

Matsuda et al.: Effects of wildfires on
ground foraging ants

Submitted to
Environmental Entomology
Community and Ecosystem Ecology

Tritia Matsuda
USGS-WERC
San Diego Field Station
4165 Spruance Rd, Suite 200
San Diego, CA 92101
Phone: 619-225-6449
Fax: 619-225-6436
E-mail: tmatsuda@usgs.gov

DRAFT

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

Tritia Matsuda*, Greta Turschak*, Cheryl Brehme, Carlton Rochester, Milan Mitrovich, and
Robert Fisher

U.S. Geological Survey - Western Ecological Research Center, San Diego Field Station, 4165
Spruance Road, Suite 200, San Diego, CA 92101

*co-first authors

1 **Abstract** We investigated the effect of broad-scale wildfire on the diversity, abundance,
2 and community structure of ground foraging ants within southern California. In October and
3 November of 2003, two wildfires burned a total of approximately 130,000 hectares of wildlands
4 within San Diego County. Between January 2005 and September 2006, we surveyed 63 plots
5 across four sites to measure the effect of the fires on the native ant assemblage present in four
6 vegetation types, (1) coastal sage scrub, (2) chaparral, (3) grassland, and (4) woodland riparian.
7 Thirty-six of the 63 plots were previously sampled before the fires between March 2001 and
8 June 2003. Mixed model regression analyses, accounting for burn history and pre- and post-fire
9 sampling efforts, revealed that fire had an overall, net negative effect on ant diversity.
10 Multivariate analyses showed that ant community structure varied significantly among
11 vegetation types, but only the ant assemblage associated with coastal sage scrub exhibited a
12 significant difference between burned and unburned plots. Most notably, the relative abundance
13 of *Messor andrei* (Mayr), increased from less than 1% of pre-fire coastal sage scrub ant samples
14 to 32.1% in burned plots post-fire. We theorize that *M. andrei* was able to capitalize on the use
15 of bare ground and post fire seed production, leading to an increase in abundance. Collectively,
16 our results suggest that wildfires can have substantial short-term impacts on the diversity and
17 species composition of ground foraging ants in coastal sage scrub. We discuss these impacts in
18 relation to management implications and directions for future research.

19

20 **Keywords:** ant community, species diversity, wildfire, southern California, coastal sage scrub

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

33 Ants are ecologically diverse and constitute a large proportion of the total animal biomass
34 within many of the vegetative communities they occupy (Hölldobler and Wilson 1990, Alonso
35 and Agnosti 2000). Ants play keystone roles as herbivores, predators, and seed dispersers in
36 many of the communities they inhabit (Hölldobler and Wilson 1990, Alonso and Agnosti 2000).
37 Ants improve soil quality (Folgrait 1998), often increasing plant mass in the vicinity of their
38 nests (Hölldobler and Wilson 1990). Locally, the native ant community constitutes the dietary
39 staple of several sensitive or endangered species including the coastal horned lizard
40 (*Phrynosoma coronatum*, Suarez et al. 2000), the night lizard (*Xantusia henshawii*, Brattstrom
41 1952), and the arroyo toad (*Bufo californicus*, Sweet and Sullivan 2005). Species-specific
42 variation in migration patterns and longevity of colonies provide for a range of responses to
43 disturbance (Alonso and Agnosti 2000). Their sensitivity to changes in the local environment

44 (Luque et al. 2007) and relatively small foraging range, closely link ants to the microhabitat they
45 occupy. Lack of movement at a broader scale makes ants good indicators of local habitat changes
46 because they are strongly linked to local conditions at the nest and foraging sites (Bromham et al.
47 1999, Stephens and Wagner 2006). Ground foraging ants are especially good indicators of
48 disturbance, as they are moderately diverse, sensitive to microclimate change, and can be easily
49 sampled (Alonso and Agnosti 2000).

50 In October and November of 2003, large-scale mega-fires swept across southern
51 California, consuming over 300,000 hectares of wildlands. The total burned area included over
52 130,000 hectares in San Diego County, burning as a result of the Cedar and Otay fires. In
53 addition to the loss of nearly 5,000 structures and 15 human fatalities, these two broad-scale fires
54 are likely to have impacted local invertebrate communities in a region already recognized as
55 being at great risk for biodiversity loss (Mittermeier et al. 1997). Ant communities are likely
56 useful indicators for assessing ecosystem health and change following catastrophic fire. The
57 effects of large wildfires on ant diversity and community structure, however, have not been
58 widely evaluated (but see Zimmer and Parmenter 1998, Ratchford et al. 2005, Stephens and
59 Wagner 2006), and to our knowledge this relationship has not been explored in southern
60 California. In the short term, fire may affect ants by causing direct mortality, loss of habitat and
61 changes in resource availability (Arnan et al. 2006). Fire may also have positive impacts,
62 especially for those species that favor open or disturbed habitats for nest sites, foraging, or
63 reproduction. Species that forage upon the pollen, nectar, or seeds of early successional plants
64 may also show a positive response to fire.

65 The objective of this study was to determine the effect of the fires on ant diversity,
66 community composition, and the distribution of individual species in multiple habitat types

67 common to the coastal areas of southern California. Ongoing monitoring of sample sites is likely
68 to determine whether observed changes reported in this study are transient or permanent.
69 Additional impetus for this project came from the Natural Communities Conservation Planning
70 (NCCP) efforts within the city of San Diego. Multiple Species Conservation Plan (MSCP) lands
71 make up one of the first large habitat reserves created in the country (Hierl et al. 2008). The
72 MSCP lands were directly in the footprint of these two fires with half of the protected areas
73 within the reserve affected. This research was driven largely by the concern over the recovery of
74 the natural areas within the reserve system given the great potential for biodiversity loss
75 associated with the fires. The threats and challenges to maintaining biodiversity and ecosystem
76 function within urbanized landscapes are not well understood and these large-scale
77 “experiments” provide information regarding functional reserve design for the region.

78

79

Methods

80 **Study Areas.** This research was conducted within San Diego County, California at four
81 separate study areas, (1) Elliot Chaparral Reserve, (2) Little Cedar Ridge, (3) Rancho Jamul
82 Ecological Reserve-Hollenbeck Canyon Wildlife Area and (4) Santa Ysabel Open Space
83 Preserve (Fig. 1). Elliott Chaparral Reserve (Elliot) has an average elevation of 195 m. The site
84 completely burned in October 2003. Prior to the Cedar Fire, the majority of the reserve burned in
85 1944 or 1945. Major vegetation communities are chaparral and coastal sage scrub, dominated by
86 chamise (*Adenostoma fasciculatum*), California buckwheat (*Eriogonum fasciculatum*), and
87 annual, non-native grasses (*Avena* and *Bromus*). Little Cedar Ridge (Cedar) is located on the
88 northern slopes of the Otay Mountain Wilderness. The Otay Wilderness encompasses
89 approximately 6,800 ha and ranges in elevation from 250 to 1,000 m. Our study plots cover a

90 small portion of the wilderness with an average elevation of 400 m. The majority of vegetation is
91 characterized as chaparral and coastal sage scrub. Dominant plants include chamise, Tecate
92 cypress (*Cupressus forbesii*), annual, non-native grasses, and California buckwheat. The entire
93 area burned during the Otay Fire in October 2003. No record of previous fire could be found for
94 the area. The Rancho Jamul Ecological Reserve and Hollenbeck Canyon Wildlife Area
95 (collectively referred to as Rancho Jamul) has an average elevation of 250 m. It covers
96 approximately 3,000 ha. Southern portions of this site burned during the Otay Fire of 2003.
97 Rancho Jamul encompasses a diversity of vegetation communities, including native and non-
98 native grasslands, coastal sage scrub, and upland and riparian woodlands dominated by oaks,
99 sycamores, and willows. In addition to natural vegetation communities, there are extensive,
100 fallow agricultural fields. Dominant plant species at the site include annual, non-native grasses,
101 California buckwheat, California sagebrush (*Artemisia californica*), coast live oak (*Quercus*
102 *agrifolia*), western sycamore (*Platanus racemosa*), laurel sumac (*Malosma laurina*), and San
103 Diego sunflower (*Viguiera laciniata*). Elliot, Cedar, and Rancho Jamul all experience similar
104 weather patterns and temperatures. Average July maximum temperatures range from 28°C to
105 29°C. Average January low temperatures fall between 5°C and 6°C. Annual precipitation
106 averages between 28 and 31 cm. At an average elevation of 1,078 m, Santa Ysabel Open Space
107 Preserve (Santa Ysabel) covers 1,500 ha and is the highest of our four study sites. The area
108 supports oak and pine woodlands, native and non-native grasslands, chaparral, coastal sage
109 scrub, and riparian woodlands. Dominating the various vegetation communities are coast live
110 oak, annual, non-native grasses, chamise, Engelmann oak (*Quercus engelmannii*), and white sage
111 (*Salvia apiana*). The average July high is 33°C; the average January daily low temperature is

112 1°C, and the average annual rainfall is 53 cm. The eastern portion of the site burned in 2003
113 Cedar fire.

114

115 **Ground Foraging Ant Sampling.** Within each of the four sites, we used pitfall traps to
116 sample the ground foraging ant assemblage. Data on ant species abundance and distribution
117 obtained through pitfall trapping have been used extensively (Andersen 1995, Suarez et al. 1998,
118 2000, Bess et al. 2002, Boulton et al 2005, Wilkinson et al. 2005, Stephens and Wagner 2006).
119 Pitfall trapping techniques give a reasonable estimate of ant species composition (Andersen
120 1991, Stephens and Wagner 2006). Bestelmeyer et al. (2000) evaluated pitfall traps as a
121 sampling method for ground-dwelling ants and found that most epigaeic species are well
122 represented, especially in open vegetation communities. Pitfall sampling also provides an
123 efficient, and low cost method of collecting a relatively complete sample of ground foraging ants
124 (Andersen 1991, Alonso and Agnosti 2000, Stephens and Wagner 2006).

125 In total, we sampled 63 locations, across the four sites. Sample locations were associated
126 with herpetofauna arrays established as part of a large multi-taxa project conducted by the U.S.
127 Geological Survey. At each of the 63 sampling locations, we set five ant traps in a “+” pattern
128 overlaying the herpetofauna arrays, with a center trap and four end traps, with each end trap 15
129 m from the center. Ant pitfall traps were 28-mm diameter, 115-mm deep, 50-mL plastic
130 centrifuge tubes partially filled with propylene glycol (antifreeze). Propylene glycol is a safer,
131 non-toxic alternative to traditional ethylene glycol and serves as a preservative for the specimens
132 (Suarez et al. 1998). We nested the traps in 2.54-cm diameter PVC pipe buried at ground level,
133 so the top of the tube was flush with the ground surface (Majer 1978). The PVC pipe and a
134 closed, empty centrifuge tube remained in place between sampling periods to prevent trap

135 locations from filling with soil and debris. Sampling locations were classified into four general
136 vegetation communities: grassland, woodland riparian, chaparral, or coastal sage scrub (CSS).
137 Classification was based on pre-fire vegetation transect surveys conducted between 1995 and
138 2002 using a 50-m point-intercept technique (Sawyer and Keeler-Wolf 1995) centered at each
139 herpetofaunal array. Post fire vegetation surveys were performed in spring 2005 and spring 2006
140 to assess the recovery (i.e., changes in shrub and tree cover estimates) of the vegetation
141 surrounding each plot.

142 We sampled ground foraging ants prior to the fires between March 2001 and June 2003 at
143 two sites, Rancho Jamul and Santa Ysabel (Table 1). Post-fire sampling was conducted between
144 January 2005 and September 2006 at all four study sites. Plots that did not burn are referred to as
145 ‘reference’ plots. Plots that burned are referred to as ‘impact’ plots. We collected the first post-
146 fire samples 14 months following the fire. Samples were collected twice per year, once during
147 winter (January – March) and again in summer months (June – September). Due to site access
148 issues, there were two exceptions regarding when the Santa Ysabel winter sample was taken; on
149 one occasion the sample was taken in November and another time in May. Each sample period
150 consisted of ten consecutive days after which the traps were closed and collected. We transported
151 the contents of each pitfall trap back to the laboratory for sorting, identification, and vouchers.
152 Ant specimens were separated from other invertebrates, stored in 95% ethanol, and identified to
153 species whenever possible. Only workers were counted. Winged queens and males were noted,
154 but not used in analyses since they might have originated outside the sampling locations. Most
155 voucher specimens are stored at the U.S. Geological Survey San Diego Field Station, San Diego,
156 CA (see appendix 1 for total specimens collected and specimen locations).

157

158 **Data Analyses.** Capture rates of ants can be highly variable over short time periods due
159 to shifts in activity levels related to variation in daily and seasonal environmental factors. Traps
160 located next to established foraging trails can also yield exceptionally large capture numbers. To
161 account for variability in captures across sample periods, we averaged the results from multiple
162 trapping sessions at each sample location into two samples (a pre and post-fire average) per
163 location. In the cases where locations were not surveyed in the pre-fire period, we averaged the
164 results into a single, post-fire sample. Within the pre- and post-fire samples we averaged the
165 count data per species to generate a single, averaged number of ants captured for each species. In
166 total, we had 99 averaged samples for each species, with 36 samples from the pre-fire period and
167 63 samples from the post-fire period.

168 In order to test for an effect of fire on ant diversity, we employed hierarchical linear
169 modeling (mixed or multilevel modeling) techniques. We used the Shannon Diversity Index
170 (Shannon 1948) as our response variable, applying the Shannon diversity calculation to the
171 averaged count data for each of the samples from the pre- and post-fire periods. We used mixed
172 models to test a set of *a priori* hypotheses in which the main effects and interactions of habitat
173 type, burn condition (reference vs. impact plots), percent shrub and tree cover, and elevation
174 explain differences in the diversity measure among samples. In all models, we included site as a
175 random effect. To account for correlations among multiple observations from individual plots,
176 we also tested for random plot effects by nesting plot location within sites. We checked for
177 deviations from normality of residuals using Shapiro-Wilk and Kolmogorov-Smirnov tests.
178 Models satisfying the normality assumption were then evaluated and weighted using Akaike's
179 Information Criterion (AIC) as described by Burnham and Anderson (2002). We then used
180 contrast tests of least squares means of four different conditions: (post-fire impact- pre-fire

181 impact) - (post-fire reference - pre-fire reference) to investigate the effects of ‘burn condition’ on
182 changes in species diversity following the fire. All models were run using SAS Statistical
183 Software (Version 9.1, SAS Institute, Cary, North Carolina).

184 Because changes in the ground-foraging ant assemblage may not be reflected in a single
185 diversity measure, we also tested for changes in the abundance of individual species and for
186 shifts in the overall ant community structure by additional multivariate and univariate
187 techniques. We performed multivariate analyses first, using the statistical software PRIMER-E
188 (Version 6, Plymouth, UK; Clarke 1993). To have sufficient power to test whether fire had a
189 significant effect on community composition within or among vegetation types, we reclassified
190 burn condition into a condensed data classification, specifically, razed (post-fire impacted plots)
191 and non-razed (pre-fire reference plots, post-fire reference plots, and pre-fire impact plots).
192 Before analyzing the data with PRIMER-E, we square-root transformed the data to remove some
193 weight from the most abundant species for a more balanced community analysis and created a
194 Bray-Curtis similarity matrix (Clarke and Green 1988). Using the Bray-Curtis similarity
195 matrices, we tested our hypotheses in a stepwise fashion using two-way crossed analysis of
196 similarity (ANOSIM) tests, a multivariate permutation-based test similar to the analysis of
197 variance (ANOVA) test in univariate statistics (Clarke and Green 1988). We first tested whether
198 the factors of vegetation type, site, or both were significantly predictive of differences in
199 community composition. If vegetation was significant, the effect of the fire was tested separately
200 for each vegetation type. If site was significant, it was used as a blocking factor in individual
201 ANOSIM tests. To visualize the results of the similarity matrix, PRIMER-E generates multi-
202 dimensional scaling (MDS) plots to ordinate the similarities between samples (Kruskal 1964),
203 with similar samples appearing closer together and dissimilar samples farther apart (Clark and

204 Warwick 2001). Because we used a condensed data classification to compare our non-razed
205 samples to the razed samples, we carefully reviewed MDS plots for each subset of samples to
206 ensure no systematic effects of time or burn condition were causing erroneous test results. We
207 used the ANOSIM results as an omnibus test for limiting Type I error and determining if any
208 further analyses were warranted. First, we thoroughly reviewed these multivariate data for any
209 potential systematic bias that could give erroneous results. If condensed burn condition (i.e.,
210 razed vs. non-razed) was not a significant predictor of community composition within or among
211 vegetation types, we conducted no further tests. If the condensed burn condition was significant,
212 we used the BIO-ENV procedure (Clarke 1993) to determine if the total cover of shrubs and
213 trees was significantly associated with observed patterns.

214 Prior to testing for the effects of fire on the relative abundance of individual species
215 within and between vegetation types, we first log-transformed species-specific capture data to
216 decrease the weight of the most frequently captured ant species in the analyses. We calculated
217 relative abundance by dividing transformed species-specific capture rates by the total sum of
218 transformed capture rates for all species within the assemblage. We conducted contrast tests to
219 check if changes in the relative abundance of individual species at the impact plots were
220 significantly different from changes at reference plots. Contrasts were not paired tests due to the
221 lack of pre-fire data at two of the sites. Variances were pooled across sample plots within each
222 vegetation type. We used the Fisher's Exact Test to determine if there were significant changes
223 in the proportion of sites occupied by each species after the fire. We considered any test result to
224 be significant when its p-value < 0.10 . Because there were a large number of species captured
225 across all habitat types, many of which had low capture rates, we chose to focus our analyses and
226 interpretation on the species which comprised the majority of the pre-fire and post-fire

227 communities. Therefore, we report results for the species which comprised > 5% of the
228 community within each habitat (Table 3).

229 **Results**

230 **Vegetation.** Across the burned plots, percent shrub and tree cover declined in chaparral
231 and CSS but remained relatively constant in grassland and woodland riparian pre to post-fire. At
232 impacted chaparral plots shrub and tree cover dropped from a mean of 67% (SE = 5.4) pre-fire to
233 31% (SE = 3.9) post-fire, while reference plots showed little change, with a mean of 68% (SE =
234 5.5) pre-fire compared to 66% (SE = 10.8) post-fire. Similarly, impact plots in CSS showed large
235 declines in shrub and tree cover, dropping from 50% (SE = 6.3) pre-fire to 12.6% (SE = 3.7)
236 post-fire, while reference plots showed modest differences between pre-fire (58% [SE = 8.2])
237 and post-fire (55% [SE = 8.6]) cover. Both the reference and impact plots in GRASS had very
238 low shrub and tree cover pre-fire, at 8% (SE = 5.6) and 1% (SE = 0.8), respectively. Post-fire, we
239 only measured 2% (SE = 1.3) in the impact plots and 3% (SE = 1.7) shrub and tree cover in
240 reference plots. Our impact plots in woodland riparian did decline in shrub and tree cover. Pre-
241 fire averages on the woodland riparian impact plots were 35% (SE = 10.8) and post-fire
242 measured 24% (SE = 6.4). Shrub and tree cover on the reference woodland riparian plots
243 remained relatively unchanged pre-fire to post-fire, with 30% (SE = 34.4) and 37% (SE = 31.3)
244 cover values, respectively. The woodland riparian plots had highly variable shrub and tree
245 coverage as this grouping included not only oak woodlands and pine forest, but also seeps, which
246 typically had lower cover values.

247

248 **Ant Species Diversity and Community Structure.** A total of 34,371 worker ants
249 encompassing 23 genera and 61 separate species were sampled during the course of this study.

250 The total species captures represented 51% of 45 genera and 23% of the 270 species present in
251 California (California Academy of Sciences, 2008). Eight species, *Dorymyrmex bicolor*
252 (Wheeler), *Formica francoeuri* (Bolton), *Forelius mccooki* (McCook), *Forelius pruinosus*
253 (Roger), *Messor andrei* (Mayr), *Pheidole vistana* (Emery), *Pogonomyrmex rugosus* (Emery) and
254 *Solenopsis xyloni* (McCook) represented the majority (82%) of all ants collected before and after
255 the 2003 fires. Regardless of vegetation type, whether an array burned or not was the most
256 predictive factor of differences in ant diversity measures among samples. Results of the
257 hierarchical modeling efforts showed the top mixed regression model included the fixed effect,
258 ‘burn condition’, and random effects of site and array (Table 2). This top model accounted for
259 74% of the total model weights and was six times more likely than the next highest-ranking
260 model to be selected as the best-fitting model if the data were to be collected again under
261 identical conditions. Contrast tests revealed an overall increase in diversity after the fire in both
262 the reference and impact plots, with the increase significantly less pronounced (Estimate= -
263 0.220, $Z = -1.786$, $p = 0.074$) in the impact plots than the unburned reference plots, suggesting an
264 overall negative effect of fire on ant diversity.

265 The initial ANOSIM test revealed that structure of the ant assemblage varied significantly
266 among vegetation types and sites. Subsequent ANOISM analyses performed within each
267 vegetation type separately with site included as a blocking factor, showed that ant community
268 composition in razed plots was significantly different from the community composition in non-
269 razed plots in CSS ($R = 0.578$, $p=0.003$), but not chaparral ($R = -0.213$, $p = 0.935$), grassland (R
270 $= 0.096$, $p = 0.227$), or woodland riparian ($R = 0.070$, $p = 0.157$). Results of the BIO-ENV for
271 CSS showed that percent shrub and tree cover was a significant predictor of change in

272 community composition ($\rho = 0.292$, $p < 0.001$; Fig. 2). On average, shrub and tree cover in razed
273 CSS plots was only 13% (SE = 3.7) compared to 53% (SE = 4.3) in non-razed plots.

274 The proportions (relative abundance) of dominant individual species by vegetation type
275 and burn condition are presented in Table 3. Because changes in ant community composition
276 were significant only in coastal sage scrub, we conducted contrast tests on the most abundant ant
277 species (species comprising > 5% of the total ant abundance) recorded in this community during
278 pre-fire and post-fire sampling. Contrast tests allowed us to evaluate the effects of the burn on
279 the relative proportions of individual species, while controlling for post-fire changes in the
280 reference plots. The eight focal species were *Crematogaster californica* (Wheeler),
281 *Crematogaster hespera* (Wheeler), *Forelius mccooki*, *Forelius pruinosus*, *Messor andrei*,
282 *Pogonomyrmex rugosus*, *Pheidole vistana*, and *Solenopsis xyloni*. In CSS, results of the contrast
283 tests showed that the single species, *M. andrei*, largely accounted for much of the difference
284 between the structure of the pre- and post-fire ant communities. *Messor andrei* comprised less
285 than 1% of all pre-fire ant captures across all plots. However, in CSS the species comprised
286 32.1% of all captures in the impact plots following the fires in comparison to 3% of the post-fire
287 reference plots (Diff = 0.29, SE = 0.12, $p = 0.022$). The proportion of impacted plots occupied by
288 *M. andrei* increased from ~1% pre-fire to 86.7% post-fire in CSS. Although not significant, *M.*
289 *andrei* also appeared to increase across all other vegetation types following the fire (Fig. 3).
290 Further results of the individual species contrast tests showed a significant net decrease in
291 *Crematogaster californica*, an acrobat ant (Diff = -0.10, SE = 0.04., $p = 0.019$). It comprised
292 21.2% of the pre-fire CSS community, but only 2.3% of the total population in impact plots.
293 Although the relative abundance of only *M. andrei* and *C. californica* populations showed the

294 only significant effects of the burn, net changes for the most abundant species in CSS are
295 represented in Fig. 4.

296

297 **Discussion**

298 Overall, in the second and third year following wildfire, we found a negative effect of fire on the
299 diversity of ground foraging ants in southern California. The most significant changes to ant
300 community structure occurred in the native ant assemblage present in coastal sage scrub habitat.
301 In this vegetation type, burned plots lost more shrub and tree cover than any other vegetation
302 type, including chaparral, woodland riparian, and grassland. Native ants present in coastal sage
303 scrub declined in diversity and showed significant shifts in community composition. In general,
304 ecologists have found the response of ant communities to landscape change to be varied and
305 often erratic (Alonso and Agnosti 2000). Wilkinson et al. (2005) found greater ant species
306 richness and abundance in burned plots compared to unburned plots in the first year following
307 fire, but not after a second year in Sonora, Mexico. Andersen and Yen (1985) found increased
308 species richness one year after a wildfire in Victoria, Australia. In the Siskiyou Mountains in
309 northern California and southern Oregon, Ratchford et al. (2005) found a fire effect to be
310 dependent upon vegetation type, with fens retaining more species in burned areas, while forested
311 sites retained less species in burned areas. Underwood and Fisher (2006) reviewed several
312 studies on ants and disturbance and found disturbance from fire to result in wide range of
313 responses ranging from significant to no response. Observed variation in ant community
314 responses to fire may in part be due to individual fire properties: time since a fire, fire intensity,
315 and habitat (Ratchford et al. 2005, Arnan et al 2006).

316 Although we found a negative effect of fire on species diversity, across all study sites, ant
317 diversity increased between the pre- and post-fire periods. The patchy nature of the fire at
318 Rancho Jamul and Santa Ysabel left a mixture of burned and unburned habitats. This mosaic
319 may provide a larger variety of microhabitats that could support more species. The changes in
320 species diversity in the impact and reference plots suggest that ant communities had some
321 resiliency to the effects of fire. Favorable landscape factors likely contributed to the recovery of
322 the ant community. The high diversity at reference plots suggests that unburned areas retained
323 healthy, viable ant populations in that area. Unburned patches within a fire site can provide
324 refuge and source populations from which to re-colonize (Kaspari and Majer 2000, Ferrenberg et
325 al. 2006). In addition, ants may be well equipped to survive fire due to limited foraging activity
326 and available refugia. Stephens and Wagner (2006) found that a mature ant colony has only 2%
327 of its total population active on the surface, so if fire breaks out, direct mortality is limited to this
328 small percentage of foragers while the majority of the colony survives. Ants active on the surface
329 at the time of fire may be able to find shelter in rocks, downed wood, and soil cracks
330 (Underwood and Fisher 2006). Insulation provided by soil is the largest source of refuge. The
331 insulating properties of soil (Sweeney 1956, Force 1981, Andersen 1991) shelter nests containing
332 the majority of the colony from high temperatures of the fire. These factors may help explain
333 why a number of impact plots did not lose species following the fire.

334

335 **Community Composition and Individual Species Responses.** Overall, our study
336 showed that the ant community composition was significantly different in coastal sage scrub
337 after the fire. This habitat had the largest decline in average shrub and tree cover two to three
338 years after the fire. Although average shrub and tree cover also declined in chaparral, the plants

339 of this community are fire adapted (Keeley and Keeley 1984), and therefore the ant community
340 may also be equally resilient to fire. The low number of non-raided plots in chaparral also may
341 have decreased the power to which we could estimate and detect burn effects. However, Suarez
342 et al. (2000) sampled ants before the fire using pitfall traps at the Elliot Chaparral Reserve and
343 reported the native ant community consisted primarily of the same species we detected post-fire:
344 *P. vistana*, *F. mccooki*, *C. californica*, *M. andrei*, *Temnothorax andrei* (Emery), and *S. xyloni*.
345 We did not find significant differences in woodland or grassland plots. Woodland riparian plots
346 may be more fire resistant as generally higher soil and plant moisture levels prevent the habitat
347 from completely burning, retaining some of its structure and possibly serving as refugia for ants
348 during the fire (Keeley and Keeley 1984). Grasslands may retain much of their native ant
349 diversity by being able to recover quickly after fires (Keeley and Keeley 1984). Coastal sage
350 scrub may be the most vulnerable vegetation type (Keeley and Keeley 1984), with post-fire
351 changes in structure and species composition being reflected in the ant community.

352 In our study, the difference in the post-fire ant community in coastal sage scrub was
353 primarily shaped by the increase in abundance of *Messor andrei*, as well as a decrease in
354 abundance of *Crematogaster californica*. *Messor andrei*, a harvester ant, increased in abundance
355 following the fire across all vegetation types and most significantly in coastal sage scrub.
356 Favorable changes in landscape and habitat resources appear to have benefited *M. andrei*. Along
357 with environmental changes, inter-specific competition may have shifted, allowing *M. andrei* to
358 expand from its pre-fire distribution (Andersen and Yen 1985). Fire cleared land consists of bare
359 soil with higher surface temperatures. The increase of bare soil affects the availability of nesting
360 sites and temperature affects foraging activity of some species (MacKay and MacKay 1989,
361 Ratchford et al. 2005, Lafleur et al. 2006). *M. andrei* may tolerate or prefer the prolonged higher

362 ground temperatures associated with the retention of heat by exposed soil. This tolerance would
363 allow for increased foraging and increased food availability to the colony, which in turn can lead
364 to an increase in abundance. Fire may also affect available food sources, such as the seeds that
365 harvester ants gather (Ratchford et al. 2005). Underwood and Christian (2009) found an increase
366 in burned plots of seed harvesters in the genus *Messor*, including *M. andrei*. (which was the most
367 abundant species in their study) which they attributed to changes in vegetation related
368 characteristics, such as forb cover. Arnan et.al (2006) found that congener *Messor capitatus*
369 (Latreille) benefited from increased production of seeds after fire. Altered habitat structure and a
370 potential increase in resource availability after the fire may have given *M. andrei* a similar
371 competitive advantage.

372 It is also expected then that species with specialized adaptations to closed-canopy habitats
373 would decline after a fire due to a reduction in suitable habitat. There was a significant decline in
374 *C. californica* in burned plots. The decline may be related to direct mortality and nesting habits.
375 *C. californica* is known to cultivate aphids and coccids at the bases and on roots of various
376 plants, so their decline may be due to the vulnerability of these plants and/or non-soil nests
377 (<http://www.utep.edu/leb/ants/Crematogaster.htm>, 2001). *Crematogaster* species make nests in
378 plants, logs or decaying wood, or nests fashioned out of carton they manufacture themselves,
379 these colonies are more susceptible to mortality than *Crematogaster* colonies that nest under
380 rocks in the soil (Wheeler and Wheeler, 1986). Losing these colonies and the habitat they
381 occupied during the fire is a likely source of decline.

382

383 **Conservation and Management Implications.** In general, the MSCP reserve system
384 supports a diverse assemblage of native ground foraging ants. To date, the MSCP reserve system

385 remains relatively free of invasion by exotic ants and protects a number of vegetation types
386 supporting this ant assemblage. The difference in the number of species occupying reference and
387 impact plots following the wildfires suggests that the ant diversity has declined in the burn areas
388 within the San Diego MSCP lands. Severe fires appear to be occurring more frequently in recent
389 years in southern California and San Diego County (e.g., Cedar and Otay Fires in 2003, Harris
390 and Witch Creek Fires in 2007). Shorter fire intervals and/or high intensity fires may disrupt
391 populations beyond their ability to recover successfully after a fire, permanently altering natural
392 systems in wilderness areas. This shift in the natural fire cycle is predicted to lead to the
393 conversion of coastal sage scrub and chaparral vegetation to grassland (Zedler et al. 1983,
394 Keeley 2005). The results of our work suggest conversion of native shrubland to exotic grassland
395 may lead to a reduction in ant species diversity, favoring ant species best suited to open habitat
396 and frequent disturbance. Changes in ant species distributions are likely to affect the abundance
397 of other plants and animals. For instance, the coastal horned lizard, *Phrynosoma coronatum*,
398 prefers to forage in open habitats (Stebbins 1985), with harvester ants making up a large portion
399 of the diet of adults (Suarez et al. 2000). At our study sites, an increase was detected in the
400 number of *P. coronatum* in CSS post-fire plots (R Fisher, unpublished data). The increased
401 presence of *M. andrei* in the burned scrub habitats is potentially benefiting *P. coronatum*.
402 Because *M. andrei* plays a key role as a seed disperser, the increased abundance of *M. andrei*
403 may also affect the distribution of plants in the vicinity of its nest (Brown and Human 1997,
404 Hobbs 1985). The association between increased *M. andrei* presence and fire may allow *M.*
405 *andrei* to serve as an indicator species of fire in southern California coastal sage scrub. In
406 general, ants are good indicators of environmental change as they require minimal effort to
407 sample and are linked closely with the microhabitats they occupy (Alonso and Agnosti 2000).

408 Ants have effects on soil, vegetation, and other animals (Hölldobler and Wilson 1990, Folgrait
409 1998, Alonso and Agnosti 2000). Since most ants are not directly affected by fire, changes in the
410 ant community could provide valuable information about how a landscape has changed as a
411 result of fire. Longer term studies are needed to monitor the long-term effects of fire on ants,
412 including the growth and reproduction of colonies (Arnan et al. 2006). Future studies designed to
413 sample changes in ant community structure in the months immediately following a fire may
414 provide valuable information on the short term impacts of fire that may only last a few months
415 (Underwood and Christian 2009). Incorporating studies using ant functional groups or trophic
416 structure could provide information about the competitive interactions in our local ant fauna.
417 Functional groups provide insight into whether ants can continue to perform their ecosystem
418 functions with increased fire frequency. If severe fire weather is to become a frequent occurrence
419 in the future of southern California, discovering patterns of ant recovery following wildfire may
420 serve as a valuable tool in the overall assessment and prediction of the region's ability to recover
421 from large-scale wildfire.

422 **Acknowledgements**

423 We are grateful for the many hours of technical assistance provided by Denise Clark, Krista
424 Mendelsohn and Jim Starrett in support of this project. We would also like to thank Dr. Andrew
425 Suarez at University of Illinois Champaign-Urbana and Dr. Phil Ward at University of
426 California, Davis, for assistance with identification of specimens. We thank Julie Yee for
427 providing statistical advice. For site access, we thank the managers of the four study sites (Tim
428 Dillingham of California Department of Fish & Game; James Stowers, Bobbi Thompson, and
429 Jeffrey Rundell of San Diego County Parks & Recreation Department; Isabelle Kay of the
430 University of California, San Diego - Elliott Chaparral Reserve; Joyce Schlachter and Janaye
431 Byergo of Bureau of Land Management). Funding for this project was provided in part by the
432 San Diego MSCP Initiative, the San Diego Association of Governments – *TransNet*
433 Environmental Mitigation Program, and the US Geological Survey – Western Ecological
434 Research Center. All work was performed under US Fish and Wildlife permit TE-045994-7 and
435 individually held California Department of Fish and Game scientific collecting permits. Any use
436 of trade, product, or firm names is for descriptive purposes only and does not imply endorsement
437 by the U.S. government.

438 **References Cited**

- 439 Alonso, L.E. and D. Agosti. 2000. Biodiversity studies, monitoring, and ants: an overview, pp. 1-
440 8. In Agosti et al. (eds.), *Ants: standard methods for measuring and monitoring*
441 *biodiversity*. Smithsonian Institution Press, Washington DC.
- 442 Andersen, A.N. 1991. Responses of ground-foraging ant communities to three experimental fire
443 regimes in a savanna forest of tropical Australia. *Biotropica*. 23: 575-585.
- 444 Andersen, A.N. 1995. A classification of Australian ant communities based on functional groups
445 which parallel plant-life forms in relation to stress and disturbance. *J. Biogeogr.* 22: 15-
446 29.
- 447 Andersen, A.N. and A.L. Yen. 1985. The immediate effects of fire on ants in the semi-arid
448 mallee region of south-western Victoria. *Aust. J. Ecol.* 10: 25-30.
- 449 Arnan, X., A. Rodrigo, and J. Retana. 2006. Post-fire recovery of Mediterranean ground ant
450 communities follows vegetation and dryness gradients. *J. Biogeogr.* 33: 1246-1258.
- 451 Bess, E.C., R.R. Parmenter, S. McCoy, and M.C. Molles, Jr. 2002. Responses of a riparian
452 forest-floor arthropod community to wildfire in the middle Rio Grande Valley, New
453 Mexico. *Environ. Entomol.* 34: 96-104.
- 454 Bestelmeyer, B.T., D. Agosti, L. E. Alonso, C. R. F. Brandão, W. L. Brown Jr., J. H. C.
455 Delabie, and R. Silvestre. 2000. Field techniques for the study of ground-dwelling ants:
456 an overview, description, and evaluation, pp. 122-144. In Agosti et al. (eds.), *Ants:*
457 *standard methods for measuring and monitoring biodiversity*. Smithsonian Institution
458 Press, Washington DC.

459 Boulton, A. M., K. F. Davies, and P. S. Ward. 2005. Species richness, abundance, and
460 composition of ground-dwelling ants in northern California grasslands: Role of plants,
461 soil, and grazing. *Environ. Entomol.* 34 (1): 96-104

462 Brattstrom, B. H. 1952. The food of the night lizards, Genus *Xantusia*. *Copeia* 1952 (3): 168-
463 172.

464 Bromham, L., M. Cardillo, A.F. Bennett, and M.A. Elgar. 1999. Effects of stock grazing on the
465 ground invertebrate fauna of woodland remnants. *Aust. J. Ecol.* 24: 199-207.

466 Brown, M.J.F and K.G. Human. 1997. Effects of harvester ants on plant species distribution and
467 abundance in a serpentine grassland. *Oecologia* 112:237-243.

468 Burnham, K.P. and D.R. Anderson. 2002. Model selection and multimodel inference: a practical
469 information-theoretic approach. 2nd ed. Springer-Verlag, New York, New York, USA.

470 California Academy of the Sciences. 2008. California Ants.
471 <http://www.antweb.org/california.jsp>. Accessed on March 31, 2008.

472 Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community composition.
473 *Aust. J. Ecol.* 18: 117-143.

474 Clarke, K.R. and R. H. Green. 1988. Statistical design and analysis for a 'biological effects'
475 study. *Marine Ecology Progressive Series* 46: 213-26.

476 Clarke, K.R., and R.M. Warwick. 2001. Change in marine communities: an approach to
477 statistical analysis and interpretation, second edition. PRIMER-E: Plymouth, United
478 Kingdom.

479 Ferrenberg, S. M., D.W. Schwilk, E.E. Knapp, E. Groth, and J.E. Keeley. 2006. Fire decreases
480 arthropod abundance but increases diversity: early and late season prescribed fire effects
481 in a Sierra Nevada mixed-conifer forest. *Fire Ecol.* 2: 79-102.

482 Folgrait, P.J. 1998. Ant biodiversity and its relationship to ecosystem functioning: a review.
483 Biodivers. Conserv. 7: 1221-1244.

484 Force, D.C. 1981. Postfire insect succession in southern California chaparral. Am. Nat. 117: 575-
485 582.

486 Hanes, T. L. 1971. Succession after fire in the chaparral of southern California. Ecological
487 Monographs. 41: 27-52.

488 Hierl, L.A., J. Franklin, D. H. Deutschman, H. M. Regan, and B. S. Johnson. 2008. Assessing
489 and prioritizing ecological communities for monitoring in a regional habitat conservation
490 plan. Environmental Management 42: 165-179

491 Hobbs, R.J. 1985. Harvester ant foraging and plant species distribution in annual grassland.
492 Oecologia 67: 519-523.

493 Hölldobler, B., and E.O. Wilson. 1990. The ants. Harvard University Press, Cambridge, MA.

494 Kaspari, M. and J.D. Majer. 2000. Using ants to monitor environmental change. pp. 89-98. In
495 Agnosti et al. (eds.), Ants: standard methods for measuring and monitoring biodiversity.
496 Smithsonian Institution Press, Washington DC.

497 Keeley, J.E. and S.C. Keeley. 1981. Post-fire regeneration of southern California chaparral. Am.
498 J. Botany. 68: 524-530.

499 Keeley, J.E. and S.C. Keeley. 1984. Postfire recovery of coastal sage scrub. Am. Midl. Nat. 111:
500 105-117.

501 Keeley, J. E., C. J. Fotheringham, and M. Morais. 1999. Reexamining fire suppression impacts
502 on brushland fire regimes. Science. 284: 1829-1832.

503 Keeley, J.E. and C.J. Fotheringham. 2001. Historic Fire Regime in southern California
504 shrublands. Con. Bio. 15: 1536-1548.

505 Keeley, J.E., C.J. Fotheringham, and M.A. Moritz. 2004. Lessons from the October 2003
506 wildfires in southern California. *J. Forestry*. 102: 26-31.

507 Keeley, J.E. 2005. Fire as a threat to biodiversity in fire-type shrublands. USDA Forest Service
508 Gen. Tech. Rep. PSW-GTR-195.2005

509 Kruskal, J.B. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric
510 hypothesis. *Psychometrika* 29:1-27.

511 Lafleur, B., W.F.J. Parsons, R.L. Bradley, and A. Francoeur. 2006. Ground-nesting ant
512 assemblages and their relationships to habitat factors along a chronosequence of postfire-
513 regenerated lichen-spruce woodland. *Environ. Entomol.* 35: 1515-1524.

514 Luque, G.M., J. Reyes-López, and J. Fernández-Haeger. 2007. Recovery of ground ant
515 (Hymenoptera: Formicidae) communities six years after a major environmental disaster.
516 *Environ. Entomol.* 36: 337-347.

517 MacKay, W.P. and E.E. MacKay. 1989. Diurnal foraging patterns of *Pogonomyrmex* harvester
518 ants (Hymenoptera: Formicidae). *Southwest. Nat.* 34: 213-218.

519 Majer, J. D. 1978. An improved pitfall trap for sampling ants and other epigaeic invertebrates.
520 *Journal of the Australian Entomological Society*. 17: 261-262.

521 Mittermeier, R.A., P. Robles Gil, and C.G. Mittermeier. 1997. Megadiversity: Earth's
522 biologically wealthiest nations. Monterrey, Mexico: CEMEX.

523 Primer E Ltd. 2006. Primer 6. Version 6.16. Primer E, Plymouth, U.K.

524 Ratchford, J. S., S. E. Wittman, E. S. Jules, A. M. Ellison, N. J. Gotelli, and N. J. Sanders. 2005.
525 The effects of fire, local environment, and time on ant assemblages in fens and forests.
526 *Diversity Distrib.* 11: 487-497.

527 SAS Institute. 2002-2003. SAS Statistical Software, Version 9.1. SAS Institute, Cary, N C.

528 Sawyer, J.O. and T. Keeler-Wolf. 1995. A Manual of California Vegetation. Sacramento:
529 California Native Plant Society.

530 Shannon, C.E. 1948. A mathematical theory of communication. Bell System Technical Journal
531 27: 379-423 and 623-656.

532 Stebbins, R. C. 1985. A field guide to Western reptiles and amphibians. Houghton Mifflin,
533 Boston.

534 Stephens, S.S. and M.R. Wagner. 2006. Using ground foraging ant (Hymenoptera: Formicidae)
535 functional groups as bioindicators of forest health in northern Arizona ponderosa pine
536 forests. Environ. Entomol. 35: 937-949.

537 Suarez, A.V., D.T. Bolger, and T.J. Case. 1998. Effects of fragmentation and invasion on native
538 ant communities in coastal Southern California. Ecol. 79: 2041-2056.

539 Suarez, A. V., J. Q. Richmond, and T. J. Case. 2000. Prey selection in horned lizards following
540 the invasion of Argentine ants in Southern California. Ecol. Appl. 10 (3): 711-725

541 Sweeney, J. R. 1956. Responses of vegetation to fire. Univ. Calif. Publ. Bot. 28: 143-216.

542 Sweet, S. S. and B. K. Sullivan. 2005. *Bufo californicus* In M. Lannoo (eds.), Amphibian
543 Declines, pp396-400. University of California Press, Berkeley and Los Angeles.

544 Underwood E. C. and C.E. Christian. 2009. Consequences of prescribed fire and grazing on
545 grassland ant communities. Environ. Entomol. 38(2): 325-332.

546 Underwood, E. C. and B. L. Fisher. 2006. The role of ants in conservation monitoring: If, when,
547 and how. Biol. Conserv. 132: 166-182

548 University of El Paso Texas. Laboratory for Environmental Biology. 2001. *Crematogaster*NA.
549 <http://www.utep.edu/leb/ants/Crematogaster.htm>. Accessed on March 12, 2008.

- 550 Vogl, R.J and P.K. Schorr. 1972. Fire and manzanita chaparral in the San Jacinto mountains,
551 California. Ecol. 53: 1179-1188.
- 552 Wheeler, G. C. and J. N. Wheeler. 1986. The Ants of Nevada. Natural History Museum of Los
553 Angeles County, Los Angeles, California.
- 554 Wilkinson, E.B., E.G. Lebrun, M.L. Spencer, C. Whitby, and C. Kleine. 2005. Short-term effects
555 of fire on sky island ant communities, pp. 550-552. In USDS Forest Service Proceedings
556 RMRS-P-36.
- 557 Zedler, P.H., C.R. Gautier, and G.S. McMaster. 1983. Vegetation change in response to extreme
558 events: the effect of a short interval between fires in California chaparral and coastal
559 scrub. Ecol. 64: 809-818.
- 560 Zimmer, K., and R.R. Parmenter. 1998. Harvester ants and fire in a desert grassland: ecological
561 responses of *Pogonomyrmex rugosus* (Hymenoptera: Formicidae) to experimental
562 wildfires in central New Mexico. Pop. Ecol. 27: 282-287.

Table 1. Total number of sample plots for both post and pre-fire periods by site, condition, and habitat type. Number of plots sampled during the pre-fire period is in parentheses.

Habitat	Site								Total
	Elliot		Cedar		Rancho Jamul		Santa Ysabel		
	Reference	Impact	Reference	Impact	Reference	Impact	Reference	Impact	
Chaparral	-	5	-	5	-	-	2	4	16 (6)
							(2)	(4)	
Coastal Sage	-	5	-	4	4	4	2	2	21
Scrub					(4)	(4)	(1)	(1)	(10)
Grassland	-	-	-	-	4	4	2	1	11
					(4)	(4)	(2)	(1)	(11)
Woodland	-	-	-	-	2	2	4	7	15 (9)
Riparian					(2)	(1)	(2)	(4)	
Total	-	10	-	9	10	10	10	14	63
					(10)	(9)	(7)	(10)	(36)

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)	Condition	5	0.000	0.738	-54.65
Array(Site)	Elevation	5	3.500	0.128	-56.40
Array(Site)	Condition+Habitat	8	3.800	0.110	-53.55
Site	ShrubCover*Habitat	8	8.400	0.011	-55.85
Array(Site)	Null	4	10.500	0.004	-60.90
Array(Site)	ShrubCover	5	10.700	0.004	-60.00
Array(Site)	Condition*Habitat	9	11.200	0.003	-56.25
Array(Site)	Habitat	7	14.700	0.000	-60.00
Array(Site)	ShrubCover*Habitat	9	14.800	0.000	-58.05
Site	ShrubCover	4	14.900	0.000	-63.10
Site	Condition+Habitat	7	16.400	0.000	-60.85
Site	Condition	4	17.100	0.000	-64.20
Site	Null	3	18.400	0.000	-65.85
Site	Habitat	6	18.800	0.000	-63.05
Site	Elevation	4	19.100	0.000	-65.20
Site	Condition*Habitat	8	20.000	0.000	-61.65

^aKey: condition (reference vs. impact); elevation (low and high); habitat (Chaparral, Coastal Sage Scrub, Grassland, Woodland Riparian); ShrubCover (Percent shrub and tree cover).

^bDifference 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.

^cAIC model weight; weights have a probabilistic interpretation: of these models, w_i is the probability that model i would be selected as the best-fitting model if the data were collected again under identical conditions.

Table 3. Pre- and post-fire relative abundance (following log-transformation of species-specific, averaged capture data) and standard error (in parentheses) of ant species at impact and reference plots by vegetation community.

Habitat	Species	Reference				Impact			
		Pre-fire		Post-fire		Pre-fire		Post-fire	
Coastal sage scrub ^a	<i>Crematogaster californica</i> *	0.15	(0.03)	0.06	(0.01)	0.21	(0.04)	0.02	(0.01)
	<i>Forelius mccooki</i>	0.08	(0.03)	0.08	(0.03)	0.20	(0.03)	0.07	(0.03)
	<i>Pogonomyrmex rugosus</i>	0.55	(0.08)	0.45	(0.07)	0.19	(0.08)	0.02	(0.01)
	<i>Pheidole vistana</i>	0.03	(0.01)	0.01	(0.00)	0.15	(0.03)	0.29	(0.04)
	<i>Solenopsis xyloni</i>	0.07	(0.02)	0.05	(0.01)	0.05	(0.01)	0.09	(0.02)
	<i>Crematogaster hespera</i>	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.05	(0.02)
	<i>Forelius pruinosus</i>	0.00	(0.00)	0.09	(0.04)	0.00	(0.00)	0.03	(0.02)
	<i>Messor andrei</i> *	0.00	(0.00)	0.03	(0.01)	0.00	(0.00)	0.32	(0.05)
	Other ^b	0.11		0.22		0.20		0.11	
	Total		1.00		1.00		1.00		1.00
Chaparral	<i>Camponotus dumetorum</i>	0.03	(0.01)	0.04	(0.01)	0.38	(0.07)	0.10	(0.04)
	<i>Pheidole hyatti</i>	0.12	(0.03)	0.02	(0.00)	0.22	(0.05)	0.05	(0.02)
	<i>Camponotus vicinus</i>	0.01	(0.00)	0.00	(0.00)	0.11	(0.04)	0.00	(0.00)
	<i>Formica moki</i>	0.01	(0.00)	0.01	(0.00)	0.06	(0.01)	0.04	(0.02)
	<i>Crematogaster mormonum</i>	0.00	(0.00)	0.03	(0.01)	0.05	(0.01)	0.05	(0.02)
	<i>Messor andrei</i>	0.14	(0.03)	0.17	(0.04)	0.00	(0.00)	0.07	(0.03)
	<i>Dorymyrmex bicolor</i>	0.28	(0.08)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
	<i>Forelius pruinosus</i>	0.00	(0.00)	0.17	(0.05)	0.00	(0.00)	0.00	(0.00)
	<i>Pheidole vistana</i>	0.15	(0.02)	0.08	(0.02)	0.00	(0.00)	0.40	(0.07)
	<i>Pogonomyrmex subnitidus</i>	0.00	(0.00)	0.27	(0.03)	0.00	(0.00)	0.00	(0.00)
	<i>Solenopsis xyloni</i>	0.05	(0.01)	0.02	(0.00)	0.00	(0.00)	0.17	(0.05)
	Other	0.21		0.20		0.18		0.12	
	Total		1.00		1.00		1.00		1.00
Grassland	<i>Pheidole vistana</i>	0.00	(0.00)	0.00	(0.00)	0.27	(0.07)	0.35	(0.06)
	<i>Crematogaster californica</i>	0.17	(0.05)	0.04	(0.01)	0.18	(0.04)	0.01	(0.00)
	<i>Solenopsis xyloni</i>	0.03	(0.01)	0.12	(0.03)	0.11	(0.04)	0.13	(0.04)
	<i>Pheidole hyatti</i>	0.04	(0.02)	0.01	(0.00)	0.11	(0.05)	0.05	(0.02)
	<i>Messor andrei</i>	0.00	(0.00)	0.13	(0.04)	0.10	(0.04)	0.30	(0.08)
	<i>Pheidole clementensis</i>	0.05	(0.02)	0.01	(0.00)	0.03	(0.01)	0.05	(0.01)
	<i>Forelius mccooki</i>	0.25	(0.08)	0.36	(0.10)	0.03	(0.01)	0.00	(0.00)
	<i>Monomorium ergatogyna</i>	0.06	(0.02)	0.04	(0.02)	0.03	(0.01)	0.00	(0.00)
	<i>Camponotus semitestaceus</i>	0.06	(0.03)	0.03	(0.02)	0.01	(0.00)	0.01	(0.00)
	<i>Pogonomyrmex rugosus</i>	0.15	(0.07)	0.05	(0.02)	0.00	(0.00)	0.02	(0.01)
	<i>Pogonomyrmex subnitidus</i>	0.11	(0.04)	0.08	(0.04)	0.00	(0.00)	0.00	(0.00)
	Other	0.09		0.12		0.14		0.08	
	Total		1.00		1.00		1.00		1.00

Habitat	Species	Reference				Impact			
		Pre-fire		Post-fire		Pre-fire		Post-fire	
Woodland	<i>Dorymyrmex bicolor</i>	0.00	(0.00)	0.00	(0.00)	0.20	(0.09)	0.11	(0.06)
Riparian	<i>Formica francoeuri</i>	0.24	(0.10)	0.30	(0.09)	0.17	(0.08)	0.11	(0.06)
	<i>Pheidole hyatti</i>	0.03	(0.01)	0.03	(0.01)	0.14	(0.03)	0.14	(0.06)
	<i>Camponotus semitestaceus</i>	0.01	(0.00)	0.04	(0.02)	0.13	(0.03)	0.03	(0.01)
	<i>Tapinoma sessile</i>	0.02	(0.00)	0.05	(0.01)	0.12	(0.03)	0.03	(0.01)
	<i>Formica moki</i>	0.05	(0.01)	0.05	(0.02)	0.06	(0.02)	0.05	(0.02)
	<i>Messor andrei</i>	0.01	(0.00)	0.07	(0.03)	0.04	(0.01)	0.10	(0.04)
	<i>Forelius mccooki</i>	0.06	(0.02)	0.03	(0.01)	0.01	(0.01)	0.09	(0.05)
	<i>Liometopum occidentale</i>	0.18	(0.05)	0.17	(0.05)	0.01	(0.00)	0.04	(0.02)
	<i>Crematogaster californica</i>	0.00	(0.00)	0.05	(0.02)	0.00	(0.00)	0.01	(0.01)
	<i>Forelius pruinosus</i>	0.00	(0.00)	0.01	(0.01)	0.00	(0.00)	0.10	(0.06)
	<i>Neivamyrmex californicus</i>	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.07	(0.03)
	<i>Pogonomyrmex rugosus</i>	0.12	(0.05)	0.04	(0.02)	0.00	(0.00)	0.00	(0.00)
	<i>Prenolepis imparis</i>	0.11	(0.04)	0.03	(0.01)	0.00	(0.00)	0.01	(0.00)
	<i>Solenopsis molesta</i>	0.05	(0.02)	0.02	(0.01)	0.00	(0.00)	0.05	(0.03)
	Other	0.14		0.11		0.12		0.07	
Total		1.00		1.00		1.00		1.00	

^aContrast tests comparing ant species abundance in impact vs. reference plots were only performed for coastal sage scrub (per ANOSIM results) and for *M. andrei* across all habitat types.

^bSpecies comprising < 5% in each habitat was grouped and listed as “other”

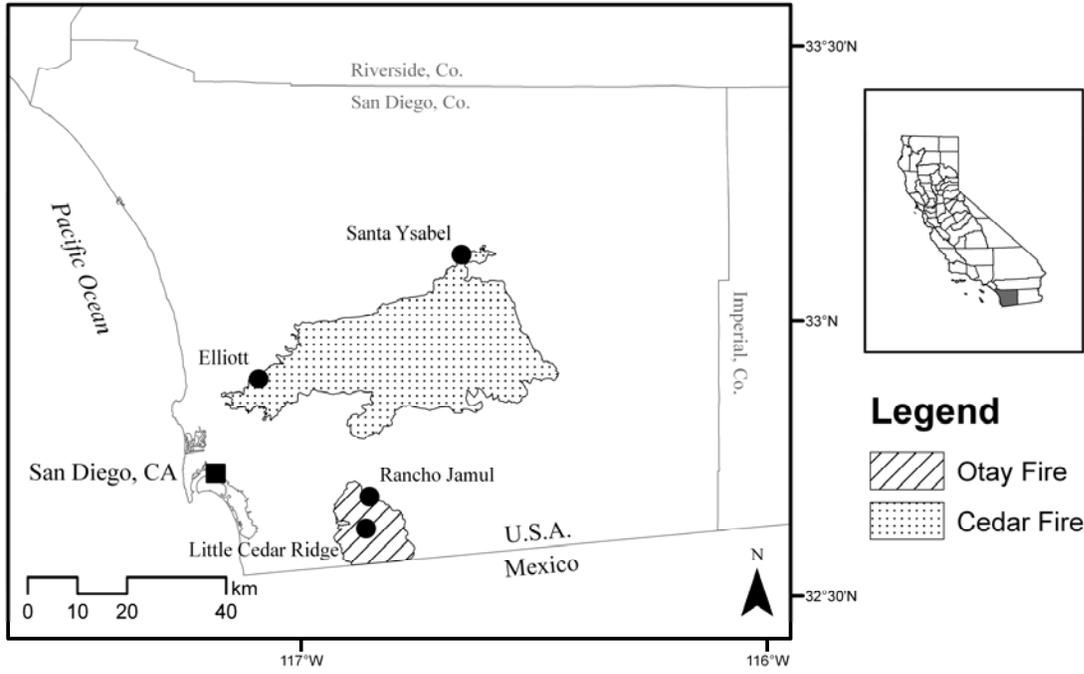
* $p < 0.10$

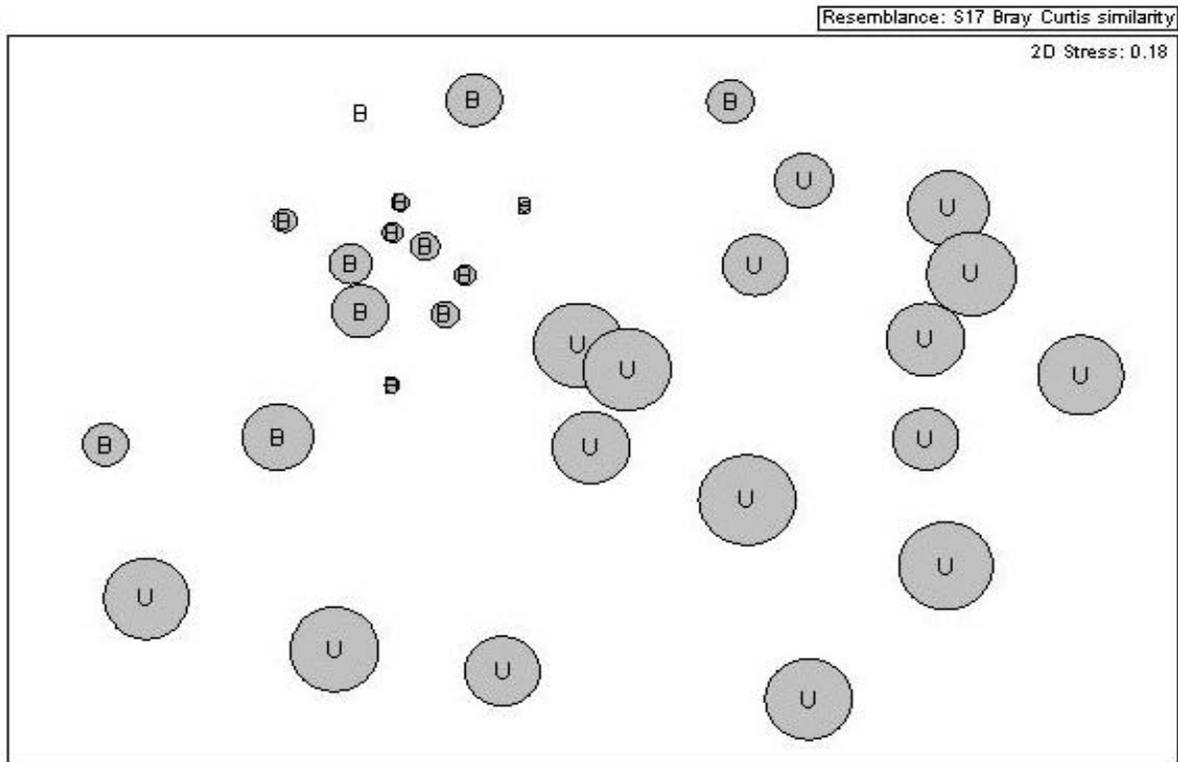
Figure 1. Map of San Diego County, California, showing the four study sites and indicating extent of the Cedar and Otay Fires of 2003.

Figure 2. Multidimensional Scaling (MDS) bubble plot of the above ground ant assemblage in Coastal Sage Scrub. Each bubble represents a single sample with “B” and “U” labels referring to razed (n = 15) and non-razed conditions (n = 16), respectively. Bubble size is proportional to percent shrub and tree cover. Relative distances between points represent the relative similarity of sampled ant assemblage.

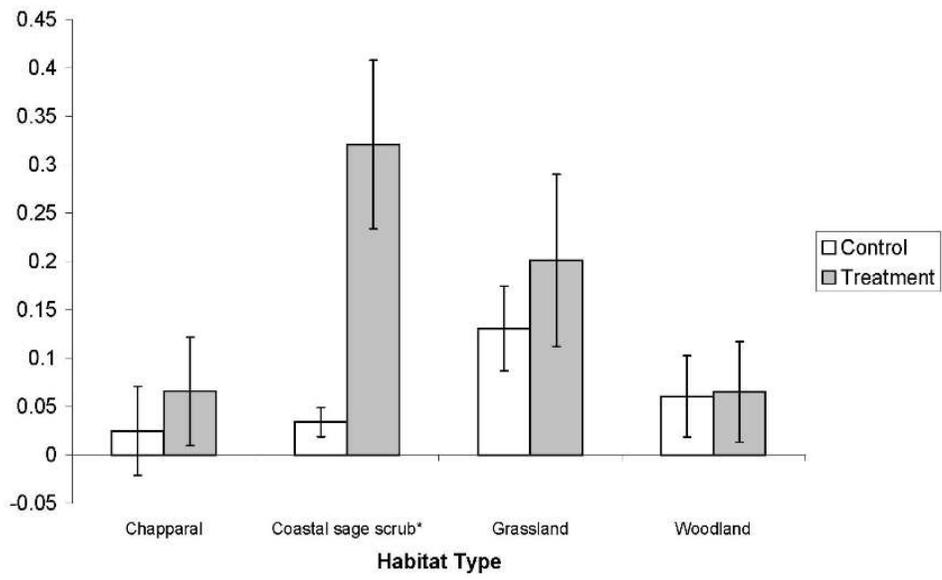
Figure 3. Change in relative abundance of *M. andrei* in pre-fire and post-fire plots across all habitat types. Error bars represent +/- one standard error. Asterisk indicates $p < 0.10$.

Figure 4. Relative abundance of ant species in coastal sage scrub. Error bars represent +/- one standard error. A) Comparison of relative abundance in razed plots versus non-razed plots. Post-fire values are subtracted from pre-fire values to determine relative abundance. B) Net change in relative abundance between razed and non-razed plots. Asterisk indicates $p < 0.10$.

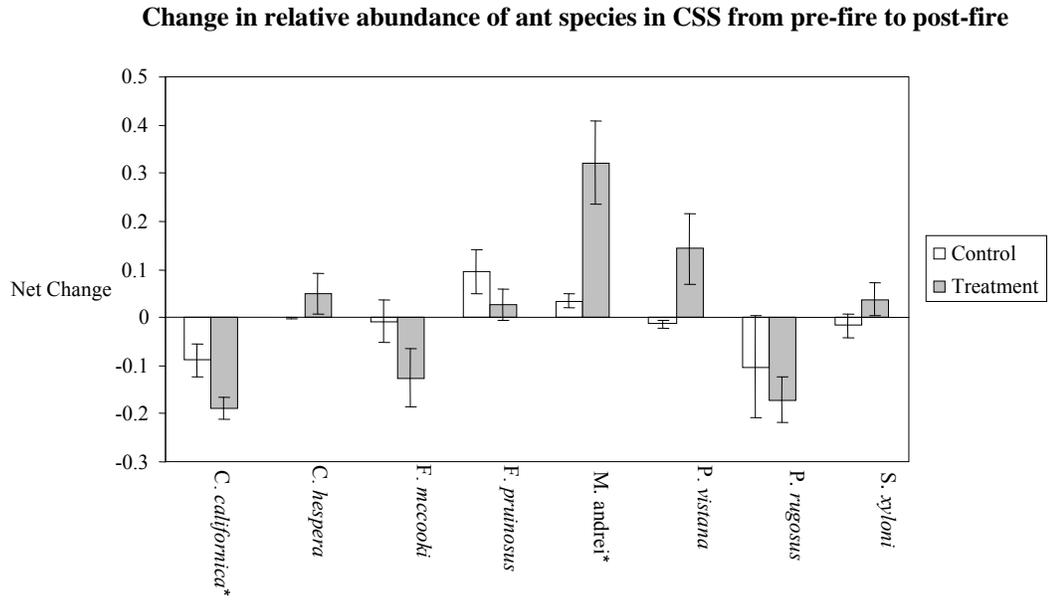




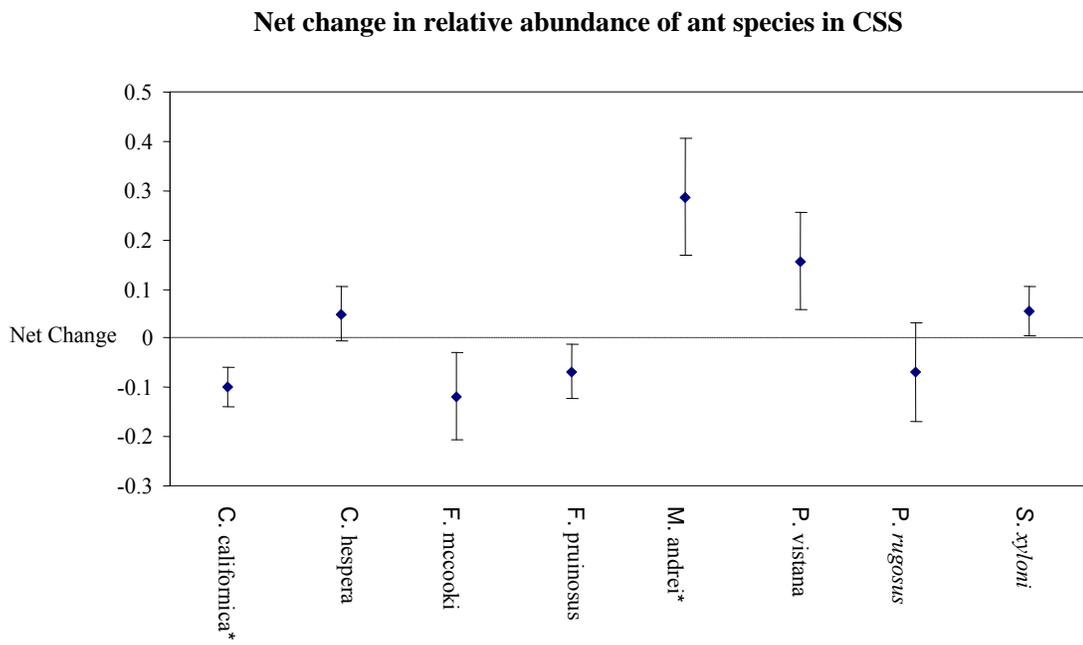
Change in relative abundance of *M. andrei* across habitat types



A)



B)



Appendix 1. Table of Species present. Count represents sum of individuals by site.

Subfamily Species	Site				Grand Total
	Cedar	Elliot	Rancho Jamul	Santa Ysabel	
Dolichoderinae					
Dorymyrmex bicolor			8271	434	8705
Dorymyrmex insanus	38		35 ^e	34	107
Forelius foetidus		269	3535	23	3827
Forelius pruinosus			1	2682	2683
Liometopum occidentale			260 ^e	119 ^d	379
Tapinoma sessile		1	64	122	187
Ecitonae					
Neviamyrmex californicus	1		166	92	259
Neviamyrmex nigrescens		16	33 ^e	145	194
Neviamyrmex opacithorax				3 ^e	3
Formicinae					
Brachymyrmex depilis			1		1
Camponotus anthrax	1			12 ^d	13
Camponotus dumetorum	18			260 ^{a, d}	278
Camponotus sayi				5 ^f	5
Camponotus semitestaceus			43	413 ^{a, d}	456
Camponotus sp ^h				9 ^f	9
Camponotus sp CA-01				47 ^d	47
Camponotus sp CA-02	1		4	74 ^{a, d}	79
Camponotus vicinus		2		44 ^{a, d}	46
Camponotus yogi				1 ^{a, d}	1
Formica francoeuri				1578	1578
Formica moki	42	1	27	190	260
Formica xerophila				2 ^{a, d}	2
Myrmecocystus mimicus		10	36 ^e	20	66
Myrmecocystus semirufus				2 ^f	2
Myrmecocystus testaceus	31			42	73
Myrmecocystus wheeleri				4 ^f	4
Paratrechina c. f. terricola			2	2	4
Prenolepis imparis	1	1	51	53 ^{a, d}	106

Subfamily	Site				Grand Total
	Cedar	Elliot	Rancho Jamul	Santa Ysabel	
Species					
Myrmicinae					
<i>Cardiocondyla ectopia</i> ^g	1				1
<i>Crematogaster californica</i>	77	78	185 ^e	383 ^{a, d}	723
<i>Crematogaster coarctata</i>	17	26	12	39 ^{a, d}	94
<i>Crematogaster depilis</i>			2		2
<i>Crematogaster hespera</i>	275	25	31	57 ^{a, d}	388
<i>Crematogaster mormonum</i>	50	164	25	80 ^{a, d}	319
<i>Messor andrei</i>	817	1068	986 ^e	1263	4134
<i>Messor stoddardi</i>				53 ^{a, d}	53
<i>Monomorium ergatogyna</i>				111	111
<i>Myrmica rugiventris</i>				2 ^{a, d}	2
<i>Myrmicina americana</i>			3		3
<i>Pheidole californica</i>		3		11 ^d	14
<i>Pheidole cerebrosior</i>		1	13 ^e	12 ^d	26
<i>Pheidole clementensis</i>			61 ^e		61
<i>Pheidole hyatti</i>			62 ^e	616	678
<i>Pheidole vistana</i>	1941	977	505	209	3632
<i>Pogonomyrmex californicus</i>			4	87 ^b	91
<i>Pogonomyrmex maricopa</i>				10 ^f	10
<i>Pogonomyrmex rugosus</i>		1	1852 ^e	2	1855
<i>Pogonomyrmex subdentatus</i>			1		1
<i>Pogonomyrmex subnitidus</i>				514 ^b	514
<i>Solenopsis amblychila</i>			2	6	8
<i>Solenopsis aurea</i>	45		22	2	69
<i>Solenopsis molesta</i>		2	71	128	201
<i>Solenopsis sp</i> ^h				3 ^f	3
<i>Solenopsis xyloni</i>	203	812	738	114	1867
<i>Stenamma diecki</i>		1			1
<i>Temnothorax andrei</i>			19 ^e	13 ^d	32
<i>Temnothorax nevadensis</i>				1 ^d	1
<i>Temnothorax nitens</i>				1 ^d	1
<i>Temnothorax sp CA-04</i>				4	4
<i>Temnothorax sp CA-07</i>		1			1
<i>Tetramorium spinosum</i>			97 ^e		97
Grand Total	3559	3459	17220	10133	34371
Species Total	17	20	35	52	61

a at least one record vouchered at UC Davis Bohart Museum

b at least one record vouchered at UC Berkeley [Essig Museum of Entomology](#)

c at least one record vouchered at [Museum of Comparative Zoology](#)

d at least one record verified by Phil Ward, UC Davis

e at least one record verified by Andrew Suarez, University of Illinois

f in process of verification

g exotic species

h Ants identified to Genus level contribute to the total number of species as different and unique from other congeners in the list