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Fire Impacts on Ant Assemblages in California Sage Scrub

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Abstract. Few studies have examined impacts of fire on invertebrates in southern California ecosystems despite the fact they harbor diverse invertebrate assemblages with many narrowly endemic species. California sage scrub, an endangered ecosystem type of low-elevation areas in southern California, is increasingly threatened by altered fire regimes and type conversion to non-native grasslands often resulting from fire disturbances. The effect of fire on ant assemblages in a patch of recovering sage scrub was examined by using adjacent intact sage scrub and non-native grassland habitats as checks. While short-term effects in ant activity potentially associated with temporary changes in habitat structure and abiotic conditions were observed, ant assemblages in the burned area did not differ between summer 2013 (pre-fire) and fall 2013 (post-fire), or between spring 2013 (pre-fire) and spring 2014 (post-fire). Results indicated that either the ant assemblages recover quickly, or more likely, pre-existing ant assemblage remained and were not directly impacted by fire. Our results, combined with the few other studies that examined impacts of fire on sage scrub invertebrates, are consistent with an emerging hypothesis that ground-dwelling ant/invertebrate assemblages are little affected by direct impacts of fire in semi-arid systems and areas where fires are common.

Introduction

While periodic fire is a natural part of many ecosystems in southern California, invasion by non-native grass species has increased the frequency of fires (D'Antonio and Vitousek 1992, Keeley et al. 1999, Talluto and Suding 2008). Increased fire frequency, or reduced fire-return intervals, facilitate further invasion by some non-native grasses because they are often the first to colonize an area after a disturbance and can outcompete natives in common environmental conditions: drought and greater nitrogen deposition rates (D'Antonio and Vitousek 1992, Cox et al. 2014, Kimball et al. 2014). The endangered California sage scrub ecosystem (hereafter, sage scrub), a native low-elevation ecosystem type dominated by drought deciduous shrubs in southern California, is particularly susceptible to the grass-fire cycle (Noss et al. 1995, Riordan and Rundel 2013). For example, 49% of the plots identified as sage scrub by the 1930s Vegetation Type Mapping Survey had been type-converted to non-native grasslands by 2005 mainly because of increased disturbance by fires (Talluto and Suding 2008).

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Preservation of biodiversity in southern California, particularly in the sage scrub ecosystem, requires understanding the influences of fire and type-conversion and which factor, if any, is responsible for changes in arthropod assemblages (Spear et al. 2017). While significant research in southern California has focused on recovery of plant and mammal communities following a fire (Malanson and O'Leary 1982, Callaway and Davis 1993, Keeley 2006, Keeley et al. 2006, Regan et al. 2010, Diffendorfer et al. 2012, Kimball et al. 2014, Shuette et al. 2014), few studies have examined impacts of fire on invertebrates (see van Mantgem et al. 2015 for the most recent review). This is unfortunate because southern California is part of the California Floristic Province, a biodiversity hotspot, and harbors diverse invertebrate assemblages with many narrowly endemic species (Pilsbry 1939, Keaton 1960, Hogue 1993, Myers et al. 2000, Roth and Sadeghian 2003).

A recent meta-analysis suggested that abundance and diversity of ground-dwelling ants, other than species that nest in litter, were not impacted by fire in semi-arid systems or in places where fire was a common disturbance (Vasconcelos et al. 2017). While most studies from semi-arid regions in Vasconceles et al. (2017) were from Australian savannahs, the pattern is supported by the few studies that examined the impacts of fire on arachnids (spiders, solfugids, and scorpions) in the region (Prentice et al. 2001, Brown et al. 2010, Spear et al. 2017). Conversely, Matsuda et al. (2011), the only study in the region that addressed the impacts of fire on ants, found that fire impacted ant assemblages 2 years after a fire. However, Matsuda et al. did not examine short-term effects or quantify changes in plant community structure, which can have profound impacts on ant assemblages (Staubus et al. 2015).

The aim of this study was to examine short-term effects of fire on ant assemblages in a sage scrub ecosystem and compare results to limited literature on fire impacts on invertebrates in sage scrub and other semi-arid ecosystems. Data were used from systematic surveys of ground-dwelling arthropods before and after a fire that burned 7 ha at the Robert J. Bernard Field Station on 11 September 2013.

Materials and Methods

The Bernard Field Station is at Claremont, CA at the eastern edge of Los Angeles County. It is primarily composed of three habitats: native California sage scrub (~25 ha), a type-converted non-native grassland (~3.5 ha), and a transitional habitat (~5.5 ha) where sage scrub shrubs were reestablishing in non-native grassland. The sage scrub habitat was characterized by a mixture of drought deciduous and evergreen shrubs, such as California sagebrush (*Artemisia californica* Lessing 1831), yerba santa (*Eriodictyon trichocalyx* Heller 1906), and California buckwheat (*Eriogonum fasciculatum* Bentham 1837). The non-native grassland was composed mostly of European grasses from the genus *Bromus*, but also contained other non-native annuals such as *Erodium* spp., patchy *Brassica* spp., and *Centaurea melitensis* L.. The non-native grassland area was once a *Citrus* grove. Hilbig (2015) found that soil legacies associated with change in microbial assemblage might favor invasion by non-native grass and limit reestablishment of native plants in citrus groves. Because there is no recent history of fire (during the last 40 years) in the non-native grassland at the Bernard Field Station, lack of shrubs might indicate the legacy effects and competitive nature of non-native grass species. Recent studies confirmed differences in soil microbial (fungal and bacterial) communities between non-native and sage scrub habitats at the Bernard Field Station, however, many other ecosystem properties key to ant assemblage structure, such as soil sediment size and differing topography, did not differ among the two habitat types (Caspi et al. 2018). The transitional habitat was dominated by *Bromus* spp. but had many reestablishing shrubs, primarily *E. trichocalyx*. Unlike non-native grassland, livestock, not a citrus grove, once (>40 years ago) occupied the area with transitional habitat. We are uncertain if there were legacy impacts of livestock other than disturbance by trampling and direct herbivory. In September 2013, a nonintentional human-ignited fire burned 7 ha at Bernard Field Station. The fire encompassed the entire transitional habitat (hereafter, burned area), but arthropod sampling sites at sage scrub and non-native grasslands were not affected. This was the first fire recorded at the Bernard Field Station in more than 40 years, excluding a small (<0.1 ha) fire that burned mostly along and outside the fence line.

Ant assemblages were sampled at 32 sites, each with three pitfall traps (3.8 cm in diameter). Pitfall traps were placed at the points of a north-facing equilateral triangle with sides 10 m long for a 2-week period each season from spring 2013 to spring 2014 and in spring 2015. Samples in spring and summer 2013 were collected before the fire and post-fire in fall 2013, winter 2014, spring 2014, and spring 2015 (see Staubus et al. 2015 and Spear et al. 2017 for dates, maps of sites, and description of sampling protocol). The sage scrub habitat had 16 sites (~75 m apart), while the non-native grassland and burned area each had eight (~40 m apart). No pitfall traps in non-native grassland or sage scrub habitats were in areas that burned.

Because the number of individual ants collected in pitfall traps did not correspond to the number of colonies, the natural units of diversity (Gotelli et al. 2011), the proportion of traps occupied by each ant species at a site, was used for all analyses. To account for loss of two to 10 traps per season, the proportion of traps occupied at a site was determined by dividing the number of traps in which a species was collected by the number of functional pitfall traps at that site.

PRIMER-E software (Clarke and Gorley 2006) was used for all analyses. Rarefaction curves were used to determine if species richness differed among the three spring collections in each habitat. Differences in species richness among years were determined when the 95% confidence intervals did not overlap.

Various ANOSIM (Analysis of Similarities) analyses were used to examine the impact of fire on ant assemblages. Before each ANOSIM test, a resemblance matrix was created using the Bray-Curtis coefficient. Initially, one-way ANOSIM (9,999 permutations) was used to compare ant assemblages in the sage scrub, non-native grassland, and transitional (pre-burned) habitats during spring 2013. We did this to test if different habitats had similar assemblages and could serve as checks to determine if changes in the ant assemblage in the burned area were associated with fire.

Two sets of ANOSIM analyses were used to test effects of fire on ant assemblages. Three one-way ANOSIMs (9,999 permutations) were used on data from summer and fall 2013 to examine if ant assemblages differed in the seasons immediately before and after fire at each habitat. Three one-way ANOSIMs (9,999 permutations) were used to analyze data from each habitat type for the three spring seasons to assess longer-term influences of fire on ant assemblages while controlling for impacts of season. The α-values for pairwise comparisons were Bonferoni corrected ($\alpha = 0.016$). Following all significant ANOSIM tests, SIMPER

(Similarity Percentages) analyses were used to analyze species-influenced changes in ant assemblages.

ANOSIMs were used to contrast changes in ant assemblages in non-native grassland and sage scrub areas with those in the burned area to control for external factors such as drought that might have confounded the impact of fire. For example, if ant assemblages differed in the burned area pre- and post-fire but did not differ in the check habitats, fire was assumed to have a significant impact.

Results

A total of 22 ant species was collected (Table 1). Sixteen species were collected in sage scrub, 12 in non-native grassland, and 12 in burned habitat. Two species were known to be non-natives: *Linepithema humile* (Mayr 1868), a widespread ant species known to displace other arthropods (Tillberg et al. 2007), and *Cardiocondyla mauritanica* Forel 1890, a scarce ant with little reported impact.

Rarefaction curves illustrated that species richness differed among years (2013, 2014, and 2015 spring collections) at each habitat, but inter-annual differences were unique among habitats (Fig. 1). In the burned area, species richness was greater in spring 2014, the spring immediately after fire, than in spring 2013 or 2015. Conversely, species richness was less in 2014 than 2013 in the non-native grassland. In sage scrub, ant richness was greater in 2013 and 2014 than in 2015.

Ant assemblages differed among habitat types before the fire in September 2013 (R = 0.155, P = 0.024; Fig. 2). However, pairwise comparisons revealed that the ant assemblages in the sage scrub and non-native grassland habitats differed (R = 0.259, P = 0.009), but the transitional/burned area did not differ from either the sage scrub habitat (R = 0.104, P = 0.146) or non-native grassland (R = 0.054, P = 0.235). This implied that comparisons between the burned habitat and sage scrub and non-native grassland might reveal important insights into the effects of fire.

Ant assemblages in the burned area did not differ between summer 2013, the season before the fire, and fall 2013, the season immediately following the fire (R = -0.053, P = 0.772). However, ant assemblages did differ between those seasons in the sage scrub (R = 0.247, P = 0.002) and non-native grassland habitats (R = 0.184, P = 0.035) (Fig. 3). SIMPER analyses indicated that differences among seasons in sage scrub and non-native grassland were driven by fewer traps and sites (Table 2).

Ant assemblages differed among spring seasons in the burned (R = 0.133, P = 0.021) and sage scrub habitats (R = 0.071, P = 0.023) but not in the non-native grassland (R = -0.052, P = 0.756). Pairwise comparisons revealed that ant assemblages differed only between spring 2014 and spring 2015 (both post-fire) in the burned and sage scrub habitats (Table 3). Differences within the burned and sage scrub habitats were driven by fewer pitfall traps and sites occupied by *Pheidole hyatti* Emery 1985, *L. humile*, and *Solenopsis molesta* Emery 1985 at both habitats.

Table 1. Average Proportion of Traps Occupied for Each Ant Species at California Sage Scrub, Non-native Grassland, and Burned Habitats in Spring 2013 (SP13), Summer 2013 (SU13), Fall 2013 (FA13), Spring 2014 (SP14), and Spring 2015 (SP15) Seasons

Species	California sage scrub					Non-native grassland					Burned area				
Season	SP13	SU13	FA13	SP14	SP15	SP13	SU13	FA13	SP14	SP15	SP13	SU13	FA13	SP14	SP15
Brachymyrmex depilis	0	0	0.02	0	0	0	0	0	0	0	0	0	0	0	0
Cardiocondyla mauritanica	0	0	0	0	0	0	0	0	0	0	0	0	0	0.04	0
Dorymyrmex insanus	0.05	0.32	0.07	0.13	0.04	0.10	0.05	0.08	0.04	0	0	0.04	0.14	0.08	0
Forelius mccooki	0.02	0.34	0.02	0	0	0.09	0.50	0.09	0	0	0.22	0.625	0.61	0.21	0
Hypoponera opacior	0	0	0	0	0	0	0	0	0	0.04	0	0	0	0	0
Linepithema humile	0.27	0.53	0.21	0.23	0.15	0.09	0	0	0	0.08	0.13	0.08	0.30	0.17	0.17
Myrmecocystus mimicus	0	0	0	0	0.02	0	0.08	0.04	0	0	0	0	0	0	0
Myrmecocystus testaceus	0	0	0	0.09	0	0	0	0	0	0	0	0	0	0	0
Myrmecocystus wheeleri	0	0.03	0	0	0	0	0	0	0	0	0	0	0	0	0
Pheidole cerebrosior	0	0	0	0	0	0.05	0.08	0.09	0	0.13	0	0	0.13	0	0.04
Pheidole hyatti	0.15	0.26	0.21	0.13	0.19	0.14	0.21	0.04	0.08	0.17	0.22	0.50	0.22	0.29	0.04
Pheidole pilifera	0.02	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pogonomyrmex californicus	0	0.03	0	0	0	0	0.04	0	0	0	0	0	0	0	0
Prenolepis impairs	0	0	0	0	0	0	0	0	0	0	0	0	0	0.04	0.09
Solenopsis molesta	0.27	0.61	0.14	0.34	0.11	0.05	0.04	0.04	0	0	0.26	0.43	0.13	0.21	0
Solenopsis xyloni	0.10	0.16	0.12	0.04	0.11	0.17	0.42	0.26	0.04	0.25	0.04	0.38	0.22	0.17	0.17
Stenamma californicum	0	0	0	0	0	0	0	0	0	0	0.04	0	0	0.04	0
Stenamma diecki	0.15	0	0	0.11	0	0	0	0	0	0.04	0	0	0	0	0
Temnothorax andrei	0.10	0.29	0	0.11	0	0	0	0	0	0	0.04	0.08	0.04	0.04	0
Temnothorax nevadensis	0.02	0	0	0.02	0	0	0	0	0	0	0	0	0	0	0
Veromessor andrei	0	0	0	0	0	0	0.17	0.09	0.04	0.08	0	0	0	0	0
Veromessor chamberlini	0	0.05	0	0.02	0	0	0	0	0	0	0	0.08	0.04	0	0

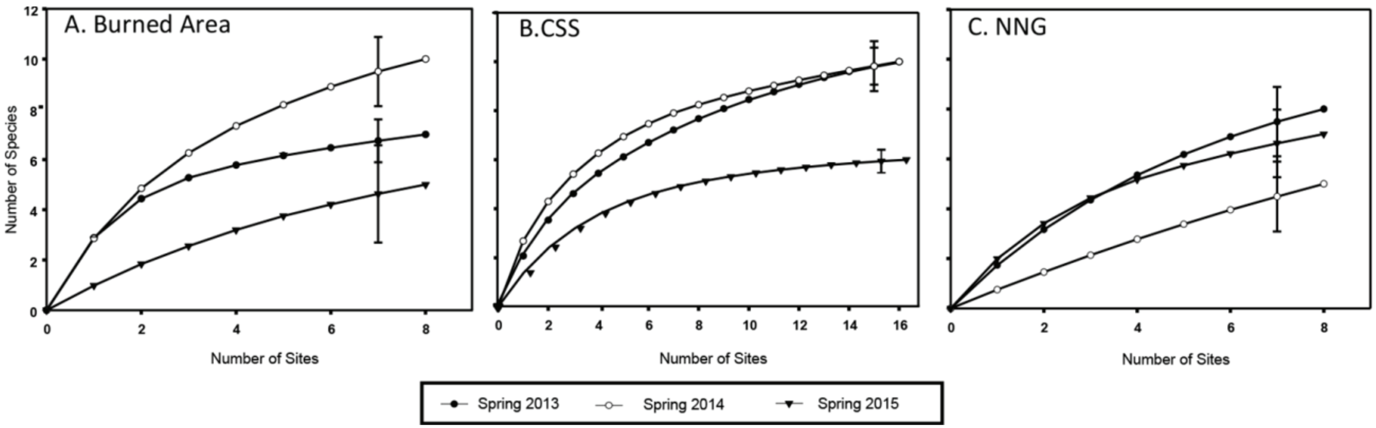

Fig. 1. Rarefaction curves of ant species richness in (A) burned area, (B) California sage scrub (CSS), and (C) non-native grassland (NNG) in spring 2013 (pre-fire), spring 2014 (post-fire), and spring 2015 (post-fire) seasons.

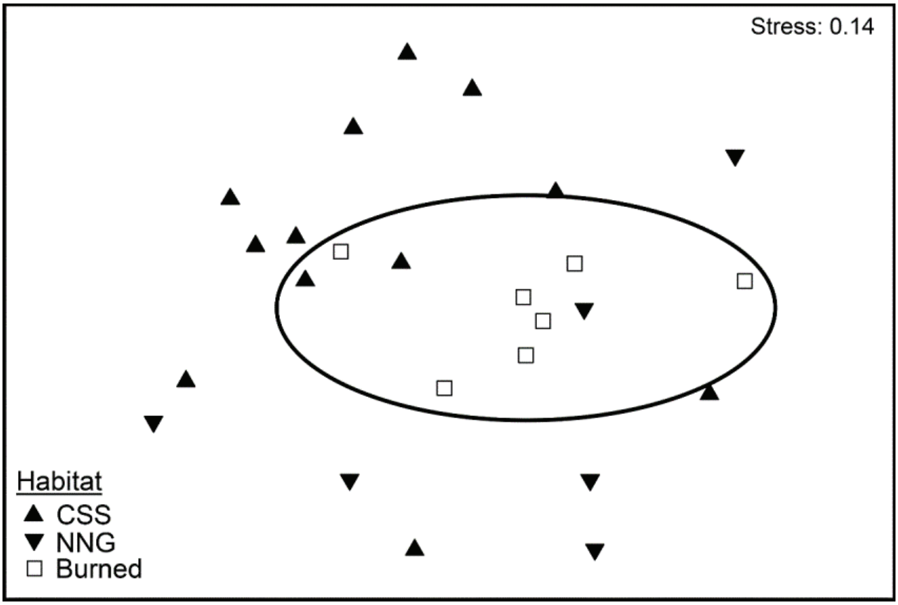

Fig. 2. Multi-dimensional scaling ordination of sites by composition of ants at three habitat types: California sage scrub (CSS), non-native grassland (NNG), and burned area. Similarity determined by Bray-Curtis similarity coefficient. Sites closer together were more similar in ant composition. Oval encompasses ordinal space occupied by transitional sites. Sites with one or fewer ant species were removed.

Discussion

Overall, results indicated that fire had little impact on ant assemblages in sage scrub. The only effect was that the assemblage in the burned area did not differ in the seasons immediately before (summer 2013) and after (fall 2013) fire, while the assemblages in sage scrub and non-native grassland check areas did. The fire, by removing vegetation that might have provided shade, increased surface temperatures, prolonged summer-like conditions in the burned area, and slowed seasonal changes in ant assemblage. In support of this assertion, *Dorymyrmex insanus* (Buckley 1866) which prefers open, warmer environments (Hölldobler and Wilson 1990), was more active in a burned area following fire, but less active in sage scrub, and maintained a limited presence in non-native grassland. However, increased activity of *L. humile* in the burned area between the two seasons suggested other factors might have influenced ant activity in the burned area, because *L. humile* is desiccation intolerant (Holway et al. 2002). Despite the initial differences between the burned and two check habitats, ant assemblages did not differ significantly between any habitat type in the spring before and the spring immediately following fire. This suggested the ant assemblages either recovered quickly, or the pre-existing ant assemblage remained and was not impacted by

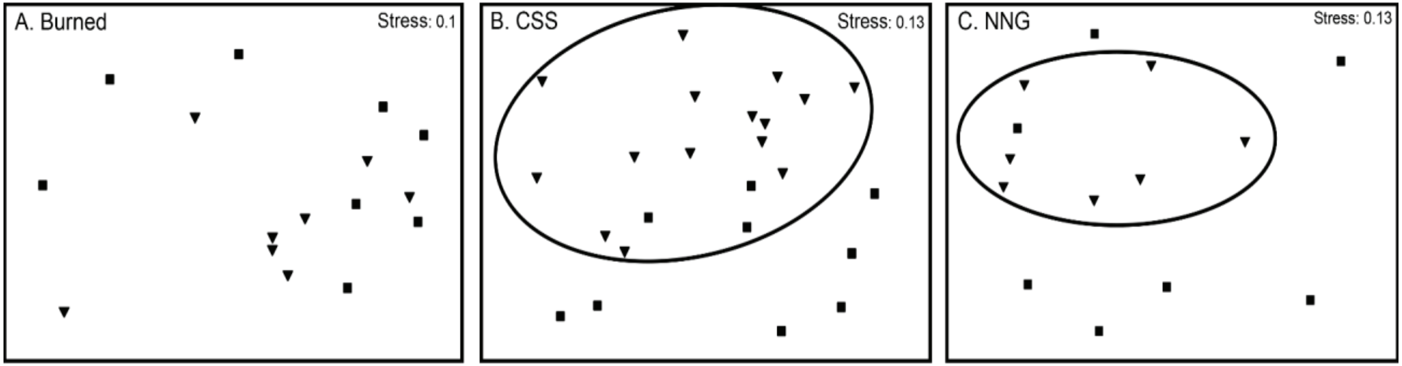

Fig. 3. Multi-dimensional scaling ordination plots of sites illustrating pre- (summer 2013) and post-fire (fall 2013) differences in ant assemblages based on species composition at (a) burned, (b) California sage scrub (CSS), and (c) non-native grassland (NNG) sites. Ovals encompass sites that surveyed in summer 2013 for habitats where ant assemblages were found to differ between pre- and post-fire seasons.

Table 2. Results from SIMPER Analyses Listing the Five Most Important Species according to Contribution to Dissimilarity between Ant Assemblages Collected Pre- (Summer 2013, SU13) and Post-Fire (Fall 2013, FA13) at California Sage Scrub and Non-native Grassland Habitats. Ant assemblages did not differ between seasons in the burned area.

Habitat *Species*	Proportion of traps		Avg. dissimilarity	SD	% contribution
Sage scrub	SU13	FA13			
Solenopsis molesta	0.61	0.14	16.06	1.06	21.65
Linepithema humile	0.53	0.21	13.08	1.32	17.63
Pheidole hyatti	0.26	0.21	9.60	0.82	14.30
Temnothorax andrei	0.29	0.00	8.84	0.75	11.92
Forelius mccooki	0.34	0.02	8.47	0.75	11.42
Non-native grassland	SU13	FA13			
Forelius mccooki	0.50	0.10	20.79	2.55	28.84
Solenopsis xyloni	0.42	0.26	15.67	1.06	21.74
Pheidole hyatti	0.21	0.04	8.21	0.81	11.39
Veromessor andrei	0.17	0.09	6.73	0.83	9.34
Pheidole cerebrosior	0.08	0.10	6.39	0.69	8.87

Table 3. Pairwise Comparison Following Significant One-way ANOSIMs of Differences in Ant Assemblages at Habitats in Pre- (Spring 2013) and Post-fire (Spring 2014 and Spring 2015) Seasons with α-values Adjusted for Multiple Testing Using the Conservative Bonferroni Correction Procedure (Three Pairwise Habitat Comparisons Each Season: α = 0.016). Bold indicates significant differences.

Habitat	Pairwise comparison	*R*	*P*
Burned	Spring 2013 vs. Spring 2014	-0.058	0.699
	Spring 2013 vs. Spring 2015	0.202	0.019
	Spring 2014 vs. Spring 2015	**0.219**	**0.007**
Sage scrub	Spring 2013 vs. Spring 2014	-0.029	0.719
	Spring 2013 vs. Spring 2015	0.052	0.107
	Spring 2014 vs. Spring 2015	**0.162**	**0.002**

direct effects of fire. The fire at the Bernard Field Station was fast moving with grasses composing most of the fuel. Much arthropod activity, although not measured, was observed weeks following the fire (Spear et al. 2017).

The ant assemblage at burned or sage scrub habitat did not differ between spring 2013 (pre-fire) and spring 2014 (post-fire), but did between spring 2014 and spring 2015 (6 and 18 months after the fire, respectively). While this suggested that inter-annual variation might have a more significant impact than fire on ant assemblage, interpretations need to consider all potential drivers. This study during 3 drought years, including the driest 2 consecutive rain years (2012-2013 and 2013-2014) since precipitation records began in 1877 (Mann and Gleick 2015), might have had a substantial impact on assemblages at all three habitats. However, disproportionate declines in arid specialist species such as *P. hyatti* and *D. insanus* (Hölldobler and Wilson 1990, Wilson 2003) at the burned area and sage scrub, respectively, seemed an unlikely consequence of drought, unless such conditions influenced availability of food. It is likely that differences reflected slight changes in the timing of spring collection, because samples in spring 2015 were collected 2 weeks earlier than in spring 2014. Although not recorded, cooler surface temperatures earlier in the season might have contributed to less *P. hyatti* and *D. insanus* activity in 2015. This highlights the complexity of factors that must be considered when determining impacts of inter-annual variation or effects of a disturbance over multiple years. Despite differences among years, it was unclear to what extent inter-annual variation and drought influenced ant assemblages. Long-term studies that span multiple drought and wet years are needed to ascertain which changes might be associated with the conditions.

Previous studies of the effect of fire on ant assemblages in sage scrub did not examine immediate post-fire changes in ant assemblages. For example, Matsuda et al. (2011) found differences in ant assemblages in burned and nonburned sage scrub plots by examining ant assemblages in sage scrub 2 years after a fire. Differences in sage scrub were driven by increased abundance of the harvester ant *Veromessor andrei* (Mayr 1886) in areas that burned. However, it was difficult to determine if increased abundance of *V. andrei* was because of direct impacts of fire or potential invasion by non-native grasses into sage scrub sites. *V. andrei* feeds on grass seeds (Hölldobler and Wilson 1990) and at our research site was found at non-native grassland areas but not sage scrub habitats (Staubus et al. 2015). Because increased abundance of non-native grasses is common following fire (D'Antonio and Vitousek 1992, Talluto and Suding 2008), it is unclear if fire or invasion by grass caused the change. Understanding the extent to which direct and indirect effects of fire, e.g., changes in plant composition, are responsible for changes in ant assemblage is critical in determining when fire disturbances will impact ants and other invertebrates (Spear et al. 2017).

Our results are consistent with those of Vasconcelos et al. (2017) who indicated that ground-dwelling ant assemblages in semi-arid systems and areas where fires were common were little affected by fire. In addition, the patterns are consistent with the few studies that examined the impact of fire on arthropods in the region (Prentice et al. 2001, Brown et al. 2010, Matsuda et al. 2011, Spear et al. 2017). While direct (short-term) impacts of fire might be limited, indirect (long-term) effects, particularly changes in plant composition following fire, can be significant depending on the taxa examined. For example, conversion of sage scrub to non-native grassland at our study sites influenced assemblages of ants but not ground-dwelling spiders (Staubus et al. 2015, Spear et al. 2017). Because direct impacts of fire probably are limited, but indirect effects can be significant, management to preserve biodiversity of ground-dwelling invertebrates requires consideration only when type conversion is expected.

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