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# Post-fire spatial heterogeneity alters ground-dwelling arthropod and small mammal community patterns in a desert landscape experiencing a novel disturbance regime



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## ABSTRACT

Anthropogenic activities have resulted in novel disturbance regimes which have unknown impacts on biodiversity. A notable example is the establishment of fire regimes in ecosystems that have not historically burned. These new disturbance regimes leave behind a complex spatial matrix with varying patterns of landscape heterogeneity. Research on novel disturbance regimes often ignores remnant vegetation within disturbed habitats, even though landscape variation in a disturbed area can influence population and community dynamics. Our objective was to understand the influence of spatial heterogeneity, characterized by varying levels of isolation and remnant vegetation, within a landscape disturbed by a novel fire regime in the Mojave Desert where wildfire was exceedingly rare to non-existent in this landscape prior to recent times. We found that community patterns of both ground-dwelling arthropods and small mammals varied based on the amount of remnant vegetation and isolation levels within burned habitats. Ground-dwelling arthropod abundance and richness measurements were highest in burned habitats that had remnant long-lived vegetation present, whereas small mammal abundance and richness measurements were highest in continuous expanses of unburned habitat. We also found that the negative impacts of fire on arthropods and small mammal communities in isolated, burned habitats were masked by the presence of long-lived perennial vegetation. Our study highlights the importance of incorporating habitat heterogeneity into future studies of novel disturbance regimes and provides evidence for the utility of restoration plantings in desert ecosystems.

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## 1. Introduction

Disturbance is a key component of ecological systems, altering landscapes across a wide range of scales (Turner, 2010). Disturbances can be defined as “any relatively discrete event that disrupts the structure of an ecosystem, community, or population and changes resource availability or the physical environment” (White and Pickett, 1985). Naturally occurring events such as fires, floods, hurricanes, and volcanic eruptions are agents that frequently disrupt continuous expanses of natural habitat (Dale et al., 2000; Schelhaas et al., 2003). However, human activities have directly or indirectly altered disturbance components such as their frequency, size, and/or severity in many ecosystems (see Turner, 2010 for disturbance component details). The resulting novel disturbance regimes often leave behind a mosaic of diverse

land covers that are historically atypical of the affected landscape (Dale et al., 2000; Turner, 2010).

Post-disturbance spatial heterogeneity has been shown to influence the structure and dynamics of populations and communities across multiple landscapes (Prugh et al., 2008; Tews et al., 2004). Disturbance theory predicts that spatial heterogeneity can influence the persistence of species, the stability of populations, and the coexistence of interacting species (summarized in Chesson (2000)). Most commonly, a positive correlation with diversity and habitat heterogeneity is hypothesized to result from an increase in ecological niches and resources (habitat heterogeneity hypothesis; Bazzaz, 1975; summarized in Tews et al. (2004)). A meta-analysis by Tews et al. (2004) found strong evidence for a positive correlation between habitat heterogeneity and diversity for multiple taxonomic groups, and these patterns suggest that habitat heterogeneity may mitigate the negative impacts of disturbances (Benton et al., 2003; Caswell and Cohen, 1991).

While it is well-documented that spatial heterogeneity within landscapes can influence population and community dynamics,

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the explicit influence of spatial heterogeneity within the disturbed landscape that results from novel disturbance regimes is largely unknown. Rather, the focus of studies exploring the impacts of novel disturbance regimes has typically been with the disturbance components, such as disturbance size and/or timing (e.g. Gibson et al., 2005; Miller et al., 2012; Poff and Allan, 1995). Studies investigating how novel disturbance regimes influence population and community dynamics focus on effects across the entire disturbed habitat (e.g. Franklin et al., 2005; Vamstad and Rotenberry, 2010) but do not consider spatial heterogeneity within the remaining disturbed landscapes. This gap partially stems from the fact that small scale disturbances were long recognized as sources of spatial heterogeneity while the occurrence of large “catastrophic” disturbances often associated with novel disturbance regimes were recognized as homogenous areas or were considered destroyed (Turner, 2010). Because of this, habitat heterogeneity is often incorporated into small-scale disturbance studies, but heterogeneity within landscapes experiencing large-scale disturbances is uncharacterized. However, even severe disturbances typically do not homogenize the landscape. Thus, understanding the impacts of novel disturbance regimes on biodiversity therefore necessitates explicitly incorporating resulting patterns of spatial heterogeneity into studies of affected landscapes.

Fire regimes have significantly altered many ecosystems (Franklin et al., 2005; Vamstad and Rotenberry, 2010) and are one of the most studied disturbances where components are being altered by human activities. Altered fire regimes have been shown to cause shifts in the relative dominance of vegetation types (e.g. Franklin et al., 2005; Vigilante and Bowman, 2004) which can alter higher trophic levels and lead to biodiversity loss (e.g. Bradstock et al., 1997; Wardell-Johnson et al., 2007). Fires may leave behind remnant vegetation in the landscape, creating a mosaic of patch types that vary in resource availability, species composition, vegetation structure, and ecosystem processes within a region. Post-fire spatial habitat heterogeneity has been shown to influence the recovery of plants and wildlife (Freckleton, 2004; Parr et al., 2004; Vandvik et al., 2005). However, despite the evidence of the importance of post-disturbance spatial heterogeneity, the influence of spatial heterogeneity within landscapes experiencing a novel disturbance regime is largely ignored.

In the Mojave Desert, wildfire was exceedingly rare to non-existent prior to recent times (Brooks and Matchett, 2006). However, fires are now increasingly common due to the invasion of non-native grass species which have been facilitated by climate change and on-going nitrogen soil deposition from urban California (Allen et al., 2009; Lenihan et al., 2003). This increase somewhat mirrors the increase in fire frequency seen in other southern California ecosystems and in many forested landscapes (e.g. Flannigan et al., 2000; Brooks et al., 2004), although many frequently burned ecosystems have experienced a historical fire regime. Despite the historical regime and that species in other systems exhibit adaptations to fire, the Mojave Desert ecosystem provides a striking case study that can be used as a standard for other systems that are experiencing fires more frequently or at larger scales.

Our objective was to quantify the influence of spatial heterogeneity on arthropod and small mammal community patterns within burned habitats in the Mojave Desert. Within our study landscape, the variation within burned habitats (i.e. heterogeneity) was created by the amount and configuration of remnant vegetation in burned habitats and the distance of the burned habitats from continuous expanses of unburned habitats (isolation level). Fires in the Mojave ecosystem have left behind a mosaic of varying levels of remnant vegetation, making it important to quantify the influence of spatial heterogeneity on multiple taxa. Arthropods generally have short generation times and have been documented to respond to changing food availability (de Groot et al., 2007) and

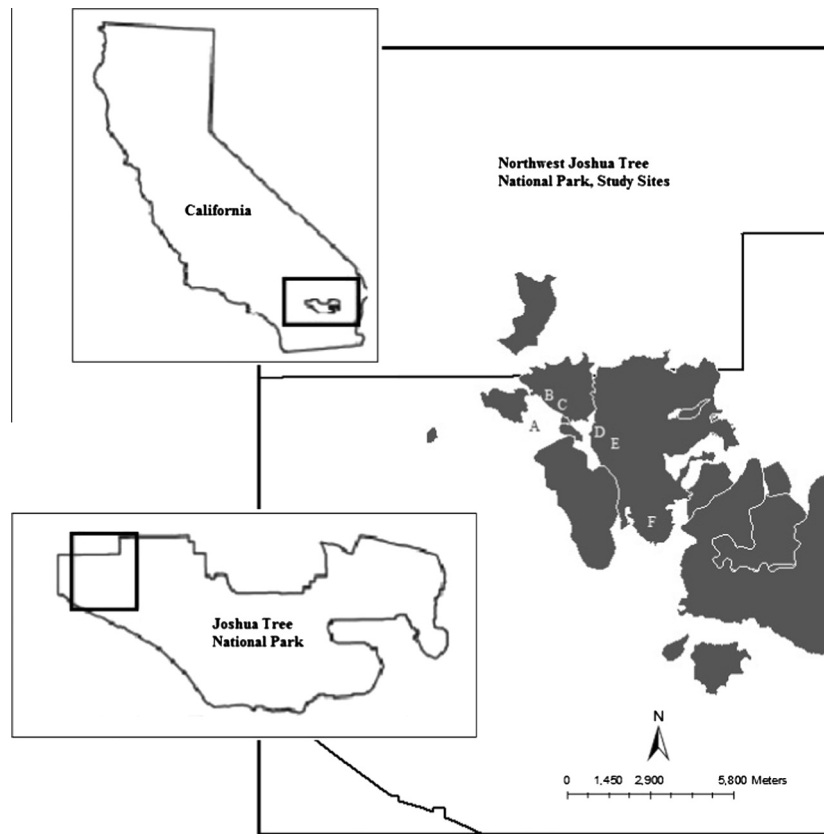
habitat structure (Pearson, 2009), making those ideal candidates for monitoring community responses to small changes in habitat (Longcore, 2003). Small mammals are a key component of desert ecosystems (Brown et al., 2000) as they are important consumers of plant materials (Price and Joyner, 1997) and are a significant portion of the prey base for a variety of carnivores. Furthermore, seed predation by small mammals has shown to significantly influence desert ecosystem structure and dynamics (Longland, 2007; Montiel and Montana, 2003). Within the Mojave Desert, Vamstad and Rotenberry (2010) found changes in small mammal diversity between burned and unburned habitats, yet abundance was not significantly different. Nevertheless, their study was taxonomically and spatially limited as it focused solely on small mammals and ignored spatial heterogeneity within burned sites. Specifically, the study did not consider whether burned areas included remnant unburned vegetation that could harbor organisms intolerant of burned areas and how isolated this vegetation was from unburned areas.

We measured abundance and richness for both ground-dwelling arthropods and small mammals across five burned habitats that naturally vary in remnant vegetation and relative isolation to answer the following two questions in a system experiencing a novel disturbance regime: (1) does spatial heterogeneity created by remnant vegetation and isolation levels within burned landscapes influence arthropod and small mammal community patterns; and (2) do taxonomic groups respond similarly to patterns of remnant vegetation and isolation levels in these landscapes? We expected that arthropod and small mammal communities would respond positively to increasing amounts of remnant vegetation in the burned landscape, but both taxonomic groups would exhibit lower abundance and richness in all burned habitats when compared to continuous expanses of unburned habitat, especially in burned habitats that were isolated from unburned habitats. We did not expect either taxonomic group to respond to heterogeneity positively as predicted by the habitat heterogeneity hypothesis as there is no recent evolutionary history of these groups with fire or other large disturbance events, making it likely that the burned matrix could not be effectively utilized by most species. We anticipated that this was particularly likely for rare and specialized species that may not be able to recover quickly or utilize burned habitats as they are naturally low in abundance and/or have specific habitat requirements. However, spatial heterogeneity introduced by fire may simultaneously increase the diversity of generalists that may be more capable of using resources in the new burned landscape.

## 2. Methods

### 2.1. Study site

Our study site is located in the northwestern region of California's Joshua Tree National Park (Fig. 1) and is part of the Mojave Desert scrub biome (Brown, 1994). The study site is characterized by slow-growth, long-lived perennial species such as California juniper (*Juniperus californica*), Joshua tree (*Yucca brevifolia*), blackbrush (*Coleogyne ramosissima*), and Muller's live oak (*Quercus cornelius mulleri*). Our study took place in the spring (April–June) of 2012. Mean monthly maximum temperatures for April, May, and June are 30.2 °C, 34.9 °C, and 38.0 °C, respectively, and mean monthly minimum temperatures are 7.4 °C, 12.2 °C, and 15.0 °C, respectively (NCDC, 2013). Mean monthly precipitation for April, May, and June are 2.54 mm, 8.38 mm, 1.02 mm, respectively (NCDC, 2013). Our 2012 sampling season was dry, receiving 0.25 mm of precipitation in June only; however, this ecosystem is accustomed to dry years.



**Fig. 1.** Map of study site in reference to California. Dark sections represent burned habitats. Letters represent habitat type as follows: (A) unburned habitat, (B) 2006 burned habitat without remnant vegetation, (C) 2006 burned habitat with remnant scattered vegetation, (D) 1995 burned habitat that is close to the unburned habitat without remnant vegetation, (E) 1995 burned habitat that is isolated from the unburned habitat without remnant vegetation and (F) 1995 burned habitat that is isolated from the unburned habitat with remnant patches.

We surveyed ground-dwelling arthropods and small mammals in two disturbed landscapes; one that burned in 1995 and one that burned in 2006. The burned landscapes varied in the amount, configuration, and isolation of remnant vegetation (see Table 1 and Fig. 2a–e for detailed habitat descriptions and visualizations). Preliminary vegetation surveys allowed us to characterize five distinct burned habitat types within the two burned landscapes. Within the 1995 burn, we surveyed three burned habitat types: (1) burned habitat that was isolated from unburned habitat that contained remnant habitat patches, (2) burned habitat that was isolated from unburned habitat that did not contain remnant habitat patches,

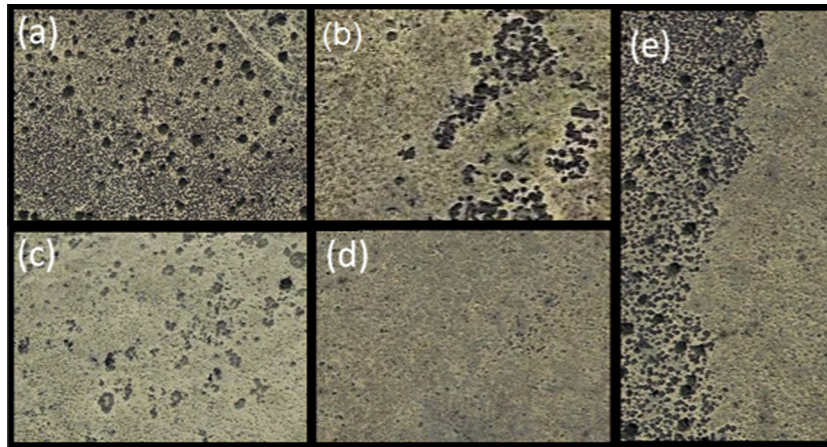
and (3) burned habitat that was close to the unburned habitat that did not contain remnant habitat patches. We did not have burned habitat that was close to the unburned habitat with remnant vegetation within the 1995 burn area. We defined habitat patches as dense clusters of remnant, long-lived perennial vegetation that were at least 200 m<sup>2</sup>, making them large enough to fit a sampling plot (described in Section 2.2).

We determined the relative isolation of habitats using our largest bodied organism, Merriam's kangaroo rat, *Dipodomys merriami*, since home range is typically proportional to body size in mammals (Swihart et al., 1988). We defined “close” burned habitats

**Table 1**

Description of burned habitat types in the 2006 burn (a) and the 1995 burn (b). See Figs. 1 and 2a–e for visual representation of habitat types.

Habitat type	Description of burned habitats
<b>2006 Burn (401 ha)</b>	
Burned; close, with scattered vegetation	Burned habitats that contain remnant, long-lived perennials. Remnant vegetation is scattered throughout the burned area, usually standing alone, and the vegetation does not exhibit a dense, clumped configuration (i.e. not patches). The habitats are between 25 m and 175 m from unburned habitat
Burned; close, without remnant vegetation	Burned habitats that do not contain remnant, long-lived perennials. All vegetation is considered regrowth. The habitats are between 25 m and 175 m from unburned habitat
<b>1995 Burn (2234 ha)</b>	
Burned; isolated, with patches (patches are considered different from scattered remnant vegetation)	Burned habitats that contain remnant habitat patches. Habitat patches are defined as dense clusters of remnant, long-lived perennial vegetation that are at least 200 m <sup>2</sup> – similar in size to the sampling plots. These habitats are considered relatively isolated from unburned habitat, being between 600 and 750 m from any unburned area. Arthropod and small mammal sampling only took place within the burned habitat
Burned; isolated, without patches	Burned habitats without any long-lived perennial vegetation left after the burn. These habitats are considered isolated from unburned habitat, being between 600 and 750 m from unburned area
Burned; close, without patches	Burned habitats without any long-lived perennial vegetation left after the burn. These habitats are considered close to the unburned habitat and are between 150 and 300 m to unburned area



**Fig. 2.** (a–e) Aerial photographs of varying types of habitat heterogeneity, described at the amount, clustering, and relative isolation of perennial vegetation, at our study locations. Darker vegetation is long-lived perennial vegetation. The above photographs represent (a) unburned habitat, (b) burned habitat with habitat patches, (c) burned habitat with scattered, remnant vegetation, (d) burned habitat without remnant vegetation, and (e) the unburned/burned habitat border. Images from Google Earth (Google Inc., 2009).

as burned habitats within the lifetime dispersal distance of kangaroo rats (300 m, Jones, 1989) to the edge of unburned habitat. We defined “far” or “isolated” burned habitats as burned habitats at least twice the lifetime dispersal distance from the edge of unburned habitat (600 m, Jones, 1989). In the 1995 burn, all habitats sampled were defined as either “close” and ranged from 150 m to 300 m from the burn/unburned edge or “far” (isolated) and ranged from 600 m to 750 m from the burn/unburned edge.

Within the 2006 burn, we surveyed two more burned habitat types: (1) burned habitat with scattered remnant vegetation and (2) burned habitat without remnant vegetation. We defined scattered vegetation as remnant perennial vegetation that did not exhibit a dense, clumped configuration (i.e. not patches). Both 2006 burn habitats were defined as “very close” as the topography of the landscape limited our sampling area to 25–175 m from the burn/unburned edge. We surveyed 12 replicates of each of the five burned habitat types. In addition, we surveyed 24 unburned control sites. We classified unburned habitats as large expanses of undisturbed habitat that were at least the size of the largest burn in our study, 2234 ha.

## 2.2. Data collection

We surveyed vegetation, ground-dwelling arthropods, and small mammal communities within the five burned habitats and within the unburned habitat. We measured vegetation composition using the point intercept method (Caratti, 2006). We randomly placed five 50-m transects in each habitat type and ten 50-m transects in the unburned habitat, totaling 35 vegetation transects. Along each transect, we marked 50 random, computer-generated locations between 0.0 m and 50.0 m. At each measurement, we dropped a meter stick and recorded all vegetation as well as bare ground and litter that touched the meter stick. We identified perennial plants to the species level and annual plants to the genus level.

We surveyed ground-dwelling arthropods using dry, un-baited plastic pitfall traps. Pitfall traps were 11 cm wide at the mouth, 14 cm deep, 1.0 L in volume, and included a tight-fitting funnel that inhibited arthropod escape once they had fallen into the trap. We placed a 1–2 cm elevated board measuring approximately 20 cm × 20 cm × 0.5 cm over the pitfall trap to prevent sand from blowing into the trap. We set four pitfall traps at each sampling plot in a 2 × 2 arrangement five meters apart before sunset. We checked the traps immediately after sunrise, and we identified ground-dwelling arthropods to the family level except for

the family Formicidae where species were grouped as either Formicidae-granivores or Formicidae-nectivores.

We surveyed small mammals using perforated Sherman live-traps (model LFATDG-P 3" × 3.5" × 9"). For each sampling plot, we set traps 8–10 m apart in a 5 × 2 configuration at dusk and checked the traps the following morning. We had more Sherman-live traps than pitfall traps; however, the pitfall traps are able to capture multiple individuals per trap. We avoided Full moon effects on small mammal activity (Price et al., 1984) by suspending sampling on weeks with full moons. We used bait that consisted of a mixture of rolled oats and peanut butter. At the time of capture, we identified each small mammal to species level using a number of recorded morphologic measurements as described by Jameson and Peters (1988). We corrected for detectability of small mammals and arthropods using a jack-knife estimator (see Section 2.3). In total, we surveyed five habitat types each with 12 sampling plots along with 24 sampling plots in the unburned habitat, totaling 840 Sherman-live traps and 336 pitfall traps.

## 2.3. Data analyses

We classified vegetation as invasive grass species, ephemeral plant species (annuals), quick-growth, short-lived perennials, or slow-growth, long-lived perennials (see Appendix A.1 for the species list). Percent cover for each vegetation type, along with bare ground and litter cover, was calculated as explained by Caratti (2006), and averaged for each habitat type. We ran Kruskal–Wallis rank-sum tests to test for differences in vegetation cover within each burn area. We then ran a post-hoc multiple comparison tests following Siegel and Castellan's (1988) methods to determine which vegetation types were responsible for the differences at the  $\alpha \leq 0.05$  significance level.

To assess the adequacy of our *a priori* habitat classifications, we used a non-parametric test, the multi-response permutation procedure (MRPP), to validate differences between vegetation compositions among habitat types. The MRPP tests for differences between two or more groups of sampling units by calculating the chance-corrected within-group agreement (A), a test statistic that describes within group homogeneity compared to a random expectation (McCune and Grace, 2002). We ran a MRPP test based on vegetation types and litter coverage, followed by an Indicator Species Analysis to identify vegetation that corresponded to particular habitat types. The MRPP analysis assigns indicator values to each

species to identify the sampling group that the species have the highest positive association with (Dufrene and Legendre, 1997).

We corrected for both arthropod and small mammal richness detectability using a jack-knife estimator (Colwell and Coddington, 1994; Palmer, 1990). We summarized arthropod and small mammal abundance and corrected species richness at each sampling plot and averaged across habitat type. We ran Kruskal–Wallis rank-sum tests for each burn area for both arthropod and small mammal metrics. We then ran post-hoc multiple comparison tests following Siegel and Castellan's (1988) methods to determine which vegetation types were responsible for the differences at the  $\alpha \leq 0.05$  and the  $\alpha \leq 0.10$  significance levels.

To further quantify differences in arthropod and small mammal species composition between habitat types, we used the MRPP to test for differences in habitat association in both taxonomic groups (see Appendix A.2 for the arthropod family and small mammal species list). We ran three different MRPP tests for each taxon in each burn by categorizing habitats by their habitat type (Table 1), their burned/unburned classification, and by the presence/absence of long-lived perennial vegetation. (Note that this final classification groups burned habitats containing remnant vegetation with unburned habitat). For tests that were significant at the  $\alpha \leq 0.10$ , we ran an indicator species analyses to understand which species were changing based on the MRPP classifications. All data analyses were carried out using the statistical software, R (R Core Team, 2012; see Appendix A.3 for function and package information).

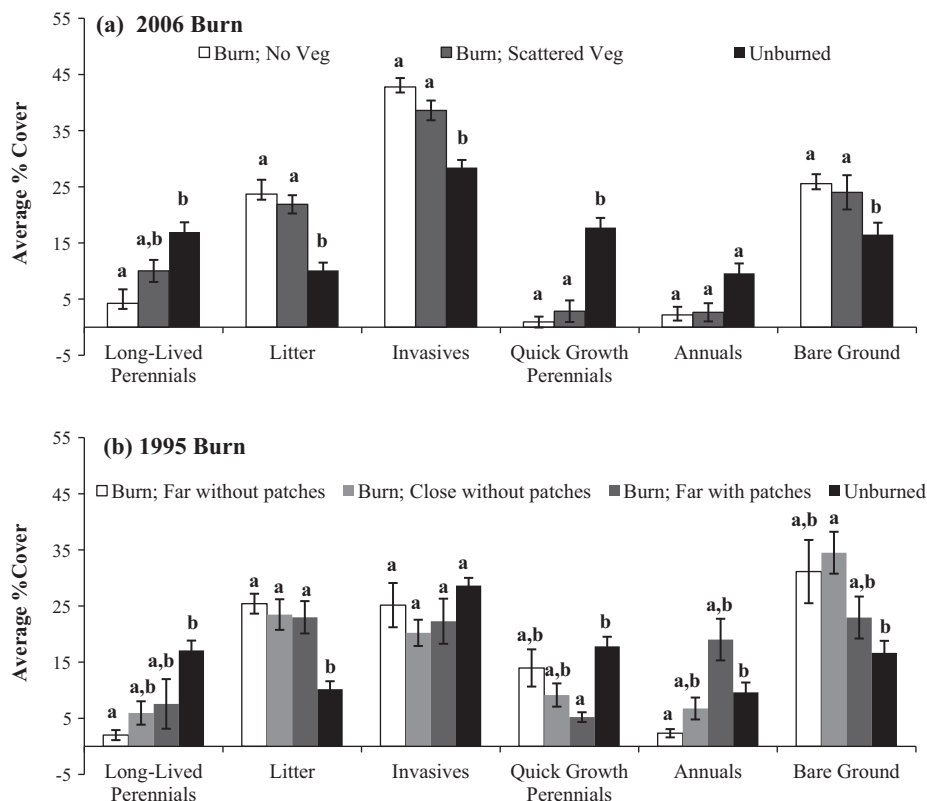
### 3. Results

Long-lived perennial vegetation cover was highest in unburned habitats, and litter cover was highest in burned habitats for both

burns at the  $\alpha \leq 0.05$  (Fig. 3a and b). We found that habitat types were significantly different based on vegetation type cover in both the 2006 burn and the 1995 burn (MRPP results;  $A_{2006} = 0.4105$ ,  $p_{2006} = 0.001$ ;  $A_{1995} = 0.2763$ ,  $p_{1995} = 0.001$ ). Long-lived perennials and quick-growth perennials had a significant positive association with the unburned habitat in both burns (Indicator Species Analysis; long-lived perennials  $p_{2006} = 0.003$ ; quick-growth perennials  $p_{2006} = 0.001$ ; long-lived perennials  $p_{1995} = 0.001$ ; quick-growth perennials  $p_{1995} = 0.012$ ; Table 2). Invasive species had a significant positive association with burned habitats without remnant vegetation in the 2006 burn (Indicator Species Analysis;  $p = 0.022$ ; Table 2).

We did not find significant differences in arthropod family-level abundances between habitat types for either the 2006 burn ( $p = 0.122$ ) or the 1995 burn ( $p = 0.5608$ ; Fig. 4a and b). However, we found significant differences in corrected arthropod family-level richness between habitat types for the 2006 burn (Kruskal–Wallis rank sum test;  $p = 0.041$ , Fig. 3a) and the 1995 burn (Kruskal–Wallis rank sum test;  $p = 0.0002$ ; Fig. 3b). In the 2006 burn, we did not find significant differences for in arthropod abundance or richness based on habitat type. However, we did find trends that the burned habitat with scattered vegetation maintained higher arthropod richness than both the burned habitat without remnant vegetation and the unburned habitat at the  $\alpha \leq 0.10$  level. In the 1995 burn, the unburned habitat had significantly lower arthropod richness than all burned habitats except for the isolated burned habitat with remnant habitat patches at  $\alpha \leq 0.05$  (Fig. 4a and b).

We found significant differences in arthropod community composition in the 2006 burn based on habitat type (MRPP results;  $p = 0.017$ ) and on the presence of long-lived perennial vegetation (MRPP results;  $p = 0.040$ ; Table 3). Arthropod compositional differences were mainly driven by the families Scarabaeidae (scarab



**Fig. 3.** (a,b) Vegetation type mean percent cover by burn year. Vegetation type differs among habitat types within the 2006 burn (a) and within the 1995 burn (b), particularly long-lived perennials and litter cover for both burns. Significant differences between habitats is assessed at the  $\alpha \leq 0.05$  level based on a post-hoc multiple comparison test following Siegel and Castellan's (1988) methods. Error bars represent one standard error.

**Table 2**  
List of vegetation types that are positively associated with particular habitat types in each burn based on the indicator species analyses. Perennials are highly significantly associated with unburned habitats as expected based on a *a priori* habitat classifications.

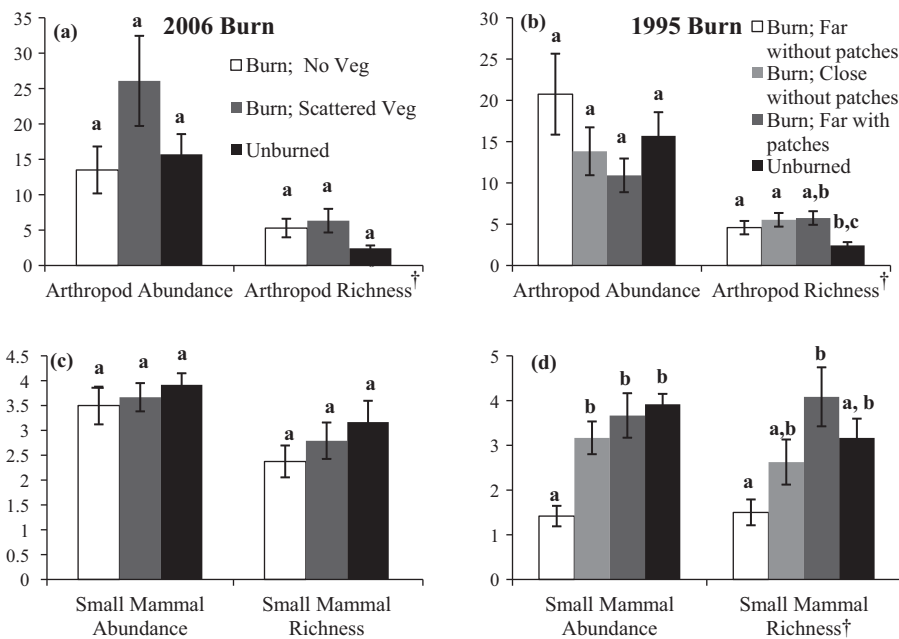
2006 Burn		1995 Burn	
Vegetation type	Habitat type	Vegetation type	Habitat type
Long-lived perennials	Unburned**	Long-lived perennials	Unburned***
Litter	Burn, no vegetation	Litter	Burn, far without patches
Invasive species	Burn, no vegetation†	Invasive species	Unburned†
Quick-growth perennials	Unburned***	Quick-growth perennials	Unburned†
Annuals	Unburned**	Annuals	Burn, far with patches***

\*  $p \leq 0.05$ .

\*\*  $p \leq 0.01$ .

\*\*\*  $p \leq 0.001$ .

†  $p \leq 0.10$ .



**Fig. 4.** (a–d) Mean richness and abundances for arthropods (a, b) and small mammals (c, d) in the 2006 burn (a, c) and 1995 burn (b, d). Richness levels are corrected for detectability using a jack-knife estimator (Colwell and Coddington, 1994; Palmer, 1990). Results differ more by taxonomic group than by burn year. Significant differences between habitats is assessed at the  $\alpha \leq 0.05$  level based on a post-hoc multiple comparison test following Siegel and Castellan's (1988) methods. Error bars represent one standard error. The symbol, †, after the x-axis label indicates additional trends found at the  $\alpha \leq 0.10$  level. Arthropod richness in the 2006 burn (a) was higher in the burned habitat with scattered vegetation than both the burned habitat without remnant vegetation and the unburned habitat at the  $\alpha \leq 0.10$  level. Arthropod richness in the 1995 burn (b) was lower in the unburned habitat than all burned habitats at  $\alpha \leq 0.10$ . Small mammal richness in the 1995 burn (d) was lower in the far (isolated) burned habitat without remnant habitat patches than both the far (isolated) burned habitat with remnant habitat patches and the continuous unburned habitat at  $\alpha \leq 0.10$  level.

beetles; generalist) and Stenopelmatidae (Jerusalem crickets; detritivore generalist); both families had a significant positive association with the burned habitat without remnant vegetation (Indicator Species Analysis;  $p = 0.037$  and  $p = 0.018$ , respectively; Table 4). Pholcidae (web-building spiders) and unknown beetle larvae had a positive association with the burned habitat with scattered remnant vegetation within the 2006 burn (Indicator Species Analysis;  $p = 0.10$  and  $p = 0.001$ , respectively; Table 4).

Within the 1995 burn, we found differences at the  $\alpha \leq 0.05$  level in arthropod community composition based on habitat type and burned/unburned classifications; we found a trend for differences in community composition based on the presence of perennial vegetation (MRPP results; Table 3). Nectivorous-Formicidae (nectivore specialists) had a significant positive association with the unburned habitat and perennial vegetation (Indicator Species Analysis;  $p = 0.003$ ; Table 4). Granivorous-Formicidae (detritus generalists) had a significant positive association with the burned habitat that was close without habitat patches (Indicator Species Analysis;  $p = 0.011$ ; Table 4). Ixodida (ticks and mites) and unknown beetle

larvae had significant positive associations with isolated burned habitat without habitat patches (Indicator Species Analysis;  $p = 0.001$  and  $p = 0.001$ , respectively; Table 4). Pholcidae had a significant positive association with the burned habitat without perennial vegetation (Indicator Species Analysis;  $p = 0.002$ ; Table 4).

We did not find any significant differences in small mammal abundance or corrected richness values within the 2006 burn (Kruskal–Wallis rank-sum test;  $p = 0.389$  and  $p = 0.751$ , respectively; Fig. 4c and d), although there was a non-significant trend of increasing abundance and richness with increasing vegetation. However, we found significant differences in small mammal abundance (Kruskal–Wallis rank-sum tests;  $p \leq 0.001$ ) and corrected richness (Kruskal–Wallis rank-sum tests;  $p = 0.006$ ) among habitat types in the 1995 burn. Within the 1995 burn, the isolated burned habitat without remnant habitat patches had lower small mammal abundance compared to all other habitat types at  $\alpha \leq 0.05$  (Fig. 3d). Small mammal richness was lower in the isolated burned habitat without remnant habitat patches than the isolated burned habitat with remnant habitat patches and in the continuous unburned

habitat at  $\alpha \leq 0.10$  level (Fig. 3d); however, the isolated burned habitat without remnant patches does not differ in richness from the isolated burned habitat with remnant patches at  $\alpha \leq 0.05$ .

We found marginal differences in small mammal community composition based on the presence of long-lived perennials in the 2006 burn (MRPP results;  $p = 0.086$ ; Table 3). *Peromyscus maniculatus* (a generalist) had a significant positive association with the burned habitat without remnant perennial vegetation (Indicator Species Analysis;  $p = 0.013$ ; Table 4) and *Onychomys torridus* (an omnivore/predator) had a positive association with all habitats with remnant perennial vegetation (Indicator Species Analysis;  $p = 0.086$ ; Table 4).

For the 1995 burn, we found significant differences in small mammal community structure based on habitat type (MRPP results;  $p = 0.039$ ; Table 3) and whether the site was burned or unburned (MRPP results;  $p = 0.067$ ; Table 3). *D. merriami* (generalist granivore), *O. torridus*, and *Ammospermophilus leucurus* (diurnal generalist) had positive associations with the unburned habitat (Indicator Species Analysis;  $p = 0.021$ ,  $p = 0.011$ , and  $p = 0.081$ , respectively; Table 4). *Peromyscus truei* (a habitat specialist) had a significant positive association with the isolated burned habitat that contains remnant habitat patches ( $p = 0.045$ ; Table 4), while *Peromyscus crinitus* had a significant positive association with isolated burned habitat that does not contain remnant habitat patches (Indicator Species Analysis;  $p = 0.003$ ; Table 4).

#### 4. Discussion

Anthropogenic influences have created many novel disturbance regimes, leaving behind a complex spatial matrix with high habitat heterogeneity. Within the Mojave Desert, a landscape experiencing a novel fire regime, we found that both ground-dwelling arthropods and small mammal communities responded to habitat heterogeneity within burned landscapes based on the amount of remnant vegetation and isolation levels, suggesting the importance of incorporating spatial heterogeneity into studies of novel disturbance regimes. However, we found that the taxa surveyed responded differently to landscape heterogeneity. Within the arthropod group, most taxa favored burned habitats, while most small mammal species favored continuous expanses of unburned habitat. An unexpected important finding of our study was that the presence of remnant long-lived perennial vegetation within burned habitats buffered against the impact of the burn with respect to faunal biodiversity.

Classifying habitats as simply “burned” or “unburned” had the lowest ability to detect differences in community structure across both burns and both taxa (Table 3). The best predictors of differences in community structure were habitat type descriptions where both remnant vegetation and isolation levels (when applicable) were considered. The only time habitat type did not differ in community composition was for the small mammals in the 2006 burn where the habitats were considered very close to the unburned habitat which may have masked the ability to detect differences in community structure.

Community responses to habitat type differed more by taxonomic group rather than burn year. We found that arthropods preferred burned habitats with remnant vegetation while small mammals preferred continuous expanses of unburned habitat regardless of burn year. However, the species that responded to particular habitat types differed. Thus, while abundance and richness values may have similar trends, different species may respond to environmental characteristics that change with increasing time since burn. Succession can play a large role in the resulting community (summarized in Lugo (2009)), and our data suggests that species may become more habitat-specific through time as there

are more species associating with habitat types in the 1995 burn compared to the 2006 burn.

Long-lived perennial plant cover corresponded to expectations based on our *a priori* habitat classifications where the unburned habitat contained significantly more long-lived perennial plant coverage than all burned sites, and burned sites with remnant vegetation contained intermediate amounts of perennial plant coverage (Fig. 3a and b). Invasive grass cover was higher in all burned habitats compared to the unburned habitat within the 2006 burn. The dominance by invasive grasses was not revealed in the 1995 burn since most annuals were dead, and the invasive grass species would have been recorded as litter cover; thus we see high litter cover in all burned habitats. This observation is consistent with the invasive grass fire cycle hypothesis, where burned desert habitats shift to invasive grasslands because invasive grasses promote frequent fires and are also the first species to colonize recently burned areas (Brooks et al., 2004).

Contrary to our predictions, arthropod richness responded to remnant vegetation as predicted by the habitat heterogeneity hypothesis, where the highest richness corresponded to areas that contain remnant long-lived vegetation within burned habitats (i.e. high habitat heterogeneity, Fig. 4a and b). Arthropod family richness and composition were influenced by a combination of distance to unburned habitat and/or perennial vegetation presence in all burned habitats (Fig. 3a and b; Table 3). Arthropods generally have fast generation times which may allow them to recover quickly to an altered fire regime relatively quickly, creating a typical response based on the habitat heterogeneity hypothesis. Furthermore, arthropod richness has been shown to respond positively to spatial complexity in areas that are naturally disturbed by fire (Gardner et al., 1995).

Most generalist arthropod families were positively associated with all burned habitat types while specialist species were positively associated with the unburned habitat or burned habitats with long-lived perennial vegetation. Formicidae-nectivore, was positively associated with unburned habitats and long-lived perennial presence (Table 4). Nectivores rely heavily on flowering vegetation for resources, but since it was a dry year, nectivores may have been restricted to habitats with long-lived perennials for consistent resources. Generalist detritivores and two predator families, Ixodida and Pholcidae, were positively associated with burned habitats (Table 4). Detritivores may respond to an increase in their food source (litter coverage), and Pholcidae (a sit-and-wait spider), may

**Table 3**

Multi-response permutation procedure (MRPP) test results for differences in small mammals and ground-dwelling composition. *Habitat type* categories are based on habitat classifications as described in Table 1 plus unburned habitat. The *burned-unburned* classification groups all habitats into either burned or unburned categories. *Perennial presence* is a binary classification based on whether the habitat contains remnant, long-lived perennial plants. Burned/unburned classifications are generally less adequate at explaining community structure when compared to classifications representing changes in vegetation composition.

Small mammals		Arthropods	
Comparison	A	Comparison	A
<b>2006 Burn</b>			
<i>Habitat type</i>	0.012	<i>Habitat type</i>	0.048*
<i>Burned-unburned</i>	-0.004	<i>Burned-unburned</i>	0.015
<i>Perennials presence</i>	0.018†	<i>Perennials presence</i>	0.024*
<b>1995 Burn</b>			
<i>Habitat type</i>	0.038*	<i>Habitat type</i>	0.086***
<i>Burned-unburned</i>	0.017†	<i>Burned-unburned</i>	0.028**
<i>Perennials presence</i>	0.011	<i>Perennials presence</i>	0.011†

\*  $p \leq 0.05$ .

\*\*  $p \leq 0.01$ .

\*\*\*  $p \leq 0.001$ .

†  $p \leq 0.10$ .



**Table 4**  
Indicator Species Analysis results from MRPP tests. Each taxonomic group is listed with the habitat type that it is positively associated with. Only those species with significant relationships at the  $\alpha \leq 0.10$  level are given below. Habitat type categories are based on classifications as described in Table 3.

Family	Habitat type	Burned–unburned	Perennials–no perennials
<i>Arthropods burn 2006</i>			
Pholcidae	Burn, scattered vegetation <sup>†</sup>	–	Perennials
Scarabaeidae	Burn, no vegetation <sup>*</sup>	–	No perennials <sup>†</sup>
Stenopelmatidae	Burn, no vegetation <sup>*</sup>	–	No perennials <sup>†</sup>
Unknown beetle larva	Burn, scattered vegetation <sup>†</sup>	–	No perennials
<i>Arthropods burn 1995</i>			
Diptera	Unburned	Unburned <sup>*</sup>	Perennials
Formicidae (Granivore)	Burn, close without patches <sup>*</sup>	Unburned	Perennials
Formicidae (Nectivore)	Unburned <sup>**</sup>	Unburned <sup>***</sup>	Perennials <sup>***</sup>
Ixodida	Burn, far without patches <sup>***</sup>	Burned <sup>†</sup>	No perennials <sup>†</sup>
Pholcidae	Burn, far without patches <sup>***</sup>	Burned <sup>**</sup>	No perennials <sup>†</sup>
Unknown beetle larva	Burn, far without patches <sup>***</sup>	Burned <sup>†</sup>	No perennials <sup>†</sup>
Species	Habitat type	Burned–unburned	Perennials–no perennials
<i>Small mammals burn 2006</i>			
<i>Peromyscus maniculatus</i>	–	–	No perennials <sup>†</sup>
<i>Onychomys torridus</i>	–	–	Perennials <sup>†</sup>
<i>Small mammals burn 1995</i>			
<i>Dipodomys merriami</i>	Unburned <sup>†</sup>	Unburned <sup>**</sup>	–
<i>Peromyscus truei</i>	Burn, far with patches <sup>*</sup>	Unburned	–
<i>Onychomys torridus</i>	Unburned <sup>†</sup>	Unburned <sup>**</sup>	–
<i>Ammospermophilus leucurus</i>	Unburned <sup>†</sup>	Unburned <sup>†</sup>	–
<i>Peromyscus crinitus</i>	Burn, far without patches <sup>**</sup>	Burned	–

\*  $p \leq 0.05$ .

\*\*  $p \leq 0.01$ .

\*\*\*  $p \leq 0.001$ .

†  $p \leq 0.10$ .

respond to the increase in detritivores, their food source. Furthermore, spiders have been shown to readily recolonize habitats after a fire due to their ballooning dispersal behavior (Buddle, 2000).

Alternatively, the positive association between arthropod richness and burned habitats may contain artifacts due to pitfall trap sampling of ground-dwelling arthropods. Unburned habitats may contain more shrub-dwelling rather than ground-dwelling arthropods, but pitfall traps are biased towards the latter. Higher detection of ground-dwelling arthropods would downplay shrub-dwelling arthropods where they are most abundant, and create an apparent increase in arthropod richness in burned habitats where ground-dwelling arthropods dominate. Future studies examining changes in both ground and shrub-dwelling arthropods within these landscapes are needed to determine if this shift exists.

Arthropod abundances did not differ by habitat type regardless of burn year (Fig. 4a and b). Within all habitat types, there may be enough resources to support arthropod survival, but the arthropod families that were present changed based on habitat type. Therefore, we were able to detect differences in richness and composition of ground-dwelling arthropods based on habitat type, but we were unable to detect differences in total arthropod abundance.

Small mammal abundance and richness values were highest in continuous expanses of unburned habitat, while burned habitats with remnant vegetation maintained moderate occupancy metrics (Fig. 4c and d). A review by Tews et al. (2004) found only a few studies exhibited a negative relationship with natural and/or disturbance-induced habitat heterogeneity, and the majority of the studies were mammals, suggesting that mammals may respond to habitat heterogeneity atypically compared to other taxonomic groups. The relationship between diversity and heterogeneity may be influenced by how the landscape is defined in structural variability and by the scale of the study, and we may not be measuring true heterogeneity as perceived for mammals. Nevertheless, our study found that the presence of remnant patches may mask the negative impacts of isolation levels in burned habitats (Fig. 3d). A study by Estrada et al. (1994) found similar results where fences containing native vegetation mitigated the negative

effects of agricultural disturbances on small mammals, suggesting the importance of remnant vegetation within disturbed habitats for small mammal conservation.

We did not find differences in small mammal occupancy metrics within the 2006 burn (Fig. 3c). Due to the topography of the landscape, we were restricted to surveying burned habitats that were very close to the unburned habitat. The proximity to the unburned habitat may have reduced our ability to detect differences in small mammal abundance and richness levels. Still, small mammal community structure differed based on long-lived perennial vegetation presence (Table 3). These results suggest that the presence of perennial vegetation is a more useful habitat descriptor than simply whether a habitat burned when the habitat is very close to large, unburned areas.

The majority of small mammal species were positively associated with unburned habitat, indicating that large expanses of long-lived perennial vegetation are needed to promote small mammal diversity. Disturbances have been shown to have negative effects on small mammals through the creation of patchy food sources and an increase in predation pressure due to the reduction of shrub cover (Simonetti, 1989). Exceptions were a few species that have unusual habitat requirements that were more likely to be covered in burned habitats (Table 4). A less common mammal species, *P. truei*, was positively associated with burned habitats with remnant habitat patches. Some of the remnant habitat patches included Piñon pine habitats containing Mueller's live oak, a key resource for *P. truei* (Linzey and Hammerson, 2008). *P. crinitus*, a species typically found in areas with bare rock (Linzey et al., 2008), was positively associated with isolated burned habitats without remnant vegetation.

Understanding the distribution and abundance of organisms is a fundamental goal of ecology; however, dramatic human alterations of disturbance regimes have created an increased need to understand how communities are structured in novel landscapes. Our study shows that there are many factors—patterns of spatial heterogeneity, time since disturbance, and choice of focal taxa—that can influence how disturbances affect community structure

and how those effects are perceived. Thus, we encourage both researchers and land managers to consider many variables within their system, including habitat heterogeneity, to provide a more holistic and unified understanding of the effects of altered disturbance regimes. From a desert restoration point of view, we encourage the promotion of long-lived native perennial vegetation within isolated habitats as perennial vegetation may mitigate the negative impacts of isolation within disturbed habitats.

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### Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2014.11.046>.

### References

- Allen, E., Leo, R., Steers, Robert, Bythnerowicz, Andrzej, Fenn, Mark, 2009. Impacts of atmospheric nitrogen deposition on vegetation and soils at Joshua Tree National Park. In: *The Mojave Desert Ecosystem: Processes and Sustainability*. University of Nevada Press, Las Vegas, NV.
- Bazzaz, F.A., 1975. Plant species-diversity in old-field successional ecosystems in southern Illinois. *Ecology* 56, 485–488.
- Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.* 18, 182–188.
- Bradstock, R.A., Tozer, M.G., Keith, D.A., 1997. Effects of high frequency fire on floristic composition and abundance in a fire-prone heathland near Sydney. *Aust. J. Bot.* 45, 641–655.
- Brooks, M.L., Matchett, J.R., 2006. Spatial and temporal patterns of wildfires in the Mojave Desert, 1980–2004. *J. Arid Environ.* 67, 148–164.
- 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.
- Brown, D., 1994. *Biotic Communities: Southwestern United States and Northwestern Mexico*. University of Utah Press, Salt Lake City, UT.
- Brown, J.H., Fox, B.J., Kelt, D.A., 2000. Assembly rules: Desert rodent communities are structured at scales from local to continental. *Am. Nat.* 156, 314–321.
- Buddle, C.M., 2000. Life history of *Pardosa moesta* and *Pardosa mackenziana* (Araneae, Lycosidae) in central Alberta, Canada. *J. Arachnol.* 28, 319–328.
- Caratti, J.R., 2006. In: Keane, R.E., Lutes, D.C., Caratti, J.F., Key, C.H., Benson, N.C., Sutherland, S., Gangi, L.J. (Eds.), *Point Intercept (PO): FIREMON: Fire Effects Monitoring and Inventory System*. USDA.
- Caswell, H., Cohen, J.E., 1991. Disturbance, interspecific interaction and diversity in metapopulations. *Biol. J. Linn. Soc.* 42, 193–218.
- Chesson, P., 2000. General theory of competitive coexistence in spatially-varying environments. *Theor. Popul. Biol.* 58, 211–237.
- Colwell, R.K., Coddington, J.A., 1994. Estimating terrestrial biodiversity through extrapolation. *Philos. Trans. R. Soc. Lond., B* 345, 101–118.
- Dale, V.H., Brown, S., Haeuber, R.A., Hobbs, N.T., Huntly, N., Naiman, R.J., Riebsame, W.E., Turner, M.G., Valone, T.J., 2000. Ecological principles and guidelines for managing the use of land. *Ecol. Appl.* 10, 639–670.
- de Groot, M., Kleijn, D., Jogan, N., 2007. Species groups occupying different trophic levels respond differently to the invasion of semi-natural vegetation by *Solidago canadensis*. *Biol. Conserv.* 136, 612–617.
- Dufrene, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* 67, 345–366.
- Estrada, A., Coatesestrada, R., Meritt, D., 1994. Non-flying mammals and landscape changes in the tropical rain-forest region of Los-Tuxtlas, Mexico. *Ecography* 17, 229–241.
- Flannigan, M.D., Stocks, B.J., Wotton, B.M., 2000. Climate change and forest fires. *Sci. Total Environ.* 262, 221–229.
- Franklin, J., Sypard, A.D., He, H.S., Mladenoff, D.J., 2005. Altered fire regimes affect landscape patterns of plant succession in the foothills and mountains of southern California. *Ecosystems* 8, 885–898.
- Freckleton, R.P., 2004. The problems of prediction and scale in applied ecology: the example of fire as a management tool. *J. Appl. Ecol.* 41, 599–603.
- Gardner, S.M., Cabido, M.R., Valladares, G.R., Diaz, S., 1995. The influence of habitat structure on arthropod diversity in Argentine semiarid Chaco forest. *J. Veg. Sci.* 6, 349–356.
- Gibson, C.A., Meyer, J.L., Poff, N.L., Hay, L.E., Georgakakos, A., 2005. Flow regime alterations under changing climate in two river basins: implications for freshwater ecosystems. *River Res. Appl.* 21, 849–864.
- Google Inc., 2009. *Google Earth (Version 5.1.3533.1731) [Software]*.
- Jameson, E.W., Peeters, H.J., 1988. *California Mammals*. University of California Press, Berkeley, CA.
- Jones, T., 1989. Dispersal distance and the range of nightly movements in Merriam's kangaroo rats. *J. Mammal.* 70, 27–34.
- Lenihan, J.M., Drake, R., Bachelet, D., Neilson, R.P., 2003. Climate change effects on vegetation distribution, carbon, and fire in California. *Ecol. Appl.* 13, 1667–1681.
- Linzey, A.V., Hammerson, G., 2008. *Peromyscus truei*. [www.iucnredlist.org](http://www.iucnredlist.org) (accessed 28.10.13).
- Linzey, A.V., Timm, R., Álvarez-Castañeda, S.T., Lacher, T., 2008. *Peromyscus crinitus*. [www.iucnredlist.org](http://www.iucnredlist.org) (accessed 28.10.13).
- Longcore, T., 2003. Terrestrial arthropods as indicators of ecological restoration success in coastal sage scrub (California, USA). *Restor. Ecol.* 11, 397–409.
- Longland, W.S., 2007. Desert rodents reduce seedling recruitment of *Salsola pauciflora*. *West. North Am. Nat.* 67, 378–383.
- Lugo, A.E., 2009. The emerging era of novel tropical forests. *Biotropica* 41, 589–591.
- McCune, B., Grace, J., 2002. *Analysis of Ecological Communities*. MjM Software, Gleneden Beach, Oregon, USA.
- Miller, A., Reilly, D., Bauman, S., Shea, K., 2012. Interactions between frequency and size of disturbance affect competitive outcomes. *Ecol. Res.* 27, 783–791.
- Montiel, S., Montana, C., 2003. Seed bank dynamics of the desert cactus *Opuntia rastrera* in two habitats from the Chihuahuan Desert. *Plant Ecol.* 166, 241–248.
- NCDC, 2013. *National Climatic Data Center*. <http://www.ncdc.noaa.gov/> (accessed 28.10.13).
- Palmer, M.W., 1990. The estimation of species richness by extrapolation. *Ecology* 71, 1195–1198.
- Parr, C.L., Robertson, H.G., Biggs, H.C., Chown, S.L., 2004. Response of African savanna ants to long-term fire regimes. *J. Appl. Ecol.* 41, 630–642.
- Pearson, D.E., 2009. Invasive plant architecture alters trophic interactions by changing predator abundance and behavior. *Oecologia* 159, 549–558.
- Poff, N.L., Allan, J.D., 1995. Functional-organization of stream fish assemblages in relation to hydrological variability. *Ecology* 76, 606–627.
- 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., Waser, N.M., Bass, T.A., 1984. Effects of moonlight on microhabitat use by desert rodents. *J. Mammal.* 65, 353–356.
- Prugh, L.R., Hodges, K.E., Sinclair, A.R.E., Brashares, J.S., 2008. Effect of habitat area and isolation on fragmented animal populations. *Proc. Natl. Acad. Sci. USA* 105, 20770–20775.
- R Core Team, 2012. *R: a language and environment for statistical computing*. Vienna, Austria.
- Schelhaas, M.J., Nabuurs, G.J., Schuck, A., 2003. Natural disturbances in the European forests in the 19th and 20th centuries. *Glob. Change Biol.* 9, 1620–1633.
- Siegel, S., Castellan, N.J., 1988. *Nonparametric Statistics for the Behavioral Sciences*, second ed. McGraw-Hill, Boston.
- Simonetti, J.A., 1989. Microhabitat use by small mammals in central Chile. *Oikos* 56, 309–318.
- Swihart, R.K., Slade, N.A., Bergstrom, B.J., 1988. Relating body size to the rate of home range use in mammals. *Ecology* 69, 393–399.
- Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *J. Biogeogr.* 31, 79–92.
- Turner, M.G., 2010. Disturbance and landscape dynamics in a changing world. *Ecology* 91, 2833–2849.
- Vamstad, M.S., Rotenberry, J.T., 2010. Effects of fire on vegetation and small mammal communities in a Mojave Desert Joshua tree woodland. *J. Arid Environ.* 74, 1309–1318.
- Vandvik, V., Heegaard, E., Maren, I.E., Aarrestad, P.A., 2005. Managing heterogeneity: the importance of grazing and environmental variation on post-fire succession in heathlands. *J. Appl. Ecol.* 42, 139–149.
- Vigilante, T., Bowman, D.M.J.S., 2004. Effects of fire history on the structure and floristic composition of woody vegetation around Kalumburu, North Kimberley, Australia: a landscape-scale natural experiment. *Aust. J. Bot.* 52, 381–404.
- Wardell-Johnson, G.W., Williams, M.R., Mellican, A.E., Annells, A., 2007. Floristic patterns and disturbance history in karri (*Eucalyptus diversicolor*: Myrtaceae) forest, south-western Australia: 2. Origin, growth form and fire response. *Acta Oecol.-Int. J. Ecol.* 31, 137–150.
- White, A.S., Pickett, S.T.A., 1985. Natural disturbance and patch dynamics: an introduction. In: Pickett, S.T.A., White, P.S. (Eds.), *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York, pp. 3–13.