

UNIVERSITY OF CALIFORNIA
RIVERSIDE

Effects of Fire on Vegetation and Small Mammal Communities in a Mojave Desert
Joshua Tree Woodland

A Thesis submitted in partial satisfaction
of the requirements for the degree of

Master of Science

in

Evolution, Ecology, and Organismal Biology

by

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March 2009

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ACKNOWLEDGEMENTS

This thesis was made possible by funding from the National Park Service and the Community Foundation of San Bernardino and Riverside Counties. Jane Cipra, Erin Hailstones, Mitsy Harding and Kristen Lalumiere deserve recognition for many long hours in the field handling hundreds of rodents. I also would like to thank Katy Matthews, Jason Van Warmerdam, Miriam Lara, Tasha LaDoux, 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 made this work possible. The Rotenberry lab at UC-Riverside provided many helpful comments in the preparation and presentation of this work. Special thanks go to my advisors, Dr. John Rotenberry, Dr. Edith Allen and Dr. Michael Allen who provided copious amounts of advice and time to guide me through this project. Finally, very special thanks go to Miriam Lara who was able to tolerate me during stressful times as well as wonderfully raise our children when I was unavailable.

DEDICATION

This work is dedicated to Miriam Lara as well as my children who had to unfairly share the stress that this endeavor required.

ABSTRACT OF THE THESIS

Effects of Fire on Vegetation and Small Mammal Communities in a Mojave Desert
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Master of Science, Graduate Program in Evolution, Ecology, and Organismal Biology
University of California, Riverside, March 2009
Dr. John Rotenberry, Chairperson

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 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 seemed to converge to paired unburned plots over time. The abundance of rodents however, was not significantly different between the burned and unburned plots. The model of arrested succession and its effects on this ecosystem will be of strong interest to Joshua tree woodland land managers. Vegetation showed a directional change in species composition with time since fire. Annual plants responded rapidly after perennial

vegetation was eliminated by fire, and then sub-shrub cover increased in sites as the cover of annual plants decreased. Finally, the cover of sub-shrubs declined with increased cover of long-lived perennials at the 65-year old site. Long-lived perennial species cover was comparable to paired un-burned plots only at the 65-year old plot. However, vegetation assemblages seem to differ greatly from 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 exotic species, nitrogen deposition, and global climate change may initiate a fire cycle in this ecosystem that will arrest succession before a Joshua tree woodland is allowed to establish.

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Introduction

Natural disturbances are key processes in the vast majority of ecosystems and a range of ecological theories have been developed in an attempt to predict biotic responses to them (Lindenmayer et al. 2008). Disturbance in desert ecosystems seems to reset an ecosystem that is especially slow to recover. Evidence of this slow recovery comes from study of well documented human developments (military camps, ghost towns and mines) that were long abandoned from human use (Webb and Wilshire 1980, Prose et al. 1987, Webb et al. 1987, Knapp 1992, Belnap and Warren 2002). Soil compaction from these types of disturbances appears to be a significant factor in retarding the establishment of desert plants (Webb and Wilshire 1980, Prose et al. 1987). Fire, as a natural vegetative denudation event, avoids substrate disturbance and soil compaction and may lead to a different trajectory of ecosystem response.

Large fires have been historically infrequent in Joshua tree (see Appendix A for scientific names of plants) woodlands found within the Mojave desert, and the recent increase in fire size is partially due to invasion of exotic grasses, principally from the genera *Bromus* and *Schismus* (Brooks 2000). Winter seasons with relatively high amounts of precipitation produce a native and/or non-native annual plant biomass that can carry fire in these habitats. The most dramatic impacts have occurred in middle elevation shrublands dominated by creosotebush, Joshua tree, and/or blackbrush, 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 considered to be not adapted to fire, partially due to its lack of a previously documented fire regime and in part its seemingly slow recovery from fire (Steers 2008). Many species of long-lived perennial plants (e.g., Joshua tree, blackbrush, California juniper) in these habitats tend to have low recruitment and low mortality rates. Over time, these species tend to dominate other perennial species that have higher recruitment and mortality rates (e.g., *Hymenoclea salsola*, *Salazaria mexicana*, *Sphaeralcea ambigua*). Sampling the cover of vegetation for 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 community structure (Brown et al. 2000). They are important consumers of plant materials (Price and Joyner 1997) and are significant prey items 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). Results of studies of rodent response to fire in arid environments have been inconsistent (Fox 1982, Price and Waser 1984,

Fitzgerald et al. 2001, Valone et al. 2002, Letnic 2003, Letnic et al. 2004, Letnic and Dickman 2005). 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 Coastal Sage Scrub habitats where species composition responded to the availability of structural microhabitats (Price and Waser 1984, Price and Reichman 1987). As fire removes much of the vegetation structure, I predict a reduction of rodent diversity to this type of disturbance. By exploring sites across a relatively large gradient of time-since-burn, the rodent community should provide an additional metric in which to sample the level of ecosystem response to fire.

My study investigates trends in vegetation and small mammal reestablishment (secondary succession) following fire in a chronosequence in the Mojave Desert. Specifically, I examined the abundance and distribution of both vegetation and small mammal species along a time-since-burn gradient in a Joshua tree woodland habitat. I hypothesized that the longer a site is allowed to re-colonize with long-lived perennial vegetation initially removed from the system by fire, early-colonizing disturbance-adapted rodent species will be joined or replaced by species with more complex habitat structural requirements.

Heightened understanding of these patterns is critical for improved biodiversity conservation, a goal of natural resource management. This work coupled with the known

increased fire frequency resulting from nitrogen deposition (Brooks 2003, Fenn et al. 2003, Rao 2008) and exotic grass invasion (Brooks et al. 2004), may provide valuable insights for better management of wildfire and recovery from wildfire in these habitats.

Methods

Study Area

The Mojave Desert is topographically and vegetatively diverse. 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 southwestern deserts (McLaughlin 1986).

The northwestern half of Joshua Tree National Park (JOTR), where this work was performed, is considered part of the Mojave Desert biome. The Mojave Desert is characterized by hot, dry summers and cool winters with low and variable amounts of precipitation. Located entirely within the boundary of JOTR, the area I sampled is characterized by long-lived perennial species such as California juniper, Joshua tree, and blackbrush. The elevation of the sites sampled was between 1342 and 1481 m and is considered mid- to high-elevation for the Mojave Desert.

Study sites were chosen on a “time-since-burn” basis. Using National Park Service fire maps, which have recorded fire history in JOTR since 1943, I located six sites of 2, 9, 13, 15, 19 and 65 years since burn (Table 1, Fig. 1). Adjacent to each burned site I 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 I 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 of the park, with little additional disturbance and no management manipulation.

Table 1. Burn Site Descriptions

Name	Burn Year	Years Since Burn	Hectares	Elevation
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

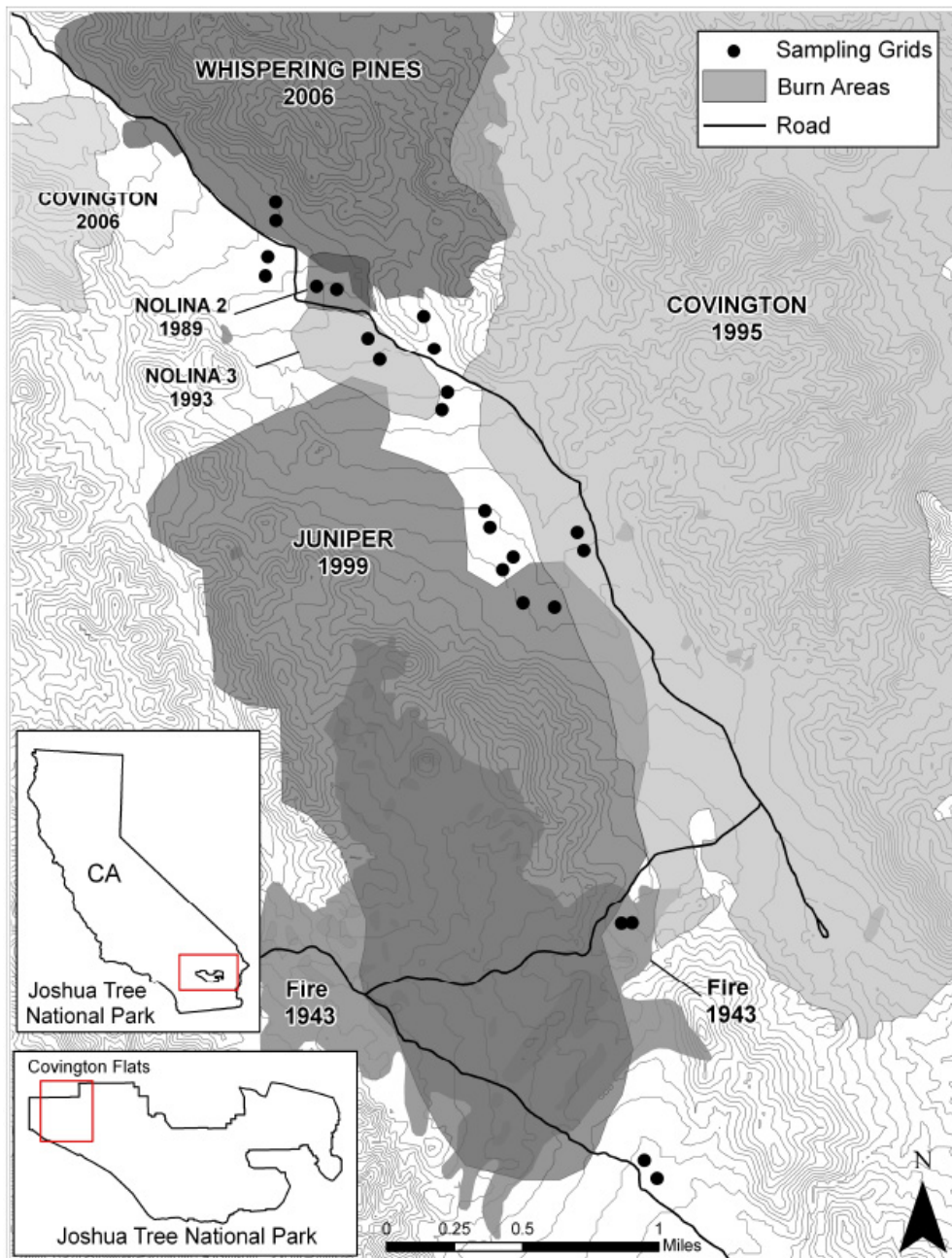


Figure 1. Study area in Joshua Tree National Park showing approximate extent of burns and details of sampling grid locations.

Survey and Sampling Design

Two sampling grids were placed at each burned and unburned plot in which 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, I was 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.

Vegetation

I sampled vegetation at the sites using the Point Intercept (PI) method (Caratti 2006). 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 plant species and ground cover classes that touched the pin were recorded as “hits” along the transect line. Percent cover values were calculated by dividing the number of hits 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) I placed twelve 50-m line transects along which I recorded PI data. Points were randomly placed and hits recorded 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.

Rodents

Each burned and un-burned 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 3x3.5x9”) set 10 m apart in a 6 x 3 configuration. For three consecutive nights, traps were opened and baited, then checked and closed the following morning. Bait consisted of an easy manageable 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 across all six burn and six un-burned plots.

Statistical Analysis

Vegetation

To describe the structure of the vegetation community, I 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. 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 across the species.

Furthermore, we used detrended correspondence analysis (DCA; (Hill and Gauch 1980, Gauch 1982 , Pielou 1984) to describe the composition of the vegetation community. DCA is an eigenvalue-based technique that is particularly suited for community data gathered along environmental gradients (ter Braak 1995). DCA 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. DCA uses detrending and rescaling to eliminate the arch effect and axis compression often associated with non-linear

datasets subjected to other ordinations (Gauch 1982 , Pielou 1984, McGarigal et al. 2000). I 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, I 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, I examined Spearman rank correlation between DCA scores and years since burn for the burned grids.

To better visualize the similarities between unburned and burned grids, I analyzed the data with Sørensen's distance. For each site I calculated the mean Sørensen distance between the two burned and two un-burned grids; the more the grids had converged, the smaller the distance. To provide context, I also calculated the distance between each pair of burned grids and each pair of un-burned grids; because each pair were intended to be replicates, I expected a relatively small distance. Using the Sørensen distance rather than Euclidean distance, allows for better retention of sensitivity to heterogeneous data sets as well as less weight given to outliers (McCune and Grace 2002).

Rodents

In general, the rodent community was subjected to the same analyses as the vegetation. However, I also used canonical correspondence analysis (CCA) to describe the relationship between the small mammal community relative to the vegetation community and other environmental variables. Other multivariate analyses such as principle components analysis (PCA), reciprocal averaging (RA) and DCA use a single set of variables to seek out major patterns in the data (McGarigal et al. 2000). CCA, on the other hand, uses regression on second set of variables to guide or “constrain” the ordination on the community species data. For this, CCA allows for better interpretation of ecological data as it is able to extract major gradients in the data that can be accounted for by measured explanatory variables (McGarigal et al. 2000). The main matrix was constructed using the rodent captures across the sites. The second (constraining) matrix was constructed using vegetation data grouped into types (Appendix A) and substrate variables. I used 998 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).

Results

Vegetation

We detected 56 different plant species (Appendix A) which could be grouped into five vegetation types based on size and life history (Table 2). The percent cover values of long-lived perennial plants after fire showed an expected reduction (Table 2) as well as a

return to un-burn cover levels between 19 and 65 years since burn. Sub-shrubs established in the 9 and 13 years since burn and then declined. Annual plant cover showed a general increase through time in sites that had burned. Exotic grass coverage (from genera *Bromus*, *Erodium* and *Schismus*) appeared to rapidly invade the burn sites, achieving cover values similar to all other sites between 2 and 9 years since burn.

Table 2. Vegetation Sampling Results – Percent cover of vegetation types

Year since burn	Burned					Unburned				
	Annual	Exotic Grass	Bunch- grass	Sub-shrub	Long- lived Perennial	Annual	Exotic Grass	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

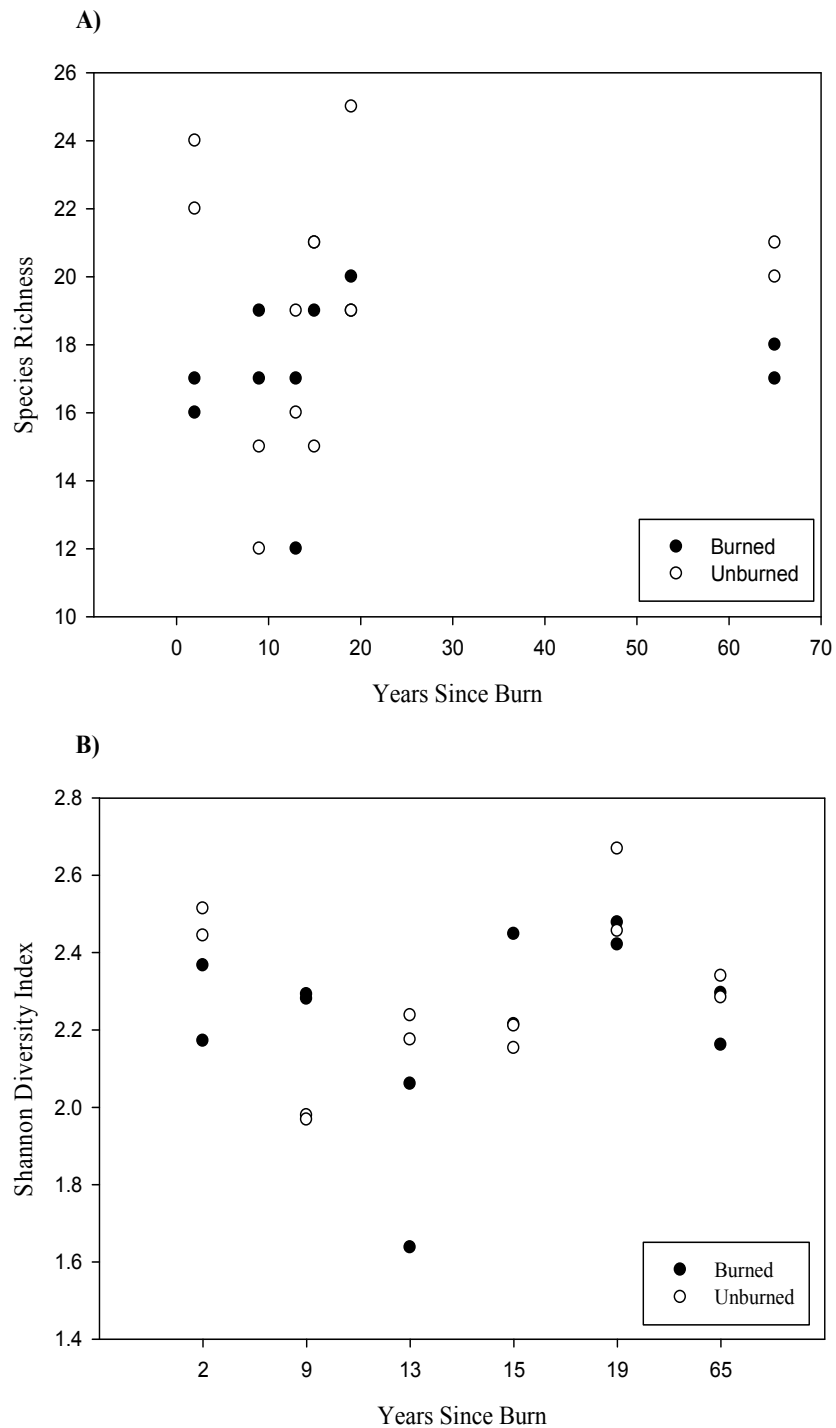


Figure 2. Species richness (A) and Shannon Diversity Index (B) of the vegetation vs. time since fire.

There were no consistent relationships between burned and unburned grids with respect to either plant species richness or SDI (Figure 2). Richness levels and the diversity index scores for the burned grids compared with the unburned grids were not significantly different (Mann-Whitney U test, $U = 90.5$, $p = 0.149$ and $U = 76$, $p = 0.421$). The rank order correlation between species richness and time since burn was marginally significant ($r_s = 0.435$, $p = 0.079$) however, the SDI values and time since burn was not significant ($r_s = 0.212$, $p = 0.253$).

The vegetation community composition was then compared among all the sampling sites by multivariate analysis using DCA (Figure 3). 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. DCA revealed a gradient in the vegetation composition ranging from grids dominated by long-lived perennials *Coleogyne ramosissima* and *Juniperus californicus* at one end and sub-shrubs *Mentzelia albicaulis* and *Sphaeralcea ambigua* on the other end; the middle was dominated by *Ephedra nevadensis*, *Hymenoclea salsola*, *Linanthus aureus* (Figure 3).

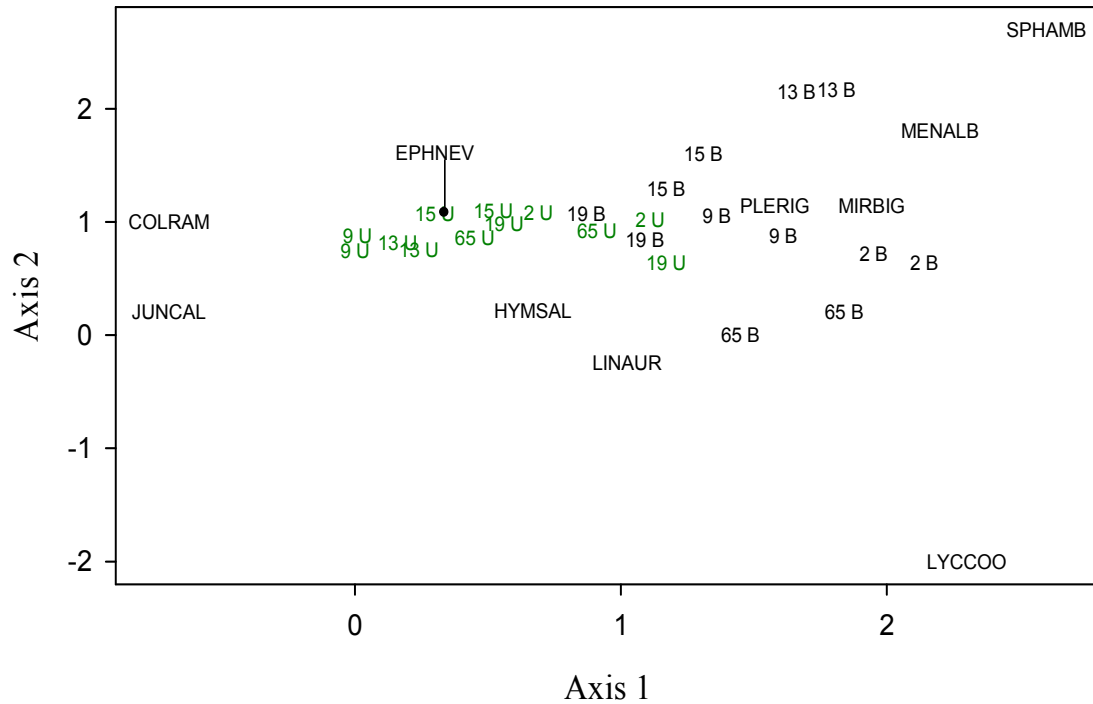


Figure 3. First two axes from DCA on the vegetation data. Numbers are years since burn. Burned and Unburned plots are delineated by B and U, respectively. Plant species descriptive to the ordination are shown. COLRAM = *Coleogyne ramosissima*; JUNCAL = *Juniperus californicus*; EPHNEV = *Ephedra nevadensis*; HYMSAL = *Hymenoclea salsola*; LINAUR = *Linanthus aureus*; PLERIG = *Pleuraphis rigida*; MIRBIG = *Mirabilis bigelovii*; SPHAMB = *Sphaeralcia ambigua*; MENALB = *Mentzelia albicaulis*; LYCCOO = *Lycium cooperi*.

Scores from the burned and unburned sites differed significantly on DCA axis 1 ($U = 4$, $p < 0.0001$; mean of burned grids = 18.2, mean of unburned grids = 6.8), indicating a strong difference in overall plant community composition. Scores from axis 2 burned and unburned sites, however, were not significantly different ($U = 84.5$, $p = 0.2451$; burned grid mean = 11.5, unburned grid mean = 13.5). The rank correlation between DCA axis 1 scores of burned plots and time since burn 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-burn successional gradient.

The vegetation differences between burned and unburned grids at each plot were greater than within-grid differences in either burn replicates or unburned replicates in 11 of 12 cases (Figure 4). Moreover, distances between burned and unburned did not seem to narrow with time, implying that burned grids were not converging in their vegetation composition to those of unburned grids nearby, even after 65 years.

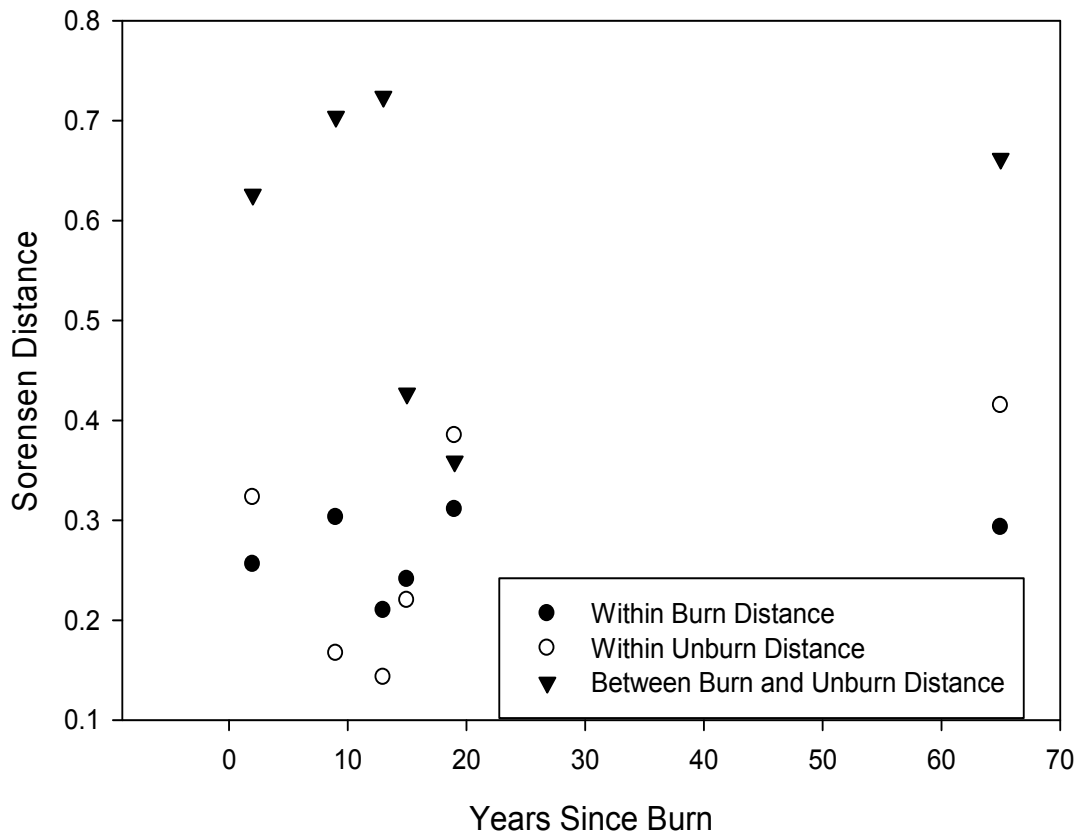


Figure 4. Sørensen distance between grids

Rodents

Trapping across the entire season resulted in 1886 captures (Table 4). Of this, 1328 were first captures rather than recaptures, representing unique individuals. 15 different species of small mammals were identified, with five species trapped 2 or fewer times. With 5182 total trap nights, trap success rate was 36.4% for all captures and 25.63% for unique individual captures.

Table 3. Rodent capture results; see Appendix E, for complete results.

Year since burn	Burn				Un-burn			
	<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

Total abundances between the burn and un-burn sites (Table 5) were not statistically different (Mann-Whitney U test, $U = 20$, $p = 0.4052$) implying that the total abundance of rodents was not effected by fire. However, Shannon Diversity Index values were significantly larger in the unburned sites (Mann-Whitney U test, $U = 30$, $p = 0.0329$; Figure 5). Species richness values were not statistically different at the $p < 0.05$ level but, nearly so ($U = 28.5$, $p = 0.0548$).

Table 4. Shannon Diversity Index and species richness of rodents

Years Since Burn	Burned			Unburned		
	Shannon Diversity Index	Species Richness	Total Abundance	Shannon Diversity Index	Species Richness	Total Abundance
2	0.3	2	48	0.6	4	44
9	0.3	3	54	1.2	7	71
13	0.2	2	46	1	7	55
15	0.5	5	55	1.1	6	56
19	0.9	6	60	1.2	7	46
65	1.6	8	61	1.9	9	67

The rank correlation of rodent species richness and SDI was significant ($r_s = 0.806$, $p = 0.001$; $r_s = 0.721$, $p = 0.004$) showing an increase in richness and diversity over time since burn. Surprisingly, however, the same trends were apparent on the unburned control grids in terms of richness and SDI values ($r_s = 0.618$, $p = 0.016$; $r_s = 0.707$, $p = 0.005$).

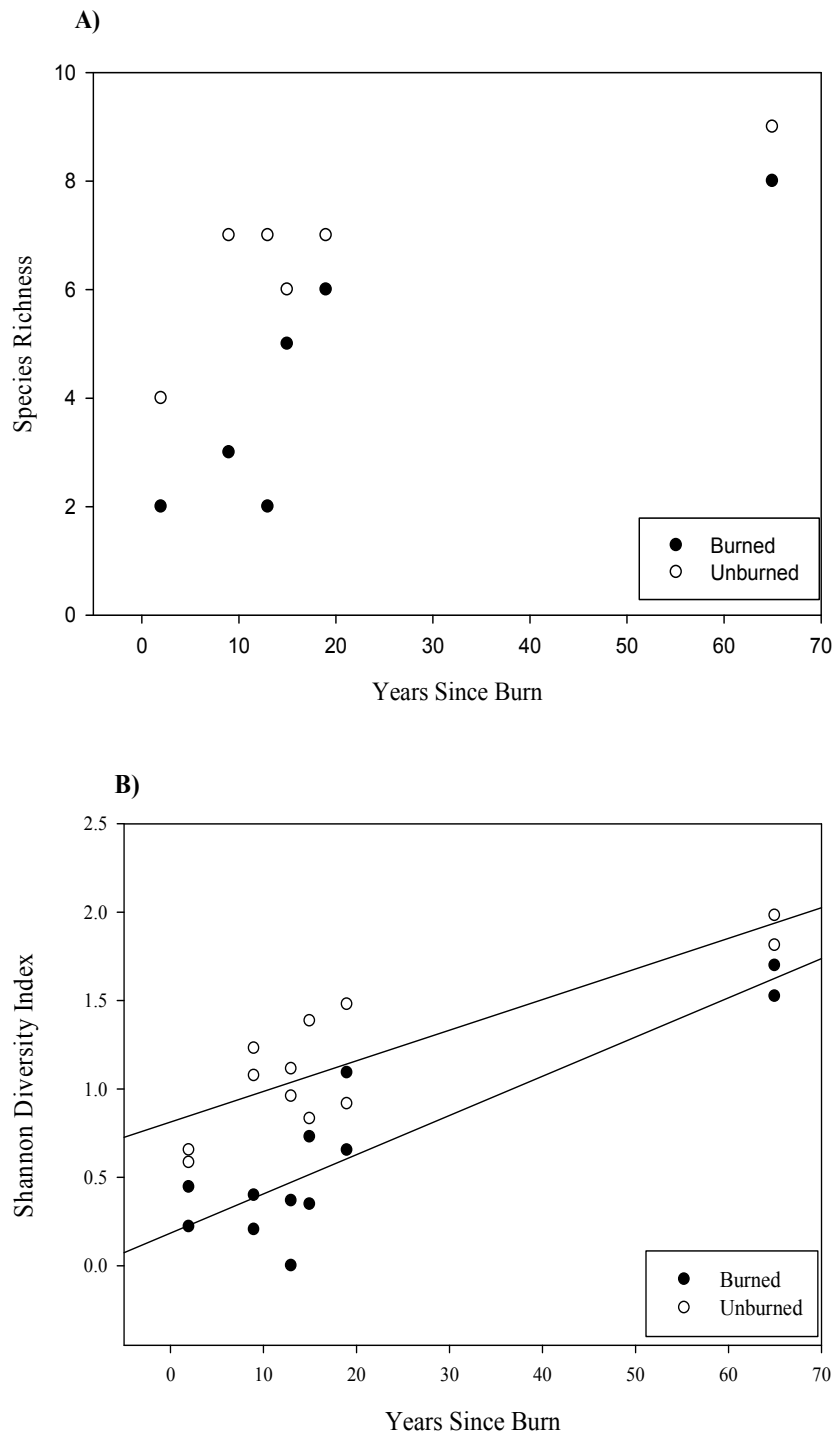


Figure 5. Species richness (A) and Shannon Diversity Index (B) of the rodents vs. time since fire.

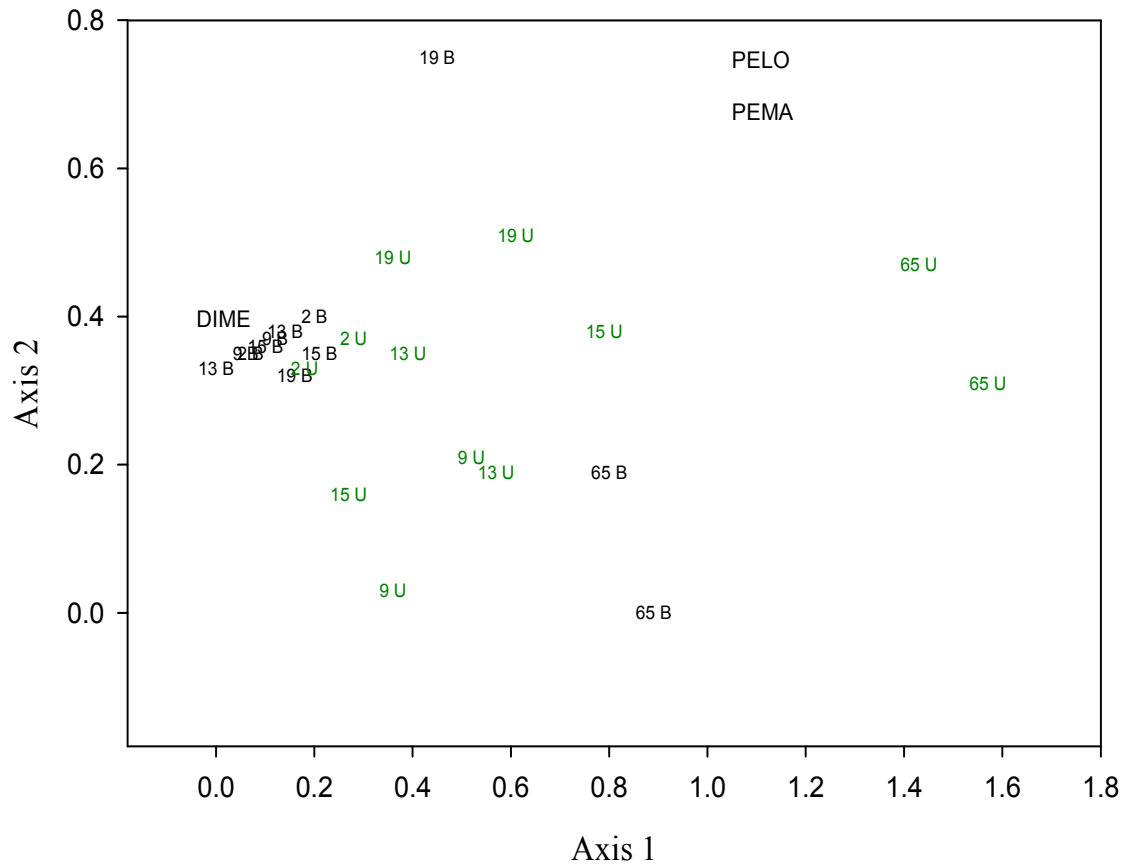


Figure 6. DCA of rodent data. Numbers represent years since burn and U and B are unburned and burned grids, respectively. Some rodent scores are shown (DIME = *Dipodomys merriami*, PELO = *Perognathus longimembris*, PEMA = *Peromyscus maniculatus*).

DCA was used to compare the rodent assemblage among all the sampling sites (Figure 6). The total variance (inertia) in the rodent species data was 0.4967 and the eigenvalues of the first two axes were 0.291 and 0.050, respectively.

Scores from DCA axis 1 differed between burn and un-burn sites (Mann-Whitney U test, $U = 116$, $p = 0.006$; burned grid mean = 8.8, unburned grid mean = 16.2). This DCA results indicate that the rodent composition was different between the burn and un-burn sites. Site scores compared on axis 2 were not significantly different ($U = 67.5$, $p = 0.409$; burned grid mean = 12.9, unburned grid mean = 12.1). Site DCA scores from both axis 1 and 2 were significantly correlated with time-since-burn ($r_s = 0.679$, $p = 0.008$; $r_s = -0.049$, $p = 0.049$), implying a successional gradient in rodent community composition.

The rodent differences found by using Sørensen's similarity coefficient between burned and unburned grids were highly variable (Figure 7). Structural heterogeneity within the rodent community assemblage at the grids is too great to elucidate any patterns relating to response from fire.

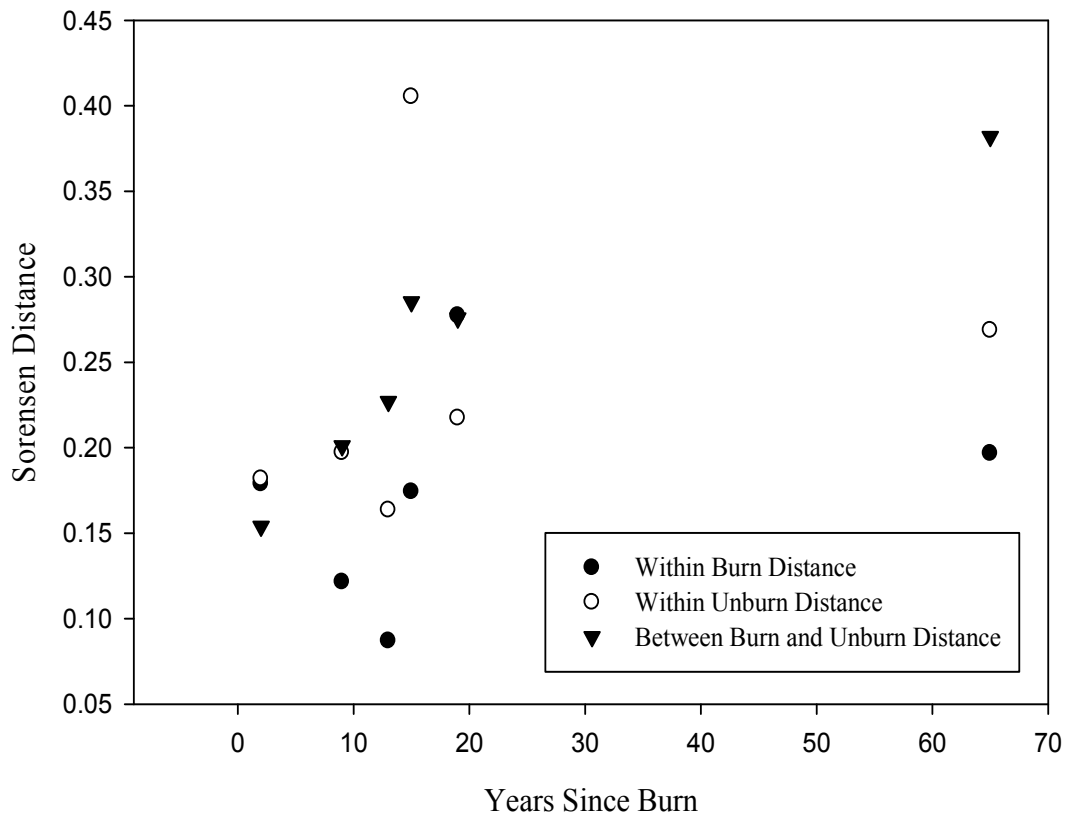


Figure 7. Sørensen's similarity coefficient statistic on the rodent data vs. time since fire.

Vegetation and Rodents

When I ordinated the rodent data constrained by the regression of the vegetation data using Canonical Correspondence Analysis (CCA), I found that *Dipodomys merriami* was correlated with the burn sites, whereas, *Peromyscus crinitus*, and *Perognathus longimembris* correlated more with the old burn and control sites (Figure 8 below). Long-lived perennial plant species were associated more with un-burned sites and subshrubs and bunchgrasses were more closely associated with the burn sites (Table 6 below). The total variance or inertia in the dataset was 0.502 and the percent of variance

explained was 41.8% on the first axis and an additional 9.9% on 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 ($p = 0.019$).

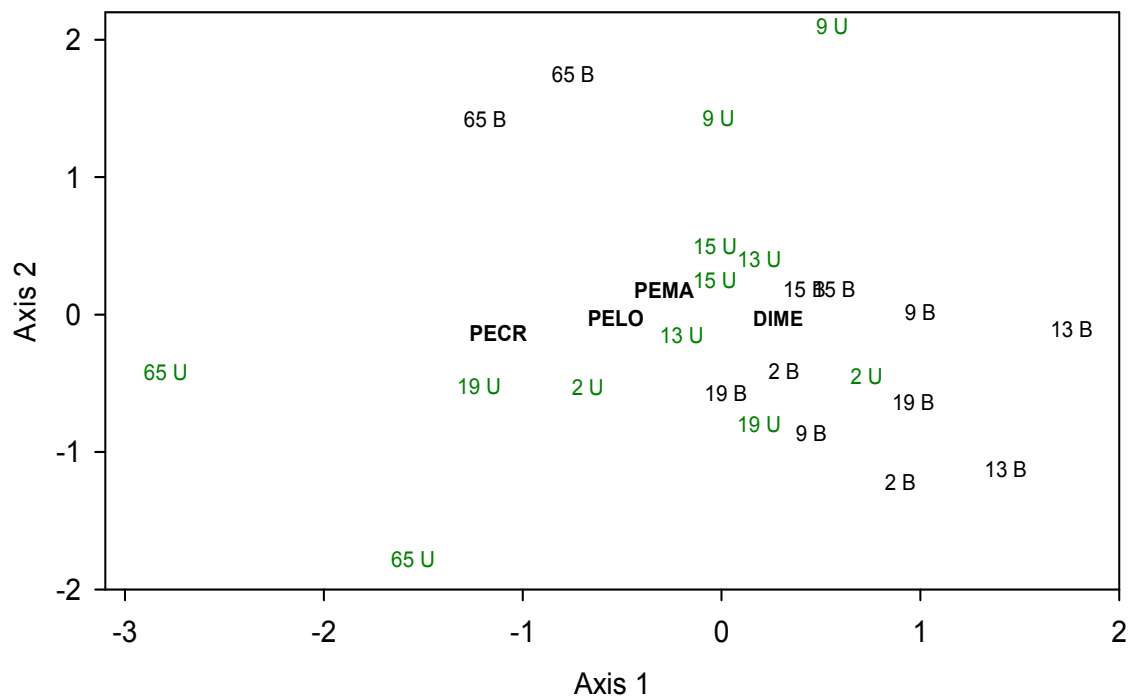


Figure 8. Canonical correspondence analysis. Site scores are indicated by years since burn. Rodent scores are shown (DIME = *Dipodomys mirriami*; PEMA = *Peromyscus maniculatus*; PELO = *Peromyscus longimembris*; PECR = *Peromyscus crinitus*).

Table 6. Vegetation type correlations from CCA

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

DISCUSSION

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. Fire did not increase the coverage of exotic annual plants in this system and took between two and nine years to establish to levels found across all burned and unburned plots.

The removal by fire of the complex vegetation structure provided by the 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 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 in southwest deserts in that bipedal species (e.g., *Dipodomys merriami*)

seem to prefer more open habitats (burns) and that quadrupedal species (e.g., *Peromyscus crinitus* and *Perognathus longimembris*) preferred the more complex structural habitat from increased cover of long-lived perennial plants (unburned grids).

Succession

The use of this chronosequence data set 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 (Luken 1990). Although it can be argued that these were not identical across these sites, the sites were similar enough to broadly describe the patterns witnessed in this system.

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. Subshrubs, especially *Sphaeralcea ambigua* and *Mentzelia 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 first saw appreciable values at 19 years post-burn 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 was further supported by the Sørensen distance measure between the 65-year since burn grids and the paired unburned grids (Figure 4). It is probable that 65 years is not long enough to witness a full reestablishment of vegetative components found in the unburned sites. Joshua Trees were still rare even in the oldest site and it has been suggested that it may require blackbrush as a host plant before it can germinate (Loik et al. 1997). This host plant dynamic may further retard the reestablishment of certain species that require a host plant to first establish.

Previous studies of secondary succession in deserts describe the critical period for biota regeneration after disturbance as that involving establishment (ecesis; (West et al. 1981). Variable rainfall events in the desert may make germination and subsequent establishment an episodic event, with reestablishment taking 40 years or so (Vasek et al. 1975). It is quite possible that such episodic events have occurred in the burn sites that I 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 do compete with native species in the Mojave desert (Brooks 2000, Steers 2008). If the exotic species do have a significant effect on the native species by reduction of habitat and species diversity through competition, one can predict 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 (Rao 2008, Allen 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. If a quickened 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-burn condition.

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 (Brooks and Matchett 2006, Rao 2008, Allen 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 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.

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 mice or canyon mice, the rates of reestablishment of these species will have to be more closely measured and considered in the context of a much quickened 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 which cause such soil disruptions in the Mojave Desert is well documented (Webb and Wilshire 1980, Webb et al. 1986, Prose et al. 1987, Knapp 1992, Belnap and Warren 2002, Webb 2002) and should be avoided.

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APPENDIX A. Plant species detected, grouped by vegetation type.

Annuals	Exotic Grasses	Bunchgrasses	Sub-shrubs	Long-lived Perennials
<i>Amsinkia tessellata</i>	<i>Bromus diandrus</i>	<i>Achnatherum hymenoides</i>	<i>Acamptopappus sphaerocephalus</i>	<i>Atriplex canescens</i>
<i>Aster sp.</i>	<i>Bromus rubens</i>	<i>Achnatherum speciosum</i>	<i>Encelia actoni</i>	Blackbrush - <i>Coleogyne ramosissima</i>
<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 ssp. juncifolia</i>	<i>Gutierrezia sarothrae</i>	California Juniper - <i>Juniperus californicus</i>
<i>Cryptantha sp.</i>	<i>Schismus barbatus</i>		<i>Hymenoclea salsola</i>	<i>Lycium cooperi</i>
<i>Calyptridium 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>				Joshua Tree - <i>Yucca brevifolia</i>
<i>Eriogonum plumatella</i>				<i>Yucca schidigera</i>
<i>Eriophyllum pringlii</i>				
<i>Eriogonum sp.</i>				
<i>Gilia sp.</i>				
<i>Layia glandulosa</i>				
<i>Lepidium lasiocarpum var. 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 ssp. cal.</i>				
<i>Phacelia distans</i>				
<i>Salvia columbariae</i>				
<i>Stephanomeria exigua</i>				

APPENDIX B. Number of vegetation hits per 120 pin drops. Species detected ≤ 3 grids across all sites were removed.

Burned										
Years Since Burn	<i>Achnatherum speciosum</i>	<i>Amsinkia tessellata</i>	<i>Atriplex canescens</i>	<i>Bromus rubens</i>	<i>Bromus tectorum</i>	<i>Chamaesyce albomarginata</i>	<i>Chaenactis fremontii</i>	<i>Coleogyne ramosissima</i>	<i>Ephedra nevedensis</i>	<i>Eriogonum fasciculatum</i>
2	0	0	0	2	9	0	24	0	0	0
2	0	12	0	2	6	0	21	0	0	0
9	0	0	0	9	49	1	12	0	6	0
9	0	4	0	10	59	7	32	0	5	0
13	2	1	0	1	47	2	3	0	1	0
13	4	0	0	0	68	1	0	0	0	0
15	3	5	0	10	42	0	4	8	2	0
15	3	4	0	6	44	1	0	1	4	0
19	5	1	0	15	53	0	7	12	8	0
19	9	0	0	17	34	0	18	3	12	2
65	0	4	0	2	33	0	29	0	0	1
65	0	1	0	19	22	0	37	0	1	0
Unburned										
Years Since Burn	<i>Achnatherum speciosum</i>	<i>Amsinkia tessellata</i>	<i>Atriplex canescens</i>	<i>Bromus rubens</i>	<i>Bromus tectorum</i>	<i>Chamaesyce albomarginata</i>	<i>Chaenactis fremontii</i>	<i>Coleogyne ramosissima</i>	<i>Ephedra nevedensis</i>	<i>Eriogonum fasciculatum</i>
2	0	0	0	10	37	0	11	15	7	1
2	0	1	0	18	48	0	8	24	4	0
9	0	0	0	36	17	0	5	43	2	0
9	0	0	0	41	26	0	4	41	4	0
13	1	0	0	42	23	0	5	22	4	0
13	0	0	0	37	27	2	10	25	3	2
15	0	1	0	36	39	0	0	39	5	0
15	0	0	0	24	32	0	0	30	10	0
19	0	2	6	15	46	0	14	5	4	2
19	0	0	2	17	34	2	4	13	9	0
65	1	0	1	34	12	2	0	0	8	0
65	2	2	3	21	49	1	4	0	0	7

APPENDIX B. Continued.

Burned										
Years Since Burn	<i>Eriophyllum pringlei</i>	<i>Erodium cicutarium</i>	<i>Gilia</i> sp.	<i>Hymenoclea salsola</i>	<i>Juniperus californicus</i>	<i>Lepidium lasiocarpum</i>	<i>Linanthus aureus</i>	<i>Lycium cooperi</i>	<i>Mentzelia albicaulis</i>	<i>Mirabilis bigelovii</i>
2	0	0	32	0	1	0	1	0	7	0
2	1	0	25	0	0	0	0	2	9	1
9	0	0	2	2	0	1	4	2	4	0
9	0	2	3	0	0	0	12	7	11	7
13	0	12	2	0	0	13	1	1	6	2
13	0	6	4	0	0	8	0	0	3	0
15	0	0	3	1	0	0	6	0	7	1
15	0	0	0	1	0	0	1	1	6	0
19	0	0	6	0	4	0	5	0	3	0
19	0	0	5	2	0	0	14	3	3	0
65	1	0	5	0	0	0	0	26	3	0
65	3	0	0	0	0	0	3	26	0	0
Unburned										
Years Since Burn	<i>Eriophyllum pringlei</i>	<i>Erodium cicutarium</i>	<i>Gilia</i> sp.	<i>Hymenoclea salsola</i>	<i>Juniperus californicus</i>	<i>Lepidium lasiocarpum</i>	<i>Linanthus aureus</i>	<i>Lycium cooperi</i>	<i>Mentzelia albicaulis</i>	<i>Mirabilis bigelovii</i>
2	1	0	13	3	3	0	2	2	3	0
2	0	1	3	5	3	0	0	1	2	1
9	0	0	1	0	10	0	0	0	1	0
9	0	0	0	0	10	0	0	0	0	0
13	0	0	3	0	16	0	1	1	0	1
13	1	0	1	0	18	0	0	0	1	0
15	0	0	0	2	5	0	0	1	3	1
15	0	0	0	0	1	0	1	3	4	0
19	4	1	0	5	2	0	4	11	1	0
19	0	0	3	4	11	0	6	0	0	0
65	0	0	0	0	6	1	12	0	1	2
65	0	0	0	0	4	0	26	2	3	1

APPENDIX B. Continued.

Burned										
Years Since Burn	<i>Phacelia distans</i>	<i>Pleuraphis rigida</i>	<i>Poa secunda</i>	<i>Prunus fasciculata</i>	<i>Salvia columbariae</i>	<i>Salazaria mexicana</i>	<i>Schismus barbatus</i>	<i>Sphaeralcia ambigua</i>	<i>Stephanomeria exigua</i>	<i>Yucca brevifolia</i>
2	5	2	0	0	3	1	0	0	8	0
2	5	6	0	0	1	0	0	0	6	0
9	0	2	0	0	0	4	1	9	19	0
9	0	0	0	0	0	0	1	9	15	0
13	0	0	1	0	0	0	0	23	0	0
13	0	1	0	0	0	0	0	25	1	0
15	2	2	0	0	0	0	0	6	2	1
15	1	7	0	0	0	0	0	10	2	0
19	4	1	0	0	0	0	12	2	3	0
19	0	0	0	0	2	0	11	0	4	0
65	7	0	0	0	0	0	0	1	14	1
65	16	0	0	1	0	0	1	0	6	2
Unburned										
Years Since Burn	<i>Phacelia distans</i>	<i>Pleuraphis rigida</i>	<i>Poa secunda</i>	<i>Prunus fasciculata</i>	<i>Salvia columbariae</i>	<i>Salazaria mexicana</i>	<i>Schismus barbatus</i>	<i>Sphaeralcia ambigua</i>	<i>Stephanomeria exigua</i>	<i>Yucca brevifolia</i>
2	1	21	0	0	0	0	1	1	3	3
2	5	0	1	0	1	3	6	2	5	3
9	6	0	1	0	3	0	0	0	5	0
9	10	0	0	0	6	1	0	0	0	0
13	7	0	3	0	0	3	0	0	0	0
13	10	1	1	0	0	1	1	0	0	0
15	4	0	1	0	0	0	5	3	4	0
15	2	5	0	0	0	0	0	3	9	0
19	3	12	0	1	0	0	4	0	6	4
19	4	3	0	0	0	0	1	0	2	0
65	1	0	1	11	0	0	0	0	2	2
65	3	0	0	8	0	0	0	0	4	0

APPENDIX C. Percent cover of vegetation types by grid.

Years since burn	Burned					Unburned				
	Annual	Exotic Grass	Bunch- grass	Sub- shrub	Long- lived Perennial	Annual	Exotic Grass	Bunch- grass	Sub- shrub	Long- lived Perennial
2	75.0	9.2	1.7	0.8	0.8	29.2	40.0	17.5	5.8	25.0
2	70.0	6.7	5.0	0.8	1.7	22.5	60.8	0.8	9.2	29.2
9	50.0	49.2	1.7	12.5	6.7	21.7	44.2	0.8	0.0	45.8
9	73.3	60.0	0.0	13.3	10.0	19.2	55.8	0.0	0.8	45.8
13	23.3	50.0	2.5	20.8	1.7	16.7	54.2	3.3	3.3	35.8
13	15.0	61.7	4.2	20.8	0.0	25.0	54.2	1.7	2.5	38.3
15	17.5	43.3	4.2	8.3	9.2	14.2	66.7	0.8	5.8	42.5
15	30.0	41.7	9.2	9.2	5.0	15.0	46.7	4.2	2.5	36.7
19	38.3	66.7	5.0	4.2	20.0	30.8	56.7	10.0	5.8	27.5
19	30.0	51.7	7.5	4.2	15.8	18.3	43.3	2.5	5.8	29.2
65	60.8	29.2	0.0	1.7	23.3	16.7	38.3	1.7	2.5	25.8
65	57.5	35.0	0.0	2.5	27.5	38.3	58.3	1.7	7.5	13.3

APPENDIX D. Vegetation Sampling Results – Sørensen distance

Years since burn	Between-plot distance for burns	Between-plot distance for unburns	Between burned and unburned sites (average of 4 distances)
2	0.256	0.323	0.626
9	0.303	0.167	0.704
13	0.210	0.143	0.724
15	0.241	0.220	0.427
19	0.311	0.385	0.359
65	0.293	0.415	0.662

APPENDIX E. Number of new rodent captures per 216 trap-nights by sampling grid

Years Since Burn	Burned					
	<i>Ammospermophilus leucurus</i>	<i>Chaetodipus fallax</i>	<i>Chaetodipus penicillatus</i>	<i>Dipodomys merriami</i>	<i>Onychomys torridus</i>	<i>Peromyscus boylii</i>
2	0	0	0	49	0	0
2	0	0	0	36	0	0
9	0	0	0	55	0	0
9	0	0	0	44	0	0
13	0	0	0	44	0	0
13	0	0	0	42	0	0
15	0	0	0	54	0	0
15	1	0	0	41	1	0
19	1	1	0	53	2	0
19	7	0	0	36	0	0
65	0	0	0	23	3	0
65	0	0	1	28	7	2

Years Since Burn	Unburned					
	<i>Ammospermophilus leucurus</i>	<i>Chaetodipus fallax</i>	<i>Chaetodipus penicillatus</i>	<i>Dipodomys merriami</i>	<i>Onychomys torridus</i>	<i>Peromyscus boylii</i>
2	0	0	0	42	1	0
2	0	0	0	31	0	0
9	1	0	0	43	2	0
9	0	0	0	53	7	0
13	0	0	0	36	2	0
13	1	0	0	41	1	1
15	0	0	0	46	3	1
15	0	0	0	25	0	0
19	2	2	0	36	0	0
19	3	3	0	25	0	0
65	5	0	1	8	0	1
65	1	0	0	13	0	4

APPENDIX E. Continued.

Years Since Burn	Burned				
	<i>Peromyscus crinitus</i>	<i>Peromyscus eremicus</i>	<i>Perognathus longimembris</i>	<i>Peromyscus maniculatus</i>	<i>Peromyscus truei</i>
2	0	0	3	0	0
2	0	0	7	0	0
9	0	0	3	0	0
9	0	0	3	2	0
13	0	0	0	6	0
13	0	0	0	0	0
15	0	0	2	3	0
15	0	1	4	2	0
19	0	0	5	1	0
19	1	0	5	7	0
65	5	4	13	6	0
65	11	2	12	4	0

Years Since Burn	Unburned				
	<i>Peromyscus crinitus</i>	<i>Peromyscus eremicus</i>	<i>Perognathus longimembris</i>	<i>Peromyscus maniculatus</i>	<i>Peromyscus truei</i>
2	0	0	5	2	0
2	2	0	4	1	0
9	4	6	3	8	0
9	1	4	5	4	1
13	6	2	8	0	1
13	3	0	6	2	0
15	0	2	1	6	0
15	3	3	14	5	2
19	3	0	6	0	0
19	4	1	4	1	1
65	12	7	15	8	2
65	19	2	17	11	7