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**Author**

Hulton VanTassel, Heather Lynn

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Ground-Dwelling Arthropod and Small Mammal Responses to Anthropogenic
Disturbances Within Southern California Deserts:  From Plant Invasions to Altered Fire
Regimes


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


Doctor of Philosophy

in

Evolution, Ecology, and Organismal Biology

by

Heather Lynn Hulton VanTassel


June 2015


Dissertation Committee:
        Dr. Kurt Anderson, Chairperson
        Dr. Rick Redak
        Dr. Darrel Jenerette

The Dissertation of Heather Lynn Hulton VanTassel is approved:

_____

_____

_____

Committee Chairperson

University of California, Riverside

Velasquez-Macedo, Tory Lamanivong, Andrea Munive, Alexis Ann Diaz, Austin Stypa,

Kasumi Tsai, Kelly Tran, Nicole Pownall, Malissa Perkins, Lora Roame, Patrick Liu,

Ryan Yuan, Victoria Autelli, Sierra Miller, and Christian Padilla.

I dedicate my dissertation to my supportive husband, Brandon.

ABSTRACT OF THE DISSERTATION


Ground-Dwelling Arthropod and Small Mammal Responses to Anthropogenic
Disturbances Within Southern California Deserts:  From Plant Invasions to Altered Fire
Regimes


by


Heather Lynn Hulton VanTassel

Doctor of Philosophy, Graduate Program in Evolution, Ecology, and Organismal Biology
University of California, Riverside, June 2015
Dr. Kurt Anderson, Chairperson

Habitat loss and fragmentation are the leading causes of biodiversity loss and are

considered to be the principal threats to the sustainability of the biosphere. Historically,

fragmentation literature focuses on direct anthropogenic disturbances, such as

deforestation and urbanization. However, many ecosystems now face novel disturbances,

such as the invasion of non-native species and climate change-induced disturbances,

further exasperating the rate of habitat loss and fragmentation. Thus, it is critical to

understand the influence of these novel disturbance events on biodiversity in order to

identify the long-term consequences of global change. My dissertation focused on two

types of landscapes facing novel disturbances:  1) the invasion of an exotic plant species

in California's Coachella Valley, and 2) altered fire regimes in Joshua Tree National Park

(JTNP).

Sahara Mustard (*Brassica tournefortii*; hereafter mustard), has invaded habitats throughout the arid southwestern United States, including five distinct sand habitats in the eastern Coachella Valley, California. I examined trends in ground-dwelling arthropod community structure concurrent with mustard invasion within those habitats from 2003–2011. I found strong negative relationships with arthropods and mustard even when controlling for non-target environmental correlates and for potential factors that we suspected of mediating mustard effects.

My second study site took place in JTNP, where wildfire was once non-existent or exceedingly rare. However, fires are now increasingly common due to the invasion of non-native grass species – an invasion facilitated by climate change and an on-going nitrogen soil deposition from urban California. This altered fire regime has left behind varying patterns of landscape heterogeneity. Within this landscape, I quantified the influence of fire-induced spatial heterogeneity on ground-dwelling arthropods and small mammal communities. I found that community patterns of both arthropods and mammals varied based on type of heterogeneity. I also found that spatial heterogeneity increased movement patterns for a general small mammal.

My dissertation research focused on the influence of multiple species in two types of disturbed landscapes across multiple habitats to provide a broad, cohesive understanding of novel disturbances influence community structure and patterns. This multifaceted approach provides a more realistic tactic to the understanding the long-term consequences of novel disturbances.

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**INTRODUCTION** – Habitat destruction and fragmentation are the leading causes of biodiversity loss (Wilcove et al. 1998; Balmford and Bond 2005), and the ecological consequences of fragmentation differ depending on the spatial landscape and how it influence rates and trajectories of recovery (Hanski 1999; Jansen 2005). Nevertheless, fragmentation of habitats generally has negative effects on population viability (Jansen 2005), and landscape transformations are occurring at such a rate that entire ecosystems are unable to recover after disturbances (Armenteras et al. 2003; Vamstad and Rotenberry 2010).

Southern California, one of the world's biodiversity hotspots (Myers et al. 2000), is experiencing a multitude of anthropogenic disturbances leading to habitat loss and fragmentation, including but not limited to climate change, urbanization, air pollution, altered fire regimes, and the introduction of non-native species (*summarized in* Lovich and Bainbridge 1999). Within southern California deserts, invasive plants and altered fire regimes have further exasperated the rate of habitat loss and fragmentations. Invasive plants have been shown to compete with native plants, alter wildlife habitat, and alter fire regime cycles. Furthermore, the increased fire frequency in the Mojave and Sonoran deserts has converted native shrublands to alien annual grasslands (*summarized in* Brooks and Pyke 2001). The natural recovery of desert ecosystems following disturbances is relatively slow (Bainbridge et al. 1993), and because of this, understanding the persistence of populations along with how space and time influence community dynamics in anthropogenically altered desert landscapes is critical in order to explain long-term consequences of habitat loss and fragmentation.

My dissertation aimed to further our understanding of the impacts of habitat fragmentation created from the invasion of exotic plant species and altered fire regimes. Particularly, my research focused on two anthropogenically altered desert landscapes in Southern California: 1) the invasion of an exotic plant species in the Coachella Valley, and 2) fire altered landscapes in Joshua Tree National Park (JTNP). The exotic plant species Sahara mustard (*Brassica tournefortii*; hereafter mustard) has reached high densities across desert sand habitats of the southwestern deserts, including five distinct sand habitats in the eastern Coachella Valley. Using a ten-year data set, I examined how mustard alters the diversity of ground-dwelling arthropods in this disturbed landscape. My second study site was in JTNP, where wildfire was once non-existent or exceedingly rare. However, fires are now increasingly common due to the invasion of non-native grass species – an invasion facilitated by climate change and an on-going nitrogen soil deposition from urban California (Allen et al. 2009). In JTNP, I quantified the influence of post-fire heterogeneity on ground-dwelling arthropod and small mammal community patterns within fragmented landscapes in JTNP, and the altered movement patterns and habitat use of a generalist small mammal, Merriam's Kangaroo Rat, in fragmented landscapes in Joshua Tree National Park.

# CHAPTER 1: DECLINES IN A GROUND-DWELLING ARTHROPOD COMMUNITY DURING AN INVASION BY SAHARA MUSTARD (BRASSICA TOURNEFORTII) IN AEOLIAN SAND HABITATS

*Co-authors – Anne Hansen, Cameron Barrows, Quresh Latif, Maggie Simon, and Kurt Anderson*

**ABSTRACT –** Sahara Mustard (*Brassica tournefortii*; hereafter mustard), an exotic plant species, has invaded habitats throughout the arid southwestern United States. Mustard has reached high densities across aeolian sand habitats of southwestern deserts, including five distinct sand habitats in the eastern Coachella Valley, California. We examined trends in ground-dwelling arthropod community structure concurrent with mustard invasion in 90 plots within those habitats from 2003–2011 (n = 773 plot·years). We expected arthropod communities to respond negatively to mustard invasion because previous work documented significant negative impacts of mustard on diversity and biomass of native plants, the primary resource base for many of the arthropods. Arthropod abundance and species richness declined during the study period while mustard cover increased, and arthropod metrics were negatively related to mustard cover across all plots. When controlling for non-target environmental correlates (e.g. perennial frequency and precipitation) and for potential factors that we suspected of mediating mustard effects (e.g. native cover and sand compaction), negative relationships with mustard remained statistically supported. Nevertheless, arthropod richness's relationship decreased slightly

in strength and significance suggesting that mechanistic pathways may be both direct (via habitat structure) and indirect (via native cover suppression and sand compaction). However, mechanistic pathways for mustard effects, particularly on arthropod abundance, remain unclear. Most arthropod taxa, including most detritivores, decreased through time and were negatively related to mustard cover. In contrast, many predators were positively related to mustard. In total, our study provides substantial evidence for a negative effect of Sahara mustard on the structure of a ground-dwelling arthropod community.

*Keywords*– *community structure, arid environments, invasive species impacts, bottom-up effects, aeolian sand dunes*

**INTRODUCTION –** Invasive exotic plants have wide ranging effects on community structure, ecosystem properties, and ecosystem services (Levine et al. 2003, Pejchar and Mooney 2009, Vila et al. 2011). Extensive literature describes what makes an exotic plant species invasive (Vilà and Weiner 2004, van Kleunen et al. 2010a, van Kleunen et al. 2010b), how they invade (Von Der Lippe and Kowarik 2007, Pyšek et al. 2011), and the consequences of invasion for native communities (Powell et al. 2011, Vilà et al. 2011). Studies have mainly focused on direct negative effects of invasion on native plant species through competition and the alteration of abiotic processes (White et al. 2006), as well as consequences of plant community alterations for ecosystem properties such as total biomass, size of nutrient pools, and disturbance regimes (Ehrenfeld 2010).

In contrast, bottom-up and indirect effects of invasive plants on higher trophic levels are poorly studied. Impacts on consumers are documented but tend to be less consistent and lower in magnitude than direct impacts on native plants (Vilà et al. 2011), and effects on consumers can be weak to non-existent (Osunkoya et al. 2011) or specific to certain functional groups (Herrera and Dudley 2003, de Groot et al. 2007, Fork 2010). Furthermore, studies that simultaneously investigate impacts of plant invasions on multiple trophic levels are scarce (Valtonen et al. 2006; de Groot et al. 2007; Gerber et al. 2008). Further study is needed to understand invasive plant impacts on consumers (Levine et al. 2003, Vilà et al. 2011).

Many deserts of the southwestern U.S. and northwestern Mexico have been invaded by exotic plant species despite challenges imposed on survival by hot, arid conditions, resulting in severe impacts to these systems (Mooney et al. 1986; Rejmanek and Randall 1994; Van Devender et al. 1997). Invasive plants often form large, monotypic stands in these deserts, negatively influencing both species diversity and landscape processes such as sand movement (Thomson 2005; Hart et al. 2012) and fire cycles (Brooks et al. 2004). Sahara mustard (*Brassica tournefortii*) is widespread in the Mojave and lower Sonoran deserts (Sanders and Minnich 2000) and has occurred in Coachella Valley, California for approximately 80 years. Sahara mustard (hereafter mustard) is an annual plant that germinates and fruits earlier in the year than native annual species. Mustard stands are therefore particularly dense in wet years with early precipitation. Previous mustard outbreaks peaked during El Niño-associated wet periods in the late 1970s to early 1980s (Sanders and Minnich 2000), in 1994–1995 (Barrows,

*unpubl.*), and in 2005 (Barrows et al. 2009). Mustard has dominated certain sand habitats within the Coachella Valley's dune landscape each year since 2005 independent of extreme wet periods (Barrows et al. 2009).

Barrows et al. (2009) documented strong negative impacts of Sahara mustard on native annual plant biomass and diversity in the Coachella Valley, but impacts on native fauna were less consistent. The Coachella Valley fringe-toed lizard (*Uma inornata*) exhibited negative responses to Sahara mustard, but arthropod responses were generally weak, although limited evidence for taxon- and context-specific responses were reported. However, Barrows et al.'s (2009) analysis of arthropods was taxonomically, spatially, and temporally, limited. In particular, they only studied mustard impacts within two of five aeolian sand communities described in this system (*see* Barrows and Allen 2007a).

In addition to affecting trophic structure, invasions can affect ecosystem function in ways that alter the physical structure of the environment with consequences for population densities and species diversity (Schwartz et al. 2000; Loeuille et al. 2002). Many arthropod species are endemic to aeolian sand systems of North American deserts, and changes to food availability and environmental structure within these systems could contribute to species extinctions (Andrews et al. 1979; Barrows 2000). In particular, studies have documented responses by arthropods to changing food availability (de Groot et al. 2007) and environmental structure (Pearson 2009) caused by invasive plants. Arthropods typically account for a large proportion of species membership and biomass of multiple trophic levels and functional guilds (Price et al. 2011). Furthermore, they typically have short generation times and are small in size, making terrestrial arthropods

ideal focal organisms for monitoring annual variation in ecosystem health (Longcore 2003).

Our overall objective was to examine the effects of the mustard invasion in the Coachella Valley on ground-dwelling arthropods. We examined trends in two measures of arthropod community structure, abundance and richness, for a nine-year period (2003-2011). During this period, mustard transitioned from being uncommon to being nearly the only annual plant species that flowers and goes to seed every year. First, we analyzed temporal trends in arthropod community structure and mustard cover, and the relationship between these trends across the landscape. Second, we further explored arthropod-mustard relationships, using multivariate models that controlled for potentially confounding environmental drivers of community structure, as well as potential mechanistic factors mediating mustard effects. Lastly, we examined mustard relationships with individual arthropod taxa to assess variation in mustard impacts among functional groups and trophic levels.

**MATERIALS AND METHODS** – Data were collected within Coachella Valley aeolian sand habitats (33° 47' N, 116° 20' W), in southeastern California (Figure 1) during 2003–2011. These included approximately 1,700 ha of historically contiguous, but now fragmented sand dunes and sand fields distributed across a strong east-west gradient in both wind disturbance intensity and rainfall. Rainfall was also extremely variable among years; minimum rainfall (3-7 mm/year) occurred in 2002 and 2007, and maximum rainfall (210–326 mm/year) occurred in 2005. Intra-annual daily temperatures also

varied, ranging from a low of ~0ºC in winter to highs of ~45ºC in summer. All precipitation data reported here are based on a July-to-June rain year and were recorded at 3 rain gauges distributed across the valley floor.

Coachella Valley's desert ecosystem consists of five different aeolian sand habitats: 1) *active sand dunes*, characterized by low shrub density, high levels of sand movement, and high topographic relief; 2) *stabilized dunes*, with high topographic relief but low sand movement due to stabilization by honey mesquite, *Prosopis glandulosa*; 3) *eastern stabilized sand fields*, with relatively high shrub density, low topographic relief, and compacted sand with low-to-moderate sand movement; 4) *western stabilized sand fields*, similar to *eastern stabilized sand fields* but more mesic and differing in both plant and animal species composition; and 5) *ephemeral sand fields* consisting of high perennial shrub density, hummock topography, and intense wind disturbance. For in-depth descriptions of vegetation and landscape attributes on these communities, see Barrows and Allen (2007a). All aeolian sand habitats were located in the western half of the Coachella Valley. *Active dunes* and *eastern stabilized sand field* habitats were located near the valley center, *ephemeral sand fields*, and *stabilized dunes* habitats were located further west, and *western stabilized sand fields* habitats were located in the western end of the valley (Fig 1). The five habitats varied in the extent to which they were invaded. *ephemeral sand fields* had little mustard cover throughout the study period. In contrast, *active dunes, eastern stabilized sand fields,* and *stabilized dunes* habitats experienced substantial increases in mustard cover, particularly following the 2007 drought. Additionally, mustard cover increased dramatically in *active dunes* and *eastern stabilized*

*sand fields* habitats in 2005, an extremely wet year. Mustard cover peaked twice in *western stabilized sand fields* during the study period, but both peaks were followed by declines.

**Data Collection** – Various aspects of the physical environment and biological communities were sampled yearly at a series of plots from 2003 to 2011. Ninety 0.1 ha (100m x 10 m) plots were sampled in total, of which 68 were sampled in 2003, 75 in 2004, and all 90 in 2005–2011, resulting in 773 plot·years sampled. Plots were separated by $\geq$ 50m, a distance greater than the diameter of many ground-dwelling arthropod home ranges, to minimize spatial dependence. We note, however, that home ranges of ground-dwelling arthropod taxa are highly variable and some small degree of spatial overlap could be present.

We measured sand compaction, a fundamental component of habitat structure and driver of plant community structure in aeolian sand habitats of the Coachella Valley (Barrows 1997; Barrows and Allen 2007a), every year and at each plot. We used a pocket penetrometer with an adapter foot for loose soils (Ben Meadows Company, Janesville, WI, USA) to measure sand compaction ($kg/cm^2$) at 25 points distributed evenly along plot midlines. Precipitation was measured with two rain gauges in relatively xeric *active dunes* and *eastern stabilized sand field* habitats, and one in a *western stabilized sand field* habitat (the most mesic habitat). Study plots were assigned precipitation values recorded by rain gauges nearest to them.

We measured annual plant cover using a one m$^2$ sampling frame placed at 12 locations along the midline of each plot. Four sampling locations were on alternating sides of the center line at each end of the plot (8 of 12 locations) and two locations were on each side of the plot center point (4 of 12 locations). We measured percent cover rather than abundance to account for size differences among individual plants. The percent cover of each plant species was visually estimated at each location. Mean cover estimates were then calculated for either individual species (mustard) or species groups (native and other exotic annual plants) for each plot in each year. The number of perennial shrubs was also recorded at each plot for each year.

Arthropods were sampled using dry, un-baited plastic pitfall traps 11 cm wide at the mouth, 14 cm deep, 1.0 L in volume, and fitted tightly with a funnel that inhibited the ability of arthropods to escape once captured. A 20 cm x 20 cm x 0.5 cm board was placed over each trap and elevated 1-2 cm with three wooden blocks. Three pitfall traps were deployed at each plot, one at each end and the third at the plot center, during each sampling occasion. Traps were typically set before sunset and checked in early morning. Contents were examined within 24 hours of trap deployment and arthropods were released alive. Specimens identified to the genus or species level were used in our analyses. Consequently, some arthropod groups, such as mites, were left out. However, individuals in these groups were impossible to count accurately because of their very small size and large numbers (in the 1000's). From these data, we summarized the relative abundance and species richness across all species at each plot during each year.

In a preliminary arthropod inventory conducted prior to 2003, arthropods were sampled with pitfall traps once a month for 10-12 months per year. Arthropod composition varied little within seasons, and abundance and species richness peaked in April–June. We therefore focused our sampling effort towards these months and restrict our inferences to species active during spring.

**Data Analysis** – We analyzed temporal trends in Sahara mustard cover and arthropod community structure using linear mixed models:

$$Y'_{ij} = \beta_0 + \beta_1 T + \varepsilon_i + \varepsilon_{ij} \quad \text{(Model 1)},$$

For these models, $Y'_{ij}$ represents a standardized measure of either relative arthropod abundance, relative arthropod richness, or mustard cover for the $i^{th}$ plot ($i = 1, \ldots, 90$) during the $j^{th}$ year ($j = 1, \ldots, 9$). $T$ represents the year (2003-2011). We included a plot-level random effect and thus accounted for two sources of error:  among-plot error ($\varepsilon_i$) and within-plot error ($\varepsilon_{ij}$). This error structure was suited to the nested structure of our data generated by repeated measurements of each plot. Within-year variance in $Y_{ij}$ varied substantially among years. We standardized $Y_{ij}$ values by dividing them by the sample standard deviation in the $i^{th}$ year, focusing models on temporal trends by removing potentially confounding effects of inter-annual variation in variances. Models were fitted using the *lmer()* function in *R* (R Core Team 2012). P-values were calculated based off of the estimation and inference assumptions in linear mixed models explained by

Fitzmaurice et al (2004). Response variables were checked for overdispersion following Zuur et al (2007). The standardized data did not exhibit overdispersion.

We then analyzed the direct relationship between mustard cover trends and arthropod metrics (abundance and richness) using a general linear mixed model of the form:

$$log(Y_{ij}) = \beta_0 + \beta_1 Mustard\_Cover + \varepsilon_i + \varepsilon_{ij} \quad \text{(Model 2)},$$

where $Y_{ij}$ represents either arthropod abundance or species richness, $\varepsilon_i$ represents residual inter-plot variation, and $\varepsilon_{ij}$ represents residual within-plot inter-annual variation (*glmer()* function in *R*; R Core Team 2012). We again checked for over dispersion in our response variables (Zuur et al 2007). We found that arthropod abundance was exhibiting a small degree of overdispersion. We, therefore, corrected our standard errors and p-values to account for overdispersion following methods described by Zuur et al (2007) by using the following equation:

$$P' = 2 * pnorm\left(\frac{Z-score}{\sqrt{\rho}}\right) \quad \text{(Equation 1)},$$

where *P'* is the new p-value that accounts for overdispersion, *pnorm()* is a function in R (R Core Team 2012) that computes the probability that a normally distributed random number will be less than that number, and Z-score is the original z-score before overdispersion correction. The overdispersion parameter, $\rho$, is calculated using *the qcc.overdispersion.test()* function in R (R Core Team 2012). New standard errors are calculated by multiplying the original standard error by $\sqrt{\rho}$ (Zuur et al 2007).

We further analyzed relationships between mustard and arthropod community metrics using generalized linear models with additional covariates representing other potential environmental drivers of community structure. These included precipitation, perennial shrub frequency, native annual cover, and sand compaction, which we expected to have negative, positive, positive, and negative relationships, respectively, with arthropod community metrics (for importance of these environmental features as drivers, *see* Barrows and Allen 2007a; Barrows et al. 2009). Both native annual cover and sand compaction are potential environmental drivers known to be influenced by mustard cover (*see* Barrows et al. 2009), and could be possible mechanistic pathways for mustard's indirect influence on the ground-dwelling arthropod community. We fit our data using a generalized linear mixed model of the form:

$$log(Y_{ij}) = \beta_0 + \beta_1 Mustard\_Cover_{ij} + \beta_2 Perennial\_Frequency_{ij}$$
$$+ \beta_3 Precipitation_{ij} + \beta_4 Native\_Annual\_Cover_{ij} + \beta_5 Sand\_Compaction_{ij} + \boldsymbol{\varepsilon_i} +$$
$$\boldsymbol{\varepsilon_{ij}}$$

(Model 3),

where $Y_{ij}$ represents either arthropod abundance or species richness, $\varepsilon_i$ represents residual inter-plot variation, and $\varepsilon_{ij}$ represents residual within-plot inter-annual variation (*glmer()* function in *R*; R Core Team 2012). We adjusted standard errors and p-values for arthropod abundance results similar to model 2 using equation 1.

Strong correlations among explanatory variables can obscure interpretation of regression parameters. We tested for such correlations by examining variance inflation factors, where a variance inflation factor greater than five indicates unacceptable levels of co-linearity between the covariates (Mendenhall and Sincich 2003). Variance inflation factors never exceeded two in our models, so we maintained all environmental variables in our analyses. In addition, there were no obvious patterns that emerged among the residuals.

We explored changes in arthropod community structure in more detail by analyzing temporal and spatial variability in arthropod rarity and occurrences. Arthropod taxa were assigned to a "rarity" subset based on the number of years observed (e.g. all nine years, eight years, etc.). We then compared the rarity subsets based on the number of years observed to both time and average mustard cover using Pearson's Correlation Coefficients (*rcorr()* function, R Core Team 2012). In addition, we calculated the number of plots occupied in each year for each species to better understand spatial changes in the arthropod community.

Finally, we examined temporal trends and relationships with mustard for individual arthropod taxa. We used univariate Poisson regression models to relate species-specific abundances with either time or mustard cover. We grouped arthropod taxa according to ecological functional guilds (detritivore, herbivore, omnivore, nectivore, or predator) and examined which guilds exhibited abundance relationships consistent with overall community patterns. Additionally, we analyzed the relationships to understand whether negative mustard relationships were associated with negative

temporal trends in abundance. We grouped arthropod taxa according to the direction of their temporal abundance trends and mustard relationships (positive versus negative) and excluded species that did not exhibit a significant ($p < 0.05$) relationship with either of these. We tested for independence in group membership using a Fisher's exact test (*fisher.test()* function, R Core Team 2012).

**RESULTS** – During the study period, we observed a positive temporal trend in mustard that was associated with negative trends in both arthropod richness and abundance. Mustard cover increased significantly ($\beta_1 = 0.079 \pm 0.023$, p<0.001; trend estimates from Model 1) during the study period from mean values of 0.58% (2003) to 9.35% (2011) across all plots (Figure 2). Furthermore, the proportion of total annual plant cover that consisted of mustard cover increased through time (Figure 3). Concurrent with this increase in mustard, arthropod abundance declined ($\beta_1 = -0.082 \pm 0.014$, p<0.001) from a mean of 44.18 (2003) to 12.39 (2011; Figure 2). Similarly, arthropod richness declined ($\beta_1 = -0.12 \pm 0.014$, p<0.001) from a mean of 8.514 (2003) to 4.54 (2011; Figure 2). When compared directly, both arthropod abundance and richness are negatively related to mustard cover ($\beta_1 = -0.049 \pm 0.005$, p' $\leq 0.001$; $\beta_1 = -0.12 \pm 0.043$, p = 0.004, respectively).

After controlling for possible confounding effects of environmental drivers other than mustard (Model 3), negative arthropod relationships with mustard continued to be apparent for both arthropod abundance ($\beta_1 = -0.049 \pm 0.0051$, p'= 0.0013) and arthropod richness ($\beta_1 = -0.03 \pm 0.002$, p = 0.067). The possible mechanistic pathways, native

annual cover and sand compaction, have significant positive relationships with arthropod richness (Model 3 $\beta_1 = 0.006 \pm 0.002$, p=0.003 and Model 3 $\beta_1 = 0.072 \pm 0.022$, p=0.001, respectively), but these do not appear to influence arthropod abundance (table 1).

The different arthropod rarity categories showed strong differences in their negative correlations with time (Figure 4) as rarer taxa were more likely to be negatively correlated than common taxa. Mustard correlations with species rarity are not significant; however, we still see that the rare species have a negative relationship with average mustard cover. The average number of plots occupied by each species in each year decreased from $4.8 \pm 0.89$ in 2003 to $3.40 \pm 0.77$ in 2011. This decreasing trend had a significant negative relationship with time (r =-0.68, one-tailed p = 0.022). When the average number of plots occupied per species is plotted together with mustard cover (Figure 5), we see occupancy drop in peak years of Sahara mustard and peak in years of low mustard cover, with the strongest relationship appearing after 2007. The correlation between plots occupied and mustard cover was marginally significant (r = -0.48, one-tailed p = 0.098).

Of the 122 arthropod taxa observed, 99 exhibited negative temporal trends (35 were significant), 23 exhibited positive trends (9 were significant), 93 exhibited negative relationships with mustard cover (20 were significant), and 29 were related positively to mustard cover (11 were significant; Table 2). Arthropod species exhibiting significant negative trends and mustard relationships consisted mainly of detritivores with inclusion of some granivores and nectivores but not predators (Table 2). Eight species exhibited positive temporal trends and mustard relationships. These consisted mainly of predators,

largely spiders and beetles (Table 2). In total, 56 species exhibited either a significant temporal trend or relationship with mustard. For this set of species, positive temporal trends tended to be associated with positive mustard relationships and negative trends with negative mustard relationships more frequently than expected by chance (table 3; $p = 0.014$; observed deviated from expected by ~3.9 species).

**DISCUSSION –** We found substantial evidence for a negative effect of Sahara mustard on the structure of a ground-dwelling arthropod community. During the study period, declines in both arthropod species richness and total abundance paralleled an overall increase in mustard cover. Arthropod species that declined in abundance tended to be those that experienced significant negative relationships with mustard more often than expected by chance. Finally, negative arthropod-mustard relationships were apparent even when controlling for other potential environmental drivers of community structure, suggesting some direct effect of mustard on arthropods.

A negative relationship between arthropod metrics and mustard was apparent even after controlling for the effects of native annual plants. We anticipated a negative relationship between mustard and ground-dwelling arthropods because of the strong negative mustard impacts on native annual plants (Barrows et al. 2009), and the importance of native annual plants as a resource base for arthropods. Native annual cover was positively related to arthropod species richness as expected. Yet, contrary to our expectations, native annual cover tended to be negatively related to arthropod abundance, albeit not strongly enough for the relationship to be statistically supported. Even though

both native annual cover and mustard cover increase simultaneously, albeit in different

proportions, the relationship between arthropod richness and mustard cover is opposite in

direction to that of richness and native annual cover. This further supports the hypothesis

that mustard is one of the factors contributing to the decline of the arthropod community

as its negative relationship remains strong even after including factors that might mask its

negative impacts. Nevertheless, when other environmental covariates were added to the

analyses, mustard cover's influence on arthropod richness decreased in strength and in

significance. This suggests these environmental covariates may contribute to the

mechanisms that are influencing arthropod richness. Mustard effects on arthropod

abundance may be more of a direct influence, while the influence of mustard on

arthropod richness may be a combination of both indirect and direct mechanisms. Thus,

from the data presented here, we have not been able to easily attribute negative impacts

of mustard and associated declines in arthropod abundance to mustard impacts on native

plants.

Native plants may still mediate mustard impacts on arthropods in ways not

observable from regression analysis. For example, arthropods may exhibit a lagged

response to declines in native annual plants, which could explain why broad mustard

impacts on arthropods were only apparent after long-term study (*contra* Barrows et al.

2009). Alternatively, other factors may mediate negative impacts of mustard on

arthropods or contribute to arthropod declines. Arthropods were also related with

precipitation and sand compaction after controlling for relationships with mustard and

native annual plants, so the role of these drivers in mediating arthropod declines and negative relationships with mustard would be of further interest.

Aside from direct competitive effects on native plant diversity, mustard also influences native plant communities, and consequently food resources for arthropods, by altering the physical structure of the landscape. The excessive biomass created by Sahara mustard can stabilize the sand surface (Hart et al. 2012) and alter habitat structure. Arid landscapes in southwestern North America experience reduced sand transport rates when highly vegetated (Lancaster and Baas 1998, Reinhardt et al. 2010, Munson et al. 2011), and vegetation growth, driven by increased precipitation, appears to explain transitions between active and stabilized states of arid aeolian landscapes. In coastal dunes, stabilization by invasive plants (particularly *Ammophila* grasses) has long been recognized as a core threat to biodiversity and ecosystem function (Wiedemann and Pickart 1996, Hacker et al. 2012, Hart et al. 2012). Interestingly, ground-dwelling arthropods in this study were positively related with sand compaction after controlling for effects of mustard and precipitation. Non-invaded annual plant communities are richer and provide more standing biomass in stabilized sand habitats (i.e., *eastern stabilized sand fields*, *stabilized dunes*, and *western stabilized sand fields*), which may benefit arthropods. If arthropods benefit from stabilization via this pathway, mustard invasion should counter-act the benefits of sand stabilization. The overall negative mustard relationship with arthropods found here would be consistent with this hypothesized relationship between sand compaction and ground-dwelling arthropod diversity.

We also see that we are losing rare species through time. However, the trend of the total number of species observed is not significantly related with average mustard. Mustard is highly variable between plots, and when we average mustard cover, we may lose the ability to predict trends since rare species may be only disappearing on heavily invaded plots. Additionally, we see species becoming rarer (occupying less plots) within the landscape, and this trend loosely follows mustard cover through time. Mustard cover may reduce habitability of plots as well as reduce access from neighboring plots by colonizers. Reduced native annual cover and above ground structural changes may operate in concert to inhibit dune arthropod populations and limit diversity. Both trophic and habitat structural impacts of plant invasions on particular insect communities have been observed, resulting in reduced detritivore foraging rates (Srivastava 2006) and changes in predator hunting efficiency (Denno et al. 2002, Finke and Denno 2002, Pearson 2009).

When examined individually, the majority of arthropod taxa decreased through time and had a negative relationship to mustard cover. Many of the arthropods in the Coachella Valley aeolian desert ecosystem are detritivores and seed predators (Ayal et al. 2005, Barrows 2012).The species that were negatively related to both time and mustard cover were largely detritivores whereas predators tended to be positively related to mustard. Dead mustard may not readily disarticulate into fine particles of detritus and may instead maintain its standing structure for long periods. Thus, the size and structure of mustard detritus may be creating an ideal hunting space for some generalist predators. However, most of the arthropod taxa that were positively related with mustard cover were

still decreasing with time. A recent study by Engelkes et al. (2012) found that invasive plant species harbored greater arthropod predator pressure on arthropod herbivores than native plants. This effect may help explain why we are observing a positive relationship between mustard and predators and a negative relationship with detritivores and herbivores. The increased aboveground biomass arising from mustard invasion may also physically impede arthropod movement (Crist and Wiens 1994, Shelef and Groner 2011) or change habitat selection cues.

Diverse native plant assemblages may provide a mix of essential nutrients or other resources not available in monotypic mustard stands, causing a decline in species richness. Dead mustard may not readily disarticulate into fine particles of detritus and may instead maintain its standing structure for long periods, leaving less food for detritivores. Additionally, chemical defenses may make mustard unpalatable to many native arthropods that have not encountered such defenses during their evolutionary histories. Our observations suggested low abundance of native phytophagous insects on mustard at our study sites (C. Barrows personal observation). In contrast, two non-native species, a Homopteran (an aphid) and a Hemipteran (*Bagrada hilaris*) were commonly observed on mustard and at heavily invaded plots. *Bagrada hilaris* is indigenous to the same region of North Africa and the southern Mediterranean where Sahara mustard originated, and therefore may be especially adapted for taking advantage of food resources provided by mustard. A pilot experiment with a saprophagous tenebrionid beetle failed to find differences in beetle survival or maintenance of mass when fed native

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versus mustard detritus (Simon et al., unpublished data), but additional studies are required to fully address this issue.

We did not account for spatial or temporal variation in detectability, which can influence measurements of diversity and abundance (Kéry et al. 2009, Kéry and Royle 2010). Reduced movement of arthropods could diminish detectability by reducing the chances of arthropods encountering traps, which in return may inflate apparent negative effects on arthropod diversity and abundance. Nevertheless, if mustard does impede arthropod movement, negative impacts on arthropod fitness are likely to occur along with any effects mustard might have on detectability via pitfall traps. However, pitfall traps were never covered by or even touched any vegetation as that would potentially offer an arthropod a "ladder" to climb out of the pitfall. The pitfall traps were always set to have open ground on all sides (360° access), but were set near vegetation so an arthropod could easily move from the cover of the vegetation to the pitfall trap. Estimation of arthropod detectability and examination of the factors that influence arthropod mobility would further inform interpretation of the results from this study.

Our results suggest some potential directions for a future study of mechanisms underlying mustard impacts on arthropods. Specifically, researchers should consider impacts via changes in trophic structure and physical aspects of the environment. Understanding system-wide impacts of invasive species on native biodiversity is critical for informing land management decisions and directing limited funding to maximize conservation objectives (Barrows and Allen 2007b). Mustard cover appears to influence both community structure and the amount of spatial coverage by arthropod taxa. Our data

suggest that the invasion of mustard negatively impacts the arthropod community across multiple aeolian sand habitats within the Coachella Valley, and a better understanding of the mechanisms responsible may help mitigate mustard impacts.

**FIGURES –**
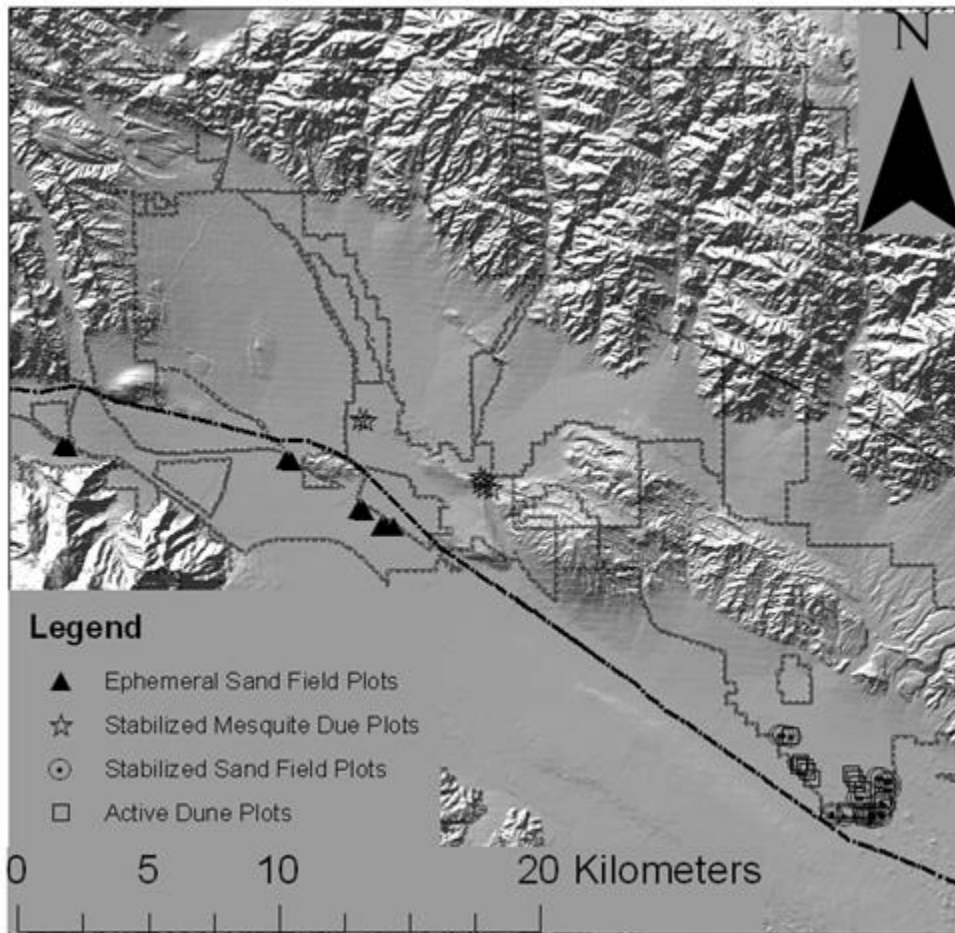


Figure 1: Map of the study site.
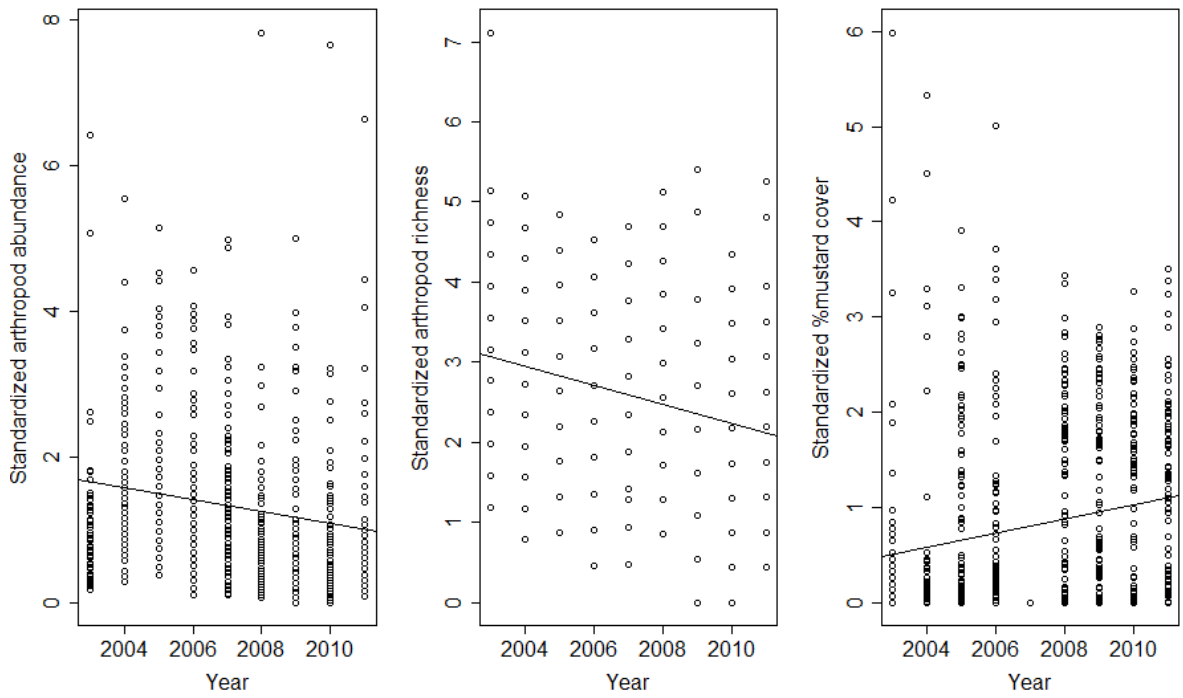
Figure 2: Temporal trends in percent mustard cover, arthropod abundance, and arthropod richness throughout the study area. Dots represent standardized values (raw values divided by within-year sample standard deviations) for each observation. Solid lines depict temporal trends estimated by regression models.
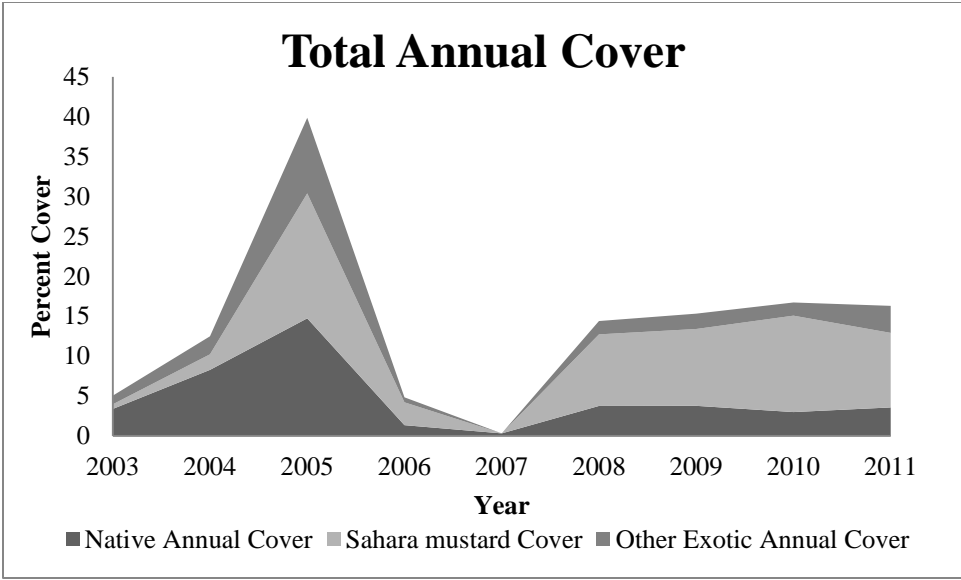
**Total Annual Cover**

Figure 3:  Contributions of constituent annual vegetation categories to total yearly mean annual plant cover.

Exotic annual cover includes all annual exotic species other than mustard.
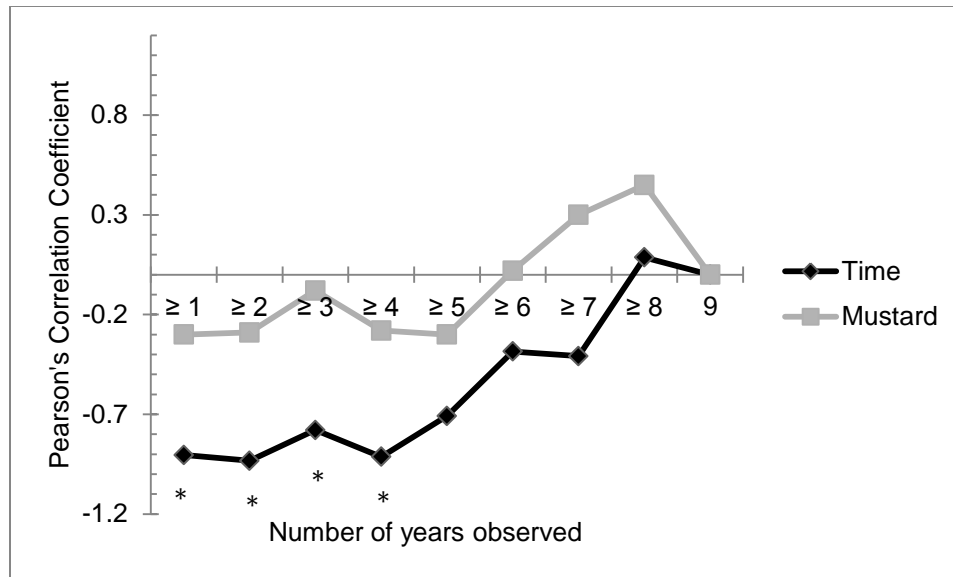
Figure 4: Rarity influences trends in species richness. Pearson's correlation coefficients *r* for relationships between richness and time are compared across subsets of the data defined by rarity. "Number of years observed" refers to the number of years a species needed to be observed in order to be included in the data subset. For example, a species in the "≥ 7" category could have been observed in 7, 8, or all 9 of the sampling years. For the "9" category, only species that were seen every year were included in the analyses. Asterisks denote correlations that were significant.
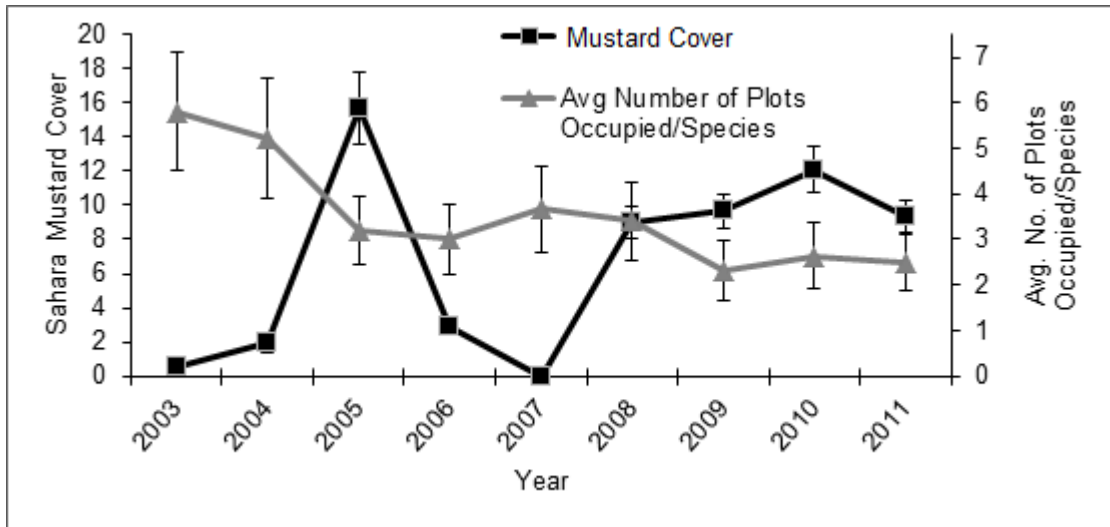
Figure 5:  Mean Sahara mustard cover plotted against the average number of plots a species occupied

through time. Error bars represent standard error.

# TABLES –

Table 1:  Regression parameters (β ± s.e.) from the multivariate model with mustard cover and other potential environmental drivers of arthropod community structure as predictor variables (Model 3).

| | Model 3 | |
| --- | --- | --- |
| | Arthropod Abundance[†] | Arthropod Richness |
| *Mustard Cover* | -0.016 ± 0.005 * | -0.003±0.002 · |
| *Perennial Frequency* | 0.004 ± 0.002 | -0.001±0.001 |
| *Precipitation* | -0.001 ± 0.001 | -0.001±0.000 *** |
| *Native Annual Cover* | -0.01 ± 0.007 | 0.006±0.002 ** |
| *Sand Compaction* | 0.063 ± 0.081 | 0.072±0.022 ** |

[†] Results are adjusted for overdispersion

*** α≤0.001        **  α≤0.01        * α≤0.05              · α≤0.10

Table 2: Relationships between arthropod taxa and time and mustard as determined by generalized linear models. The arthropod taxa are grouped by the direction the estimated slopes have with time and mustard cover.

| Species | Guild | Common Guild | Temporal Trend | Mustard Relationship |
|---|---|---|---|---|
| *Messor pergandei* | Granivore | Ant | -0.051 ± 0.02 | -0.112 ± 0.013 *** |
| *Myrmecocystus kennedyi* | Nectivore | Ant | -0.131 ± 0.015 *** | -0.016 ± 0.004 *** |
| *Myrmecocystus tenuinodis* | Nectivore | Ant | -0.094 ± 0.025 *** | -0.103 ± 0.014 *** |
| *Pogonomymex magnacanthus* | Granivore | Ant | -0.406 ± 0.018 *** | -0.037 ± 0.005 *** |
| *Crematogaster opuntiae* | Detritivores | Ant | -0.007 ± 0.083 | -0.862 ± 0.398 * |
| *Dorymyrex spp.* | Omnivore | Ant | -0.009 ± 0.026 | -0.131 ± 0.02 *** |
| *Forelius pruinosus* | Omnivore | Ant | -0.039 ± 0.042 * | -0.387 ± 0.091 *** |
| *Pheidole barbata* | Detritivore | Ant | -0.003 ± 0.024 | -0.173 ± 0.024 *** |
| *Pheidole psammophila* | Detritivore | Ant | -0.005 ± 0.162 * | -0.283 ± 0.218 |
| *Solenopsis xyloni* | Detritivore | Ant | -0.01 ± 0.075 | -0.101 ± 0.04 * |
| *Solenopsis aurea* | Detritivore | Ant | -0.006 ± 0.193 * | -0.063 ± 0.054 |
| *Niptus venticulus* | Detritivore | Beetle | -0.009 ± 0.023 | -0.02 ± 0.007 ** |
| *Cymatodera punctata* | Detritivore | Beetle | -0.002 ± 0.436 * | -0.094 ± 0.129 |
| *Sibinia spp.* | Herbivore | Beetle | -0.003 ± 0.39 * | -0.305 ± 0.336 |
| *Trigonoscuta imbricata* | Detritivore | Beetle | -0.005 ± 0.078 * | -0.035 ± 0.025 |
| *Corticaria spp.* | Detritivore | Beetle | -0.004 ± 0.243 ** | -0.528 ± 0.497 |
| *Catops spp.* | Detritivore | Beetle | -0.002 ± 3500 * | -0.148 ± 0.236 |
| *Trichocrus spp.* | Detritivore | Beetle | -0.002 ± 0.293 * | -0.116 ± 0.132 |
| *Cysteodemus armatus* | Herbivore | Beetle | -0.007 ± 2100 * | -2.167 ± 1.645 |
| *Eupompha spp.* | Detritivore | Beetle | -0.002 ± 0.293 * | -0.014 ± 0.052 |
| *Asidina confluens* | Detritivore | Beetle | -0.005 ± 0.144 | -0.063 ± 0.049** |
| *Batulius setosus* | Detritivore | Beetle | -0.092 ± 0.024 *** | -0.015 ± 0.006 * |
| *Chilometopon abnorme* | Detritivore | Beetle | -0.008 ± 0.055 | -0.011 ± 0.014* |
| *Chilometopon brachystomum* | Detritivore | Beetle | -0.017 ± 0.045 * | -0.085 ± 0.022 *** |
| *Chilometopon pallidum* | Detritivore | Beetle | -0.027 ± 0.161 *** | -0.5 ± 0.203 * |
| *Edrotes barrowsi* | Detritivore | Beetle | -0.001 ± 0.035 | -0.057 ± 0.014 *** |
| *Edrotes ventricosus* | Detritivore | Beetle | -0.341 ± 0.014 *** | -0.036 ± 0.004 *** |
| *Eupsophulus castaneus* | Detritivore | Beetle | -0.004 ± 0.115 | -0.142 ± 0.085* |

| Species | Guild | Common Guild | Temporal Trend | Mustard Relationship |
|---|---|---|---|---|
| *Notibius puberulus* | Detritivore | Beetle | -0.075 ± 0.02 *** | -0.001 ± 0.004 |
| *Telabis aliena* | Detritivore | Beetle | -0.015 ± 0.098 *** | -0.119 ± 0.049 * |
| *Loxosceles spp.* | Predator | Spider | -0.003 ± 0.455 ** | -0.123 ± 0.14 |
| *Smeringurus mesaensis* | Predator | Other Arachnid | -0.011 ± 0.241 *** | -0.108 ± 0.062 |
| *Vaejovis spp.* | Predator | Other Arachnid | -0.012 ± 0.07 *** | -0.003 ± 0.015 |
| *Tetragonoderus pallidus* | Predator | Beetle | 0.0545 ± 0.03 *** | 0.037 ± 0.004 *** |
| *Araeoschizus hardyi* | Detritivore | Beetle | 0.005 ± 0.018 | 0.017 ± 0.003 *** |
| *Eleodes armata* | Herbivore | Beetle | 0.011 ± 0.074 ** | 0.008 ± 0.013 |
| *Embaphion depressum* | Detritivore | Beetle | 0.003 ± 0.163 * | 0.045 ± 0.016 ** |
| *Tarsonops spp.* | Predator | Spider | 0.036 ± 0.033 *** | 0.018 ± 0.006 *** |
| *Syspira spp.* | Predator | Spider | 0.009 ± 0.050 | 0.021 ± 0.008 ** |
| *Psilochorus spp.* | Predator | Spider | 0.089 ± 0.016 *** | 0.019 ± 0.016 |
| *Steatoda triangulosa* | Predator | Spider | 0.005 ± 0.197 ** | 0.015 ± 0.003 *** |
| *Mecynotarsus delicatulus* | Detritivore | Beetle | 0.014 ± 0.089 | -0.064 ± 0.03 * |
| *Asbolus laevis* | Detritivore | Beetle | 0.023 ± 0.009 | -0.02 ± 0.003 *** |
| *Callilepis spp.* | Predator | Spider | 0.001 ± 0.076 | -0.086 ± 0.039 * |
| *Dermacentor spp.* | Predator | Other Arachnid | 0.17 ± 0.036 ** | -0.059 ± 0.009 *** |
| *Pogonomyrmex califonricus* | Granivore | Ant | -0.483 ± 0.005 * | 0.01 ± 0.001 *** |
| *Calosoma spp.* | Predator | Beetle | -0.009 ± 0.111 ** | 0.058 ± 0.009 *** |
| *Calosoma pravicollis* | Predator | Beetle | -0.02 ± 0.075 *** | 0.03 ± 0.009 ** |
| *Ophryastes desertus* | Herbivore | Beetle | -0.008 ± 0.06 * | 0.006 ± 0.012 |
| *Asbolus verrucosa* | Detritivore | Beetle | -0.025 ± 0.031 * | 0.002 ± 0.007 |
| *Cheriodes celifornica* | Detritivore | Beetle | -0.021 ± 0.072 *** | 0.033 ± 0.008 *** |
| *Cryptoglossa muricata* | Detritivore | Beetle | -0.124 ± 0.062 * | 0.014 ± 0.011 |
| *Oonops spp.* | Predator | Spider | -0.009 ± 0.121 ** | 0.001 ± 0.024 |
| *Scopoides spp.* | Predator | Spider | -0.006 ± 0.141 ** | 0.002 ± 0.005 |
| *Steatoda fulva* | Predator | Spider | -0.062 ± 0.025 *** | 0.039 ± 0.017 * |
| *Averivaga spp.* | Predator | Other Arachnid | -0.017 ± 0.042 ** | 0.004 ± 0.009 |

*** α≤0.001      ** α≤0.01      * α≤0.05           · α≤0.10

Table 3: Summary of the direction of regression parameters for arthropod taxa with time and mustard cover. Only arthropod taxa with significant parameters at the α≤0.05 are included. Expected cell frequencies are reported in parentheses. A test of independence (Fisher's exact test) fund cell frequencies to deviate significantly from expected frequencies (p = 0.014).

| Arthropod Taxa & Time | Arthropod Taxa  & Mustard | | |
|---|---|---|---|
| | *Relationship* | *Positive* | *Negative* |
| | *Positive* | 8 (4.1) | 4 (7.9) |
| | *Negative* | 11 (14.9) | 33 (29.1) |

**CHAPTER 2: POST-FIRE SPATIAL HETEROGENEITY ALTERS GROUND-DWELLING ARTHROPOD AND SMALL MAMMAL COMMUNITY PATTERNS IN A DESERT LANDSCAPE EXPERIENCING A NOVEL DISTURBANCE REGIME**

*Co-authors – Cameron Barrows and Kurt Anderson*

**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.

*Keywords* – Small mammals, ground-dwelling arthropods, spatial heterogeneity, habitat fragmentation, novel disturbance regimes, fire, arid environments

**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, 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 2005). 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 et al. 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

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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.

**MATERIALS AND METHODS** – Our study site is located in the northwestern region of California's Joshua Tree National Park (Figure 6) 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, 8.38mm, 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.

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 4 and Figures 7a-7e 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$^2$, making them large enough to fit a sampling plot (described in 2.2 Data Collection).

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 1988). We defined "close" burned habitats as burned habitats within the lifetime dispersal distance of kangaroo rats (300m, 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 (600m, Jones 1989). In the 1995 burn, all habitats sampled were defined as either "close" and ranged from 150m to 300m form the burn/unburned edge or "far" (isolated) and ranged from 600m to 750m 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 25m to 175m 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.

**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-meter transects in each habitat type and ten 50-meter 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 x 20 cm x 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 $2 \times 2$ 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 $3'' \times 3.5'' \times 9''$). For each sampling plot, we set traps 8-10 m apart in a $5 \times 2$ 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 Data Analyses). 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.

**Data Analyses** –We classified vegetation as invasive grass species, ephemeral plant species (annuals), quick-growth, short-lived perennials, or slow-growth, long-lived

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perennials. 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 $\alpha \le 0.05$ 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 arthropods and small mammal metrics. We then ran post-hoc multiple

comparison tests following Siegel and Castellan's (1988) methods to determine which

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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. We ran three different MRPP tests for each taxon in each burn by categorizing habitats by their habitat type (Table 4), 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).

**RESULTS –** Long-lived perennial vegetation cover was highest in unburned habitats, and litter cover was highest in burned habitats for both burns at the $\alpha \leq 0.05$ (Figures 3a, 3b). 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 5). Invasive species had a significant positive association with burned habitats

without remnant vegetation in the 2006 burn (Indicator Species Analysis; p = 0.022; Table 5).

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; Figures 9a, 9b). 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, Figure 8a) and the 1995 burn (Kruskal-Wallis rank sum test; p = 0.0002; Figure 8b). 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 α ≤ 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 α ≤ 0.05 (Figures 9a, 9b).

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 6). Arthropod compositional differences were mainly driven by the families Scarabaedae (scarab 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). Pholcidaes (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 α ≤ 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 6). 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, respectfully; Figures 9c, 9d), 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 ≤ 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 $\alpha \leq 0.05$ (Figure 8d). 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 (Figure 8d); 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 6). *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 6) and whether the site was burned or unburned (MRPP results; $p = 0.067$; Table 6). *Dipodomys merriami* (generalist granivore), *Onychomys 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

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a significant positive association with isolated burned habitat that does not contain remnant habitat patches (Indicator Species Analysis; p = 0.003; Table 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. 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.

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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. 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). Arthropod family richness and composition were influenced by a combination of distance to unburned habitat and/or perennial vegetation presence in all burned habitats. 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. 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. Detritivores may respond to an increase in their food source (litter coverage), and Pholcidae (a sit-and-wait spider), may 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 et al. 2000).

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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. 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. 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

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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. 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 (Figure 8c). 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. 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. A less common mammal species, *Peromyscus 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). *Peromyscus 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.

**FIGURES –**
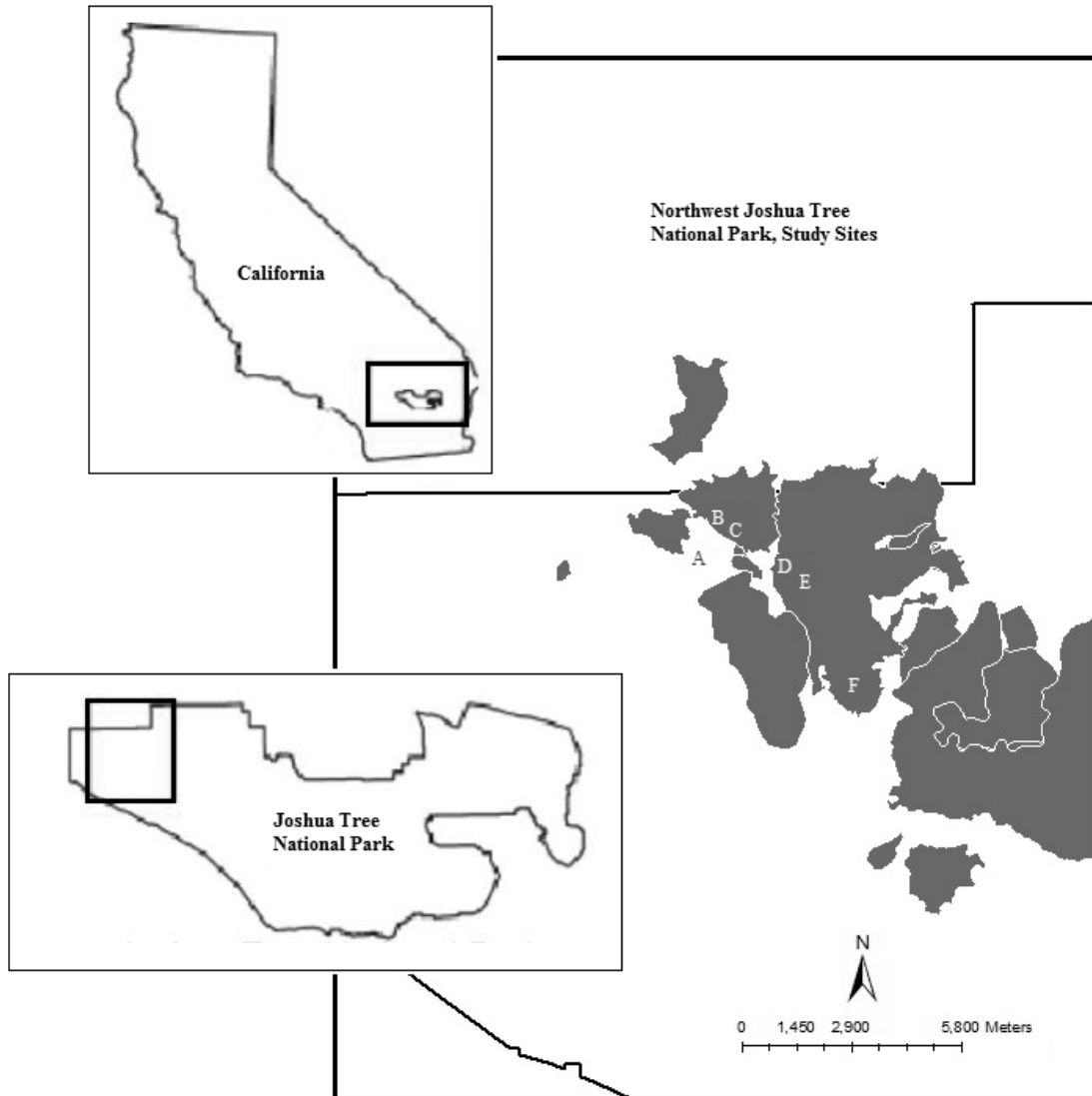


Figure 6: Map of study site in reference to California. Dark sections represent burned habitats. Letters represent habitat type as follows: A) Unburned habitat, B) 2006 Burned habitat without remnant vegetation, C) 2006 Burned habitat with remnant scattered vegetation, D) 1995 Burned habitat that is close to the unburned habitat without remnant vegetation, E) 1995 Burned habitat that is isolated from the unburned habitat without remnant vegetation, F) 1995 Burned habitat that is isolated from the unburned habitat with remnant patches.
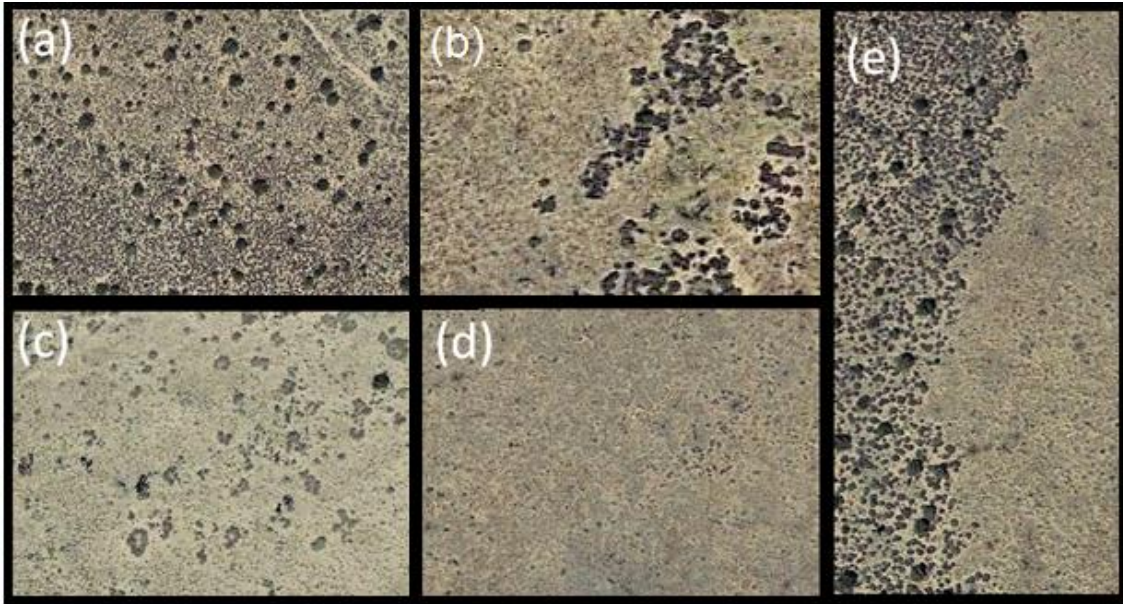
Figures 7a-7e: Aerial photographs of varying types of habitat heterogeneity, described at the amount, clustering, and relative isolation of perennial vegetation, at our study locations. Darker vegetation is long-lived perennial vegetation. The above photographs represent (a) Unburned habitat, (b) burned 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).
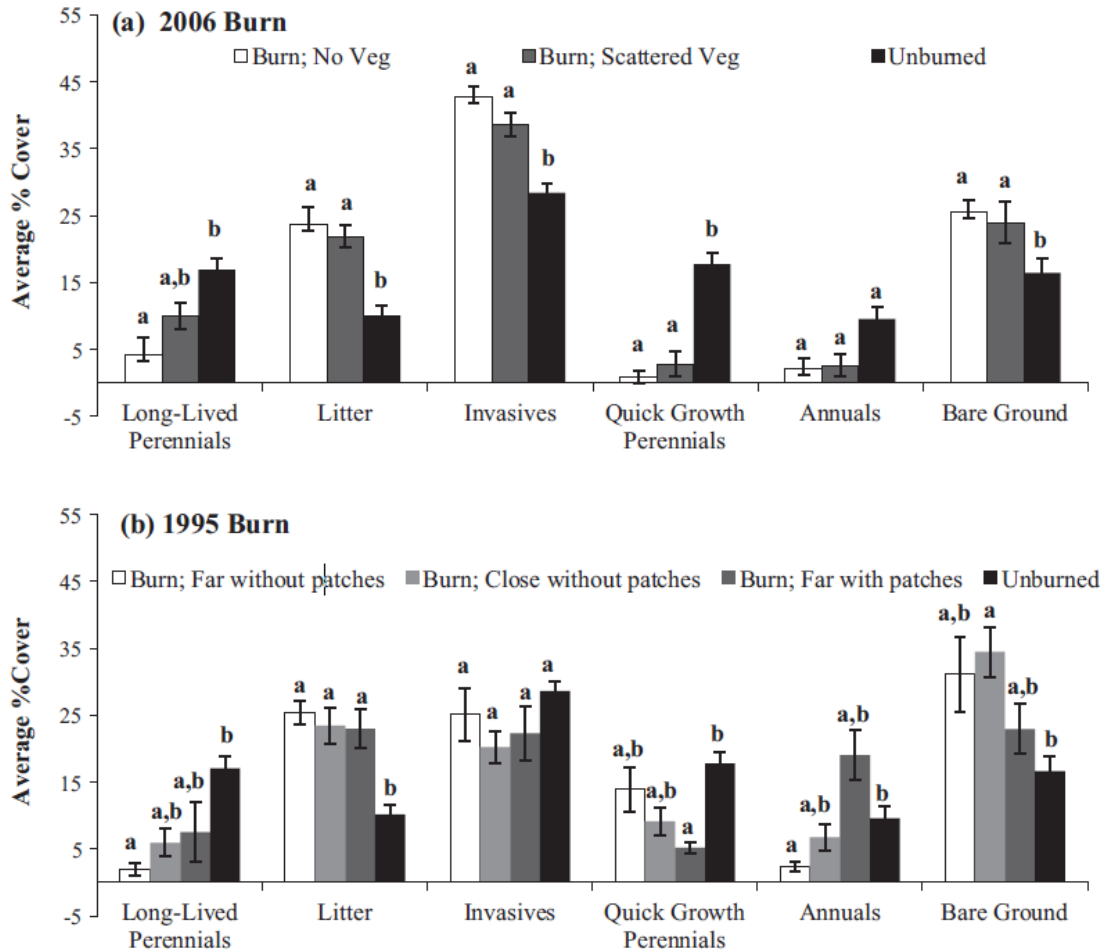
Figures 8a-8b: Vegetation type mean percent cover by burn year. Vegetation type differs among habitat types within the 2006 burn (a) and within the 1995 burn (b), particularly long-lived perennials and litter cover for both burns. Significant differences between habitats is assessed at the $\alpha \leq 0.05$ level based on a post-hoc multiple comparison test following Siegel and Castellan's (1988) methods. Error bars represent one standard error.
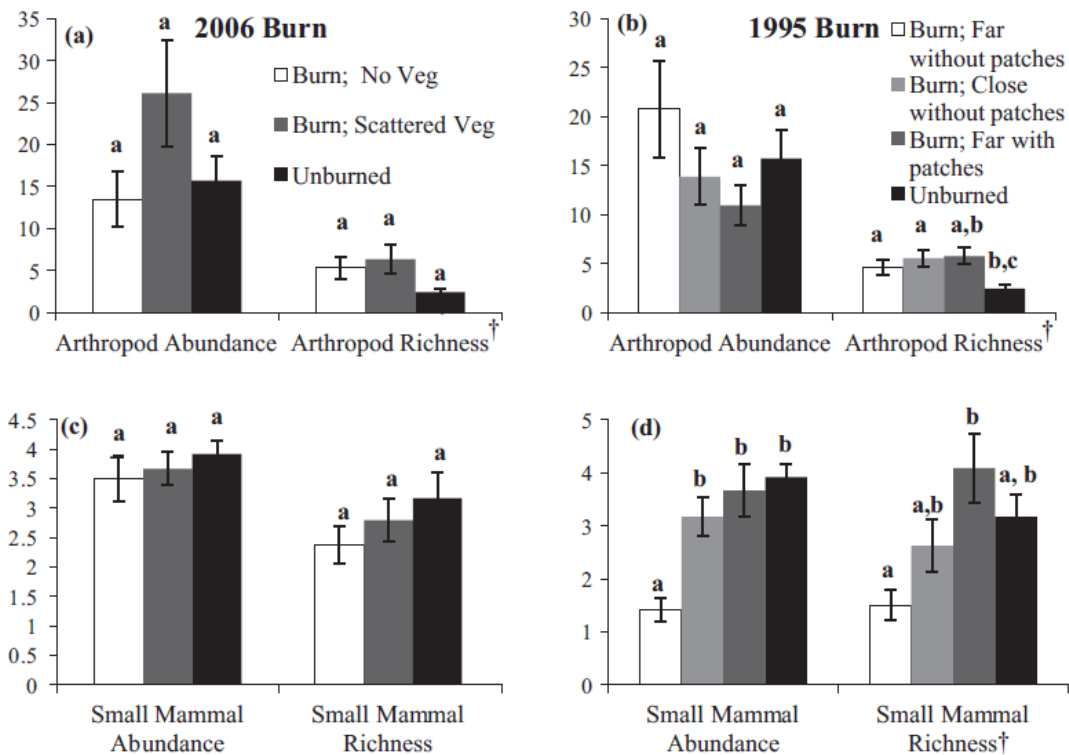
Figures 9a-9d: Mean richness and abundances for arthropods (a,b) and small mammals (c,d) in the 2006 burn (a,c) and 1995 burn (b,d). Richness levels are corrected for detectability using a jack-knife estimator (Colwell and Coddington 1994; Palmer 1990). Results differ more by taxonomic group than by 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 995 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.

## TABLES –

Table 4: Description of burned habitat types in the 2006 burn (a) and the 1995 burn (b). See Figures 6 and

7a-7e for visual representation of habitat types.

| (a)  2006 Burn (401 ha) | |
| --- | --- |
| Habitat Type | Description of Burned Habitats |
| 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 25m and 175m 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 25m and 175m from unburned habitat. |
| (b)  1995 Burn (2,234 ha) | |
| 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 $m^2$– similar in size to the sampling plots. These habitats are considered relatively isolated from unburned habitat, being between 600 and 750m from any unburned area. Arthropod and small mammal sampling only took place within the burned habitat. |
| Burned; Far (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 750m 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 150-300m to unburned area. |

Table 5: 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 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≤0.001;     ** p≤0.01;     * p≤0.05;     † p≤0.10

Table 6: 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 3 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 habit 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 | |
|---|---|---|---|
| 2006 Burn | | | |
| <u>Comparison</u> | <u>A</u> | <u>Comparison</u> | <u>A</u> |
| *Habitat Type* | 0.012 | *Habitat Type* | 0.048 * |
| *Burned-Unburned* | -0.004 | *Burned-Unburned* | 0.015 |
| *Perennials Presence* | 0.018 † | *Perennials Presence* | 0.024 * |
| 1995 Burn | | | |
| <u>Comparison</u> | <u>A</u> | <u>Comparison</u> | <u>A</u> |
| *Habitat Type* | 0.038 * | *Habitat Type* | 0.086 *** |
| *Burned-Unburned* | 0.017 † | *Burned-Unburned* | 0.028 ** |
| *Perennials Presence* | 0.011 | *Perennials Presence* | 0.011 † |

*** $p \leq 0.001$;    ** $p \leq 0.01$;    * $p \leq 0.05$;    † $p \leq 0.10$

# CHAPTER 3:  ALTERED MOVEMENT PATTERNS OF MERRIAM'S KANGAROO RAT, DIPODOMYS MERRIAMI, BASED ON SPATIAL COMPLEXITY IN POST-FIRE LANDS IN JOSHUA TREE NATIONAL PARK

*Co-author – Kurt Anderson*

**ABSTRACT –** Habitat loss and fragmentation are the leading causes of biodiversity loss and are considered to be the principal threats to the sustainability of the biosphere. Habitat fragmentation has been shown to alter many ecological processes, including shifts in animal movement patterns, resulting in particularly severe consequences. Understanding how habitat fragmentation influences movement and habitat use is critical for ecological understanding of long-term consequences of the negative impacts of disturbances in order to provide sound species conservation management within fragmented landscapes. We examined the effects of post-fire spatial complexity of burned landscapes (amount of remnant vegetation) on the influence of seasonal and daily movement patterns of Merriam's kangaroo rat, *Dipodomys merriami*, in Joshua Tree National Park. We found that Merriam's kangaroo rat increased seasonal movement patterns within habitats that are considered more spatially complex (i.e. more habitat heterogeneity). Furthermore, our data suggest that this species may increase territory size as habitat spatial complexity increases. We did not find any differences in daily movement patterns associated with post-fire spatial complexity. From a conservation view point, we highly recommend the revegetation of burned habitats to promote an

increase *D. merriami* movement, which could ultimately increase the dispersal distance of seeds to provide a faster recovery within post-fire lands.

**INTRODUCTION –** Habitat loss and fragmentation are the leading causes of biodiversity loss (Wilcove et al. 1998) and are considered to be the principal threats to the sustainability of the biosphere (Balmford and Bond 2005). Habitat loss and fragmentation create a general pattern of biological degradation and negatively affect species persistence mainly through the reduction in the amount of native habitat, an increase in isolation among remnant patches, and an increase in edge effects (Laurance et al. 2002; Fahrig 2003; Kupfer et al. 2006). Furthermore, many studies have found that remnant habitat fragments support fewer specialist species with an increase in widespread generalist species (Harrison and Bruna 1999; Bender et al. 2003; Fahrig 2003; Matthews et al. 2014).

A generalist species has fewer habitat requirements specialized adaptations than does a specialist species. Consequently a generalist has a higher potential for success in a greater variety of environments (Futuyma and Moreno 1998; Southwood 1988; Foufopoulos and Ives 1999). The remaining abundance and spatial arrangement of species after a disturbance can influence community succession trajectories (Turner et al. 1998). Given the importance of post-disturbance remnant species and the relative success of generalist species in fragmented landscapes, it's is becoming increasing critical to study the response of generalist species to habitat fragmentation. Habitat fragmentation has been shown to alter many ecological processes, including nutrient and sediment flow

in riparian ecosystems, plant dispersal, plant community dynamics, plant and animal reproduction, and animal movement patterns (summarized in Collinge 2000).

Animal movement patterns can provide insight into foraging decisions, space use, home range, spatial distributions of populations, and community interactions (summarized in Crist et al. 1992). Movement patterns have also been shown to influence population, community, and ecosystem composition and functioning via altering the genetic and demographic composition of populations, the spread of diseases and parasites, and the energy flow and nutrient transfer (*summarized in* McIntyre and Wiens 1999). Because of this, shifts in animal movement patterns are thought to produce particularly severe consequences, and understanding how habitat fragmentation influences movement and habitat use is central for both ecological understanding and species conservation within fragmented landscapes (Ims et al. 1993; Andreaseen et al. 1998).

Spatial heterogeneity within fragmented landscapes can influence movement patterns, altering dispersal rates and foraging behaviors (Milne et al. 1989). Fragmentation of terrestrial landscapes often turns the landscape into a complex mosaic of multiple land cover types. However, the movement patterns, behavior, and habitat use can be altered based on the spatial pattern of the mosaic (habitat heterogeneity) and landscape structure (Said and Servanty 2005). Furthermore, patchy environments have been shown to alter habitat use due to heterogeneity in resource availability (Milne et al. 1989) or interactions with other individuals via predation or reproduction (Weins 1992).

Thus, understanding how animal movement patterns are affected by heterogeneity within

fragmented landscapes is critical for long-term conservation and land-use planning.

In the Mojave Desert, wildfire was non-existent or exceedingly rare prior to

recent times (Brooks et al. 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). This

altered fire regime has left a patchwork of burned and unburned habitat patches which

creates a natural experiment to test the influence of spatial structure on animal movement

patterns within a fragmented landscape. Thus, we aimed to answer the following

questions: 1) does spatial structure influence seasonal movement patterns and space-use

of a generalist species and 2) does spatial structure influence daily movement patterns

and space-use of a generalist species. Our study consisted of three types of spatially

structured habitats (unburned habitat; burned habitat with remnant patches; burned

habitat without remnant patches). We hypothesized that as the amount of long-lived

perennial vegetation (consistent food source) was reduced, then the both seasonal and

daily movement patterns would increase in distance. Thus, we expected to find that the

unburned habitat would have relatively small movement patterns while the burned habitat

without remnant patches would have relatively large movement patterns, and the burned

habitat with remnant patches would have medium distance movement patterns due to the

necessity of finding food resources.

For our study, we used a generalist small mammal, Merriam's kangaroo rat

(*Dipodomys merriami*) as our focal species. *D. merriami* is a small rodent of the family

Heteromyidae, and is a solitary, nocturnal, burrow-dwelling small mammal, widespread throughout the arid southwest of North America (Behrends et al. 1986). They are known to succeed equally well on sandy soils, clays, gravels, and even among rocks. They also are characterized by long survival with documented life spans of at least 3.5 years (Zeng and Brown 1987). *D. merriami* and other 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. *D. merriami* feeds primarily on seeds, and seed depredation by desert small mammals has shown to significantly influence ecosystem structure and dynamics (Brown and Heske 1990; Hoffmann et al. 1995; Longland 2007; Montiel and Montana 2003). Furthermore, small mammals are relatively easy to mark and recapture through the use of PIT-tags, making them ideal candidates for documenting the effects of habitat fragmentation on movement patterns.

**MATERIALS AND METHODS –** Our study site is located in the northwestern region of California's Joshua Tree National Park (Figure 10) 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).

In order to understand the post-fire effects of spatial structure on *D. merriami's* movement patterns, we monitored movement in three habitat types that varied in spatial vegetation structure: 1) unburned habitat, 2) burned habitat with remnant patches, and 3) burned habitat without remnant patches. We classified the unburned habitat as a large expanse of undisturbed habitat that was the size of the burn in our study, 2,234 ha. Both burned habitats were located in a burn that took place in 1995. Within the burn, there are sections where it burned completely, and there were sections where there are remnant patches of vegetation leftover. Therefore, within the burn, we had two habitat types. One burned habitat had no remaining vegetation after the burn, and all vegetation within the burned habitat was considered regrowth. The second burned habitat had remnant patches left over within the burned area. Remnant patches were defined as possessing dense clusters of remnant, long-lived perennial vegetation that were at least 200 m$^2$. The burned habitats were considered relatively far (isolated) from unburned habitats, being between 600 and 750m from any unburned area and from the other burned site; this distance was considered far (isolated) from the unburned habitat as it was at least twice the lifetime dispersal distance of *D. merriami* from the edge of all other habitats (600m, Jones 1989).

**Seasonal Movement Patterns Data Collection** – We surveyed *D. merriami* using perforated Sherman live-traps (model LFATDG-P 3″ × 3.5″ × 9″). Within all three habitats, we set up a sampling grid of 14 traps by 11 traps spaced approximately 15m

apart. At each trap location, we recorded the plant species (when applicable) where the trap was located. For each habitat grid, we sampled half of the grid at a time due to logistical constraints, and we sampled the second half the following week. We sampled each half-grid five times, making ten captures the maximum number of times an individual could be captured in each habitat. Each habitat's grid consisted of 154 traps, totaling 2310 traps•nights. Trapping took place between April 2013 and July 2013. Full moon effects on small mammal activity (Price et al. 1984) were avoided by suspending sampling on weeks with full moons.

At the time of capture, we recorded age, sex, and location of each individual; we inserted an 8.5mm microchip under the skin between the shoulder blades using a sterilized needle provided by BIOMARK ® and recorded microchip number (PIT tags). At each subsequent trapping, we recorded trap location after microchip identification. In a study by Williams et al. (1997), it was determined that the PIT-tag method has a low marking loss rate, a low misreading rate, and it took the least amount of time to identify marked individuals when compared to ear-tagging, tattooing, and cheek-pouch tags. This efficiency reduces the amount of stress to the animal due to a short handling time. In addition, no infections or other pathology was related with PIT tags, while cheek and ear tags were related to a high association with infections and injuries from the tags (Williams et al. 1997).

**Daily Movement Patterns Data Collection** – In order to understand daily movement, we used a fluorescent powder tracking technique. We placed an individual into a plastic

bag with non-toxic fluorescent pigment and gently shook the bag and released the individual. The individual left behind a fluorescent trail when moving. The following night, we followed the fluorescent trail using an ultraviolet light and protective eye wear. We placed a flag at every turn and at every meter mark to allow for adequate mapping the following day as described in Lemen and Freemen (1985). We recorded turn angels and distance per turn traveled. In addition, we recorded distance to burrow and foraging behavior whenever possible. We followed 30 individuals from each habitat type; however, we decided to analyze adult *D. merriami* only as we were unable to get large enough sample sizes of juveniles in one trap night. We had 25, 29, 28 adults for the unburned habitat, the burned habitat with remnant patches, and the burned habitat without remnant patches, respectively.

**Seasonal Movement Patterns Data Analysis** – We checked for differences in the proportion of males to females and juveniles to adults captured among habitats using chi-squared tests. In order to test for possible influences of vegetation type of capture rates, we calculated the number of average captures for each plant associated with the trap, and we used a Kruskal-Wallis rank sum test to test for differences in plant preference within each habitat. We, then, utilized Bayesian hierarchical models following the multinomial spatial-capture-recapture model as described in (Royle and Dorazio 2008, Ch. 7) to calculate relative abundance (N), effective sampling area (ESA), probability of capture ($p_o$), and typical distance moved between sample sites ($\sigma$). We calculated ESA since all of our habitats had open populations, and ESA provides us with a better understanding of

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the true size of our sampling area. Bayesian analysis of the model was conducted using data augmentation as described in Royle et al. (2007). For N, we assume a discrete uniform prior on the integers 0 to 180; we chose 180 individuals for our upper bound of N was much larger than the observed number of individuals for all habitats. We deduced that 180 was a sufficiently large upper bound for the uniform prior because the posterior distribution of N was concentrated well below the value 180. For the parameter $p_o$ we used a uniform prior on (0, 1) to represent probability of capture. For the parameter $\sigma$, we used a uniform prior on (0, 15) since our traps were 15 m apart. Each MCMC algorithm was run for 10,000 iterations, the first 2000 were discarded, and posterior summaries were computed from the remaining 8,000 iterations.

We then calculated the following for each habitat with basic analyses of movement: 1) furthest distance captured per individual and 2) the propensity to return to traps (trap loyalty). We compared average furthest distance captured among habitats by calculating the average furthest distance moved (distance between the two furthest traps captured at for each individual) using a Kruskal-Wallis rank-sum test. We then compared the number of individuals who were found in just one trap by counting the number of individuals recaptured in only one trap location and the number of individuals that were captured in multiple trap locations. We compared the proportions using a chi-square test. We calculated the propensity to return for each habitat by calculating the number of times an individual was captured divided by the number of unique trap locations for each individual, and we used a Kruskal-Wallis rank-sum test to test for differences among habitats. We conducted all analysis described above using the whole population. We then

re-did each analysis by sub-setting the data by 1) males only, 2) females only, 3) juveniles only, and 4) adults only.

To understand trap overlap (territory overlap), we calculated the average number of individuals captured per trap, and we used a Kruskal-Wallis rank sum test to test for differences among habitats. For each Kruskal-Wallis rank-sum test that was significant at the $\alpha \leq 0.10$ significance level, we ran a post-hoc multiple comparison tests following Siegel and Castellan's (1988) methods to determine which vegetation types were responsible for the differences. Within our study site, home range using the maxim polygon method was not calculable as many individuals were only captured at 2 trap locations at most.

**Daily Movement Patterns Data Analysis** – For each habitat, we calculated the average length of each trail segment, the average turning angle, the average straight-line distance to burrow from trap (distance from point A, trap location, to point B, burrow), and the average straight-line distance traveled (distance from point A, trap location, to point B, burrow or lost trail). We compared each value among habitat types using Kruskal-rank sum tests. We then re-did each analysis by grouping the data by males only and by females only.

We calculated the net squared displacement assuming an uncorrelated random walk using the following equation described in Turchin (1998).

$$\bar{R}_n^2 = nm_2 \text{ equation (1)},$$

Where $m_2$ is the average squared distance and $n$ is the number of moves. $\bar{R}_n^2$ is net squared displacement, and under the assumption of no correlations between moves, it increases linearly with time. We assumed a uniform sampling time between flags since we were unable to record movement times. We then plotted net squared displacement versus move number to observe whether it increases linearly with each move. If net squared displacement increases faster than linearly (curves up), then it is thought that there is significant directionality in movement. If net squared displacement curves down, then it is thought that dispersal rate is decreasing with time or there is a barrier to dispersal. If the movements are within home range, then net squared displacement should approach a constant asymptote Turchin (1998).

**RESULTS –**

**Seasonal Movement Patterns –** The proportion of males to females and juveniles to adults caught in traps did not differ based on habitat type ($p = 0.335$ and $p = 0.748$, respectively; Table 7). The traps local vegetation did influence the capture rate regardless of habitat ($p_{unburned} = 0.3113$; $p_{burnedwithpatches} = 0.7263$; $p_{burnedwithoutpatches} = 0.816$). Because of these results, it was not necessary to control for differences in age or sex of the individuals or the vegetation type at each trap location.

Actual abundance for the unburned habitat, the burned habitat with remnant patches, and the burned habitat without remnant patches was 137, 91, and 111 individuals, respectively. Estimated abundance (N) for the unburned habitat, the burned habitat with remnant patches, and the burned habitat without remnant patches was 145

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(140,152 [2.5%, 97.5%]; Table 8) individuals, 98 (93, 104) individuals, 123 (116, 133)

individuals, respectively (Table 8). Estimated effective sampling area for the unburned

habitat, the burned habitat with remnant patches, and the burned habitat without remnant

patches was 38.06 (37.23, 38.79) km$^2$, 38.06 (37.23, 38.79) km$^2$, 38.06 (37.23, 38.79)

km$^2$, respectively (original sampling grid = 34.65 km$^2$; Table 8). Probability of capture

($p_o$) for the unburned habitat, the burned habitat with remnant patches, and the burned

habitat without remnant patches was estimated to be 0.73 (0.62, 0.99), 0.33 (0.20, 0.40),

0.25 (0.20, 0.32), respectively (Table 8). Typical distance moved between sample sites

($\sigma$) for the unburned habitat, the burned habitat with remnant patches, and the burned

habitat without remnant patches was estimated to be 1.51 m (1.32, 1.74), 14.7 m (13.8,

15), 11.47 m (9.28, 14), respectively (Table 8). These distances are equivalent to being

captured in the same trap for the unburned habitat and being captured in one trap over for

both burned habitats on consecutive sampling periods.

　　　For the remaining analyses of movement data for seasonal movement patterns, we

will only describe those with significant tests due to the large number of tests conducted.

We found that the burned habitat with remnant patches moved marginally significantly

further distances than the burned habitat without patches and the unburned habitat ($p$ =

0.0916) for the whole population; we also found similar results when we analyzed only

the adult's furthest movement ($p$ = 0.048; Table 9a). We also found that that there was a

significant grouping of the number of individuals found only in one trap versus those that

were found in multiple traps ($p$ = 0.039; Table 4); the unburned habitat did not differ

from the expected values; the burned habitat with remnant patches had more individuals

found in more traps than expected (moving more than expected; Table 4); and the burned

habitat without remnant patches had more individuals found in only one trap than

expected (moving less than expected; Table 4). We found that the burned habitat with

remnant patches had a significantly lower propensity to return than the burned habitat

without patches and the unburned habitat when we analyzed the whole population ($p =$

$0.08182$); we also found similar results when we analyzed only the adult's propensity to

return ($p = 0.01303$; Table 9b). We found that the number of individuals captured per trap

were lower in the burned habitats compared to the unburned habitat ($p < 0.001$) showing

evidence of a decrease in home range overlap ($mean_{unburned} = 1.66 \pm 0.075$;

$mean_{urnedwithpatches} = 1.21 \pm 0.073$; $mean_{burnedwithoutpatches} = 1.23 \pm 0.069$).

**Daily Movement Patterns** – We did not find any difference in the average length of

each trail segment, the average turning angle, the average straight-line distance to burrow

from trap, and the average straight-line distance traveled ($p = 0.1997, 0.1270, 0.524,$ and

$0.4624$, respectively), nor did we find any differences when we analyzed only males ($p =$

$0.73424, 0.7217, 0.9801, 0.5914$, respectively) or only females ($p = 0.3401, 0.2919,$

$0.1829, 0.38$, respectively).

For all habitats, net squared displacement exhibits a uncorrelated random walk,

where the unburned habitat, burned habitat with remnant patches, and the burned habitat

without remnant patches have significant linear trends ($p < 0.001, p < 0.001, p = 0.010,$

respectively). The net squared displacement for the burned habitat without remnant

patches is about half that of both the unburned habitat and the burned habitat with

remnant patches. All analyses were conducted using the statistical software, R (R Core Team 2012).

**DISCUSSION –** Contrary to our hypothesis, our study found that *D. merriami* moves more within burned habitat with remnant patches (spatially complex; heterogeneous habitat) compared to the unburned and burned habitat without remnant patches (more homogenous landscapes) during a season. This suggests that the individuals living in the more heterogeneous landscape are moving further distances. Based on our data, we hypothesize two possible mechanisms for this behavior:  1) the kangaroo rats may be becoming more territorial by occupying larger home ranges in order to maintain territories in the burned habitat and remnant patches, or 2) the kangaroo rats have more resources in the burned habitat with remnant patches compared the burned habitat without remnant patches, and they are able to move further distances for resource acquisition, and the individuals in the unburned habitat do not need to move far distances to acquire adequate resources. Our study provides evidence for the importance of incorporating spatial heterogeneity when examining the impacts of habitat fragmentation on animal movement patterns. From a conservation perspective, we found that *D. merriami* appears to be highly adaptable to fragmentation and could be of particular interest for restoration via seed dispersal efforts within the burned landscapes in the Mojave Desert.

     *D. merriami* may be moving further seasonal distances to cover both the burned habitat and the remnant patches within the landscape for foraging purposes and acquiring

resources. A study by Diffendorfer et al. (1995) found that two species of small mammals moved longer distances as fragmentation within landscapes increased, and a study by Szacki et al. (1993) found that two more species of small mammals also increased their movement distances in heterogeneous landscapes. Szacki et al. (1993) concluded that this increase in movement within heterogeneous landscapes is most likely because the small mammals are trying to encapsulate the "minimum dynamic area" (Pickett and Thompson 1978) by covering multiple landscapes via increasing travel distances. However, we still see a reduced movement in the burned habitat without remnant patches. We found this very interesting since resources may be scarce in burned habitat without remnant patches, and we expected an increase in movement for resource acquisition.

Another hypothesis for our findings is that there may be an increase in movement behavior in the burned habitat with remnant patches because those habitats theoretically have more resources, providing them with more energy to increase the distances needed to find additional resources. The burned habitat without remnant patches may not provide enough resources for increased movement while the unburned habitat may have enough resources in a relatively small area of land. An alternative reason for decreased movement within burned habitats without remnant patches is that the individuals within the burned habitat without remnant patches may be exhibiting behavioral predatory avoidance by reducing movement rates within the modified landscape (Wilcove et al. 1986; Laurance and Bierregaard 1997).

Our data also suggest another possible mechanism for increasing movement distances within burned habitat with remnant patches may be due to an increase in

territoriality (not just an increase in types of habitat covered). Each individual may choose to have access to both the burned sections and the remnant patches, and those individuals may become more territorial to maintain access to both sections of the burned habitat with remnant patches. The increase in territoriality is supported as we also see a reduction in the number of individuals in the burned habitat with remnant patches in addition to an increase in movement and the home range proxy. Furthermore, the propensity to return to (or be found in) the same trap was decreased and the number of individuals captured at each trap is reduced. In other words, the individuals in the burned habitat with remnant patches are found in more traps but each trap has fewer individuals captured. Our data also suggests that the increased movement is a learned behavior as the juveniles do not exhibit differences in movement among habitats, only the adults do.

The burned habitat with remnant patches had the lowest actual and estimated abundance. A previous study within the same study sites found that the burned habitat with remnant patches maintained higher values of richness of small mammals but not abundance (Hulton VanTassel et al. 2015), and our study also incidentally trapped more small mammal species in the burned habitat with remnant patches than the burned habitat without remnant patches. Thus, the lower estimated abundance within the burned habitat with patches compared to the burned habitat without remnant patches may be due to the burned habitat with remnant patches supporting more species which could reduce the number of *D. merriami* that the habitat can support.

Surprisingly, we did not find any differences among habitats in daily movement patterns. However, the net squared displacement revealed interesting movement pattern

as the individuals showed no bias in movement direction, and their patterns exhibited an uncorrelated random walk. This may be due to *D. merriami* responding to our presence and viewing us a predator, and they are moving away from us, not towards anything. *D. merriami* within the burned habitat without remnant patches is moving shorted distances between moves, almost half that of the other habitats. With reduced vegetation cover, rapid turns may be to increase possibility of predatory avoidance.

Fahrig (2007) found that movement parameters of many species have not been able to track landscape change and have therefore become non-optimal. However, we found that *D. merriami* is altering their movement behavior based on the spatial complexity (habitat heterogeneity), and may be able to readily adapt to the changing landscape. *D. merriami* is considered a generalist species, which may increase their ability to adapt. Nevertheless, more research on changes in movement patterns in altered landscapes is needed for specialized and rare species.

Our study shows that *D. merriami* has increased movement patterns within spatially heterogeneous landscapes compared to homogenous landscapes. Even though this species has not evolved with fire, they appear to readily adapt to the new landscapes. Our study also provides evidence of the possible utility of revegetation within burned habitats in the Mojave Desert. A previous study found that the burned habitats with remnant patches maintains higher small mammal diversity compared to burned habitats remnant patches (Hulton VanTassel et al. 2015), and we found that remnant patches within burned landscapes can increase movement behavior. Thus, our data suggest that the revegetation of burned habitats could be used to promote an increase in small

mammal diversity and an increase *D. merriami* movement, which ultimately could

increase the dispersal of seeds to provide a faster recovery.
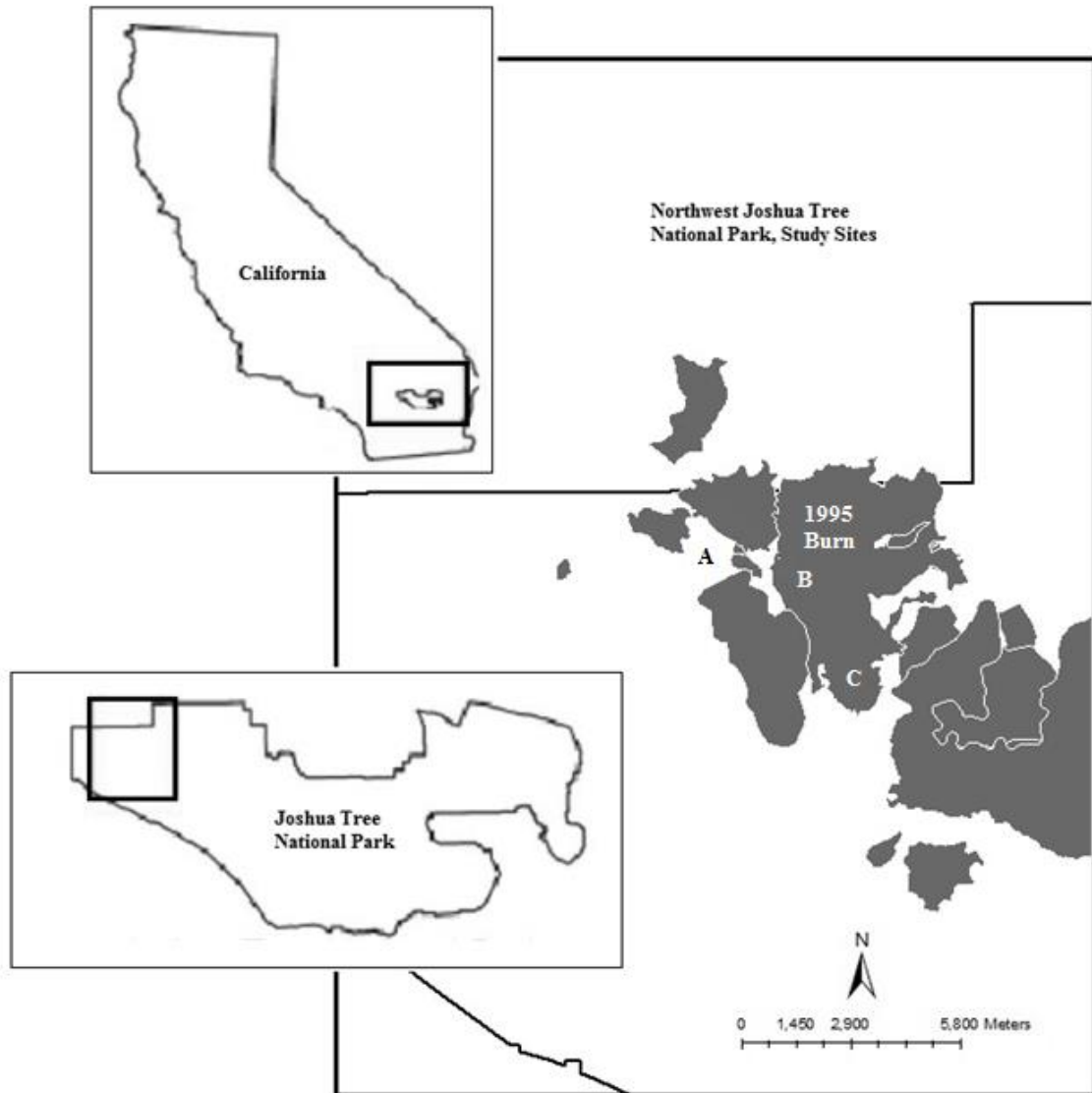
**FIGURES –**



Figure 10:  Map of study site in reference to California. Dark sections represent burned habitats. Letters represent habitat type as follows:  A) Unburned habitat, B) 1995 Burned habitat without remnant patches, and C) 1995 Burned habitat with remnant patches.

# TABLES –

Table 7: Proportion of males to females (a) and adults to juveniles (b). We did not find any significant differences in the proportion of males to females (p =0.335) nor adults to juveniles (p = 0.748) based on the chi-squared test. Expected values based on the chi-squared test in parentheses.

| Habitat | (a) Male vs Female abundances | | (b) Adult vs Juvenile abundances | |
|---|---|---|---|---|
| | Males | Females | Adults | Juveniles |
| *Unburned* | 53 (47.3) | 84 (89.7) | 113 (114) | 24 (22.6) |
| *Burned habitat with remnant patches* | 31 (31.4) | 60 (59.6) | 75 (76) | 16 (15) |
| *Burned habitat without remnant patches* | 33 (38.3) | 78 (72.7) | 96 (93.6) | 16 (18.4) |

Table 8: Summary of parameter estimates from the multinomial spatial-capture-recapture model as described in (Royle and Dorazio 2008, Ch. 7). Abundance (N) units are the number of individuals; effective sampling area (esa) is in units of $km^2$, probability of captured ($p_o$) is a probability. Typical distance moved between sample sites ($\sigma$) is in meters.

| | N | ESA | $p_o$ | $\sigma$ |
|---|---|---|---|---|
| *Unburned Habitat* | 145 (140, 152) | 38.07 (37.19, 38.79) | 0.73 (0.36, 0.99) | 1.51 (1.32, 1.74) |
| *Burned Habitat with Remnant Patches* | 98 (93, 104) | 37.82 (36.67, 38.75) | 0.30 (0.20, 0.40) | 14.7 (13.8, 15) |
| *Burned Habitat without Remnant Patches* | 123 (116, 133) | 36.48 (34.94, 37.69) | 0.25 (0.20, 0.32) | 11.47 (9.28, 14) |

Table 9:  Results from the Kruskal-wallis rank-sum tests that were significant at the α ≤ 0.10. The burned habitat with remnant patches was significantly different than the unburned habitat and the burned habitat without remnant patches for all of the tests below.

| (a) Mean Furthest Distance | | | |
|---|---|---|---|
| Treatment | | Whole Population (p = 0.092) | |
| *Habitat* | Unburned | Burned habitat with remnant patches | Burned habitat without remnant patches |
| *Mean  ± Standard Error* | 22.71 ± 2.06 | 28.88 ± 3.13 | 23.61 ± 3.22 |
| *Group Membership* | a | b | a |
| Treatment | | Adults Only (p = 0.048) | |
| *Habitat* | Unburned | Burned habitat with remnant patches | Burned habitat without remnant patches |
| *Mean  ± Standard Error* | 22.73 ± 2.24 | 30.81 ± 3.36 | 24.34 ± 3.44 |
| *Group Membership* | a | b | a |
| (b) Propensity to Return to the Same Trap | | | |
| Treatment | | Whole Population (p = 0.082) | |
| *Habitat* | Unburned | Burned habitat with remnant patches | Burned habitat without remnant patches |
| *Mean  ± Standard Error* | 1.68  ± 0.08 | 1.38  ± 0.06 | 1.65  ± 0.08 |
| *Group Membership* | a | b | a |
| Treatment | | Adults Only (p = 0.013) | |
| *Habitat* | Unburned | Burned habitat with remnant patches | Burned habitat without remnant patches |
| *Mean  ± Standard Error* | 1.73 ± 0.09 | 1.32 ± 0.05 | 1.67 ± 0.09 |
| *Group Membership* | a | b | a |

**DISCUSSION AND FINAL CONCLUSIONS** – My dissertation aimed to further our understanding of the impacts of habitat loss and fragmentation created from the invasion of exotic plant species and altered fire regimes. Particularly, I focused my research in two anthropogenically altered desert landscapes in Southern California:  1) the invasion of an exotic plant species in the Coachella Valley, and 2) fire altered landscapes in Joshua Tree National Park (JTNP). My dissertation research documented the impacts of anthropogenic disturbances on multiple species in two types of desert landscapes across multiple habitats to provide a broad, cohesive understanding of habitat loss and fragmentation influence population and community patterns. This multifaceted approach provides a novel and more realistic tactic to the understanding the long-term consequences of novel disturbances within desert ecosystems in Southern California.

Within the Coachella Valley, I found substantial evidence for a negative effect of Sahara mustard on the structure of a ground-dwelling arthropod community. During the study period, declines in both arthropod species richness and total abundance paralleled an overall increase in mustard cover. Arthropod species that declined in abundance tended to be those that experienced significant negative relationships with mustard more often than expected by chance. Finally, negative arthropod-mustard relationships were apparent even when controlling for other potential environmental drivers of community structure, suggesting some direct effect of mustard on arthropods.

These results suggest some potential directions for a future study of mechanisms underlying mustard impacts on arthropods. Specifically, researchers should consider impacts via changes in trophic structure and physical aspects of the environment.

Understanding system-wide impacts of invasive species on native biodiversity is critical for informing land management decisions and directing limited funding to maximize conservation objectives (Barrows and Allen 2007b). Mustard cover appears to influence both community structure and the amount of spatial coverage by arthropod taxa. My data suggest that the invasion of mustard negatively impacts the arthropod community across multiple aeolian sand habitats within the Coachella Valley, and a better understanding of the mechanisms responsible may help mitigate mustard impacts.

Within the post-fire lands in Joshua Tree National Park, a landscape experiencing a novel fire regime, I 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, I 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 my 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. 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. My research 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, I 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.

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. One mechanism that can influence distributions is via movement behavior and habitat use. We examined movement behavior of a generalist species, *Dipidomys merriami,* within the post-fire lands in JTNP that have the largest differences in distributions and abundances based on the spatial configuration of the landscape.  Contrary to my hypothesis, my study found that *D. merriami* moves more within burned habitat with remnant patches (spatially complex; heterogeneous habitat) compared to the unburned and burned habitat (more homogenous landscapes) during a season. My data suggests that the individuals living in the more heterogeneous landscape are moving further distances. Based on my data, I have two possible mechanisms for this behavior:  1) the kangaroo rats may be becoming more territorial by occupying larger home ranges in order to maintain territories in the burned habitat and remnant patches or 2) the kangaroo rats have more

resources in the burned habitat with remnant patches compared the burned habitat without remnant patches, and they are able to move further distances to resource acquisition, and the individuals in the unburned habitat do not need to move far distances to acquire adequate resources.

Fahrig (2007) found that movement parameters of many species have not been able to track landscape change and have therefore become non-optimal. However, I found that *D. merriami* is altering their movement behavior based on the spatial complexity (habitat heterogeneity), and may be able to readily adapt to the changing landscape. *D. merriami* is considered a generalist species, which may increase their ability to adapt. Nevertheless, more research on changes in movement patterns in altered landscapes is needed for specialized and rare species.

Overall, I found that the invasion of Sahara Mustard in the Coachella Valley and the altered fire regime in Joshua Tree National Park had overall negative impacts on the abundance, richness, and community composition of the faunal communities, and some species were more negatively impacted than others. Even though I found an overall negative impact of both disturbance events and desert communities are known for slow recovery periods, the desert communities of southern California appear to be fairly resilient to disturbances where some taxonomic groups maintained healthy population patterns. Nevertheless, I still found that some taxonomic groups were negatively influence by the disturbance where their population was reduced to low numbers or was absent in disturbed habitats. Furthermore, as there is an increase demand for urbanization and agricultural land use with a growing global population as well as a simultaneous

impact of climate change, there needs to be an emphasis on reducing the impacts of other

disturbance events, such as invasive species and altered fire regimes, in order to promote

the sustainability of biodiversity. Because of this, I strongly recommend the eradication

of invasive plant species as they can have negative effects on native faunal communities

through a variety of avenues, such as directly via biomass and plant compositional

changes or indirectly via alterations of fire regimes.

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