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Research article

A comparison of ant assemblages (Hymenoptera, Formicidae) on serpentine and non-serpentine soils in northern California

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Summary

In northern California, ant assemblages in 8 sites in serpentine chaparral habitat were compared with those occurring in 8 chaparral sites on adjacent non-serpentine soils. A total of 27 species of ants was found: 22 species were collected in non-serpentine chaparral and 20 species in serpentine chaparral. Seven species were collected exclusively in non-serpentine, and 5 species were found only in serpentine habitats. A *Formica* species, conspecific with or closely related to *F. xerophila*, was found only in serpentine chaparral. Subsequent collections suggest that in northern California, this species is confined to serpentine outcrops. Two other species significantly differed in frequency of occurrence in each habit: *Camponotus hyatti, C.* cf. *vicinus*. Five species showed marginal significant differences in their relative abundance between habitats: *Camponotus hyatti, C.* cf. *vicinus, Formica moki, Prenolepis imparis, Leptothorax nevadensis, Stenamma diecki.*

Introduction

The study of plant communities on serpentine soils has contributed to a broader understanding of the ecology and evolution of plant tolerance to unique edaphic environments (Kruckeberg, 1984; Baker et al., 1992; Mayer and Soltis, 1994; Mayer et al., 1994). Recent studies have shown that plant populations exhibit a range of adaptations to serpentine conditions; some populations show ecotype diversification while others have become specialized endemic species (Brooks, 1987; Kruckeberg, 1984; Kruckeberg and Kruckeberg, 1990; Westerbergh and Saura, 1992). These classic studies have added to our understanding of the role of isolation and competition in the evolution of endemism, the nature of ecotypic differentiation, and the genetic consequences of stress to local populations (Kruckeberg, 1984; Westerbergh and Saura, 1992; Mayer and Soltis, 1994; Mayer et al., 1994).

In spite of this intensive research on serpentine plant communities, few studies have addressed whether there are unique, endemic animals restricted to serpentine

(Proctor and Woodell, 1975; Ubick and Briggs, 1989). Herbivorous insects whose host plants are restricted to serpentine soils are of course endemic to serpentine habitats (e.g., Shapiro, 1981). However, for scavengers or mostly predaceous invertebrates, such as ants, it is not a foregone conclusion that they will exhibit specificity to serpentine habitats.

The objective of this study was to evaluate the effect of serpentine soils and associated endemic plant life on ant assemblages by comparing the species composition and abundance of ants in chaparral habitats on serpentine and adjacent non-serpentine soils in the North Coast Range foothills in California.

Methods

Field site

Research was conducted at the McLaughlin Homestake Mining Co. adjacent to the Sylvia McLaughlin Natural Reserve, located approximately 12 miles SE of Clear Lake in the Inner Coast Range of California (Fig. 1). The area contains a mosaic of woodland, chaparral and grassland vegetation types.

Ant assemblages of chaparral plant communities restricted to serpentine soils were compared with those occurring in chaparral communities in adjacent non-serpentine soils. The serpentine and non-serpentine sites were similar in elevation and exposure. The survey was conducted between mid-March and mid-June, 1993. Previous experience has shown that ant activity is highest during spring rains, before the onset of the summer dry season. In each of the two habitats, eight sites were inventoried. Four serpentine and non-serpentine sites were located near Red-Elephant Mine, west of the Berryessa Knoxville Road and east of Jericho Creek in Lake County, between 485 and 575 m (20 km ESE Lower Lake, 38°50′N, 122°24′W). Four additional sites in each habitat were located in Yolo County, along the Rieff Rayhose Road and Davis Creek between 525 and 650 m, approximately 5 km NNE of the Red-Elephant Mine sites (13 km W Rumsey, 38°52′N, 122°523′E). The arrangement of serpentine and non-serpentine transects is shown in Figure 1. The minimum distance between tansects within each habitat was 250 m, and therefore each transect was considered independent.

The dominant woody plant species in the two habitats were:

1) Serpentine Chaparral: *Arctostaphylos viscida* (white-leaved manzanita), *Ceanothus jepsonii* (Jepson's ceanothus), *Quercus durata* (leather oak).
2) Non-serpentine Chaparral: *Adenostoma fasciculatum* (chamise), *Quercus berberidifolia* (scrub oak), *Arctostaphylos manzanita* (Parry manzanita), *Ceanothus sorediatus* (Jim bush), *Pickeringia montana* (chaparral pea), *Heteromeles arbustifolia* (toyon).

Inventory technique

The ant inventory technique included both pitfall traps and litter sifting methods. These techniques do not sample the subterranean or arboreal ant community, but

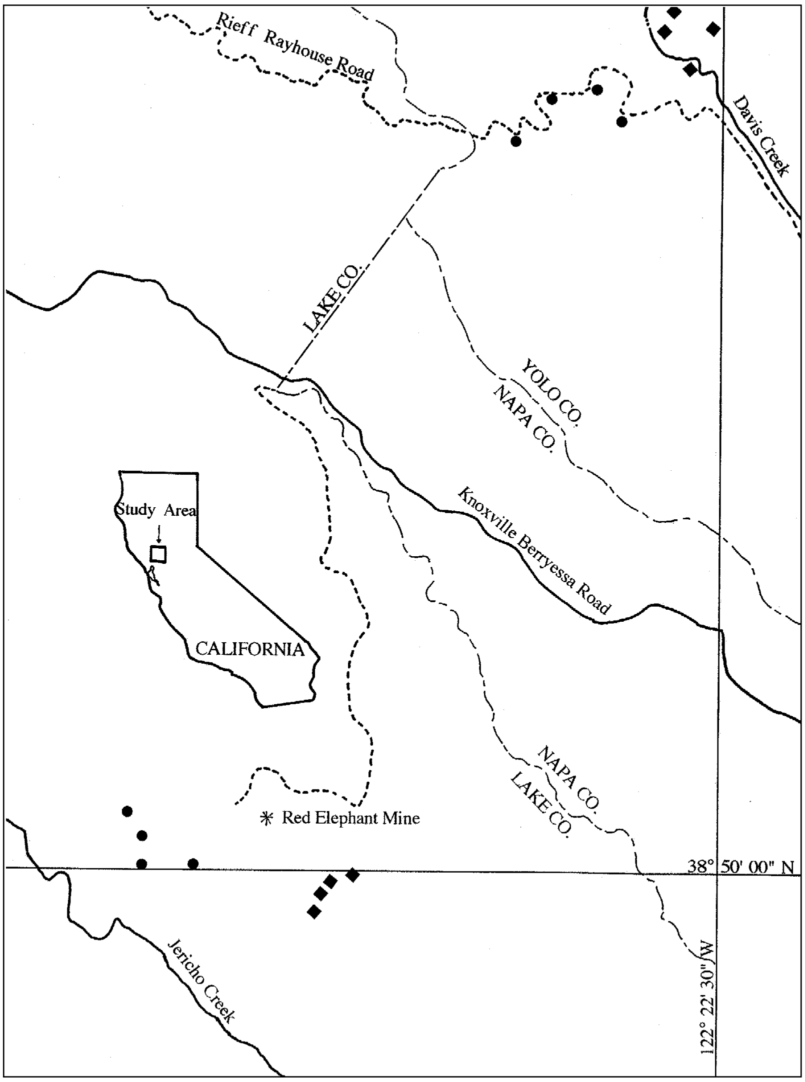

Figure 1. Map of McLaughlin Homestake study area, showing location of serpentine sites (●) and non-serpentine sites (■)

only those ant species that nest or forage on the ground or in the litter. At each site, 10 pitfall traps were installed in a 45 m transect with 5 m between each trap (160 traps total: 10 traps per site × 8 sites per habitat × 2 habitats). Traps consisted of 18 mm internal diameter test tubes partly filled with ethylene glycol/H_2O, inserted into PVC sleeves, and buried flush with the soil surface. Traps were left in the field from 24 April to 9 June 1993, with an interim collection of the contents on May 15.

At each site, 8 liters of sifted plant litter were collected at the base of trees and shrubs parallel to the pitfall transect. Arthropods were extracted over a 48 hr period using Winkler sacks (see Ward, 1987). Leaf litter samples were collected between 10–18 April 1993.

Data analysis

Only worker ants and not queens were used in the data analysis. The total number of ant species collected at each transect site from pitfall and litter methods was combined for analyses of ant species richness and abundance. The program Estimate S (R. K. Colwell, unpublished) was used to compute means and variances of two non-parametric species richness estimators: the incidence-based coverage estimator (ICE: Lee and Chao, 1994) and first-order jackknife (Heltshe and Forrester, 1983). Computations were based on 100 randomized sample orders for each habitat and for both habitats combined. Formulas for the estimates are presented in Chazdon et al. (in press). Estimates of species richness were analyzed graphically, by plotting the estimator and the observed species richness as a function of the cumulative number of sites sampled.

Two measures of species abundance (frequency of occurrence, total individuals) were used to compare ant assemblages in serpentine and non-serpentine chaparral. Because of the patchy distribution of ants (i.e., there existence in colonies), frequencies of occurrence are often a more accurate estimate of abundance than total number of individuals collected (Andersen, 1991). The relative abundances of the 15 most common species overall were analyzed separately using Chi-squared tests on their frequency of occurrence in serpentine versus non-serpentine transects. Yates'correction for continuity was used so that species with small sample sizes could be tested (Sokal and Rohlf, 1981). In addition, for each of the 15 most common species the total number of individuals collected in each transect was compared using Mann-Whitney U-tests. In both analyses, the 15 most common species were determined by ranking the frequency of occurrence of each species across all transects in both habitats. Species frequencies in pitfall traps (percentage of pitfall traps in which each species was collected) were also calculated for each site.

Results

I collected and identified 6,521 worker ants comprising 27 species and 16 genera from pitfall and leaf litter extraction methods. This does not include *Camponotus quercicola* which is an arboreal species that was recorded only from a single queen collected in a pitfall trap at a non-serpentine site. Since the presence of a queen does not necessarily signify the establishment of that species within the study site, only collections of workers were used in the analyses. In non-serpentine chaparral 22 species were collected, while 20 species were collected from serpentine chaparral. A list of ant species and the total number of individual workers collected using pitfalls and Winkler litter sifting for non-serpentine and serpentine sites are presented in Table 1. In addition, species frequencies in pitfalls (percentage of pitfall traps in which each species was collected) and mean abundance of individuals and their standard errors are presented (Table 1). The occurrence of each species in the Yolo Co. and Lake Co. sites, and percentage occurrence in each habitat are presented in Table 2.

Five species (19%) of the 27 were collected only in serpentine chaparral: *Liometopum luctuosum, Camponotus yogi, Formica* cf. *xerophila, Amblyopone pallipes*, and *Pseudomyrmex apache*. Seven species (26% of all species) were uniquely collected in non-serpentine chaparral: *Liometopum occidentale, Tapinoma sessile, Neivamyrmex californicus, Camponotus essigi, C. hyatti, Formica lasioides*, and *Messor andrei*. Most records of species that were unique to one habitat, were from few individuals: 5 species were recorded from collections of a single individual (Table 1).

Observed species accumulation curves, and ICE and first-order jackknife estimates of species richness are presented for each habitat (Fig. 2a, b). ICE, Jackknife and observed species accumulation curves approached leveling off, but were still slowly increasing. This indicates that within the area of the survey, pitfall and leaf litter extraction methods collected the majority of the ants foraging or living in the leaf litter or ground. These methods collected 82% in serpentine sites, and 81% in non-serpentine sites of the total number of ant species estimated by first-order jackknife to occur in the region (Table 3). The ICE and jackknife estimated species richness of ants in serpentine and non-serpentine soils did not significantly differ, based on comparison of 95% confidence intervals. The ICE estimator was least sensitive to sample size, performing well at low sample sizes (Fig. 2). Chazdon et al. (in press) also found ICE to be less sensitive to samples size in estimating plant species richness in Costa Rica.

In an analysis of the 15 most common species, the frequency of occurrence of 2 species was significantly different between habitats, based on Chi-squared tests with Yates' correction: *C. hyatti* ($P = 0.0098$) and *C.* cf. *vicinus* ($P = 0.044$). The abundance of 6 species were significantly different between serpentine and non-serpentine sites based on comparison of the number of individuals collected in each transect using Mann-Whitney U-tests: *Camponotus hyatti* ($U = 8$, $P < 0.02$), *C.* cf. *vicinus* ($U = 13$, $P < 0.05$), *Prenolepis imparis* ($U = 13$, $P < 0.05$), *Formica moki* ($U = 13$, $P < 0.05$), *Leptothorax nevadensis* ($U = 11$, $P < 0.03$), and *Stenamma diecki* ($U = 11.5$, $P < 0.05$).

Discussion

Serpentine specificity

Though we know that the chemical characteristics of serpentine soils restrict the diversity and abundance of plants we have no information on the effect of serpentine soils on most invertebrate assemblages. Because ants are one of the most ecologically important invertebrates through their interactions with, and effects on, soils, plants, and other animal groups (Hölldobler and Wilson, 1990), studies on their response to habitat variables are of interest.

Table 1. List of ant species and total number of individuals collected from pitfalls (PF) and Winkler leaf litter samples (W) at McLaughlin Homestake Mine Co. near the border of Yolo and Lake Counties, California. Only collections of workers are presented; *Camponotus quercicola* was recorded by a single queen from a pitfall trap in non-serpentine and is excluded from this list. NS = non-serpentine chaparral, S = serpentine chaparral. Proportion of pitfalls (out of 80) each species was recorded is given in parentheses. Mean abundance and standard errors (N = 8) are given in parentheses

Species	NS PF	NS W	Total NS	S PF	S W	Total S
Dolichoderinae						
Liometopum luctuosum Wheeler				105 (0.100)	21	126 (15.8 ± 15.47)
Liometopum occidentale Emery	718 (0.113)	1	719 (89.9 ± 89.88)			
Tapinoma sessile (Say)	1 (0.013)		1			
Ecitoninae						
Neivamyrmex californicus (Mayr)	2 (0.013)		2			
Formicinae						
Brachymyrmex depilus Emery	12 (0.625)	1	13 (1.6 ± 1.22)	4 (0.025)		4 (0.5 ± 0.33)
Camponotus cf. *vicinus*	4 (0.038)		4 (0.5 ± 0.5)	24 (0.188)	1	25 (3.1 ± 1.33)
Camponotus essigi M. Smith	1 (0.013)		1			
Camponotus hyatti Emery	9 (0.100)	1	10 (1.25 ± 0.37)			
Camponotus semitestaceus Snelling	272 (0.688)		272 (34 ± 10.70)	131 (0.663)		131 (16.4 ± 3.35)
Camponotus yogi Wheeler				3 (0.038)		3
Formica lasioides Emery		1	1			
Formica moki Wheeler	112 (0.338)	3	115 (14.4 ± 6.08)	410 (0.800)	52	462 (57.8 ± 19.87)
Formica cf. *xerophila*				3 (0.025)		3
Prenolepis imparis (Say)	357 (0.438)	63	420 (52.5 ± 22.42)	1 071 (0.813)	145	1216 (152 ± 42.27)

Table 1 (continued)

Species	NS PF	NS W	Total NS	S PF	S W	Total S
Myrmicinae						
Crematogaster coarctata Mayr	250 (0.313)	123	373 (46.6 ± 20.6)	568 (0.350)	133	701 (87.6 ± 52.00)
Leptothorax andrei Emery	27 (0.225)	126	153 (19.1 ± 8.44)	25 (0.250)	91	116 (14.5 ± 3.19)
Leptothorax nevadensis Wheeler	420 (0.709)	119	539 (67.4 ± 16.89)	152 (0.338)	10	162 (20.3 ± 9.76)
Leptothorax nitens Emery	41 (0.225)	198	239 (29.9 ± 13.20)	26 (0.200)	142	168 (21 ± 11.31)
Messor andrei (Mayr)	7 (0.025)		7			
Monomorium ergatogyna Wheeler	39 (0.088)		39 (4.9 ± 4.46)	54 (0.138)	1	55 (6.9 ± 4.54)
Pheidole californica Mayr	4 (0.038)		4	2 (0.025)		2
Solenopsis molesta (Say)	9 (0.088)	80	89 (11.1 ± 6.61)		2	2 (0.3 ± 0.25)
Solenopsis xyloni McCook	91 (0.175)		91 (11.4 ± 7.99)	81 (0.175)	7	88 (11 ± 6.32)
Stenamma diecki Emery	6 (0.050)	19	25 (3.1 ± 1.70)	7 (0.075)	77	84 (10.5 ± 2.98)
Stenamma punctatoventre Snelling	1 (0.013)	21	22 (2.8 ± 1.24)		32	32 (4 ± 2.13)
Ponerinae						
Amblyopone pallipes (Haldeman)					1	1
Pseudomyrmecinae						
Pseudomyrmex apache Creighton				1 (0.013)		1
Total individuals	2383	756	3139	2667	715	3382
Total species	21	14	22	17	14	20

Table 2. The presence of each species in transects in non-serpentine (NS) and serpentine (S) sites in Lake County and Yolo County (see Fig. 1), and their percentage of occurrences out of 8 sites. Four sites in each habitat were located in each county. Each transect consisted of 10 pitfalls and one leaf litter sample

Species	NS		S		Occurrence (%)	
	Yolo	Lake	Yolo	Lake	NS	S
Dolichoderinae						
Liometopum luctuosum	0	0	0	3	0	37.5
Liometopum occidentale	1	0	0	0	12.5	0
Tapinoma sessile	1	0	0	0	12.5	0
Ecitoninae						
Neivamyrmex californicus	0	1	0	0	12.5	0
Formicinae						
Brachymyrmex depilus	1	2	1	1	37.5	25
Camponotus cf. *vicinus*	1	0	3	3	12.5	75
Camponotus essigi	1	0	0	0	12.5	0
Camponotus hyatti	2	4	0	0	75	0
Camponotus semitestaceus	4	4	4	4	100	100
Camponotus yogi	0	0	1	1	0	25
Formica lasioides	1	0	0	0	12.5	0
Formica moki	4	4	4	4	100	100
Formica cf. *xerophila*	0	0	0	1	0	12.5
Prenolepis imparis	4	2	4	4	75	100
Myrmicinae						
Crematogaster coarctata	4	0	4	2	50	75
Leptothorax andrei	4	4	4	4	100	100
Leptothorax nevadensis	4	4	3	2	100	62.5
Leptothorax nitens	4	1	4	4	62.5	100
Messor andrei	2	0	0	0	25	0
Monomorium ergatogyna	2	0	3	0	25	37.5
Pheidole californica	1	1	1	0	25	12.5
Solenopsis molesta	3	2	0	1	62.5	12.5
Solenopsis xyloni	0	3	0	3	37.5	37.5
Stenamma diecki	3	2	4	4	62.5	100
Stenamma punctatoventre	4	0	2	2	50	50
Ponerinae						
Amblyopone pallipes	0	0	1	0	0	12.5
Pseudomyrmecinae						
Pseudomyrmex apache	0	0	0	1	0	12.5

Table 3. Observed, ICE, and jackknife estimated richness and 95% confidence intervals (CI) for serpentine (S), and non-serpentine (NS)

Habitat	Observed	ICE	CI	Jackknife	CI
S	20	23.6	0.29	24.4	0.37
NS	22	26.6	0.68	27.3	0.68

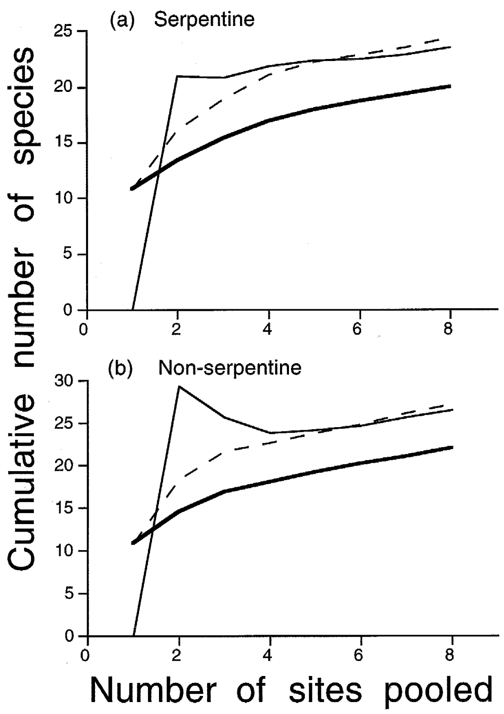

Figure 2. Assessment of leaf litter and pitfall ant, sampling technique for: (a) non-serpentine chaparral; and (b) serpentine chaparral. The lower (thick) species accumulation curve in each chart plots the observed number of species as a function of the number of sites. The upper curves display the non-parametric first order jackknife (dashed) and ICE (solid) estimated total species richness based on successively larger number of samples from the data set (Heltshe and Forrester, 1983; Lee and Chao, 1994). Curves are plotted from the means of 100 randomizations of sample accumulation order, calculated using the program EstimateS (R.K. Colwell, unpublished)

Serpentine and non-serpentine sites at McLaughlin did not differ greatly in observed species richness (Table 3) but did differ in species composition and abundance (Table 1). *F.* cf. *xerophila* is the only species recorded from serpentine chaparral that has not been recorded elsewhere in non-serpentine chaparral in northern California. The limited collection data suggest that *F.* cf. *xerophila* is limited to nesting in the soil structure found in serpentine outcrops. *C. hytti* and *C.* cf. *vicinus* differed significantly in frequency of occurrence and in abundance in each habitat. Further studies will need to determine if these differences are local or widespread. In addition, research should address susceptibility of the serpentine ant fauna to habitat change and which ant species are the most important indicators of disturbance.

Comparison with other faunas

To evaluate the efficacy of the collecting effort at McLaughlin I plotted species accumulation curves (Fig. 2). In addition, comparisons can be made with surveys conducted in similar habitats in the region. The closest site for faunal comparison to this study is Stebbins Cold Canyon Reserve in Solano Co. which is located 50 km SE of the McLaughlin study site. The Reserve is on non-serpentine soils, is dominated by chaparral, and is on the north slope of the Vaca Mountains, on the innermost ridge of the North Coast Range (Weather and Cole, 1985). Based on the work of P. S. Ward, who has studied the ant fauna of the area for over 15 years, a total of 39 ant species have been collected in the reserve, including 31 species recorded from chaparral habitat (Sudgen et al., 1985; P. S. Ward, pers. comm.). The balance of species were recorded from oak woodland and riparian habitats. In his study, ants were surveyed from an altitude range of 120 to 600 m.

Of the 31 species found in chaparral at Cold Canyon, 11 species were not recorded from McLaughlin. The absence of some of these species can be explained. Two of these species (*Leptothorax gallae, Crematogaster marioni*) are arboreal and were not targets of the sampling protocol at McLaughlin. While three other species (*Hypoponera* cf. *opacior, Proceratium californicum, Cyphomyrmex wheeleri*) are cryptobiotic species and are rarely collected (Ward, 1988). *Pogonomyrmex subdentatus, Dorymyrmex bicolor*, and *D. insanus* all require open, bare ground which was not extensively sampled in the transects.

Formica lasioides and *C.* cf. *vicinus* were collected at McLaughlin but not at Cold Canyon. In the Coastal Range, these two species are found on cooler slopes than the area surveyed at Cold Canyon (data from museum records at University of California, Davis). The closest records to Cold Canyon for these species include Mount St. Helena at 1160 m (*F. lasiodes*) and Vaca Mountain at 680 m (*C.* cf. *vicinus*). Since only one worker of *F. lasioides* was collected at McLaughlin, further studies are needed to determine if this collection represents an established population in the area or simply the chance establishment of a vagrant colony outside its normal range where it cannot maintain a viable population.

Formica cf. *xerophila* was collected only from two pitfalls at one serpentine site and is not known from Cold Canyon. The collections at McLaughlin were from SW facing slopes and were bare of vegetation. *Formica xerophila* M. Smith is known from the Great Basin (Washington, Utah, Nevada, Arizona) and from southern California, but this is the first record of a specimen similar to this species west of the Sierra Nevada Mountains. Subsequent collections by P. S. Ward have found *F.* cf. *xerophila* at other serpentine outcrops in northern California with the characteristic bare soil and south or west facing slope. Further studies are needed to determine if *F.* cf. *xerophila* is limited in distribution to just serpentine soils or if it is also found on other mafic (e.g., gabbro) or ultramafic outcrops. In addition, taxonomic studies are needed to determine if *F.* cf. *xerophila* is a distinct species from *F. xerophila*.

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