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

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ABSTRACT

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

1. Introduction

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

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

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

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

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

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

Our objective was to quantify the influence of spatial heterogeneity on arthropod and small mammal community patterns within burned habitats in the Mojave Desert. Within our study landscape, the variation within burned habitats (i.e. heterogeneity) was created by the amount and configuration of remnant vegetation in burned habitats and the distance of the burned habitats from continuous expanses of unburned habitats (isolation level). Fires in the Mojave ecosystem have left behind a mosaic of varying levels of remnant vegetation, making it important to quantify the influence of spatial heterogeneity on multiple taxa. Arthropods generally have short generation times and have been documented to respond to changing food availability (de Groot et al., 2007) and habitat structure (Pearson, 2009), making those ideal candidates for monitoring community responses to small changes in habitat (Longcore, 2003). Small mammals are a key component of desert ecosystems (Brown et al., 2000) as they are important consumers of plant materials (Price and Joyner, 1997) and are a significant portion of the prey base for a variety of carnivores. Furthermore, seed predation by small mammals has shown to significantly influence desert ecosystem structure and dynamics (Longland, 2007; Montiel and Montana, 2003). Within the Mojave Desert, Vamstad and Rotenberry (2010) found changes in small mammal diversity between burned and unburned habitats, yet abundance was not significantly different. Nevertheless, their study was taxonomically and spatially limited as it focused solely on small mammals and ignored spatial heterogeneity within burned sites. Specifically, the study did not consider whether burned areas included remnant unburned vegetation that could harbor organisms intolerant of burned areas and how isolated this vegetation was from unburned areas.

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

2. Methods

2.1. Study site

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