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Source: Environmental Entomology, 40(2):204-216. 2011.

Published By: Entomological Society of America

DOI: 10.1603/EN10061

URL: <http://www.bioone.org/doi/full/10.1603/EN10061>

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Effects of Large-Scale Wildfires on Ground Foraging Ants (Hymenoptera: Formicidae) in Southern California

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Environ. Entomol. 40(2): 204–216 (2011); DOI: 10.1603/EN10061

ABSTRACT We investigated the effect of broad-scale wildfire on ground foraging ants within southern California. In October and November of 2003, two wildfires burned large portions of the wildlands within San Diego County. Between January 2005 and September 2006, we surveyed 63 plots across four sites to measure the effect of the fires on the ant assemblages present in four vegetation types: 1) coastal sage scrub, 2) chaparral, 3) grassland, and 4) woodland riparian. Thirty-six of the 63 plots were sampled before the fires between March 2001 and June 2003. Mixed model regression analyses, accounting for the burn history of each plot and our pre- and postfire sampling efforts, revealed that fire had a negative effect on ant species diversity. Multivariate analyses showed that ant community structure varied significantly among the four vegetation types, and only the ant assemblage associated with coastal sage scrub exhibited a significant difference between burned and unburned samples. The most notable change detected at the individual species level involved *Messor andrei* (Mayr), which increased from <1% of prefire coastal sage scrub ant samples to 32.1% in burned plots postfire. We theorize that *M. andrei* responded to the increase of bare ground and postfire seed production, leading to an increase in the detection rate for this species. Collectively, our results suggest that wildfires can have short-term impacts on the diversity and community structure of ground foraging ants in coastal sage scrub. We discuss these findings in relation to management implications and directions for future research.

KEY WORDS ant community, species diversity, wildfire, southern California, coastal sage scrub

Wildfires long have been a part of the natural and human-altered environments of southern California. Large, landscape-level fires occurred in the past and will likely persist as long as southern California continues to experience episodes of severe fire weather (e.g., fast, dry winds; Keeley et al. 1999, 2004). Despite fire suppression efforts and management plans, wildfires continue to occur from both natural ignition sources and those associated with the increasing human population (Keeley et al. 2004). Native vegetation communities have evolved with episodic fire and adapted various survival strategies in response (Hanes 1971; Vogl and Schorr 1972; Keeley and Keeley 1981, 1984; Zedler et al. 1983; Keeley and Fotheringham 2001). As fire return intervals decrease, however, shrublands, such as chaparral and coastal sage scrub, are susceptible to becoming type converted to grasslands (Zedler et al. 1983, Keeley 2005). As fires alter

the vegetative composition and physical structure of habitats, we expect associated animal communities to experience concomitant shifts in structure and richness (Whelan 1995, Ostojia and Schupp 2009).

In October and November of 2003, large-scale fires swept across southern California, consuming over 300,000 ha of wildlands. The total burned area included nearly 130,000 ha in San Diego County, burning as a result of the Cedar and Otay Fires. In addition to the loss of nearly 5,000 structures and 15 human fatalities, these two broad-scale fires are likely to have affected local invertebrate communities in a region already recognized as being one of the most at risk areas for loss of biodiversity (Mittermeier et al. 1997).

Ants are ecologically diverse and constitute a large portion of the total animal biomass within the vegetation communities they occupy (Hölldobler and Wilson 1990, Alonso and Agosti 2000). Ants fill various functional roles in the environment, such as herbivores, predators, and seed dispersers (Alonso and Agosti 2000, Cuautle et al. 2005, Agarwal et al. 2007, Christianini and Oliveira 2010). Ants improve soil quality, often increasing plant mass in the vicinity of their nests (Hobbs 1985, Rissing 1986, Brown and

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Human 1997, Folgrait 1998, MacMahon et al. 2000). In southern California, the native ant community constitutes the dietary staple of several sensitive or endangered species including the coastal horned lizard (*Phrynosoma coronatum* Blainville, Suarez et al. 2000); the night lizard (*Xantusia henshawii* Stejneger, Brattstrom 1952); and the arroyo toad (*Anaxyrus californicus* Camp Sweet and Sullivan 2005).

Because they are moderately diverse with regards to species and behaviors, sensitive to microclimate change, and can be sampled easily, ground foraging ants are ideal functional measures of environmental disturbance (Majer 1978, Andersen and Yen 1985, Bromham et al. 1999, Alonso and Agosti 2000, Stephens and Wagner 2006, Underwood and Fisher 2006, Luque et al. 2007). Studies of the effects of fire on ant communities have been largely limited to the time period immediately following fire or to localized ant assemblages (Andersen and Yen 1985, Wilkinson et al. 2005, Underwood and Christian 2009). However, in a study conducted 8 yr after fire across a moisture and elevation gradient in Catalonia, Spain Arnan et al. (2006) concluded that ant communities in semiarid habitats are more resilient and recover faster than in moister habitats. Scrubland type habitats are not as frequently studied (Andersen and Yen 1985, Donnelly and Gilioee 1985, Underwood and Fisher 2006) and to our knowledge, there have been no such studies in the Mediterranean climatic region of southern California. In the short term, fire may affect ants by causing direct mortality, loss of habitat, and changes in resource availability (Arnan et al. 2006). Fire may also have positive impacts, especially for those species that favor open or disturbed habitats for nest sites, foraging, or reproduction. Species that forage upon the pollen, nectar, or seeds of early successional plants may also show a positive response to fire. The few short term studies in arid habitats suggest there may be an immediate positive response of ant abundance, particularly seed harvesters, after fire (Andersen and Yen 1985, Wilkinson et al. 2005, Underwood and Christian 2009).

The objective of this study was to determine the effects of the massive 2003 Cedar and Otay Fires on ant species diversity, community structure, and the relative abundance of individual species across a habitat and elevation gradient in southern California. Our research provides a perspective on the interaction between natural fire disturbance and ants on a large scale. Unlike most previous fire studies, we did not sample in the immediate period after the fire, beginning sampling 2 and 3 yr after the fire. We sampled across four different vegetation types, including chaparral and coastal sage scrub, two of the unique vegetation types to southern California, as well as grasslands and woodlands.

Additional impetus for this project came from the Natural Communities Conservation Planning efforts within the County of San Diego. Lands protected under the county's Multiple Species Conservation Plan (MSCP), one of the first large habitat reserves created in the country (Hierl et al. 2008), were di-

rectly in the footprints of these two fires with half of the protected areas within the reserve affected. This research was driven largely by the concern over the recovery of the natural areas within the reserve system given the potential for loss in biodiversity in the region, whether from fires or the growing human population. The threats and challenges to maintaining biodiversity and ecosystem function within urbanized landscapes are not well understood. Learning how ants, as potential indicator species, have responded to these large-scale "experiments" may provide insightful information regarding functional reserve design, environmental quality, and the postfire recovery process in the diverse wildlife communities of southern California.

Methods

Study Areas. This research was conducted within San Diego County, CA at four separate study areas: 1) Elliott Chaparral Reserve, 2) Little Cedar Ridge, 3) Rancho Jamul Ecological Reserve-Hollenbeck Canyon Wildlife Area, and 4) Santa Ysabel Open Space Preserve (Fig. 1). Elliott Chaparral Reserve (Elliott) had an average elevation of 195 m. The site completely burned in October 2003. Before the Cedar Fire, the majority of the reserve burned in 1944 or 1945. Major vegetation communities were chaparral and coastal sage scrub, dominated by chamise (*Adenostoma fasciculatum* Hook & Arn); California buckwheat (*Eriogonum fasciculatum* Benth); and annual, non-native grasses (*Avena* L. and *Bromus* L.). Little Cedar Ridge (Cedar) was located on the northern slopes of the Otay Mountain Wilderness. The Otay Wilderness encompassed $\approx 6,800$ ha and ranged in elevation from 250 to 1,000 m. Our study plots covered a small portion of the wilderness with an average elevation of 400 m. Vegetation at Cedar was characterized as chaparral and coastal sage scrub. Dominant plants included chamise; Tecate cypress (*Cupressus forbesii* Jepson); annual, non-native grasses; and California buckwheat. The entire area burned during the Otay Fire in October 2003. No record of previous fire could be found for the area. The Rancho Jamul Ecological Reserve and Hollenbeck Canyon Wildlife Area (collectively referred to as Rancho Jamul) had an average elevation of 250 m. It covered $\approx 3,000$ ha. The southern portion of this site burned during the Otay Fire of 2003. Rancho Jamul encompassed a variety of vegetation communities, including native and non-native grasslands; coastal sage scrub; and upland and riparian woodlands dominated by oaks, sycamores, and willows. In addition to natural vegetation communities, there were extensive, fallow agricultural fields. Dominant plant species at the site included annual, non-native grasses; California buckwheat; California sagebrush (*Artemisia californica* Less.); coast live oak (*Quercus agrifolia* Née); western sycamore (*Platanus racemosa* Nutt.); laurel sumac (*Malosma laurina* Nutt.); and San Diego sunflower (*Viguiera laciniata* Gray). The three low elevation sites, Elliott, Cedar, and Rancho Jamul, all experience similar weather patterns and temperatures

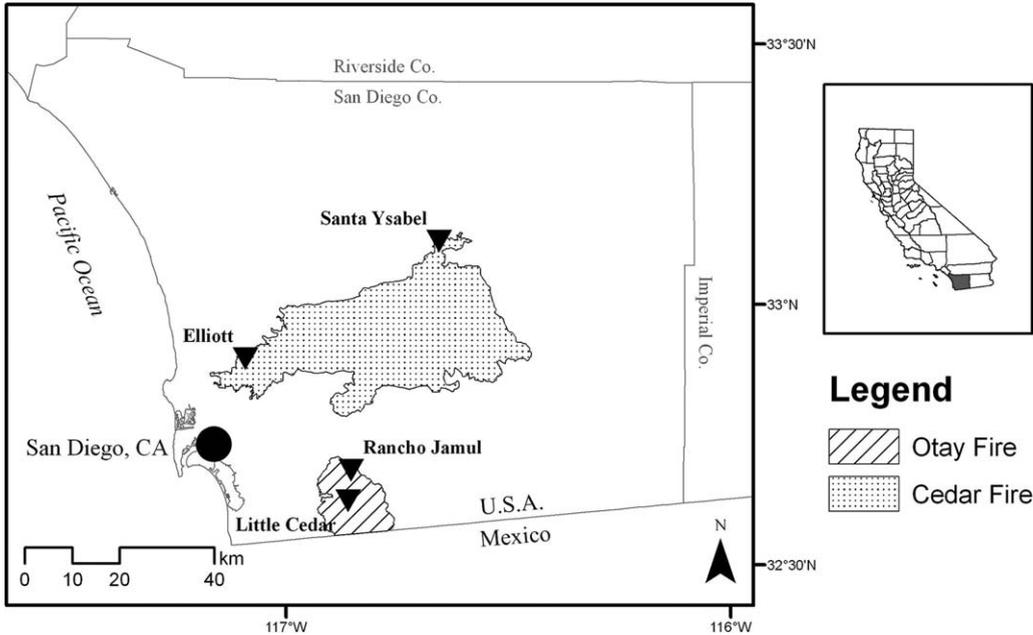


Fig. 1. Map of San Diego County, CA, showing the four study sites and indicating extent of the Cedar and Otay Fires of 2003.

based on the 30-yr averages developed by Franklin (2001) from over 100 weather stations located across southern California. Average July maximum temperatures range from 28 to 29°C. Average January minimum temperatures fall between 5 and 6°C. Annual precipitation averages between 28 and 31 cm. The actual rainfall for the three low elevation sites, as measured at Lindbergh Field, San Diego County where the long-term average is ≈ 25 cm, were as follows: 2001, 22 cm; 2002, 9 cm; 2003, 26 cm; 2005, 58 cm; and 2006, 15 cm (SDCWA 2010a). At an average elevation of 1,078 m, Santa Ysabel Open Space Preserve (Santa Ysabel) covered 1,500 ha and was our only high elevation study site. The area supported oak and pine woodlands, native and non-native grasslands, chaparral, coastal sage scrub, and riparian woodlands. Dominating the various vegetation communities were coast live oak; annual, non-native grasses; chamise; Engelmann oak (*Quercus engelmannii* Greene); and white sage (*Salvia apiana* Jepson). The average July maximum is 33°C, the average January daily minimum temperature is 1°C, and the average annual rainfall is 53 cm (Franklin 2001). Based on the rainfall measurements taken at Lake Henshaw, San Diego County, where the long-term average rainfall is nearly 70 cm, Santa Ysabel experienced the following annual precipitation rates during our survey efforts: 2002, 20 cm; 2003, 70 cm; 2005, 119 cm; and 2006, 54 cm (SDCWA 2010b). The eastern portion of the site burned in the 2003 Cedar Fire.

Vegetation Classification. We conducted linear vegetation transect surveys three times at each of the study plots. Each vegetation transect consisted of a 50-m point-intercept technique (Sawyer and Keeler-

Wolf 1995) with species composition, vegetation height, substrate, and leaf litter depth recorded every 0.5 m. Bauer's work with linear vegetation transects in southern California (Bauer 1943) has shown this technique to be comparable to the results of the more time consuming quadrat technique, especially in chaparral. The original, prefire vegetation surveys were conducted near the time when each plot was originally established and were used to classify each plot into one of four general vegetation types. Postfire vegetation surveys were conducted in 2005 and 2006 to assess the recovery (i.e., changes in shrub and tree cover estimates) of the vegetation surrounding each plot.

We grouped the study plots, based on the vegetation transect results, into four general categories: 1) chaparral, 2) coastal sage scrub, 3) grassland, and 4) woodland riparian (Table 1). We used a 25% coverage level to determine the vegetation classification of each plot. Based on the prefire vegetation survey, if 25% or more of the plants detected along the transect were typically associated with chaparral, coastal sage scrub, or one of the categories making up woodland riparian (Sawyer and Keeler-Wolf 1995, Hickman 1996), the plot was classified as such (Table 1). Where more than one vegetation type represented 25% or more of the transect, the more abundant classification was used. This classification was made regardless of the percent of the plot covered by grassland species. Because much of southern California has experienced some level of disturbance or invasion by exotic grasses, plots were only considered to be grassland if no other vegetation type represented 25% or more of the linear vegetation transect.

Table 1. Total number of sample plots for both post- and prefire periods by site, condition, and vegetation type

Vegetation Type	Site								Total
	Cedar		Elliott		Rancho Jamul		Santa Ysabel		
	Reference	Impact	Reference	Impact	Reference	Impact	Reference	Impact	
Chaparral	—	5	—	5	—	—	2 (2)	4 (4)	16 (6)
Coastal sage scrub	—	4	—	5	4 (4)	4 (4)	2 (1)	2 (1)	21 (10)
Grassland	—	—	—	—	4 (4)	4 (4)	2 (2)	1 (1)	11 (11)
Woodland riparian	—	—	—	—	2 (2)	2 (1)	4 (2)	7 (4)	15 (9)
Total	—	9	—	10	10 (10)	10 (9)	10 (7)	14 (10)	63 (36)

Number of plots sampled during the prefire period is in parentheses.

Chaparral arrays were dominated by evergreen plant species such as chamise (Sawyer and Keeler-Wolf 1995). We classified study plots as coastal sage scrub (CSS) based on the presence of such plant species as California sagebrush, white sage, and California buckwheat. A large percentage of grasslands in southern California are populated with several non-native genera of grass, including *Avena* and *Bromus*, although some native grasses are interspersed. For our analyses, we made no distinction between native and nonnative grasslands. The woodland riparian category included oak woodlands, pine forests, sycamore, and willow riparian areas, as well as seeps. Although these wooded vegetation types were diverse, we did not have sufficient numbers of replicates to test these individually. Most study plots could not be described as 100% one vegetation type or another, but were classified based on the results of the vegetation transect surveys. For all vegetation types, data for shrubs and trees were used for analyses of cover as well as plant community composition. Because we did not always conduct vegetation surveys during the same season, we did not include the data for annual forbs and herbs when determining the vegetation community of a study plot. We found that many of the herbs and annual forbs commonly disarticulated in the summer and fall periods, leaving open ground through winter.

Sampling of Ground Foraging Ants. Within each of the four sites, we used pitfall traps to sample the ground foraging ant assemblage. Pitfall traps have been used extensively to collect data on ant species abundance and distribution (Andersen 1995; Suarez et al. 1998, 2000; Bess et al. 2002; Boulton et al. 2005; Wilkinson et al. 2005; Stephens and Wagner 2006). Pitfall trapping techniques give a reasonable estimate of ant species composition (Andersen 1991, Stephens and Wagner 2006). Bestelmeyer et al. (2000) evaluated pitfall traps as a sampling method for ground-dwelling ants and found that most epigaeic species are well represented, especially in open vegetation communities. Pitfall sampling also provides an efficient, low cost method of collecting a relatively complete sample of ground foraging ants (Andersen 1991, Alonso and Agosti 2000, Stephens and Wagner 2006).

In total, we sampled 63 locations, across the four sites (Table 1). Sample locations were associated with herpetofauna arrays established as part of a large multi-taxa project conducted by the U.S. Geological

Survey (Mendelsohn et al. 2008, Rochester et al. 2010). At each of the 63 sampling locations, we set five ant traps in a cross “+” pattern overlaying the herpetofauna arrays. One trap was placed at the center of the cross and at the end of each arm 15 m from the center. Ant pitfall traps were 30-mm-diameter, 115-mm deep, 50-ml plastic centrifuge tubes partially filled with propylene glycol (antifreeze). Propylene glycol is a safer, nontoxic alternative to traditional ethylene glycol and serves as a preservative for the specimens (Suarez et al. 1998). We nested the traps in 2.54-cm-diameter (1-in.) class 200 PVC pipe buried vertically in the ground, so the top of the centrifuge tube was flush with the soil surface (Majer 1978). The PVC pipe and a closed, empty centrifuge tube remained in place between sampling periods to prevent trap locations from filling with soil and debris.

The timing of our ant sample collection efforts varied prefire to postfire and by study site. No prefire samples were collected from Elliott or Cedar. At Rancho Jamul, we conducted three rounds of prefire samples at 19 plots (March and August 2001, and January 2002). Prefire collections from 17 plots at Santa Ysabel occurred in July and November 2002, and again in March and June 2003. Postfire sampling was conducted between January 2005 and September 2006 at all four study sites with the first postfire samples collected 14 mo after the fires. Two samples were collected at each site each postfire year, one during winter (January–March) and the second in summer months (June–September). Because of site access issues, there were two exceptions regarding when the Santa Ysabel winter samples were taken: in 2002 it was taken in November, and in 2005 it was collected in May. Each sample period pitfall traps were open for ten consecutive days. After 10 d, the traps were closed and collected. We returned all samples to the laboratory for sorting, identification, and vouchering. Ant specimens were separated from other invertebrates, stored in 95% ethanol, and identified to species by the lead author whenever possible. When questionable or unknown species were encountered, specimens were sent to experienced authorities for identification or confirmation. Because alates may have originated outside the sampling locations, only workers were counted and included in analyses. Most voucher specimens are stored at the U.S. Geological Survey San Diego Field Station, San Diego, CA (see appendix 1 for total specimens collected and specimen locations).

Data Analyses. Capture rates of ants can be highly variable over short time periods because of shifts in activity levels related to variation in daily and seasonal environmental factors. Traps located next to established foraging trails also can yield exceptionally large capture numbers. To account for temporal variability in captures across sample periods, we averaged the per session capture rates of ant species for pre- and postfire sampling, thus creating a prefire and a postfire average capture rate for each ant species at each plot. In the cases where locations were not surveyed prefire, we averaged the results into a single, postfire sample. In total, we had a sample size of 99, with 36 samples from the prefire period and 63 samples from the postfire period.

To test for an effect of fire on ant diversity, we employed hierarchical linear modeling (mixed or multilevel modeling) techniques. We used the Shannon Diversity Index (Shannon 1948) as our response variable, applying the Shannon diversity calculation to the averaged count data for each of the samples from the pre- and postfire periods. We used mixed models to test a set of a priori hypotheses in which the main effects and interactions of vegetation type, burn condition (reference [unburned] versus impact [burned] plots), percent shrub and tree cover, and elevation (low versus high) might explain differences in the diversity measure among samples. In all models, we included site as a random effect. To account for correlations among multiple observations from individual plots, we also tested for random plot effects by nesting plot location within sites. We checked for deviations from normality of residuals using Shapiro-Wilk and Kolmogorov-Smirnov tests. Models satisfying the normality assumption then were evaluated and weighted using Akaike's Information Criterion as described by Burnham and Anderson (2002). We then used contrast tests of least squares means of four different conditions—postfire impact-prefire impact and postfire reference-prefire reference—to investigate the effects of burn condition on changes in species diversity following the fire. All models were run using SAS Statistical Software Version 9.1. (SAS Institute 2002–2003).

Because changes in the ground-foraging ant assemblage may not be reflected in a single diversity measure, we also tested for changes in the abundance of individuals within a species, species distribution across plots, and for shifts in the overall ant community structure using additional multivariate and univariate techniques. We performed multivariate analyses using the statistical software PRIMER-E (Version 6, Plymouth, United Kingdom; Clarke and Warwick 2001). To have sufficient power to test whether fire had a significant effect on community structure within or among vegetation types, we reclassified the variable burn condition into a condensed data classification, specifically, razed (samples from postfire impacted plots) and nonrazed (samples from prefire reference plots, postfire reference plots, and prefire impact plots). Before analyzing the data with PRIMER-E, we square-root transformed the data to remove some weight from the

most abundant species for a more balanced community analysis and created a Bray-Curtis similarity matrix (Clarke and Green 1988). Using the Bray-Curtis similarity matrices, we tested our hypotheses in a stepwise fashion using two-way crossed analysis of similarity (ANOSIM) tests, a multivariate permutation-based test similar to the analysis of variance test in univariate statistics (Clarke and Green 1988). We first tested whether the factors of vegetation type, site, or both were significantly predictive of differences in the prefire community structure. If vegetation was significant, the effect of the fire was tested separately for each vegetation type. If site was significant, it was used as a blocking factor in individual ANOSIM tests. To visualize the results of the similarity matrix, PRIMER-E generates multi-dimensional scaling (MDS) plots to ordinate the similarities between samples (Kruskal 1964), with similar samples appearing closer together and dissimilar samples farther apart (Clarke and Warwick 2001). Because we used a condensed data classification to compare our nonrazed samples to the razed samples, we carefully reviewed MDS plots for each subset of samples to ensure no systematic effects of time (pre- to postfire), site, or burn condition were causing erroneous test results. We used the ANOSIM results as an omnibus test for limiting type I error and determining if any further analyses were warranted. If condensed burn condition (i.e., razed versus nonrazed) was not a significant predictor of community structure within or among vegetation types, we conducted no further tests. If it was significant, we performed two additional multivariate tests. We used the BIO-ENV procedure (Clarke 1993) to determine if the total cover of shrubs and trees was significantly associated with observed patterns and the SIMPER analysis to identify which species contributed to the differences between samples (Clarke 1993).

Before testing for the effects of fire on the relative abundance of individual species within and between vegetation types, we first log-transformed species-specific capture data to decrease the weight of the most frequently captured ant species in the analyses. We calculated relative abundance by dividing transformed species-specific capture rates by the total sum of transformed capture rates for all species within the assemblage. We conducted contrast tests to check if changes in the relative abundance of individual species at the impact plots were significantly different from changes at reference plots. Contrasts were not paired tests because of the lack of prefire data at two of the sites. Variances were pooled across sample plots within each vegetation type. We used the Fisher Exact Test to determine if there were significant changes in the proportion of plots occupied by each species after the fire. We considered any test result to be significant when its P value < 0.10 . Because there were a large number of species captured across all vegetation types, many of which had low capture rates, we chose to focus our analyses and interpretation on the species that comprised the majority of the pre- and postfire communities. Therefore, we report results for the spe-

Table 2. Species diversity models using mixed regression techniques weighted by descending AIC values

Random effect(s)	Fixed effect(s) ^a	No. parameters	ΔAIC ^b	Model weight ^c	Log-likelihood
Array (site)	Burn condition	5	0.000	0.738	-54.65
Array (site)	Elevation	5	3.500	0.128	-56.40
Array (site)	Burn condition+Veg	8	3.800	0.110	-53.55
Site	Shrub cover*Veg	8	8.400	0.011	-55.85
Array (site)	Null	4	10.500	0.004	-60.90
Array (site)	Shrub cover	5	10.700	0.004	-60.00
Array (site)	Burn condition*Veg	9	11.200	0.003	-56.25
Array (site)	Veg	7	14.700	0.000	-60.00
Array (site)	Shrub cover*Veg	9	14.800	0.000	-58.05
Site	Shrub cover	4	14.900	0.000	-63.10
Site	Burn condition+Veg	7	16.400	0.000	-60.85
Site	Burn condition	4	17.100	0.000	-64.20
Site	Null	3	18.400	0.000	-65.85
Site	Veg	6	18.800	0.000	-63.05
Site	Elevation	4	19.100	0.000	-65.20
Site	Burn condition*Veg	8	20.000	0.000	-61.65

^a Key: Condition (Reference and Impact); Elevation (low and high); Veg (Chaparral, Coastal Sage Scrub, Grassland, and Woodland Riparian); Shrub Cover (Percent shrub and tree cover).

^b Difference in AIC values between each model and the low-AIC model; when comparing the relative fits of a suite of models, differences in AIC values among models indicate the relative support for different models.

^c AIC model weight; weights have a probabilistic interpretation and indicate the probability that the given model would be selected as the best-fitting model if the data were collected again under identical conditions.

cies which comprised >5% of the community within each vegetation type based on the raw, nontransformed detection results.

Results

Vegetation. Across the burned plots, the percent of shrub and tree cover, as measured during the vegetation transect surveys, declined in chaparral and CSS but remained relatively constant in grassland and woodland riparian pre- to postfire. At impacted chaparral plots shrub and tree cover dropped from a mean of 67% (SE = 5.4) prefire to 31% (SE = 3.9) postfire, while reference plots showed little change, with a mean of 68% (SE = 5.5) prefire compared with 66% (SE = 10.8) postfire. Similarly, impact plots in CSS showed large declines in shrub and tree cover, dropping from 50% (SE = 6.3) prefire to 12.6% (SE = 3.7) postfire, while reference plots showed modest differences between prefire (58% [SE = 8.2]) and postfire (55% [SE = 8.6]) cover. Both the reference and impact plots in grasslands had very low shrub and tree cover prefire, at 8% (SE = 5.6) and 1% (SE = 0.8), respectively. Postfire, we only measured 2% (SE = 1.3) in the impact plots and 3% (SE = 1.7) shrub and tree cover in reference plots. The prefire average on the woodland riparian impact plots was 35% (SE = 10.8) and postfire measured 24% (SE = 6.4). Shrub and tree cover on the reference woodland riparian plots remained relatively unchanged pre- to postfire, with 30% (SE = 34.4) and 37% (SE = 31.3) cover values, respectively. The woodland riparian plots had highly variable shrub and tree coverage as this grouping included not only oak woodlands and pine forest, but also seeps, which typically had lower cover values.

Ant Species Diversity and Community Structure. In total, 34,371 worker ants, encompassing 23 genera and 58 separate species, were sampled during the course of

this study. The species captured during this research represented 51% of the 45 genera and 21% of the 270 species known to be present in California (California Academy of Sciences 2008). Eight species, *Dorymyrmex bicolor* (Wheeler), *Formica francoeuri* (Bolton), *Forelius mccoooki* (McCook), *Forelius pruinosus* (Roger), *Messor andrei* (Mayr), *Pheidole vistana* (Emery), *Pogonomyrmex rugosus* (Emery), and *Solenopsis xyloni* (McCook), represented the majority (82%) of all ants collected before and after the 2003 fires. Regardless of vegetation type, whether an array burned or not was the most predictive factor of differences in ant diversity measures among samples ($F_{3,58,8} = 6.4, p < 0.001$). Results of the hierarchical modeling efforts showed the top mixed regression model included the fixed effect, burn condition, and random effects of site and array (Table 2). This top model accounted for 74% of the total model weights and was six times more likely than the next highest-ranking model to be selected as the best-fitting model if the data were to be collected again under identical conditions. Least squares means show that in reference plots, the overall diversity index increased from 1.77 (SE = 0.11) to 2.11 (SE = 0.09) after the fires. In impact plots, the overall diversity index increased from 1.73 (SE = 0.14) to 1.85 (SE = 0.13) after the fires. Contrast tests revealed the increase was significantly less pronounced (Estimate = -0.220, Z = -1.786, P = 0.074) in the impact plots than in the unburned reference plots, suggesting a negative effect of fire on ant diversity.

The initial ANOSIM test revealed that the structure of the ant assemblages varied significantly among the four vegetation types and two study sites that we sampled during the prefire effort. The ant community at Rancho Jamul was different than that at Santa Ysabel (R = 0.393, P = 0.001). The vegetation type at each plot was also predictive of differences in the ant com-

Table 3. Relative abundance and standard error (in parentheses) of ant species in impact and reference plots for Coastal Sage Scrub Habitat

Subfamily	Species	Reference (unburn)		Impact (burn)	
		Preburn	Postburn	Preburn	Postburn
Dolichoderinae	<i>F. mccooki</i>	0.08 (0.03)	0.08 (0.03)	0.20 (0.03)	0.07 (0.03)
Dolichoderinae	<i>F. pruinosus</i>	0.00 (0.00)	0.09 (0.04)	0.00 (0.00)	0.03 (0.02)
Ecitoninae	<i>Neivamyrmex nigrescens</i>	0.00 (0.00)	0.03 (0.01)	0.00 (0.00)	0.03 (0.02)
Myrmicinae	<i>C. californica</i> [*]	0.15 (0.03)	0.06 (0.01)	0.21 (0.04)	0.02 (0.01)
Myrmicinae	<i>C. hespera</i>	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.05 (0.02)
Myrmicinae	<i>Crematogaster mormonum</i>	0.00 (0.00)	0.01 (0.00)	0.00 (0.00)	0.02 (0.01)
Myrmicinae	<i>M. andrei</i> [*]	0.00 (0.00)	0.03 (0.01)	0.00 (0.00)	0.32 (0.05)
Myrmicinae	<i>P. vistana</i>	0.03 (0.01)	0.01 (0.00)	0.15 (0.03)	0.29 (0.04)
Myrmicinae	<i>P. rugosus</i>	0.55 (0.08)	0.45 (0.07)	0.19 (0.08)	0.02 (0.01)
Myrmicinae	<i>S. xyloni</i>	0.07 (0.02)	0.05 (0.01)	0.05 (0.01)	0.09 (0.02)
Myrmicinae	<i>Tetramorium spinosum</i>	0.03 (0.01)	0.01 (0.00)	0.02 (0.01)	0.01 (0.01)
	Other ^a	0.09	0.17	0.18	0.05
Total		1.00	1.00	1.00	1.00

^aSpecies comprising < 5% in each vegetation type were grouped and listed as "other".
^{*}*P* < 0.10.

munity detected ($R = 0.280, P = 0.002$). Based on these results, subsequent ANOSIM analyses were performed within each vegetation type separately with site included as a blocking factor. The individual ANOSIM tests showed that the ant community structure in razed samples was significantly different from the community structure in nonrazed samples in CSS ($R = 0.578, P = 0.003$); but not chaparral ($R = -0.213, P = 0.935$); grassland ($R = 0.096, P = 0.227$); or woodland riparian ($R = 0.070, P = 0.157$). The 2-way crossed SIMPER analysis showed that the average dissimilarity between the razed and nonrazed CSS samples was 76.04%, consisting of 13.84% from *M. andrei*, 10.25% from *P. rugosus*, 9.69% from *F. mccooki* (Buckley), 8.90% from *P. vistana*, 8.77% from *S. xyloni*, and 3.96% from *Crematogaster californica* (Wheeler). These six species account for nearly 73% of the overall 76% dissimilarity between the razed and nonrazed samples from CSS plots. Results of the BIO-ENV for CSS showed that the percent of shrub and tree cover was a significant predictor of change in community structure ($\rho = 0.292, P < 0.001$; Fig. 2). On average, shrub and tree cover in razed CSS samples was only

13% (SE = 3.7) compared with 53% (SE = 4.3) in nonrazed samples.

The proportions (relative abundance) of individual species by vegetation type and burn condition are presented in Tables 3–6. Because changes in ant community structure were significant only in coastal sage scrub, we conducted contrast tests on the most abundant ant species (species comprising >5% of the total ant abundance) recorded in this community during pre- and postfire sampling. The eight focal species were *C. californica*, *Crematogaster hespera* (Wheeler), *F. mccooki*, *F. pruinosus*, *M. andrei*, *P. rugosus*, *P. vistana*, and *S. xyloni*. *M. andrei* comprised <1% of all prefire ant captures across all plots. However, in CSS the species comprised 32.1% of all captures in the impact plots following the fires in comparison to 3% of the postfire reference plots (Diff = 0.29, SE = 0.12, $P = 0.022$). The proportion of impacted plots occupied by *M. andrei* also increased from ≈1% prefire to 86.7% postfire in CSS. Although not significant, *M. andrei* appeared to have increased slightly across all other vegetation types following the fire (Fig. 3).

Table 4. Relative abundance and standard error (in parentheses) of ant species in impact and reference plots for Chaparral Habitat

Subfamily	Species	Reference (unburn)		Impact (burn)	
		Preburn	Postburn	Preburn	Postburn
Dolichoderinae	<i>D. bicolor</i>	0.28 (0.08)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Dolichoderinae	<i>Dorymyrmex insanus</i>	0.01 (0.00)	0.00 (0.00)	0.03 (0.01)	0.02 (0.01)
Dolichoderinae	<i>F. pruinosus</i>	0.00 (0.00)	0.17 (0.05)	0.00 (0.00)	0.00 (0.00)
Formicinae	<i>Formica moki</i>	0.01 (0.00)	0.01 (0.00)	0.06 (0.01)	0.04 (0.02)
Formicinae	<i>Camponotus dumetorum</i>	0.03 (0.01)	0.04 (0.01)	0.38 (0.07)	0.10 (0.04)
Formicinae	<i>Camponotus vicinus</i>	0.01 (0.00)	0.00 (0.00)	0.11 (0.04)	0.00 (0.00)
Myrmicinae	<i>Crematogaster mormonum</i>	0.00 (0.00)	0.03 (0.01)	0.05 (0.01)	0.05 (0.02)
Myrmicinae	<i>M. andrei</i>	0.14 (0.03)	0.17 (0.04)	0.00 (0.00)	0.07 (0.03)
Myrmicinae	<i>Pheidole hyatti</i>	0.12 (0.03)	0.02 (0.00)	0.22 (0.05)	0.05 (0.02)
Myrmicinae	<i>P. vistana</i>	0.15 (0.02)	0.08 (0.02)	0.00 (0.00)	0.40 (0.07)
Myrmicinae	<i>Pogonomyrmex subnitidus</i>	0.00 (0.00)	0.27 (0.03)	0.00 (0.00)	0.00 (0.00)
Myrmicinae	<i>S. xyloni</i>	0.05 (0.01)	0.02 (0.00)	0.00 (0.00)	0.17 (0.05)
	Other ^a	0.21	0.20	0.15	0.10
Total		1.00	1.00	1.00	1.00

^aSpecies comprising < 5% in each vegetation type were grouped and listed as "other".

Table 5. Relative abundance and standard error (in parentheses) of ant species in impact and reference plots for Grassland Habitat

Subfamily	Species	Reference (unburn)		Impact (burn)	
		Prefburn	Postburn	Prefburn	Postburn
Dolichoderinae	<i>F. mccooki</i>	0.25 (0.08)	0.36 (0.10)	0.03 (0.01)	0.00 (0.00)
Ecitoninae	<i>Neivamyrmex californicus</i>	0.00 (0.00)	0.01 (0.00)	0.01 (0.00)	0.00 (0.00)
Formicinae	<i>Camponotus semitestaceus</i>	0.06 (0.03)	0.03 (0.02)	0.01 (0.00)	0.01 (0.00)
Myrmicinae	<i>C. californica</i>	0.17 (0.05)	0.04 (0.01)	0.18 (0.04)	0.01 (0.00)
Myrmicinae	<i>Crematogaster mormonum</i>	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.02 (0.01)
Myrmicinae	<i>M. andrei</i>	0.00 (0.00)	0.13 (0.04)	0.10 (0.04)	0.30 (0.08)
Myrmicinae	<i>Monomorium ergatogyna</i>	0.06 (0.02)	0.04 (0.02)	0.03 (0.01)	0.00 (0.00)
Myrmicinae	<i>Pheidole clementensis</i>	0.05 (0.02)	0.01 (0.00)	0.03 (0.01)	0.05 (0.01)
Myrmicinae	<i>Pheidole hyatti</i>	0.04 (0.02)	0.01 (0.00)	0.11 (0.05)	0.05 (0.02)
Myrmicinae	<i>P. vistana</i>	0.00 (0.00)	0.00 (0.00)	0.27 (0.07)	0.35 (0.06)
Myrmicinae	<i>P. rugosus</i>	0.15 (0.07)	0.05 (0.02)	0.00 (0.00)	0.02 (0.01)
Myrmicinae	<i>Pogonomyrmex subnitidus</i>	0.11 (0.04)	0.08 (0.04)	0.00 (0.00)	0.00 (0.00)
Myrmicinae	<i>Solenopsis molesta</i>	0.04 (0.02)	0.00 (0.00)	0.03 (0.01)	0.01 (0.00)
Myrmicinae	<i>S. xyloni</i>	0.03 (0.01)	0.12 (0.03)	0.11 (0.04)	0.13 (0.04)
Myrmicinae	<i>Tetramorium spinosum</i>	0.00 (0.00)	0.04 (0.02)	0.00 (0.00)	0.03 (0.01)
	Other ^a	0.05	0.06	0.09	0.02
Total		1.00	1.00	1.00	1.00

^aSpecies comprising < 5% in each vegetation type were grouped and listed as "other."

Further results of the individual species contrast tests showed a significant net decrease in *C. californica*, (Diff = -0.10, SE = 0.04, P = 0.019). It comprised 21.2% of the prefire CSS community, but only 2.3% of the total population in impact plots postfire. Although the relative abundance of only *M. andrei* and *C. californica* populations were the only species that showed significant effects of the burn, we present the postfire changes in relative abundance at reference and impact plots for the eight most abundant species in CSS (Fig. 4).

Discussion

Species Diversity. In the 2nd and 3rd yr following wildfires in southern California, we found a net negative effect of fire on the overall diversity of ground

foraging ants at impacted plots compared with reference plots across all habitat types. Our results suggest that this was likely because of changes in community structure rather than the loss of species richness. Although we found a negative effect of fire on ant diversity, the increases in species diversity in both the impact and reference plots suggest that ant communities had some resiliency to the effects of fire. The higher diversity at reference plots suggests that unburned areas retained healthy, viable ant populations. Unburned patches within a fire site can provide refuge and source populations from which to recolonize (Kaspari and Majer 2000, Ferrenberg et al. 2006). In addition, ants may be well equipped to survive fire. Stephens and Wagner (2006) found that only 2% of the population of a mature ant colony is active on the surface, so if fire breaks out, direct mortality is limited

Table 6. Relative abundance and standard error (in parentheses) of ant species in impact and reference plots for Woodland Habitat

Subfamily	Species	Reference (unburn)		Impact (burn)	
		Prefburn	Postburn	Prefburn	Postburn
Dolichoderinae	<i>D. bicolor</i>	0.00 (0.00)	0.00 (0.00)	0.20 (0.09)	0.11 (0.06)
Dolichoderinae	<i>F. mccooki</i>	0.06 (0.02)	0.03 (0.01)	0.01 (0.01)	0.09 (0.05)
Dolichoderinae	<i>F. pruinosus</i>	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.10 (0.06)
Dolichoderinae	<i>Liometopum occidentale</i>	0.18 (0.05)	0.17 (0.05)	0.01 (0.00)	0.04 (0.02)
Dolichoderinae	<i>Tapinoma sessile</i>	0.02 (0.00)	0.05 (0.01)	0.12 (0.03)	0.03 (0.01)
Ecitoninae	<i>Neivamyrmex californicus</i>	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.07 (0.03)
Formicinae	<i>Camponotus semitestaceus</i>	0.01 (0.00)	0.04 (0.02)	0.13 (0.03)	0.03 (0.01)
Formicinae	<i>Formica francoeuri</i>	0.24 (0.10)	0.30 (0.09)	0.17 (0.08)	0.11 (0.06)
Formicinae	<i>Formica moki</i>	0.05 (0.01)	0.05 (0.02)	0.06 (0.02)	0.05 (0.02)
Formicinae	<i>Prenolepis imparis</i>	0.11 (0.04)	0.03 (0.01)	0.00 (0.00)	0.01 (0.00)
Myrmicinae	<i>C. californica</i>	0.00 (0.00)	0.05 (0.02)	0.00 (0.00)	0.01 (0.01)
Myrmicinae	<i>C. hespera</i>	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.01 (0.00)
Myrmicinae	<i>M. andrei</i>	0.01 (0.00)	0.07 (0.03)	0.04 (0.01)	0.10 (0.04)
Myrmicinae	<i>Pheidole hyatti</i>	0.03 (0.01)	0.03 (0.01)	0.14 (0.03)	0.14 (0.06)
Myrmicinae	<i>P. vistana</i>	0.00 (0.00)	0.01 (0.00)	0.00 (0.00)	0.00 (0.00)
Myrmicinae	<i>P. rugosus</i>	0.12 (0.05)	0.04 (0.02)	0.00 (0.00)	0.00 (0.00)
Myrmicinae	<i>Solenopsis molesta</i>	0.05 (0.02)	0.02 (0.01)	0.00 (0.00)	0.05 (0.03)
Myrmicinae	<i>S. xyloni</i>	0.03 (0.01)	0.02 (0.00)	0.00 (0.00)	0.00 (0.00)
	Other ^a	0.11	0.07	0.12	0.05
Total		1.00	1.00	1.00	1.00

^aSpecies comprising < 5% in each vegetation type were grouped and listed as "other."

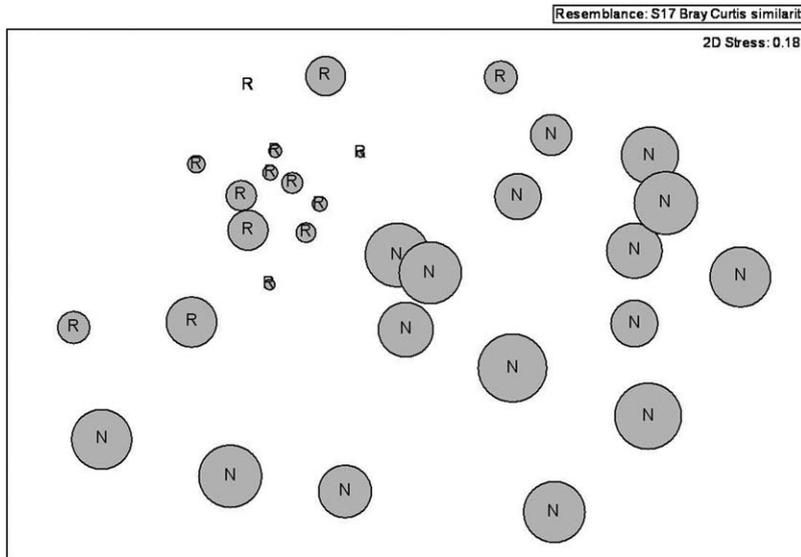


Fig. 2. Multidimensional Scaling (MDS) bubble plot of the above ground ant assemblage in coastal sage scrub. Each bubble represents a single sample with “R” and “N” labels referring to razed ($n = 15$) and nonrazed conditions ($n = 16$), respectively. Bubble size is proportional to percent shrub and tree cover. The relative distances between points (=plots) represent the relative similarity of sampled ant assemblage.

to this small percentage of foragers although the majority of the colony survives. Ants active on the surface at the time of fire may be able to find shelter in rocks, downed wood, and soil cracks (Underwood and Fisher 2006). The insulating properties of soil are the largest source of refuge and can shelter the majority of the colony from the high temperatures of a fire (Sweeney 1956, Force 1981, Andersen 1991).

Community Structure and Individual Species Responses. Significant changes to ant community structure occurred in the ant assemblage present in coastal sage scrub habitat. Coastal sage scrub may be the most vulnerable (Keeley and Keeley 1984) and structurally

complex of the four vegetation types, with the postfire changes in vegetation structure being reflected in the ant community. This habitat had the largest decline in average shrub and tree cover 2–3 yr after the fire. Although average shrub and tree cover also declined in chaparral, the plants of this community are fire adapted (Keeley and Keeley 1984), and therefore the ant community may also be equally resilient to fire. The low number of nonrazed samples in chaparral also may have decreased the power to which we could estimate and detect burn effects. However, Suarez et al. (2000) sampled ants before the fire using pitfall traps at the Elliott Chaparral Reserve and reported the

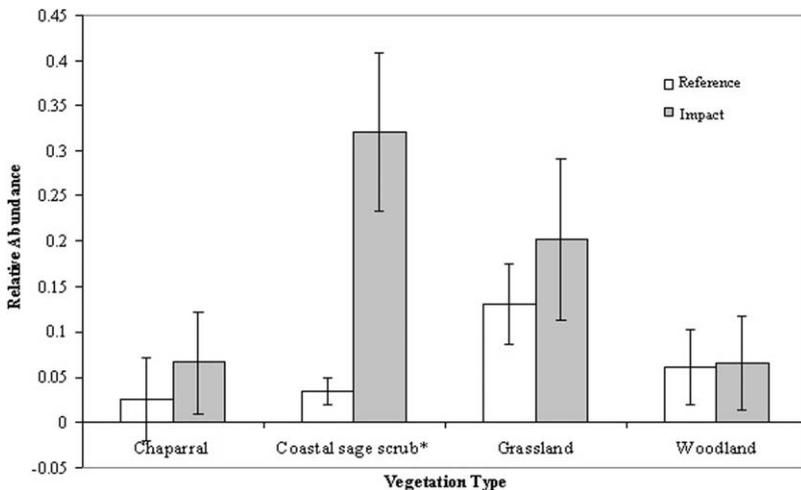


Fig. 3. Change in relative abundance of *M. andrei* in prefire and postfire plots across all vegetation types. Error bars represent \pm one standard error. Asterisk indicates $P < 0.10$.

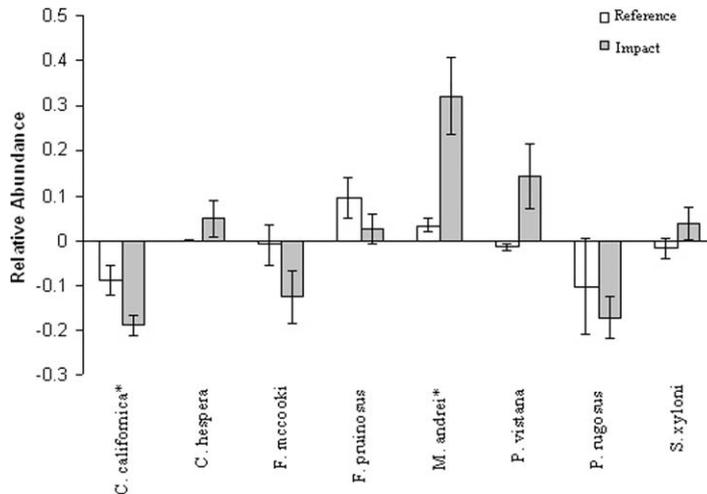


Fig. 4. Comparison of relative abundance of ant species in coastal sage scrub in impact plots versus reference plots. Postfire values are subtracted from prefire values to determine relative abundance. Error bars represent \pm one standard error.

native ant community consisted primarily of the same species we detected after the fires: *P. vistana*, *F. mccooki*, *C. californica*, *M. andrei*, *Temnothorax andrei* (Emery), and *S. xyloni*. Similarly, we did not find significant differences in ant community structure in woodland riparian or grassland plots. Woodland riparian plots may be more fire resistant as generally higher soil and plant moisture levels prevent the habitat from completely burning, retaining some of its structure and possibly serving as refugia for ants during the fire (Keeley and Keeley 1984). Grasslands may retain much of their native ant diversity by being able to recover quickly after fires (Keeley and Keeley 1984).

The difference in the postfire ant community in coastal sage scrub was shaped primarily by the increase in the abundance of *M. andrei*, as shown by both the multivariate SIMPER analysis and significant contrast tests. Favorable changes in landscape and habitat resources appear to have benefited *M. andrei*. The increase of bare soil from the fire and associated higher surface temperatures may alter availability of nesting sites and affect the foraging activities of some species (MacKay and MacKay 1989, Ratchford et al. 2005, Lafleur et al. 2006). *M. andrei* may tolerate or prefer the higher ground temperatures associated with exposed soils, translating into increased foraging opportunities and increased food availability to the colony, which in turn can lead to an increase in abundance (Wilkinson et al. 2005). Fire may also affect available food sources, such as the seeds that harvester ants gather (Ratchford et al. 2005). Underwood and Christian (2009) found an increase in burned plots of seed harvesters in the genus *Messor*, including *M. andrei* (the most abundant species in their study), which they attributed to changes in vegetation related characteristics, such as forb cover. Arnan et al. (2006) found that congener *Messor capitatus* (Latreille) benefited from increased production of seeds after fire. Altered habitat structure and a potential increase in resource

availability after the fire may have given *M. andrei* a similar competitive advantage. Along with environmental changes, inter-specific competition may have shifted, allowing *M. andrei* to expand from its prefire distribution (Andersen and Yen 1985).

It is also expected then that species with specialized adaptations to closed-canopy habitats would decline after a fire because of a reduction in suitable habitat. There was a significant decline in *C. californica* in burned plots. The decline may be related to direct mortality and nesting habits. *C. californica* is known to cultivate aphids and coccids at the bases and on roots of various plants, so their decline may be because of the vulnerability of these plants nonsoil nests, or both. (UTEF 2001). *Crematogaster* species make nests in plants, logs or decaying wood, or nests fashioned out of carton they manufacture themselves (Wheeler and Wheeler 1986). These colonies are more susceptible to mortality than *Crematogaster* colonies that nest under rocks in the soil (Wheeler and Wheeler 1986). The loss of these above ground colonies and the suitable habitat they occupied is a likely source of the declines that we detected.

Responses of ants to fire have varied among different studies (Underwood and Fisher 2006), and have been characterized as being erratic (Alonso and Agosti 2000). Variation in ant community responses to fire may be related to individual fire properties: time since a fire, fire intensity, and habitat (Ratchford et al. 2005, Arnan et al. 2006). The intensity of a fire affects recovery time, and in habitats with complex vegetation structures, the time needed to regain this complexity in the landscape would be longer (Ratchford et al. 2005). Increased ant captures after a fire may be because of changes in actual abundance or changes in activity. For example, ants may be more active recolonizing or foraging, increasing detection probability for some species (Andersen and Yen 1985, Underwood and Christian 2009). However, sampling done 2–3 yr

postfire may reflect changes in the habitat and in ant community structure, rather than short term activity.

Conservation and Management Implications. In general, the MSCP reserve system supports a diverse assemblage of native ground foraging ants. To date, the MSCP reserve system remains relatively free of invasion by exotic ants and protects a number of vegetation types supporting this ant assemblage. The results of our study showed the ant communities to be fairly resilient to the short term impacts of fire, although the impact to diversity was clearly negative and community structure was altered in coastal sage scrub within the San Diego Multiple Species Conservation Plan Lands. Severe fires appear to be occurring more frequently in recent years in southern California and San Diego County (e.g., Cedar and Otay Fires in 2003, Harris and Witch Creek Fires in 2007). Shorter fire intervals, high intensity fires, or a combination of both may disrupt populations beyond their ability to recover successfully after a fire, altering the natural systems in wilderness areas. Continued monitoring is necessary to assess the long-term impacts on ant communities as the fire cycle shifts in southern California.

Changes in ant communities are likely to affect plants and animals with which they coexist. For instance, the coastal horned lizard, *P. coronatum*, prefers to forage in open habitats (Stebbins 1985), with harvester ants making up a large portion of the adult diet (Suarez et al. 2000). At our study sites, we detected an increase in the number of *P. coronatum* in CSS postfire impact plots (Rochester et al. 2010). The increased presence of *M. andrei* in the burned scrub habitats is potentially benefiting *P. coronatum*. Because most ants are not directly affected by fire, changes in the ant community could provide valuable information about how a landscape has changed as a result of fire. Longer term studies are needed to monitor the extended effects of fire on ants (Arnan et al. 2006). If severe fires become more frequent in southern California, discovering patterns of ant recovery following wildfire may be useful in assessing the region's ability to recover from large-scale wildfire.

Acknowledgments

We are grateful for the many hours of technical assistance provided by Denise Clark, Krista Mendelsohn, and Jim Starrett in support of this project. We also thank Andrew Suarez at University of Illinois Champaign-Urbana and Phil Ward at University of California, Davis, for their expertise in identification of specimens. We thank Julie Yee for providing statistical advice and for reviewing the manuscript. We also thank Amy Vandergast, Emily Underwood, and the two anonymous reviewers for their time and input reviewing the manuscript. For site access, we thank the managers of the four study sites (Tim Dillingham of California Department of Fish & Game; James Stowers, Bobbi Thompson, and Jeffrey Rundell of San Diego County Parks & Recreation Department; Isabelle Kay of the University of California, San Diego Elliott Chaparral Reserve; Joyce Schlachter and Janaye Byergo of Bureau of Land Management). Funding for this project was provided in part by the San Diego MSCP Initiative, the San Diego Association of Governments *TransNet*

Environmental Mitigation Program, and the U.S. Geological Survey Western Ecological Research Center. All work was performed under U.S. Fish and Wildlife permit TE-045994-7 and individually held California Department of Fish and Game scientific collecting permits. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. government.

References Cited

- Agarwal, V. M., N. Rastogi, and S.V.S. Raju. 2007. Impact of predatory ants on two lepidopteran insect pests in Indian cauliflower agroecosystems. *J. Appl. Entomol.* 131: 493–500.
- Alonso, L. E., and D. Agosti. 2000. Biodiversity studies, monitoring, and ants: an overview, pp. 1–8. *In* Agosti et al. (eds.), *Ants: standard methods for measuring and monitoring biodiversity*. Smithsonian Institution Press, Washington, DC.
- Andersen, A. N. 1991. Responses of ground-foraging ant communities to three experimental fire regimes in a savanna forest of tropical Australia. *Biotropica* 23: 575–585.
- Andersen, A. N. 1995. A classification of Australian ant communities based on functional groups which parallel plant-life forms in relation to stress and disturbance. *J. Biogeogr.* 22: 15–29.
- Andersen, A. N., and A. L. Yen. 1985. The immediate effects of fire on ants in the semi-arid mallee region of southwestern Victoria. *Aust. J. Ecol.* 10: 25–30.
- Arnan, X., A. Rodrigo, and J. Retana. 2006. Post-fire recovery of Mediterranean ground ant communities follows vegetation and dryness gradients. *J. Biogeogr.* 33: 1246–1258.
- Bauer, H. L. 1943. The statistical analysis of chaparral and other plant communities by means of transect samples. *Ecology* 24: 45–60.
- Bess, E. C., R. R. Parmenter, S. McCoy, and M. C. Molles, Jr. 2002. Responses of a riparian forest-floor arthropod community to wildfire in the middle Rio Grande Valley, New Mexico. *Environ. Entomol.* 34: 96–104.
- Bestelmeyer, B. T., D. Agosti, L. E. Alonso, C.R.F. Brandão, W. L. Brown, Jr., J.H.C. Delabie, and R. Silvestre. 2000. Field techniques for the study of ground-dwelling ants: an overview, description, and evaluation, pp. 122–144. *In* Agosti et al. (eds.), *Ants: standard methods for measuring and monitoring biodiversity*. Smithsonian Institution Press, Washington, DC.
- Boulton, A. M., K. F. Davies, and P. S. Ward. 2005. Species richness, abundance, and structure of ground-dwelling ants in northern California grasslands: role of plants, soil, and grazing. *Environ. Entomol.* 34: 96–104.
- Brattstrom, B. H. 1952. The food of the night lizards, genus *Xantusia*. *Copeia* 1952: 168–172.
- Bromham, L., M. Cardillo, A. F. Bennett, and M. A. Elgar. 1999. Effects of stock grazing on the ground invertebrate fauna of woodland remnants. *Aust. J. Ecol.* 24: 199–207.
- Brown, M.J.F., and K. G. Human. 1997. Effects of harvester ants on plant species distribution and abundance in a serpentine grassland. *Oecologia* 112: 237–243.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed. Springer, New York.
- California Acad. of the Sciences. 2008. California ants. (<http://www.antweb.org/california.jsp>).
- Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* 18: 117–143.

- Clarke, K. R., and R. H. Green. 1988. Statistical design and analysis for a 'biological effects' study. *Marine Ecology Progressive Series*. 46: 213–26.
- Clarke, K. R., and R. M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd ed. PRIMER-E: Plymouth, United Kingdom.
- Christianini, A. V., and P. S. Oliveira. 2010. Birds and ants provide complementary seed dispersal in a neotropical savanna. *J. Ecol.* 98: 573–582.
- Cuautle, M., V. Rico-Gray, and C. Diaz-Castelazo. 2005. Effects of ant behaviour and presence of extrafloral nectaries on seed dispersal of the Neotropical myrmecochore *Turnera ulmifolia* (Turneraceae). *Biol. J. Linn. Soc.* 86: 67–77.
- Donnelly, D. L., and J. H. Giliomee. 1985. Community structure of epigeic ants in a pine plantation and in newly burnt fynbos. *J. Entomol. Soc. South Afr.* 48: 259–265.
- Ferrenberg, S. M., D. W. Schwilk, E. E. Knapp, E. Groth, and J. E. Keeley. 2006. Fire decreases arthropod abundance but increases diversity: early and late season prescribed fire effects in a Sierra Nevada mixed-conifer forest. *Fire Ecol.* 2: 79–102.
- Folgrait, P. J. 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodivers. Conserv.* 7: 1221–1244.
- Force, D. C. 1981. Postfire insect succession in southern California chaparral. *Am. Nat.* 117: 575–582.
- Franklin, J. 2001. Geographic information science and ecological assessment, pp. 151–161. In P. Bourgeron, M. Jensen, and G. Lessard (eds.), *An integrated ecological assessment protocols guidebook*. Springer, New York.
- Hanes, T. L. 1971. Succession after fire in the chaparral of southern California. *Ecol. Monogr.* 41: 27–52.
- Hickman, J. C. 1996. *The Jepson manual: higher plants of California*. University of California Press, Berkeley and Los Angeles.
- Hierl, L. A., J. Franklin, D. H. Deutschman, H. M. Regan, and B. S. Johnson. 2008. Assessing and prioritizing ecological communities for monitoring in a regional habitat conservation plan. *Environ. Manage.* 42: 165–179.
- Hobbs, R. J. 1985. Harvester ant foraging and plant species distribution in annual grassland. *Oecologia* 67: 519–523.
- Hölldobler, B., and E. O. Wilson. 1990. *The ants*. Harvard University Press, Cambridge, MA.
- Kaspari, M., and J. D. Majer. 2000. Using ants to monitor environmental change, pp. 89–98. In Agosti et al. (eds.), *Ants: standard methods for measuring and monitoring biodiversity*. Smithsonian Institution Press, Washington, DC.
- Keeley, J. E. 2005. Fire as a threat to biodiversity in fire-type shrublands. United States Department of Agriculture Forest Service Gen. Tech. Rep. PSW-GTR-195.2005.
- Keeley, J. E., and C. J. Fotheringham. 2001. Historic fire regime in southern California shrublands. *Conserv. Biol.* 15: 1536–1548.
- Keeley, J. E., and S. C. Keeley. 1981. Post-fire regeneration of southern California chaparral. *Am. J. Bot.* 68: 524–530.
- Keeley, J. E., and S. C. Keeley. 1984. Postfire recovery of coastal sage scrub. *Am. Midl. Nat.* 111: 105–117.
- Keeley, J. E., C. J. Fotheringham, and M. Morais. 1999. Re-examining fire suppression impacts on brushland fire regimes. *Science* 284: 1829–1832.
- Keeley, J. E., C. J. Fotheringham, and M. A. Moritz. 2004. Lessons from the October 2003 wildfires in southern California. *J. Forestry*. 102: 26–31.
- Kruskal, J. B. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 29: 1–27.
- Lafleur, B., W. F. J. Parsons, R. L. Bradley, and A. Francoeur. 2006. Ground-nesting ant assemblages and their relationships to habitat factors along a chronosequence of post-fire-regenerated lichen-spruce woodland. *Environ. Entomol.* 35: 1515–1524.
- Luque, G. M., J. Reyes-López, and J. Fernández-Haeger. 2007. Recovery of ground ant (Hymenoptera: Formicidae) communities six years after a major environmental disaster. *Environ. Entomol.* 36: 337–347.
- MacKay, W. P., and E. E. MacKay. 1989. Diurnal foraging patterns of *Pogonomyrmex* harvester ants (Hymenoptera: Formicidae). *Southwest. Nat.* 34: 213–218.
- MacMahon, J. A., J. F. Mull, and T. O. Crist. 2000. Harvester ants (*Pogonomyrmex* spp.): their community and ecosystem influences. *Annu. Rev. Ecol. Syst.* 31: 265–291.
- Majer, J. D. 1978. An improved pitfall trap for sampling ants and other epigeic invertebrates. *J. Aust. Entomol. Soc.* 17: 261–262.
- Mendelsohn, M. B., C. S. Brehme, C. J. Rochester, D. C. Stokes, S. A. Hathaway, and R. N. Fisher. 2008. Responses in bird communities to wildland fires in southern California. *Fire Ecol.* 4: 63–82.
- Mittermeier, R. A., P. Robles Gil, and C. G. Mittermeier. 1997. Megadiversity: Earth's biologically wealthiest nations. Monterrey, Mexico: CEMEX.
- Ostoja, S. M., and E. W. Schupp. 2009. Conversion of sagebrush shrublands to exotic annual grasslands negatively impacts small mammal communities. *Divers. Distrib.* 15: 863–870.
- Primer E Ltd. 2006. Primer 6. Version 6.16. Primer E, Plymouth, United Kingdom.
- Ratchford, J. S., S. E. Wittman, E. S. Jules, A. M. Ellison, N. J. Gotelli, and N. J. Sanders. 2005. The effects of fire, local environment, and time on ant assemblages in fens and forests. *Divers. Distrib.* 11: 487–497.
- Rissing, S. W. 1986. Indirect effects of granivory by harvester ants: plant species structure and reproductive increase near ant nests. *Oecologia* 68: 231–234.
- Rochester, C. J., C. S. Brehme, D. R. Clark, D. C. Stokes, S. A. Hathaway, and R. N. Fisher. 2010. Reptile and amphibian responses to large-scale wildfires in southern California. *J. Herpetol.* 44: 333–351.
- SAS Institute. 2002–2003. SAS Statistical Software, Version 9.1. SAS Institute, Cary, N C.
- Sawyer, J. O., and T. Keeler-Wolf. 1995. *A manual of California vegetation*. California Native Plant Society, Sacramento, California.
- [SDCWA]. 2010a. Annual rainfall amounts at Lindbergh Field, San Diego County. (<http://www.sdcwa.org/manage/rainfall-lindbergh.phtml>).
- [SDCWA]. 2010b. Annual rainfall amounts at Lake Henshaw, San Diego County. (<http://www.sdcwa.org/manage/rainfall-henshaw.phtml>).
- Shannon, C. E. 1948. A mathematical theory of communication. *Bell Syst. Tech. J.* 27: 379–423 and 623–656.
- Stebbins, R. C. 1985. *A field guide to western reptiles and amphibians*. Houghton Mifflin, Boston, MA.
- Stephens, S. S., and M. R. Wagner. 2006. Using ground foraging ant (Hymenoptera: Formicidae) functional groups as bioindicators of forest health in northern Arizona ponderosa pine forests. *Environ. Entomol.* 35: 937–949.
- Suarez, A. V., D. T. Bolger, and T. J. Case. 1998. Effects of fragmentation and invasion on native ant communities in coastal southern California. *Ecology* 79: 2041–2056.

- Suarez, A. V., J. Q. Richmond, and T. J. Case. 2000. Prey selection in horned lizards following the invasion of Argentine ants in southern California. *Ecol. Appl.* 10: 711–725.
- Sweeney, J. R. 1956. Responses of vegetation to fire. *Univ. Calif. Publ. Bot.* 28: 143–216.
- Sweet, S. S., and B. K. Sullivan. 2005. *Bufo californicus* In M. Lannoo (eds.), *Amphibian declines*, pp. 396–400. University of California Press, Berkeley and Los Angeles.
- Underwood, E. C., and B. L. Fisher. 2006. The role of ants in conservation monitoring: if, when, and how. *Biol. Conserv.* 132: 166–182.
- Underwood, E. C., and C. E. Christian. 2009. Consequences of prescribed fire and grazing on grassland ant communities. *Environ. Entomol.* 38: 325–332.
- [UTEP]. Laboratory for Environmental Biology. 2001. *CrematogasterNA*. (<http://www.utep.edu/leb/ants/Crematogaster.htm>).
- Vogl, R. J., and P. K. Schorr. 1972. Fire and manzanita chaparral in the San Jacinto mountains, Calif. *Ecol.* 53: 1179–1188.
- Whelan, R. J. 1995. *The ecology of fire*. Cambridge University Press, Cambridge, United Kingdom.
- Wheeler, G. C., and J. N. Wheeler. 1986. *The ants of Nevada*. Natural History Museum of Los Angeles County, Los Angeles, California.
- Wilkinson, E. B., E. G. Lebrun, M. L. Spencer, C. Whitby, and C. Kleine. 2005. Short-term effects of fire on sky island ant communities, pp. 550–552. *In* Proceedings, 11–15 May 2004, Tucson, AZ. USDA Forest Service Rocky Mountain Research Station, Fort Collins, CO.
- Zedler, P. H., C. R. Gautier, and G. S. McMaster. 1983. Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. *Ecology* 64: 809–818.

Received 4 March 2010; accepted 27 December 2010.
