

# Species Richness, Abundance, and Composition of Ground-Dwelling Ants in Northern California Grasslands: Role of Plants, Soil, and Grazing

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**ABSTRACT** We examined the role of cattle grazing, plants, and soil attributes on species richness, abundance, and composition of ground-dwelling ants in northern California serpentine and nonserpentine grasslands. In addition, we analyzed the relationship between three numerically dominant ant species and overall ant species richness and abundance. We used pitfall traps to collect worker ants at 80 sites over a 2-wk period in May 2002. Twenty species of ants were identified from a total of 5,149 worker ants; 80% of all individuals belonged to three dominant species: *Messor andrei* (Mayr), *Pheidole californica* Mayr, and *Solenopsis xyloni* McCook. Ant species richness was negatively affected by grazing on nonserpentine soils only. In general, soil chemistry and texture formed the most consistent associations with the ant community. Plants were less important than soil attributes in explaining variation in overall ant species richness and abundance, but the abundance of the three dominant ant species was significantly correlated with plant biomass or plant richness. Based on logistic regression analysis, the presence or absence of each dominant ant species was negatively correlated with the abundance of the other two dominants. However, the three numerically dominant ant species did not correlate with overall ant species richness or abundance.

**KEY WORDS** ant species richness/abundance, grazing, plant/soil effects

THE FACTORS INFLUENCING SPECIES diversity and abundance continue to be a source of ongoing debate (Magurran 1988, Gaston 1991, Rosenzweig 1995). Concern about an impending extinction crisis (Ricklefs and Schluter 1993, Vitousek 1994) has heightened interest in these issues, especially for species-rich groups of organisms. Ants (Hymenoptera: Formicidae) are a major structuring force in many terrestrial communities. They exert direct and indirect effects on both closely and distantly related taxa (Brown and Davidson 1977) and have diverse functional roles, including scavenging, predation, granivory, and omnivory (Hölldobler and Wilson 1990, Whitford 1996, Folgarait 1998). For these reasons, the factors influencing ant richness and abundance have attracted considerable attention from ecologists and biogeographers. Many studies invoke at least one of several plant attributes (e.g., richness, biomass, percentage of cover) as a causal mechanism affecting ant diversity (Caldas and Moutinho 1993, Dean and Milton 1995, Picker and Samways 1996). However, soil attributes may be equally, if not more important, than plant attributes in explaining patterns of ant diversity be-

cause the majority of ant species nest in the soil (Bestelmeyer and Wiens 2001, Wang et al. 2001). Ants seem to prefer certain soil types over others, which is probably due to a combination of factors such as ease of tunneling and chamber construction, and water-holding capacity. In this study, we examine soil and plant factors affecting ant species richness and abundance in northern California grasslands to assess the relative importance of plant versus soil attributes in regard to the ant community.

Attributes of both soil and the plant community have been shown to influence ant community structure. Wang et al. (2001) showed that ant abundance and diversity were negatively associated with high elevations and increased soil moisture in North American forests. Soil parent material also can influence ant species composition. Fisher (1997) compared ant communities at the McLaughlin Reserve in northern California from serpentine and nonserpentine chaparral and found few compositional differences between the two soil types. At least one ant species, *Formica xerophila* Smith, seems to be serpentine-specific in northern California (Fisher 1997). In short-grass prairies, soil texture can be a good predictor of ant species richness (Bestelmeyer and Wiens 2001). Clay-rich soils affect distribution patterns in some ants via their effects on foundress wetmass (Johnson 2000), whereby high-clay soils (i.e., higher moisture reten-

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tion) is associated with increased survivorship in *Pogonomyrmex rugosus* (Emery) and *Pogonomyrmex barbatus* (Smith) alates. However, clay soil also could indirectly affect ants by impacting plant distributions.

In fact, plants have often been the focus in the study of ant species richness (Caldas and Moutinho 1993, Dean and Milton 1995, Picker and Samways 1996). A number of studies (Terayama 1992, Quiroz-Robledo and Valenzuela-González 1995, Torres and Snelling 1997) have shown that attributes of the plant community are often the best predictors of ant species richness. Some studies have found an inverse correlation between ant diversity and plant biomass (Caldas and Moutinho 1993, Parr et al. 2002), whereas others have found a positive correlation between plant and invertebrate diversity (Dean and Milton 1995, Picker and Samways 1996). Still other research has found no correlation between species richness and plant variables for other insect groups, such as butterflies (Hawkins and Porter 2003). However, few of these studies examined multiple soil attributes, which could be a third variable affecting both plant and ant communities.

Because the plant community can play an important role in determining ant species richness, grazing of plants by vertebrates could indirectly affect other consumers in the community. The impact from grazing has been examined repeatedly for plant communities (Vogl 1974, Parsons and Stohlgren 1989, Noy-Meir 1995, Whelan 1995). Few studies have asked how grazing could indirectly affect the consumers in a given community, such as ants. In semiarid and arid areas, grazing seems to have little impact on ant richness or abundance (Kerley and Whitford 2000, Read and Andersen 2000, Bestelmeyer and Wiens 2001), although ungrazed areas can favor the abundance of certain ant species (Read and Andersen 2000, Bestelmeyer and Wiens 2001). Even if grazing does not affect overall ant richness, ant species composition may vary as a function of grazing. For example, opportunistic and hot-climate specialist ant species were more prevalent in excessively grazed habitats in the Argentine Chaco (Bestelmeyer and Wiens 1996). In summary, studies have shown how plants, grazing, soil attributes, or a combination affect ant richness and abundance, but none have examined these factors in a single study, as we do here.

We also wanted to examine how a numerically dominant ant species relates to overall ant species richness and abundance as well as the abundance of other numerically dominant species. A few studies have examined how a numerically dominant species affects species richness and abundance in a particular taxon, but the relationship between these two variables is often negative (Sánchez-Piñero and Aalbu 2002). Theoretically, a numerically dominant species will reduce the diversity for a given area, but its impact on diversity is not always straightforward (Green and Ostling 2003).

In this article, we survey the ground-dwelling ant community on both serpentine and nonserpentine soils at a series of grasslands in the Coast Range of

**Table 1.** Mean plant biomass and species number by treatment

	Mean plant biomass	Plant species no.
Nonserpentine	19.17	135
Serpentine	11.62	154
Grazed	18.42	150
Ungrazed	13.49	157

northern California. We address the following questions: 1) How do ant species richness, abundance, and composition vary as a function of soil attributes, grazing regimes, and the plant community? 2) How is the presence of three numerically dominant ant species related to soil attributes, plant richness, plant biomass, and other ant species?

## Materials and Methods

**Study Sites.** Using the long-term sites described in Harrison (1999), our study system was composed of 80 grassland sites on the 3,100-ha Donald and Sylvia McLaughlin University of California Natural Reserve, in Napa, Lake, and Yolo counties ( $\approx 38^{\circ} 51' N$ ,  $123^{\circ} 30' W$ ), 120 km north of San Francisco, CA. The reserve experiences a Mediterranean climate, with warm, dry summers and cool, moist winters. Annual precipitation is seasonally bimodal (160 mm in January, 0.3 mm in July), and mean annual temperature is  $\approx 18.1^{\circ}C$ . Sites were selected a priori based on Harrison (1999). Serpentine and nonserpentine soils within this area were characterized by D'Appolonia (1982). Geology, soil attributes, and the flora and fauna are described in detail by Harrison et al. (2003) and by the Natural Reserve System of the University of California, Davis (UC NRS 2003).

**Plant Data.** We collected data on plant species richness and composition at each of the eighty sites by using five 1-m<sup>2</sup> quadrats at 10-m intervals along a 40-m linear transect in mid-April and late May 2002 (after Harrison 1999). In total, 187 plant species were recorded. We also measured biomass after the end of the growing season (late July) as an estimate of productivity for each site. We clipped all vegetation down to the soil surface from a 30-cm<sup>2</sup> area adjacent to the middle 1-m<sup>2</sup> vegetation composition quadrat. The samples were dried in an oven at  $55^{\circ}C$  for 2 d and then weighed. Table 1 lists mean plant biomass and total species number for each treatment. Detailed analysis of the plant community at these sites can be found in Harrison et al. (2003).

**Ant Collections.** We placed a pitfall trap (7.5 cm in diameter, 9.5 cm in height) adjacent to each of the three middle plant quadrats along all linear transects (i.e., quadrats 2, 3, and 4). Thus, each of the 80 sites had three pitfall traps. In late April 2002, one-third of each trap was filled with 100% propylene glycol (antifreeze) to which a few drops of detergent was added to break the surface tension. Traps were opened for  $\approx 2$  wk in the second half of May, a period of high foraging activity for most ant species in the region (P.S.W., personal observation). Traps were undis-

turbed by animals, although we did catch an insignificant number of vertebrates in them (i.e., 11 mice). Specimens collected in the traps were washed and stored in 95% ethanol until identification. From each sample, all ant workers were removed, counted, and identified to species. Voucher specimens were deposited at the Bohart Museum of Entomology, University of California at Davis. We analyzed ant species richness, overall ant abundance, and the abundance of the three dominant species in relation to soil variables, grazing, and plant composition, biomass, and richness.

**Soil Attributes.** For soil analyses, we collected 300–500 g of soil from 1- to 5-cm depths adjacent to the first 1-m<sup>2</sup> plant quadrat (described above) at each study site. Soil samples were oven-dried, sieved, and analyzed by A and L Western Agricultural Laboratories (Modesto, CA) for the following soil attributes: %organic matter (OM); estimated nitrogen release (ENR); Olsen P; pH; K, Mg, Ca, Na, H, S, Zn, Mn, Fe, Cu, B, Co, and Ni; %soluble salts; %sand; %silt; %clay; and cation exchange capacity (CEC). The serpentine-nonserpentine soil classification throughout this article is based on Ca:Mg ratios from Harrison et al. (2003) for these same sites. By this measure, 41 of the 80 sites were serpentine and 39 were nonserpentine.

**Effects of Grazing.** Approximately one-half the sites on each soil type had been grazed year-round for many decades, with roughly one cow and calf per 10 ha. The remaining sites had been similarly grazed until cattle were removed from various areas during the construction of a gold mine in 1985. These sites were well interspersed around the 3,100-ha study area, such that soil type and grazing status were independent of latitude and longitude (Harrison 1999). In this study, there were 14 grazed and 25 ungrazed sites on serpentine and 21 grazed and 20 ungrazed sites on nonserpentine.

**Data Analysis.** To meet parametric assumptions, we log transformed all continuous variables and arcsine transformed all percentage data. Wherever means are reported, they are followed by their standard deviations. We analyzed the data via independent-sample *t*-tests and regressions (both linear and logistic) (Sokal and Rohlf 1995, Neter et al. 1996). To detect any interaction effects between the two independent variables, namely, soil type (serpentine and nonserpentine) and grazed versus ungrazed plots, we performed a two-way analysis of variance (ANOVA) (Sokal and Rohlf 1995) on all dependent variables. Only significant results are reported for this series of tests.

Grazing was used as an independent variable in an analysis of covariance (ANCOVA) of ant species richness and abundance with plant and soil attributes as covariates (Sokal and Rohlf 1995). Stepwise regressions, *t*-tests, ANOVAs, and ANCOVAs were carried out using the statistical computer package SPSS, version 8.0 for Windows (O'Connor 2004). Principal component analysis (PCA) was run on all soil response variables by using PC-ORD, version 4.0 (Gilliam and Saunders 2003). A correlation matrix was used for this analysis. Principal component scores were then used

as additional response variables (after Culver and Beattie 1983). Positive and negative symbols preceding a number and/or a variable indicate the direction of the association throughout the text, unless otherwise noted. We applied the Bonferroni correction to each *t*-test by multiplying its corresponding *P* value by the number of tests executed for that particular variable (Sokal and Rohlf 1995).

To determine whether soil attributes and plant composition correlated with composition of the ant community, we compared their dissimilarity matrices. First, we calculated the Sorensen–Czekanowski metric (Fortin and Gurevitch 1993, Legendre and Legendre 1998) to measure the dissimilarity in species composition (presence or absence) between sites for both plants and ants. We then used the Gower metric (Gower 1971) to measure the dissimilarity in soil attributes between sites.

To test for an association between plant and ant communities, we computed the partial Mantel statistic  $r_{A,B,C}$  (the correlation between matrix A and B, given C) (Smouse et al. 1986). We used this statistic to describe the effect of plant composition on ant community when the effect of soil attributes was removed. A positive value for  $r_{A,B,C}$  indicates an effect of the plant community on the ant community, whereas  $r_{A,B,C}$  equal to or less than zero indicates no effect. We used partial Mantel tests for positive  $r_{A,B,C}$  by the first method of Smouse et al. (1986), by using the algorithm given in Legendre and Legendre (1998) (p. 558). For each test, we used 9999 permutations and calculated one-tailed permutation probabilities. Finally, we repeated the partial Mantel test to look at the effect of soil attributes on ant community composition when the effect of the plant community composition was removed.

## Results

**Principal Component Analyses of Soil Data.** Three PCAs were run on the soil data: one on all data combined (abbreviated as PC-all hereafter), one on the serpentine portion of the data (abbreviated as PC-serp hereafter), and one on the nonserpentine data (abbreviated as PC-nonserp hereafter) (Table 2). The first three eigenvalues explained 47.6% of the cumulative variance for PC-all, 47.7% for PC-serp, and 48.3% for PC-nonserp. The PC coordinate scores from these three eigenvalues were then used as independent variables in the regressions and *t*-tests below. Due to some collinearity between PC-all and PC-serp and PC-all and PC-nonserp, PC-all scores were used for analyses on all the data combined, PC-serp scores were confined to analyses on serpentine data, and PC-nonserp, to nonserpentine data. Table 2 lists the soil factors associated with principal component. As expected, all three PC axes for the combined data were significantly associated with the serpentine/nonserpentine classification in Harrison et al. (2003): PC1-all,  $F = 120.6$ ;  $df = 1, 76$ ;  $P < 0.0001$ ; PC2-all,  $F = 6.39$ ;  $df = 1, 76$ ;  $P = 0.014$ ; PC3-all,  $F = 4.56$ ;  $df = 1, 76$ ;  $P = 0.036$ . There were no significant main effects for these three axes on

**Table 2. PCA for combined (PC-all), serpentine (PC-serp), and nonserpentine (PC-nonserp) soil data sets**

Principal component	Eigenvalue (% of explained variance)	Factors ( $\pm$ association)
PC1-all	7.881 (24.6%)	Olsen P(-), pH(+), K(-), Mg(+), Zn(-), Fe(-)
PC2-all	4.624 (14.5%)	Cation exchange capacity (CEC+), Cu(+), %sand(-), %clay(+)
PC3-all	2.740 (8.6%)	Ca(-), Mn(+), B(-), Co(+)
PC1-serp	7.476 (24.1%)	Organic matter (OM-), ENR(-), Zn(-), Cu(-), K(-)
PC2-serp	4.235 (13.7%)	Mg(-), CEC(-), Fe(+), %clay(-), %sand(+)
PC3-serp	3.060 (9.9%)	Na(+), pH(+), B(+), Co(-), soluble salts(+)
PC1-nonserp	6.454 (20.2%)	Mg(+), CEC(+), Cu(+), %sand(-), %clay(+)
PC2-nonserp	5.445 (17.1%)	pH(-), Zn(+), Mn(+), Fe(+)
PC3-nonserp	3.566 (11.1%)	Olsen P(+), K(+), Ca(+), B(+), Co(-)

The first three eigenvalues explained approximately one-half of the variance for each data set. If a variable's eigenvector was  $> \pm 0.25$ , it was included in the factor column. Symbols from the periodic table of elements were used for soil chemistry variables.

the other independent variable (grazing), nor any interaction effects.

**All Ant Species.** We identified 20 ant species from a total of 5,149 worker ants collected from 76 sites (four of the 80 sites contained no ants) with mean number of worker ants per site of  $64.4 \pm 80.1$ . The ten species that dominated these sites in overall abundance were roughly equivalent to the 10 species that occurred with the highest frequency across sites (Table 3). Three species, *Pheidole californica* Mayr, *Messor andrei* (Mayr), and *Solenopsis xyloni* McCook, represented the majority (82%) of all worker ants collected. Data from these species are analyzed individually in the next section.

There were 16 ant species collected from the nonserpentine sites and 17 species from the serpentine sites. The following four species were collected only in serpentine samples: *Aphaenogaster occidentalis* (Emery), *Liometopum luctuosum* Wheeler, *Formica xerophila*, and *Camponotus* sp. nr. *vicinus* Mayr. The following three ant species were found only on the nonserpentine sites: *Stenamma punctatovenstre* Snel-

ling, *Stenamma californicum* Snelling, and *Cyphomyrmex wheeleri* Forel. There were some slight differences in overall abundance and frequency of occurrence for all ant species and in abundance and frequency per ant species between serpentine and nonserpentine sites (Table 3). For example, *M. andrei* was the most abundant ant in nonserpentine sites, but it ranked third most abundant in the serpentine sites. Even though *M. andrei* was fairly common across the two soil types, it was trapped in only 16% of serpentine sites compared with 53% of the nonserpentine sites.

We regressed log ant abundance and log ant species richness on log plant species richness, log plant biomass, and the three PC scores unique to each data set. For the combined data analysis (Table 4), a multiple regression indicated a negative association between ant species richness and both plant biomass and PC2-all (+CEC, -%sand, +%clay, +Cu). Similarly, the serpentine data produced a positive trend between ant richness and PC2-serp (-CEC, +%sand, -%clay, +Fe, -Mg), but ant richness was negatively associated with plant biomass for the nonserpentine data

**Table 3. List of ground-dwelling ant species collected from 80 grassland sites at McLaughlin Reserve in northern California**

Ant species	Nonserpentine abundance (n = 39)	Serpentine abundance (n = 41)	Nonserpentine % occurrence (n = 39)	Serpentine % occurrence (n = 41)
<i>Aphaenogaster occidentalis</i> (Emery)	0	3	0	3
<i>Camponotus</i> sp. nr. <i>vicinus</i> Mayr	0	33	0	5
<i>Camponotus semitestaceus</i> Snelling	102	57	39	29
<i>Crematogaster coarctata</i> Mayr	49	28	18	18
<i>Cyphomyrmex wheeleri</i> Forel	10	0	8	0
<i>Formica xerophila</i> Smith	0	9	0	5
<i>Formica moki</i> Wheeler	103	70	32	29
<i>Liometopum luctuosum</i> Wheeler	0	4	0	5
<i>Liometopum occidentale</i> Emery	53	66	37	5
<i>Messor andrei</i> (Mayr)	936	487	53	16
<i>Neivamyrmex nigrescens</i> (Cresson)	32	5	5	3
<i>Pheidole californica</i> Mayr	782	1,066	34	68
<i>Prenolepis imparis</i> (Say)	42	34	21	13
<i>Solenopsis molesta</i> (Say)	13	2	5	5
<i>Solenopsis xyloni</i> McCook	457	494	37	21
<i>Stenamma californicum</i> Snelling	5	0	5	0
<i>Stenamma punctatovenstre</i> Snelling	2	0	3	0
<i>Tapinoma sessile</i> (Say)	37	19	21	18
<i>Temnothorax andrei</i> (Mayr)	2	2	3	3
<i>Temnothorax nevadensis</i> (Wheeler)	68	77	29	13

Abundance (total number of worker ants) and occurrence (percentage of sites occupied) are listed for both serpentine and nonserpentine sites.

**Table 4.** Multiple regression coefficients in an analysis of log ant species richness and log ant abundance for each of the three data sets

Dependent variable	Data set	Independent variable ( $\pm$ association)	Multiple regression Bonferroni-corrected
Ant richness	All data	Plant biomass(-), PC2-all(-)	$R^2 = 0.08, P = 0.044$
	Serpentine data	PC2-serp(+)	$R^2 = 0.08, P = 0.090$
	Nonserpentine data	Plant biomass(-)	$R^2 = 0.17, P = 0.007$
Ant abundance	All data	PC2-all(-)	$R^2 = 0.04, P = 0.077$
	Serpentine data	Plant species richness(-), PC2-serp(+)	$R^2 = 0.18, P = 0.029$
	Nonserpentine data	PC1-nonserp(-)	$R^2 = 0.18, P = 0.005$

The following independent variables were used in the analysis: log plant species richness, log plant biomass, and the three PC scores. PC scores correspond to their respective data set: PC-all used on all combined data; PC-serp used for serpentine portion of the data, and PC-nonserp used for nonserpentine component of the data. Only significant variables are listed in the independent variable column.

analysis (Table 4). Ant abundance was regressed on the same independent variables and produced results similar to ant richness (Table 4) in that ant abundance was negatively associated with %clay and CEC but was positively related to %sand. In all instances, the percentage of variation in ant abundance or richness that was explained was relatively low (4–18%).

**Dominant Ant Species.** Three ant species represented >80% of all worker individuals collected (Table 3). In total, there were 1,848 workers of *P. californica*, 1,423 of *M. andrei*, and 951 of *S. xyloni*. The abundance of each dominant showed no relationship with abundance of the other two dominants as evidenced by individual regressions and bivariate correlations, even though *S. xyloni* never co-occurred in a trap with *M. andrei* in the serpentine pitfalls.

The log abundance of each dominant ant species was regressed on the same independent variables used above for all three data sets (Table 5). *P. californica* abundance was negatively associated with plant biomass and positively associated with PC3-all (-Ca, +Mn, -B, +Co) in the combined data set. It also was negatively associated with plant biomass and positively related to PC2-nonserp (-pH, +Zn, +Mn, +Fe) in the nonserpentine analysis. *P. californica* abundance in the serpentine samples was positively related to PC2-serp (-Mg, -CEC, +Fe, -%clay, +%sand) and negatively associated with PC3-serp (+Na, +pH, +B, -Co, +soluble salts). From our two-way ANOVA, there was only a significant main effect for *P. californica* and the serpentine/nonser-

pentine-independent variable,  $F = 3.94$ ;  $df = 1, 6$ ;  $P = 0.051$ .

*M. andrei* abundance was negatively associated with PC2-all (+CEC, -%sand, +%clay, +Cu) and positively related to plant biomass in the multiple regression on the combined data (Table 5). In the nonserpentine analysis, it was similarly negatively associated with PC1-nonserp (+CEC, -%sand, +%clay, +Cu, +Mg). No significant relationships existed for *M. andrei* in the serpentine multiple regression. *S. xyloni* abundance was negatively associated with plant richness in all three data sets (Table 5). In addition, *S. xyloni* was negatively related to PC1-serp (-OM, -ENR, -Zn, -Cu, -K) and positively associated with PC3-serp (+Na, +pH, +B, -Co, +soluble salts) in the serpentine multiple regression.

Finally, logistic regressions were computed for the three dominant ant species. Presence or absence of each species was used as the binary, dependent variable, and each of the other ant, plant, and soil variables were used as continuous, independent factors as described above. There were no significant associations between the dependent variables and the following independent variables: ant species richness, overall ant abundance, plant biomass and richness, and PC scores for soil variables. Table 6 lists the results comparing each dominant species to the abundance of the other two dominants. The presence of *S. xyloni* was negatively associated with the abundance of the other two dominant species in the combined analysis. Presence of the other two dominants (*M. andrei* and *P.*

**Table 5.** Stepwise multiple regression coefficients in an analysis of log abundance of the three dominant ant species for each of the three data sets

Dependent variable	Data set	Independent variable ( $\pm$ association)	Multiple regression Bonferroni-corrected
<i>P. californica</i> abundance	All data	Plant biomass(-), PC3-all(+)	$R^2 = 0.19, P < 0.001$
	Serpentine data	PC2-serp(+), PC3-serp(-)	$R^2 = 0.19, P = 0.028$
	Nonserpentine data	Plant biomass(-), PC2-nonserp(+)	$R^2 = 0.17, P = 0.030$
<i>M. andrei</i> abundance	All data	Plant biomass(+), PC2-all(-)	$R^2 = 0.16, P = 0.001$
	Serpentine data	PC3-serp(+)	$R^2 = 0.06, P = 0.149$
	Nonserpentine data	PC1-nonserp(-)	$R^2 = 0.31, P < 0.001$
<i>S. xyloni</i> abundance	All data	Plant species richness(-)	$R^2 = 0.13, P = 0.001$
	Serpentine data	Plant species richness(-), PC1-serp(-), PC3-serp(+)	$R^2 = 0.21, P = 0.044$
	Nonserpentine data	Plant species richness(-)	$R^2 = 0.20, P = 0.003$

The following independent variables were used in the analysis: log plant species richness, log plant biomass, and the three PC scores. PC scores correspond to their respective data set: PC-all used on all combined data, PC-serp used for serpentine portion of the data, and PC-nonserp used for nonserpentine component of the data. Only significant variables are listed in the independent variable column.

**Table 6.** Logistic regression results with presence or absence of each dominant ant species used as the dependent variable and abundance of the other ant dominants as the continuous, independent variables

Dependent variable	Data set	Independent variable ( $\pm$ association)	Logistic regression Bonferroni-corrected
<i>P. californica</i> presence/absence	All data	<i>M. andrei</i> abundance(-), <i>S. xyloni</i> abundance(-)	$B = 1.8, P = 0.06$ $B = 2.7, P = 0.02$
<i>M. andrei</i> presence/absence	All data	<i>P. californica</i> abundance(-), <i>S. xyloni</i> abundance(-)	$B = 1.9, P = 0.06$ $B = 1.8, P = 0.10$
<i>S. xyloni</i> presence/absence	All data	<i>M. andrei</i> abundance(-), <i>P. californica</i> abundance(-)	$B = 3.1, P = 0.03$ $B = 2.4, P = 0.01$

*californica*) approached significant, negative associations with abundance for the other two dominant species for the combined analysis. There were no significant relationships between these three dominants and any of the other variables in the serpentine and nonserpentine analyses.

**Effects of Grazing.** Grazing was negatively associated with ant species richness in analyses with the combined ( $t = -4.0, df = 78, P < 0.001$ ) and nonserpentine data ( $t = -4.3, df = 78, P < 0.001$ ) but was unrelated to ant abundance. In the combined analysis, ant species richness was negatively associated with grazing (PCI-all was a significant covariate),  $F = 17.0; df = 1, 78; P < 0.001$ . Similarly, this negative relationship between grazing and ant richness existed in the nonserpentine analysis, but with plant biomass as the significant covariate,  $F = 20.9; df = 1, 76; P < 0.001$ . There were no significant results from the serpentine ANCOVAs. Our two-way ANOVA results supported the above-mentioned findings. There was a significant main effect for ant richness and the grazing independent variable ( $F = 16.06; df = 1, 76; P < 0.0001$ ) with fewer ant species in grazed plots and a significant interaction effect between the serpentine and grazing independent variables ( $F = 5.24; df = 1, 76; P = 0.025$ ). In other words, the grazing effect is strongest in nonserpentine soils but undetectable in serpentine plots.

**Community-Level Analysis.** There was a significant relationship between soil attributes and ant community composition (Table 7). However, there was no correlation between plant and ant communities, even though soil and plant composition were strongly correlated. When soil was taken into account, plant composition had no effect on ant composition. Soil had only a weak relationship with ant composition when plant composition was taken into account. Thus, ant composition was associated with soil attributes but not plant composition.

**Table 7.** Effects of plant community structure and soil attributes on ant composition using a Mantel test with 9999 permutations and one-tailed permutation probabilities

Variables	$r$	$P$
Ant species composition and plant species composition	0.025	0.080
Ant species composition and soil attributes	0.033	0.030
Soil attributes and plant species composition	0.500	<0.001
Partial correlation of ants and plants	0.009	0.310
Partial correlation of ants and soil	0.025	0.080

## Discussion

There were >20 independent, continuous soil variables measured at the sites where ants were surveyed. The PC scores from combined, serpentine, and nonserpentine soil data consistently produced the strongest associations with ant variables—much more often than the plant factors did. Our community analyses also supported this trend in that soil attributes were significantly associated with ant species composition (Table 7). This was not the case for plant and ant composition, even when soil attributes were used as a covariate. Given the strong association between ants and plants reported in the literature (Caldas and Moutinho 1993, Dean and Milton 1995, Picker and Samways 1996, Parr et al. 2002), it is surprising that there were so few significant associations (positive or negative) between ants and plants in this study.

**Ant-Plant Associations.** There were some examples of ant-plant associations in the results, but they were not consistent across serpentine and nonserpentine soils. For example, ant richness was negatively correlated with plant biomass across the serpentine sites and when both soil types were analyzed together (Table 4). This negative association between ants and plants could result from space competition between ant nesting sites and root zones (Caldas and Moutinho 1993, Parr et al. 2002). It also may be due to the fact that pitfall traps catch fewer insects in dense vegetation—presumably due to invertebrates moving more slowly in dense vegetation, which may make them less likely to fall in a trap (Greenlade 1964, Melbourne 1999). Another interesting exception to the lack of association between plants and ants was obtained in the analyses of the dominant ant species, (i.e., *S. xyloni*, *P. californica*, and *M. andrei*) (Tables 5 and 6). Although soil variables were correlated with the abundance of each dominant ant species, plant biomass or richness consistently produced both positive and negative correlations with these three dominants across each soil type. Plant richness negatively correlated with abundance of *S. xyloni*, regardless of soil type. Plant biomass positively related to *M. andrei* in the combined analysis, but it negatively correlated with *P. californica* abundance in nonserpentine and combined data sets (Table 5). However, when we examined how the presence of each dominant ant species related to the other variables using logistic regressions, significant plant effects did not occur.

**Ant-Soil Associations.** Soil attributes (as represented by PC scores) were consistently associated with richness and abundance for all ant species and for the three dominant ants. Overall ant species richness and abundance were negatively correlated with high concentrations of Cu and Mg and high CEC and %clay levels, but they were positively associated with high %sand content across soil types. CEC or cation exchange capacity is defined as the total exchangeable cations a soil can absorb (Brady and Weil 1996). Because CEC in a given soil is determined by the amount of colloids, lower CEC is associated with sandy soils. Likewise, higher CEC values generally occur in clay-rich soils (Brady and Weil 1996). For this reason, it is understandable that CEC and %clay consistently loaded together on the various PC axes (Table 2). Thus, it is reasonable that CEC and %clay negatively affected the ants—an effect that is probably due to difficulty ants experience nesting in such clay-rich (high CEC) soils.

All three dominant ant species exhibited some association with soil attributes. *M. andrei* abundance was negatively related to high concentrations of Cu and Mg and high CEC and %clay levels in the nonserpentine and combined analyses. In the serpentine samples, *M. andrei* abundance was negatively correlated with high Na, B, soluble salts, acidic soil, and with low levels of Co (Table 5). Abundance of *P. californica* was inconsistently related to soil attributes across the three analyses. However, its abundance tended to be positively associated with acidic, high Co, low B, high Mn, high Fe soils, but this was not consistent across data sets. *S. xyloni* was positively correlated with soils characterized by high OM, high Zn, high K, high Cu, high Na, high B, and high pH in the serpentine analysis only.

In summary, high sand-low clay/CEC soils were consistently and positively associated with both dominant and all ant species pooled. However, even these results produced relatively low correlation values. Thus, there are other variables affecting ant community structure at this reserve, such as ant interactions with vertebrates (especially competing granivorous rodents) or other invertebrates (especially prey). Based on our results though, soil texture does play a significant, albeit not the sole, role in structuring the ant community at McLaughlin. Soil texture effects on ant richness and abundance was also documented in Bestelmeyer and Wiens (2001). Because there was so much variation across soil type and ant species for the other soil characteristics, we cannot assume that these other attributes (e.g., pH, Mg, and Zn) have the same importance as soil texture did for the ground-dwelling ant community at McLaughlin Reserve. Even though soil attributes seem to play an important role in the ant community, there was not a marked difference between the ant fauna of serpentine and nonserpentine sites—a finding concordant with the results of Fisher (1997), who compared ant communities from serpentine and nonserpentine chaparral at the McLaughlin Reserve.

We suggest that, more generally, soil structure and composition may play a more important role than plant community structure in shaping ant communities. Although many studies have documented correlations between ant and plant community structure, many of these studies did not consider (or considered very few) soil attributes. A unique feature of the research we present here is that our soil data are the most comprehensive among studies examining ant species richness. If soil determines both ant and plant community structure, then ant and plant community structure will likely be correlated. Unfortunately, such a correlation would falsely suggest that plants “cause” patterns in the ant community.

**Associations among the Dominant Ant Species.** The presence of each dominant species was negatively associated with the abundance of the other two dominants across all combined analyses. Another interesting result was that *S. xyloni* and *M. andrei* were never captured in the same traps on serpentine sites. Although the abundance of *S. xyloni* was similar on serpentine and nonserpentine sites, *P. californica* abundance nearly doubled on the serpentine sites compared with nonserpentine localities. Conversely, the abundance of *M. andrei* was reduced by nearly 50% at the serpentine sites (Table 3). Thus, we have circumstantial evidence for competition among all three dominant ant species, although an alternate interpretation would be that they have differing habitat preferences.

**Effects of Grazing.** In general, grazing was associated with reduced ant species richness on nonserpentine soils. That grazing affects ants is not a new finding (Bestelmeyer and Wiens 1996, 2001; Kerley and Whitford 2000); however, no other studies have documented any impact (positive or negative) of grazing on ant species richness as we report here. We did not find any relationship between grazing and the abundance of the three dominant ant species. Our results could have been strengthened if we had tracked the ant community pre- and postgrazing. Comparisons across grazed plots in relation to the plant community are discussed elsewhere (Harrison et al. 2003).

We found that variation in overall abundance, richness, and composition of ants at McLaughlin Reserve was more often associated with variation in soil characteristics (especially low clay and high sand content) than with variation in plant richness, biomass, or composition. Percentage of clay and sand consistently affected the abundance of all ant species combined and the three dominant ants. Several soil elements also explained some of the variation in the ant community (e.g., Mg, Co, and B). These soil attributes could affect ants directly via their nesting activities or indirectly via their effect on plants (Harrison et al. 2003).

We document that ant species richness and abundance negatively correlated with soil clay content and positively correlated with soil sand content. Plant variables, however, were inconsistently related to the ant community composition. We also found that grazing reduced ant species richness, but this effect was inconsistent across soil type and ant species. The pres-

ence or absence of the three dominant ant species was negatively associated with the abundance of the other two. Contrary to findings reported in the literature, our three numerically dominant species did not negatively (or positively) correlate with ant species richness or overall ant abundance. It is important to note that most of our correlations were very small, even though they were significant for ant-soil associations. Future work should explore additional habitat characteristics (other biotic interactions and abiotic factors) as determinants of ant community structure. Also, the competitive relationship between these three native, dominant ant species needs to be further investigated and should include experimental removal and introduction to quantify their impact on plants and on one another.

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