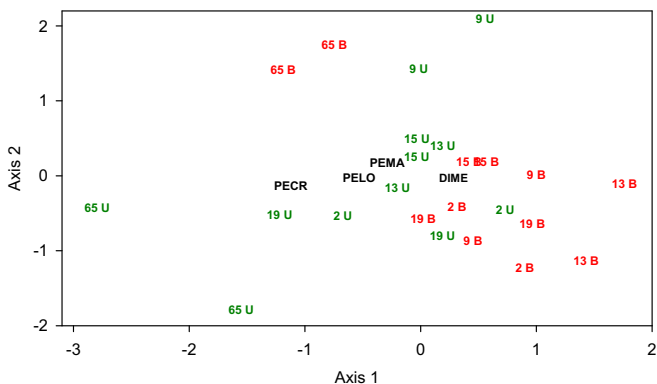
Appendix C

First two axes from DCA of rodent data. Numbers are years since burned and U and B are unburned and burned grids, respectively. Some rodent scores are shown (DIME = *Dipodomys merriami*, PELO = *Perognathus longimembris*, PEMA = *Peromyscus maniculatus*).



Appendix D

Canonical Correspondence Analysis of rodent communities constrained by vegetation composition and structure. Burned (red) and unburned (green) plots are indicated by B and U, respectively, and numbers are years since burned. Codes for rodent species are: DIME = *Dipodomys mirriami*; PEMA = *Peromyscus maniculatus*; PELO = *Peromyscus longimembris*; PECR = *Peromyscus crinitus*.



References

- Abella, S.R., 2009. Post-fire plant recovery in the Mojave and Sonoran deserts of western North America. *Journal of Arid Environments* 73, 699–707.
- Abella, S.R., 2010. Disturbance and plant succession in the Mojave and Sonoran deserts of the American southwest. *International Journal of Environmental Research and Public Health* 7, 1248–1284.
- Allen, E.B., Rao, L.E., Steers, R.J., Bytnerowicz, A., Fenn, M.E., 2009. Impacts of atmospheric nitrogen deposition on vegetation and soils in Joshua tree national park. In: Webb, R.H., Fenstermaker, L.F., Heaton, J.S., Hughson, D.L., McDonald, E. V., Miller, D.M. (Eds.), *The Mojave Desert: Ecosystem Processes and Sustainability*. University of Nevada Press, Las Vegas, Nevada, USA, pp. 78–100.
- Belnap, J., Warren, S.D., 2002. Patton's tracks in the Mojave Desert, USA: an ecological legacy. *Arid Land Research and Management* 16, 245–258.
- Bowers, J.E., Webb, R.H., Pierson, E.A., 1997. Succession of desert plants on debris flow terraces, Grand Canyon, Arizona, USA. *Journal of Arid Environments* 36, 67–86.

- Brittingham, S., Walker, L.R., 2000. Facilitation of *Yucca brevifolia* recruitment by Mojave Desert shrubs. *Western North American Naturalist* 60, 374–383.
- Brooks, M.L., 2000. Competition between alien annual grasses and native annual plants in the Mojave Desert. *American Midland Naturalist* 144, 92–108.
- Brooks, M.L., 2003. Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. *Journal of Applied Ecology* 40, 344–353.
- Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J. M., Hobbs, R.J., Pellant, M., Pyke, D., 2004. Effects of invasive alien plants on fire regimes. *Bioscience* 54, 677–688.
- Brooks, M.L., Matchett, J.R., 2006. Spatial and temporal patterns of wildfires in the Mojave Desert, 1980–2004. *Journal of Arid Environments* 67, 148–164.
- Brown, D.E. (Ed.), 1994. *Biotic Communities: Southwestern United States and Northwestern Mexico*. University of Utah Press, Salt Lake City, Utah, USA.
- Brown, J.H., Fox, B.J., Kelt, D.A., 2000. Assembly rules: desert rodent communities are structured at scales from local to continental. *American Naturalist* 156, 314–321.
- Brown, J.H., Heske, E.J., 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science* 250, 1705–1707.
- Caratti, J.F., 2006. Point Intercept (PO): FIREMON: Fire effects monitoring and inventory system. In: Lutes, D.C., Keane, R.E., Caratti, J.F., Key, C.H., Benson, N.C., Sutherland, S., Gangi, L.J. (Eds.), *General Technical Report*. US Department of Agriculture, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- D'Antonio, C.M., Vitousek, P.M., 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*, 63–87.
- DeFalco, L.A., Bryla, D.R., Smith-Longozo, V., Nowak, R.S., 2003. Are Mojave Desert annual species equal? Resource acquisition and allocation for the invasive grass *Bromus madritensis* subsp. *rubens* (Poaceae) and two native species. *American Journal of Botany* 90, 1045–1053.
- Fenn, M.E., Baron, J.S., Allen, E.B., Rueth, H.M., Nydick, K.R., Geiser, L., Bowman, W.D., Sickman, J.O., Meixner, T., Johnson, D.W., Neitlich, P., 2003. Ecological effects of nitrogen deposition in the western United States. *Bioscience* 53, 404–420.
- Fitzgerald, C.S., Krausman, P.R., Morrison, A.L., 2001. Short-term impacts of prescribed fire on a rodent community in desert grasslands. *Southwestern Naturalist* 46, 332–337.
- Fox, B.J., 1982. Fire and mammalian secondary succession in an Australian coastal heath. *Ecology* 63, 1332–1341.
- Gauch, H.G., 1982. *Multivariate Analysis in Community Ecology*. Cambridge University Press, Cambridge, UK.
- Guo, Q.F., Thompson, D.B., Valone, T.J., Brown, J.H., 1995. The effects of vertebrate granivores and folivores on plant community structure in the Chihuahuan Desert. *Oikos* 73, 251–259.
- Haim, A., Izhaki, I., 1994. Changes in rodent community during recovery from fire – relevance to conservation. *Biodiversity and Conservation* 3, 573–585.
- Hayhoe K., Cayan D., Field C.B., Frumhoff P.C., Maurer E.P., Miller N.L., Moser S.C., Schneider S.H., Cahill K.N., Cleland E.E., Dale L., Drapek R., Hanemann R.M., Kalkstein L.S., Lenihan J., Lunch C.K., Neilson R.P., Sheridan S.C., Verville J.H., 2004. Emissions pathways, climate change, and impacts on California. In: *Proceedings of the National Academy of Sciences of the United States of America*, 101:12422–12427.
- Hill, M.O., Gauch, H.G., 1980. Detrended correspondence analysis – an improved ordination technique. *Vegetatio* 42, 47–58.
- Hoffmann, L.A., Redente, E.F., McEwen, L.C., 1995. Effects of selective seed predation by rodents on shortgrass establishment. *Ecological Applications* 5, 200–208.
- Jameson Jr., E.W., Peeters, H.J., 1988. *California Mammals*. University of California Press, Berkeley, California, USA.
- Knapp, P.A., 1992. Secondary plant succession and vegetation recovery in 2 western Great-Basin desert ghost towns. *Biological Conservation* 60, 81–89.
- Letnic, M., 2003. The effects of experimental patch burning and rainfall on small mammals in the Simpson Desert, Queensland. *Wildlife Research* 30, 547–563.
- Letnic, M., Dickman, C.R., 2005. The responses of small mammals to patches regenerating after fire and rainfall in the Simpson Desert, central Australia. *Austral Ecology* 30, 24–39.
- Letnic, M., Dickman, C.R., Tischler, M.K., Tamayo, B., Beh, C.L., 2004. The responses of small mammals and lizards to post-fire succession and rainfall in arid Australia. *Journal of Arid Environments* 59, 85–114.
- Lindenmayer, D.B., Wood, J.T., MacGregor, C., Michael, D.R., Cunningham, R.B., Crane, M., Montague-Drake, R., Brown, D., Muntz, R., Driscoll, D.A., 2008. How predictable are reptile responses to wildfire? *Oikos* 117, 1086–1097.
- Loik, M.E., St. Onge, C.D., Rodgers, J., 1997. Post-fire recruitment of *Yucca brevifolia* and *Yucca schidigera* in Joshua tree National Park, California. Technical Report. Joshua Tree National Park Research Library, Twentynine Palms, California, USA.
- Longland, W.S., 2007. Desert rodents reduce seedling recruitment of *Salsola paulsenii*. *Western North American Naturalist* 67, 378–383.
- Lovich, J.E., Bainbridge, D., 1999. Anthropogenic degradation of the southern California desert ecosystem and prospects for natural recovery and restoration. *Environmental Management* 24, 309–326.
- Luken, J.O., 1990. *Directing Ecological Succession*. Chapman and Hall, New York, USA.
- McCune, B., Mefford, M.J., 1999. *PC-ORD. Multivariate Analysis of Ecological Data. Version 5.0*. MjM Software, Gleneden Beach, Oregon, USA.
- McLaughlin, S.P., 1986. Floristic analysis of the southwestern USA. *Great Basin Naturalist* 46, 46–65.

- Montiel, S., Montana, C., 2003. Seed bank dynamics of the desert cactus *Opuntia rastrera* in two habitats from the Chihuahuan Desert. *Plant Ecology* 166, 241–248.
- National Park Service, 2008. Reference Manual #18-Wildland Fire Management. U.S. Department of the Interior. Available from: http://www.nps.gov/fire/fire/fir_wil_pla_reference18.cfm.
- National Park Service Air Resources Division. NPS Air, Denver, Colorado, USA. Available from: <http://www.nature.nps.gov/air/>.
- Niering, W.A., Goodwin, R.H., 1974. Creation of relatively stable shrublands with herbicides – arresting succession on rights-of-way and pastureland. *Ecology* 55, 784–795.
- Pielou, E.C., 1984. *The Interpretation of Ecological Data: a Primer on Classification and Ordination*. John Wiley & Sons, New York, USA.
- Price, M.V., Joyner, J.W., 1997. What resources are available to desert granivores: seed rain or soil seed bank? *Ecology* 78, 764–773.
- Price, M.V., Reichman, O.J., 1987. Distribution of seeds in Sonoran Desert soils – implications for Heteromyid rodent foraging. *Ecology* 68, 1797–1811.
- Price, M.V., Waser, N.M., 1984. On the relative abundance of species – postfire changes in a Coastal Sage Scrub rodent community. *Ecology* 65, 1161–1169.
- Price, M.V., Waser, N.M., Bass, T.A., 1984. Effects of moonlight on microhabitat use by desert rodents. *Journal of Mammalogy* 65, 353–356.
- Prose, D.V., Metzger, S.K., Wilshire, H.G., 1987. Effects of substrate disturbance on secondary plant succession – Mojave Desert, California. *Journal of Applied Ecology* 24, 305–313.
- Rao, L.E., Parker, D.R., Bytnerowicz, A., Allen, E.B., 2009. Nitrogen mineralization across an atmospheric nitrogen deposition gradient in Southern California deserts. *Journal of Arid Environments* 73, 920–930.
- Rao, L.E., Allen, E.B., 2010. Combined effects of precipitation and nitrogen deposition on native and invasive winter annual production in California deserts. *Oecologia* 162, 1035–1046.
- Rosenzweig, M.L., Winakur, J., 1969. Population ecology of desert rodent communities habitats and environmental complexity. *Ecology* 50, 558–572.
- Sawyer, J.O., Keeler-Wolf, T., Evens, J.M., 2009. *A Manual of California Vegetation*, 2nd ed. California Native Plant Society Press, Sacramento, California, USA.
- Simons, L.H., 1991. Rodent dynamics in relation to fire in the Sonoran Desert Arizona USA. *Journal of Mammalogy* 72, 518–524.
- Steers, R.J., 2008. *Invasive plants, fire succession, and restoration of Creosote Bush Scrub in southern California*. PhD Dissertation. University of California - Riverside, California, USA.
- ter Braak, C.J.F., 1986. Canonical correspondence-analysis – a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67, 1167–1179.
- ter Braak, C.J.F., 1995. Ordination. In: Jongman, R.H.G., ter Braak, C.J.F., van Tongersen, O.F.R. (Eds.), *Data Analysis in Community and Landscape Ecology*. Cambridge University Press, Cambridge, UK, pp. 91–173.
- ter Braak, C.J.F., Prentice, I.C., 1988. A theory of gradient analysis. *Advances in Ecological Research* 18, 271–317.
- Valone, T.J., Nordell, S.E., Ernest, S.K.M., 2002. Effects of fire and grazing on an arid grassland ecosystem. *Southwestern Naturalist* 47, 557–565.
- Vander Wall, S.B., Esque, T., Haines, D., Garnett, M., Waitman, B.A., 2006. Joshua tree (*Yucca brevifolia*) seeds are dispersed by seed-caching rodents. *Ecoscience* 13, 539–543.
- Vasek, F.C., Johnson, H.B., Brum, G.D., 1975. Effects of power transmission lines on vegetation of the Mojave Desert California USA. *Madrono* 23, 114–130.
- Webb, R.H., 2002. Recovery of severely compacted soils in the Mojave Desert, California, USA. *Arid Land Research and Management* 16, 291–305.
- Webb, R.H., Steiger, J.W., Turner, R.M., 1987. Dynamics of Mojave desert shrub assemblages in the Panamint mountains, California. *Ecology* 68, 478–490.
- Webb, R.H., Steiger, J.W., Wilshire, H.G., 1986. Recovery of compacted soils in Mojave-Desert ghost towns. *Soil Science Society of America Journal* 50, 1341–1344.
- Webb, R.H., Wilshire, H.G., 1980. Recovery of soils and vegetation in a Mojave Desert ghost town, Nevada, USA. *Journal of Arid Environments* 3, 291–305.
- West, D.C., Botkin, D.B., Shugart, H.H., 1981. *Forest Succession: Concepts and Application*. Springer-Verlag, New York, USA.